Brown Trout

Brown Trout: Biology, Ecology and Management

Edited by

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Foreword

The brown trout is an extraordinary fish, endowed by its evolutionary history with the ability to changes its spots – literally and metaphorically – to adapt at lightning speed to new environments. Take the United States, where brown trout introduced in 1883 from a river in Germany, thrived so well and so fast that today they represent the most abundant and widely-distributed trout species in the entire USA, more numerous than the resident rainbow trout. Or Kerguelen, that isolated land mass in the southern Indian Ocean – known to the early English explorers as Desolation Island – where brown trout shipped in by French scientists in the 1950s quickly learned to go to sea, creating one of the most successful sea-trout populations in the world, many monster fish among them.

As any well-travelled angler or biologist will confirm, no two populations of brown trout are quite the same, from Russia to the Atlas Mountains and from the foothills of the Andes to the mountain lochs of Scotland. We even find different forms within the same lake, occupying different zones and breeding at different seasons in different places.

Science tells us that the brown trout's secret lies deep in its evolutionary past and has to do with the number of genes it has, which has enabled it to diversify and adapt with perhaps greater speed than any other fish. From the angler's point of view (I have been both an angler and an amateur student of aquatic natural history since childhood), the result is a fascinating fish which offers an extraordinary variety of sport. Stalking small, darting wild trout in tiny streams; casting a dry fly for wise old chalk-stream monsters; trailing a fish bait for *Salmo ferox* in the deep northern lakes; hunting the mighty silver sea trout in summer night-time rivers – all these forms of trout fishing are as different from each other as football is from tennis. Indeed, it was not until the middle of the 20th century that the angling world realised that in pursuing these varied sports, they are hunting essentially for the same species. It has taken modern genetic analysis to give us a proper understanding of speciation in the trout, as is amply dealt with elsewhere in this book. In fact the one fish most anglers thought really was different – the sea trout – has turned out to be exactly the same species as *Salmo trutta*, but pursuing a very different lifestyle. It is the mystical sea trout, with its beauty, its great speed and strength and its habitual disdain of our flies and lures, which fascinates and tantalises me most of all fish.

A carp is a carp, a cod is a cod and a pike is a pike. Trout are different. They are the chameleons of the river, the jesters and jokers, tantalising, surprising and fooling us repeatedly with their ability to adapt almost as fast as the angler can change his tackle. Where food is rich, they can grow as big as salmon; where it is in short supply, they mature when they are little more than fingerlings. There are races which have adapted to browsing the bottoms of lakes, while others spend their lives roaming the surface for wind-borne insects. River-dwelling trout may happily go to sea to feed if the cupboard is bare at home, even if their own parents had never been anywhere near salt water. You can almost imagine them swimming proudly back home to show off their smart new silver coats to the dull, stay-at-home relatives they left behind.

While the trout's beauty, elusiveness and sweet taste have put a high price on its head throughout human history, sport fishing has rarely if ever been its true enemy; most fishermen value their quarry enough to avoid overfishing and do their best to protect the waters in which 'their' trout swim. Where the brown trout has struggled, the causes have been those far more insidious human-induced problems of pollution, acid rain, water abstraction, urban development, intensive agriculture and misguided stocking of hatchery-bred fish.

I like to think that in introducing the brown trout to new dominions around the world, we have helped to atone for the damage we have done to many of its home waters in the over-developed Western world. Having been distributed far beyond its original two native continents, Europe and Asia (plus a small part of northern Africa), the brown trout now swims rivers and lakes at suitable latitudes in every continent except Antarctica. With global warming now beyond dispute, I wonder if one day in the far distant future they will make their home there too.

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Preface

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Since Linnaeus first named brown trout as *Salmo trutta* in 1758, this species has been classified under many different common and Latin names. Linnaeus reserved the original name for river trout and recognized two other species; sea-trout *S. eriox* and stream trout *S. fario*. Thus the taxonomic problems started over 200 years ago! Arguments continue as to whether brown trout, including sea-trout, belong to a single species, *Salmo trutta* L., or many species. At the end of the last glacial period in Europe, some 10,000 years ago, different populations of brown trout were geographically isolated from each other. These populations slowly evolved into many varieties which caused the early taxonomic 'splitters' of the late 19th and early 20th centuries to elevate them to the species level with over 50 species being described. Their disparity of form, colour or habit may deserve such a distinction but, in my opinion, it is no more than a semantic argument. Unfortunately, a recent handbook of European freshwater fishes lists 27 different *Salmo* species, most being for *S. trutta* (Kottelat & Freyhof, 2007). Jonsson & Jonsson (2011) list over 60 so-called species that can be synonyms of *S. trutta*. These authors conclude that systematic splitting, such as that by Kottelat & Freyhof (2007), is erroneous because it is often based on sometimes accidental species descriptions and does not take into account the high variability of this polytypic species within and among localities, even within a limited geographical area. I strongly agree!

Originally, the brown trout was chiefly a European species, occurring as far north as Iceland, northern Scandinavia and Russia. Western limits were defined by the European coastline and southern limits by the northern coastline of the Mediterranean as well as the islands of Corsica, Sardinia and Sicily, and the Atlas mountains of North Africa. The eastern limits are more difficult to define, but they are probably the Ural mountains, Caspian Sea and as far south as the upper reaches of the Orontes (Asi) river in Lebanon. Anadromous sea-trout populations occur in Western Europe from latitude 42° northwards and in countries bordering the Black and Caspian Seas, but not, surprisingly, the Mediterranean. Some resident populations have undoubtedly arisen from deliberate introductions and this stocking has been practised in some countries for at least 200 years. Brown trout have also been introduced successfully in at least

24 countries outside Europe in the past 150 years. This species is probably one of the world's 100 most invasive exotic species, and is often blamed for the reduction of native fish populations, due to predation, displacement and competition for food.

The early literature on brown trout is enormous, but is essentially descriptive with few quantitative data. Such material has provided copy for many books dealing with the natural history of brown trout and how to catch it! My 1994 book did not duplicate these texts, but emphasised the quantitative ecology of this successful species, especially the development, testing and use of realistic mathematical models for the population dynamics, growth and energetics of brown trout. This book illustrated the single author approach to a monograph on a particular species (Elliott, 1994), and a similar approach was followed in the more recent excellent text on the ecology of Atlantic salmon and brown trout by the husband and wife team of Jonsson & Jonsson (2011). The advantage of only one or two authors is that there is a coherent approach to the text that reflects the opinions of the author(s). The disadvantage is that the authors cannot be experts on all aspects of their subject. An alternative approach is the multi-author text, and this is well-illustrated by the recent excellent monograph on Atlantic salmon, edited by Aas, Einum, Klemetsen & Skurdal (2011). The obvious advantage of this approach is that it utilises the expertise of many authors and provides a wide, comprehensive coverage of the subject.

The latter approach was used in the present volume with 28 chapters divided into six sections. An introductory chapter covers in more detail some of the points mentioned in this Preface. Such an overlap is inevitable in a multi-author text and emphasises the same important points made by different authors. Section 1 covers phylogeography and genetic structure in four chapters, and reproductive traits in section 2 are also described in four chapters. This is followed by three chapters in section 3 on different aspects of the life-history. Section 4 is the largest in the book with seven chapters on different aspects of population dynamics, including those of the anadromous sea-trout. The impacts of brown trout as a global invader in North America, New Zealand, Argentina and Africa are discussed in the six chapters of section 5. Finally, important aspects of the conservation and management of brown trout are covered in four chapters in section 6. It can be seen from this brief summary that the coverage is comprehensive, and illustrates the evidence-based research that is essential for the successful management of brown trout populations. All the contributors, especially the editors, are to be congratulated on producing a book that will become one of the standard works in the future.

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1

Introduction

Princess of the Streams: The Brown Trout *Salmo trutta* L. as Aquatic Royalty

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Brown trout *Salmo trutta* is one of the most widely and collectively sought-after, studied, introduced, and actively managed salmonid species across the world, rivaled only, perhaps, by rainbow trout *Oncorhynchus mykiss* (see Crawford & Muir 2008, Newton 2013). Occurring historically on three continents, the range of the brown trout has been expanded to watersheds on all continents except Antarctica. Unlike rainbow trout, brown trout remains somewhat less ‘synthetic’ (*sensu* Halverson 2010) because of a lesser history of artificial propagation along with a broad range where the species has been less influenced by active fishery management.

Brown trout stands out as an iconic species whose values as recreational and food resources include a global interest in fishing by huge amounts of passionate, rod-and-line anglers who generate robust direct and derivative economies, leisure and other social interactions and subsequent management efforts. In addition to its value as a fishing interest, brown trout has amassed an extensive scientific value because of its complex taxonomic status, its evolutionary history, its trophic status as an apex aquatic predator, and its dizzying array of life-history expressions (Bernatchez 2001, Northcote & Lobón-Cerviá 2008). Ultimately, however, centuries of anthropogenic changes to their natural habitats at both localized and landscape scales has resulted in the extirpation of numerous populations across their historical range that has triggered substantial social and political concerns over the species and the aquatic ecosystems it occupies.

In part because of the previously described values, brown trout has been introduced widely on a global scale wherever habitat conditions have been deemed suitable. Consequently, brown trout has emerged as economically important in numerous places where it is now established (e.g., Australia, New Zealand, Argentina, Canada and the USA among others). While perhaps once heralded as a highly desirable addition to aquatic communities in decades past, brown trout are increasingly and simultaneously being viewed as one of the most destructive invaders in some watersheds where native

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species are being displaced or otherwise harmed through competition or predation. For example, brown trout is emerging as a nuisance to native and imperiled fish fauna in the Colorado River and other drainages of southwestern US (See Budy & Gaeta, Chapter 20). Consequently, as a worldwide species, its image increasingly wanders into a maze of contradictory feelings including the opposite extremes of enthusiasm, love and passion *vs.* hate and confusion. To find the way out from such a maze (if there is one!) of competing complex socio-cultural and economical values likely requires reasoned and honest dialog along with some heroic and collaborative efforts from a diversity of experts and perspectives including aquatic ecologists and evolutionary scientists, fishery resource managers, developers, land-use planners and administrators, economists, elected politicians, and even land-ethicists – among others (see Young *et al.*, Chapter 29).

Iconic in so many ways, complexity and diversity are perhaps the most definitive key words that typify brown trout. Across the wide range of aboriginal habitats, brown trout populations display an overwhelming variability of morphological and life-history traits. Interestingly, such traits may differ and prove stable even at relatively fine geographic scales – such as in adjacent streams or even sympatric within a common stream. In other cases, locally adjacent populations may display a considerable plasticity of their morphological and ecological strategies in response to the environmental heterogeneity of the habitats where they complete their life-cycles including streams, rivers, lakes, estuaries and oceans, as well as systems with high levels of periodic ecological disturbances.

An area of considerable controversy is the brown trout's taxonomic status and associated nomenclature due to the overall complexity referenced previously. Complexity and diversity are expressed dramatically in the taxonomical position of numerous populations, a controversial issue since the earliest studies of the species. Lack of awareness of this complexity, along with more typological perspectives on naming and describing species was probably the keystone of the historical confusion. Specifically, Linnaeus (1758) in his 'Systema Naturae' described several species of the genus *Salmo* of which at least three *Salmo fario, S. trutta* and *S. eriox* can be assigned to what we synonymously name Brown Trout. A decade-long effort to disentangle that puzzle triggered a constellation of papers including the proposed descriptions of new species, sub-species and 'morphas'. Nevertheless, most recent investigations benefitting from inherited molecular markers such as mitochondrial DNA sequences (Bernatchez 2001) have offered a consensus in which all populations, independently of external designs, life-history strategies and other peculiarities, belong to a common species namely, *Salmo trutta* 'species complex'. Moreover, this super-species displays divergence into five or more phylogenetic lineages across their distributional area (see Sanz, Chapter 2) and supports a hypothesis that include all populations previously described that account for, at least, 83 species and sub-species (Jonsson & Jonsson 2011).

Elucidation of the boundaries of the brown trout complex's natural distributional range has been also controversial. Over the last decades, several authors have presented detailed maps covering the natural and exotic distributional areas including, in several instances, the dates and geographical origins of the introduced individuals (Fletcher 1958, MacCrimmon & Marshall 1968, MacCrimmon, Marshall & Gots

1970, Heacox 1974, Welcomme 1988, Baglinière & Maisse 1991). An updated description of the natural distribution covers a vast territory of millions of square kilometres that cut across climates, geologies and landscapes of three continents – implying that brown trout is among the most broadly distributed salmonids worldwide. This vast territory ranges from Iceland at one extreme across the east and south of Europe, continuing down through central Asia and terminating in the north of Africa, including Morroco and Algeria. The southern and eastern distribution include the Mediterranean Islands (except Balearic) and the Black, Caspian and Aral Seas, Turkey, Irak, Iran (Mostafavi *et al.* 2014) as far east as Kazajistan, Uzbekistan, Kyrguizstan and Tajikistan at the 'buttresses of the Himalayas' (Baglinière & Maisse 1991, M. Esteve, pers. com.).

Within these vast territories, there is an exceptional amount of life-history diversity displayed by populations. For example, there are riverine populations that complete the entirety of their life-cycles as sedentary residents within a few hundred meters of a small stream (see Lobón-Cervia, Rasmussen & Mortensen, Chapter 13). Conversely, there are fluvial populations within larger rivers that migrate long distances upstream in search of suitable or natal spawning habitats. In some populations individuals grow at low rates and spawn at a later age whereas in other populations the growth rates are higher and spawn at an ealier age. There are semelparous populations that spawn only once in a lifetime and iteropareous that spawn several times (Cucherousset *et al.* 2005). Strictly riverine populations have been historically considered a sub-species or 'morpha' known as *S. t. fario*. In other populations, juveniles metamorphose into a silver-grey color and develop dark lateral marks under a process known as smoltification – which permits transition from freshwater to marine environments. Once completed, they migrate downstream towards the oceans where they spend varied time periods and is called anadromy (see Rasmussen, Chapter 14). In regions where lakes have no direct contact with the oceans, the fish migrate solely between rivers and the lakes. These migratory or, adfluvial individuals return to their original streams to spawn (see Husko *et al.*, Chapter 12) and transport back nutrients of major importance for the ecological processes of the streams (Stockner 2003). Sea-migratory and lake-migratory forms were also considered sub-species or 'morphas' known as *S. t. trutta* and *S. t. lacustris*, respectively. Yet another life-history type or set of populations known as 'slob trout' stay in estuaries under the influence of the tides where fresh- and marine waters mix. Finally, there are populations in which either 'morpha' may co-occur and may further hybridize with each other (Jonsson 1985) or with a phylogenetically-related sister species such as the Atlantic salmon, *S. salar* L. (Solomon & Child 1978; García de Leaniz & Verspoor 1989).

The anadromous marine 'morpha' or sea-trout, are distributed from Iceland and the British Islands to the Iberian Peninsula with a southern range limit at the Portuguese Mondego River (see Caballero, Vieira-Lanero & Cobos, Chapter 18) and an eastern limit at the Baltic and White Seas and the Kola Peninsula. In the Mediterranean region, sea- trout apparently also occur in the Black and Caspian Seas yet there is no evidence of their occurrence in France, Italy, Yugoslavia, Greece, Turkey, Morroco or Algeria. The lacustrine 'morpha' or lake-trout are abundant from Ireland to central and eastern Europe including sub-alpine lakes of northern Italy, Poland, the Scandinavian countries and Russian Karelia.

The morphological and genetic diversity of the southern, Mediterranean brown trout is remarkably greater than those from central and northern Europe. During the numerous inter-glacial periods over the last 2.5 million years (Darlington 1959, Brown & Lomolino 1998), the freshwater fish fauna of central and northern Europe became partially or totally extinct as glaciers covered the landmass and then retreated. Presently, most of the species that compose the fish assemblages of freshwater ecosystems and drainages of the northern versant of the Mediterranean mountains systems (Pyrenees, Alps, etc.) are recent colonizers associated with the glacial retreats during the last 500,000 years with a last retreat in the Holocene some 10,000–12,000 years ago. These processes may best explain the similarity of the fish fauna from the westernmost France to the remote extremes of Siberia. It also explains the dissimilarity between central and northern Europe and the southern versants where rivers flow south to the Mediterranean and are inhabited by an older and diverse fish fauna of endemic species, due to their resistance to glaciation effects (Crivelli & Maitland 1995).

Therefore, it is not surprising that markedly different assemblages of trout species flourish in the southern latitudes whose taxonomical positions remain somewhat controversial (Snoj *et al.* 2011). Several authors are reluctant to consider all these populations as genuine members of the *S. trutta* ‘species complex’ (see Meraner & Gandolfi, Chapter 3). This set of species include, at least, marble trout *S. marmoratus* (Cuvier 1829), a trout with a very different external design that attain uncommonly large sizes as 1.5 m length and >30 kg weight (Figure 1.1, Povz *et al.* 1996). Its distribution is limited

Figure 1.1 A 25 kg specimen of *S. marmoratus* caught by rod-and-line by a happy angler in Soça River (Eslovenia).

to the Po and Adige Rivers in northern Italy and a few rivers of Slovenia, Croatia, Bosnia-Herzegovina and Montenegro. Also *S. obtusitrostis* (Heckel 1981) endemic to the Neretva, Zeta, Jadro and Vrijika Rivers. Moreover, *S. cettii* (Rafinesque 1810), probably a synonymous of *S. macrostigma* (Dumeril 1858). These brown trout relatives were considered endemic of Algerie, but recent investigations support their occurrence in the Tyrrenian Sea and the Mediterranean Islands (Corsicans, Sardinia and Sicily), the Italian Magra River and according to Kottelat & Freyhof (2007), probably in the Easternmost Spanish and Southernmost French rivers.

Lake-dwelling species related to or synonymous with brown trout are common in central and southern Italy (Gandolfi *et al.* 1991), the Balkans (Pustovrh, Snoj & Susnik 2014) and minor Asia. These at least include *S. fibreni* (Zerunian – Gandolfi 1990) and *S. carpio* in the Italian Posta Fibreno and Garda Lakes (Melotto & Oppi 1987, Melotto & Alessio 2006). Also, *S. letnica* (Karaman 1924) and *S. Ohridanus* are found in Ohrid Lake at the border between Makedonia and Albania. *S. ischchan* (Kessler 1877) from Sevan Lake in Armenia (Berg 1962) and *S. ezenami* (Berg 1948) from Kezenoi-Am Lake in the Caucasus (Freyhof & Kottelat 2008). The populations of the Black and Azov Seas are also considered a nominal species, *S. labrax* (Pallas 1914). Another trout endemic of Turkey, *S. platycephalus* (Behnke 1968) and the unique Aral trout, *S. aralensis* (Berg 1908), are definitively extinct after one of the most important environmental cathaclysm recorded in history, the dry up of 68,000 Km^2 of freshwaters (Figure 1.2). Moreover, *S. ciscaucasicus* (Dorofeeva 1967) originally described as a

Nick Hannes - "Desert Ships (Aral Sea)" - Courtesy © the artist. Nick Hannes' works are on view at BOZAR, Brussels in "Beyond the Document: Contemporary Belgian Photographers" from June 29th through September 25th.

Figure 1.2 The Aral Sea (Kazajistan-Uzbekistan), after the drying up of 68,000 km^2 of fresh water, following one of the most important human-induced environmental cataclysms in history. Camels relaxing in the shade of shipwrecks have replaced *S. aralensis* in their natural habitat.

species or sub-species from the sub-tropical Eurasia (Kottelat & Freyhof 2007). Finally, in Morroco, the so called 'green trout', *S. pallaryi* from Isli Lake (Vivier 1948, Mouslih 1987) and the 'dwarf trout', *S. akairos* (Dellinger & Doadrio 2005, Doadrio, Perea & Yahyaoui 2015) from Ifni Lake (Figure 1.3).

Brown trout and all other brown trout-like species are also iconic in terms of their Conservation status. The status of 'vulnerable' or 'near extinction' (IUCN 2010) covers practically all eastern and southern brown trout-like species with restricted distributional areas. The recent revision by Smith & Darwall (2006) accounts for 13 species of the Salmonidae family – including the genera *Acantholingua*, *Salmo* and *Salmothymus* (see Esteves *et al.* 2014) – whose status is 'vulnerable', 'endangered' or

Figure 1.3 Trout lakes in the Atlas Mountains (Morocco). (A) 'Isni' Lake inhabited by the 'green trout', *S. pallaryi* and (B) 'Ifni' Lake inhabited by the 'dwarf trout', *S. akairo*.

'critically endangered'. In regards to the European native populations, the Red Data Books available assign no dramatic situation to any of these populations, however such status may be no more than a mirage. Since the darkness of the times, human interventions have induced dramatic changes in all salmonid habitats to the extent that just a few, scattered pristine trout habitats actually remain in the European continent. Canals, weirs, hydro-electrical stations, reservoirs and water diversions, intensive land use and the development of industries and mining operations are considered directly or indirectly related to numerous population extirpations at local and regional scales. Moreover, such changes have remarkably led to the extinction of land-locked and river-locked populations most common in the southerly latitudes.

Another human intervention became important in the wake of World War II. During the late 1940s and early 1950s, administrators and anglers began what can only be described as 'industrial-scale' stocking and transplantation as major tools to 'improve' sport fishing. Millions of captive-bred, reared and domesticated individuals from different aquaculture origins were stocked on an annual basis across the globe (Lobón-Cerviá, Elvira & De Sostoa 1989, De Sostoa & Lobón-Cerviá 1989, Vøllestad & Hesthagen 2001). Massive stocking resulted in direct and indirect risks to Salmonid biodiversity (Utter & Epifanio 2002). For example, propagation and stocking intensified the occurrence and facilitated the spread of undesirable pathogens (diseases) and parasites across broad geographical areas. Brood choice practices and the unnatural culture environment led to domestication effects and the narrowing the gene pool. The mixing of evolutionary divergent genetic lineages eroded gene pool architecture or eliminated original local adaptations (García-Marín, Sanz & Pla 1998). Inter- and intra-specific hybridization among divergent lineages actually obscures the real conservation status of many populations given the difficulty to identify natural *vs.* anthropogenic hybridization in some populations (Marzano *et al.* 2003, Sanz *et al.* 2006, Schenekar *et al.* 2014). Even where gene-level variation might remain high among populations with substantial hybridization, the reduction or extinction of evolutionarily integrated genomes may be lost albeit masked by large numbers of hybrids (Epifanio & Philipp 2001). Consequently, the conservation status of numerous European populations is still to be quantified.

In turn, brown trout is one of the most extensively introduced species globally with exceptional success to the extent to be known as the 'fish that conquered an empire' (see Newton 2013) and probably far beyond. After more than 170 years, intensive brown trout stocking is the subject of controversy and debate. Whilst it plays a similar and majestic role as the royal 'Princess of the Streams' in numerous exotic regions, as an invader it is highly problematic (see Chapters 20 to 24) to the extent to be considered one of the 30 most invasive freshwater species worldwide (McIntosh, McHugh & Budy 2012). And, despite substantive debates worldwide, developers and recreational fishery managers still consider brown trout a potential species to be further introduced in other regions where local fisheries are not possible or where under-developed economies clamor for new sources of recreational revenues.

On the other hand, the fascinating variability of the life-history modes exhibited by brown trout (Crisp, 2000; Antunes *et al.* 2006), together with the development of methods and techniques that permit manageable field sampling and population quantifications *vis-a-vis* the development of insightful genetic analysis has motivated the scientific community to focus on brown trout as an 'umbrella species'. Studies on all aspects of their biology have been published during the last 150 years and several recent books summarize the advances and knowledge acquired (Lamond 1916, Menzies 1936, Frost & Brown 1967, McClane 1971, Heacox 1974, Bagliniere & Maisse 1991, Elliott 1994, Crisp 2000, Harris & Milner 2006, O'Grady, Kelly & O'Reilly 2008, Jonsson & Jonsson 2011, Polakof & Moon 2013). Yet, such abundant literature and insightful studies may be little more than a mirage. Practically all research efforts have been focused on European populations and a few exotic regions as New Zealand, USA and South-America. Unfortunately, our knowledge about all other populations and brown trout-like species from the southern and eastern regions is often limited to genetic approaches (Hashemzadeh *et al.* 2012, Kohout *et al.* 2013, Gratton *et al.* 2014, Jadan *et al.* 2015,) whereas our knowledge on their biology and ecology is comparatively scant (Crivelli 1996).

As aforementioned, the general status of brown trout as a worldwide species wanders in a maze of confusion. In many natural and exotic regions, brown trout generates substantial economic activity. These have yet to be quantified rigorously (see Baglinièri 1991), but are undoubtedly very important in terms of GDP as those underlying important exploited marine fishes. Interestingly, social demands for sport fishing *vis-a-vis* leisure purposes are increasing at the same rates as the national economies. Simultaneously, however, the brown trout populations and habitats are deteriorating at nearly identical rates. With no need to invoke the potential effects of global change and warming trends, this situation predicts that within a reasonably short period of time the 'supply' in terms of fishable populations will not be sufficient to meet the 'demand' for sport fishing, a disequilibrium that will necessary trigger profound social concerns. While there are no guarantees, we may be just in time to react and implement proactive solutions. Priorities of management include, at the minimum, to make compatible conservation *vs.* exploitation of natural populations. Priorities in exotic regions are the protection of the native biota and the underlying ecological processes threatened by the successful invasiveness of Brown trout (see Jellyman *et al.*, Chapter 22; Budy & Gaeta, Chapter 20). Such priorities require much more efficient management strategies driven by robust scientific analyses and intensive research efforts (see Young *et al.*, Chapter 29) supported by strict ethical principles consistent with a sustainable land ethic (see Piccolo, Unfer & Lobón-Cervia, Chapter 25). Thus, brown trout might be seen as an unprecedented new emblem for science and more specifically, for conservation biology and ecology.

This new book attempts to be a step in advance to offer updated studies of major interest for the best knowledge of brown trout, for the design of new management strategies and for the amelioration of undesirable human-induced effects on both natural and exotic populations. Authors from all over the world actively involved in the study and management of these populations offer chapters including reviews and case studies that provide insight into theory and practice. If successful, this book will identify the exit from the complex maze of controversies and challenges associated with a most 'royal' fish – known to many as simply 'brown trout' and to many others as *S. trutta* 'species complex' and brown trout-like species.

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Section 1

Phylogeography and Genetic Structure

2

Phylogeographic History of Brown Trout: A Review

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Introduction

Elucidating phylogeographic patterns and inferring evolutionary histories of species is essential to understanding patterns of population divergence and to defining effective management and conservation strategies for maintaining genetic diversity. For brown trout, this is challenging due to the high diversity of phenotypes that do not always correspond to genetic differences, discordances between the phylogenetic histories inferred from different molecular markers and the lack of strongly-supported phylogeographic patterns. In addition, human-induced processes of introgression among lineages increase the complexity of this already complex evolutionary model.

The intricate evolutionary history of brown trout has been accompanied by a confused taxonomy that has led to a continuous reclassification and definition of trout species over the years (Table 2.1). Currently, the *FishBase* (http://www.fishbase.org/Nomenclature/ScientificNameSearchList.php?) catalogue recognizes up to 45 trout species within the genus *Salmo*. Because most of the described species are closely related phylogenetically, many taxonomic reviews and phylogenetic studies consider *S. trutta* (Linnaeus 1758) as a species complex that includes most of these species (Bernatchez, 2001; Simonović *et al.*, 2007; Lo Brutto *et al.*, 2010; Snoj *et al.*, 2010; Vera *et al.*, 2011; Meraner *et al.*, 2013; Gratton *et al.*, 2014).

Crête-Lafrenière *et al.* (2012) reviewed the phylogenetic relationships in the Salmonidae family based on mitochondrial and nuclear molecular markers and situated the origin of the genus *Salmo* at 26–29 million years (MY) ago. According to these authors, the Atlantic salmon (*S. salar*) split from brown trout (*S. trutta*) between 10 and 14 MY ago, and the intraspecific divergence in the *S. trutta* species complex occurred during the Pliocene, 2.5–5 MY ago, associated with the cooling climate of the Northern hemisphere. Whereas fossils of Salmonidae fish date from the Miocene (Osinov & Lebedev, 2004), the oldest recorded fossils for brown trout were found in the Caucasus and date from the upper Pliocene, 2 million years ago (Vladimirov, 1948).

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Table 2.1 Taxonomic units (species and subspecies) whose taxonomical classification has been checked by molecular markers.

Taxa	Locality	Molecular markers	Molecular validation	Source
Salmo akairos (Delling & Doadrio 2005)	Lake Ifni (Morocco)	COI + CR + microsatellites	AT lineage	1; 2
Salmo aphelios (Kottelat 1997)	Lake Ohrid (Albania)	COI	Not identified	1
Salmo carpio (Linnaeus 1758)	Lake Garca (Italy)	COI + CR + cyt*b* + 16S + nDNA + microsatellites	AD × MA lineages	1; 3; 4
Salmo cenerinus (Kottelat 1997)	North Italy-Adriatic basin	CR + nDNA + microsatellites	AD lineage	3
Salmo cettii (Rafineske 1810)	Corsica; Sardinian; Sicily; South Italy-Tyrrenian basin	COI + CR + nDNA + microsatellites	AD lineage	1; 3; 5; 6
Salmo cf. montenigrinus (Karaman 1926)	Neretva (Balkans)	CR + SNPs + microsatellites	*S. trutta* × *S. obtusirostris*	7
Salmo chilo (Turan, Kottelat & Enging 2012)	Turkey	COI	Not identified	1
Salmo dentex (Heckel 1851)	Balkans	CR + nDNA + microsatellites + nDNA	AD and MA lineages	7; 8; 9
Salmo farioides (Karaman 1938)	Northwestern Balkans	COI + CR + microsatellites	AD lineage	1; 10; 11
Salmo ferox (Jardine 1835)	Ireland (United Kingdom)	allozyme + 16S + NADH + COI + 12S	AT lineage	12;13
Salmo fibreni (Zerunian & Gandolfi 1989)	Lake Posta Fibreno (Italy)	COI + CR + cyt*b* + 16S + nDNA + microsatellites	AD lineage	1; 3; 4; 5
Salmo ischchan (Kessler 1877)	Lake Sevan (Armenian)	CR	DA lineage	14
Salmo labecula (Turan, Kottelat & Enging 2012)	Turkey	COI	Not identified	1
Salmo labrax (Pallas 1814)	Black Sea	CR + cyt*b* + 12S + 16S + NADH + microsatellites	DA lineage	15; 16; 17; 18
Salmo letnica (Karaman 1924)	Lake Ohrid (Albania)	COI + CR + NADH + microsatellites	AD lineage	3; 19; 20; 21
Salmo lourocensis (Delling 2011)	Louros River (Greece)	COI	Not identified	1
Salmo macedonicus (Karaman 1924)	FYROM; Greece	COI + cytb + 12S	AD lineage	1; 22
Salmo macrostigma (Duméril 1858)	North Africa/Lake Posta Fibreno (Central Italy); Sardinian; Sicily; Corsica	CR + cytb + 16S + NADH + microsatellites + nDNA + allozymes	AT lineage (Africa)/ AD and ME lineages	2; 4; 5; 15; 23; 24
Salmo marmoratus (Cuvier 1829)	Italy; Slovenian; Balkans; Greece	COI + cyt*b* + CR + 16S + nDNA + microsatellites	MA lineage	1; 3; 4; 9; 25; 26; 27

Salmo nigripinnis (Günther 1866)	Ireland (United Kingdom)	allozyme + 16S + NADH + COI + 12S	AT lineage	12; 13
Salmo obtusirostris (Heckel 1851)	Neretva, Zeta, Jadro and Vrljika Rivers (Balkans)	COI + CR + + cyt*b* + 16S + nDNA + ITS1 + microsatellites	*Salmo obtusirostris*	1; 9; 28; 29; 30; 31; 32
Salmo ohridanus (Steindachner 1892)	Lake Ohrid (Albania)	COI + cyt*b* + CR + 12S + nDNA + ITS1 + microsatellites	*Salmo ohridanus*	1; 9; 20; 22; 31; 32
Salmo opimus (Turan, Kottelat & Enging 2012)	Turkey	COI	Not identified	1
Salmo pallaryi (Vivier 1948)	Lake Isli (Morocco)	CR + microsatellites	AT lineage	2
Salmo pelagonicus (Karaman 1938)	FYROM	12S + cyt*b*	AD lineage	22
Salmo pellegrini (Werner 1931)	Ourika stream (Morocco)	COI + CR + microsatellites	AT lineage	1; 2
Salmo peristericus (Karaman 1938)	FYROM	COI + CR + microsatellites	AD lineage	1; 33
Salmo platycephalus (Behnke, 1969)	Turkey	COI + CR + NADH + cyt*b* + ITS1 + microsatellites	AD lineage	1; 15; 31; 34
Salmo rhodanensis (Fowler 1974)	Rhône River (France)	COI	Not identified	1
Salmo stomachicus (Günther 1866)	Ireland (United Kingdom)	allozyme + 16S + NADH + COI + 12S	AT lineage	12; 13
Salmo tigridis (Turan, Kottelat & Bektaş 2011)	Tigris River-Euphrates Basin (Turkey)	CR + cyt*b* + NADH + microsatellites	DA lineage	15; 35; 36
Salmo trutta caspius (Kessler 1887)	Caspian Basin (Iran)	CR + cyt*b* + ITS + nDNA + microsatellites	DA lineage	37; 38; 39; 40
Salmo trutta oxianus(Kessler 1874)	Aral Sea basin	CR	DA lineage	41
Salmo visovacensis (Taler 1950)	Lake Visova (Dalmatia)	COI	Not identified	1
Salmo zrmanjaensis (Karaman 1938)	FYROM	COI	Not identified	1

1: Geiger *et al.* 2014; 2: Snoj *et al.* 2011; 3: Gratton *et al.* 2014; 4: Pattarnello *et al.* 1994; 5: Gratton *et al.* 2013; 6: Zaccara *et al.* 2015; 7: Razpet *et al.* 2007; 8: Snoj *et al.* 2010; 9: Pustovrh *et al.* 2014; 10: Snoj *et al.* 2009; 11: Mrdak *et al.* 2012; 12: Ferguson & Taggart 1991; 13: McKeown *et al.* 2010; 14: Osinov 2009; 15: Bardakci *et al.* 2006; 16: Dudu *et al.* 2011; 17: Marić *et al.* 2012; 18: Lerceteau-Köhler *et al.* 2013; 19: Sell & Spirkovski 2004; 20: Sušnik *et al.* 2006; 21: Susnik *et al.* 2007b; 22: Lo Brutto *et al.* 2010; 23: Querzi *et al.* 2013; 24: Berrebi *et al.* 2015; 25: Maric *et al.* 2006; 26: Sušnik *et al.* 2008; 27: Pujolar *et al.* 2011; 28: Snoj *et al.* 2002; 29: Snoj *et al.* 2008; 30: Sušnik *et al.* 2007a; 31: Sušnik *et al.* 2004; 32: Crête-Lafrenière *et al.* 2012; 33: Berrebi *et al.* 2013; 34: Kohout *et al.* 2013; 35: Sušnik *et al.* 2005; 36: Arslan & Bardakzi 2010; 37: Vera *et al.* 2011; 38: Hashemzadeh *et al.* 2012; 39: Rezaei & Akhshabi 2012; 40: Najjar *et al.* 2015; 41: Griffiths *et al.* 2009.

In agreement with fossil records, the first brown trout molecular data suggested that the origin of the major brown trout lineages took place in the Pliocene (Bernatchez *et al.*, 1992; Osinov & Bernatchez, 1996; Apostolidis *et al.*, 1997). However, initial divergences have been obscured or modified along with the fluctuations in Quaternary climate patterns. During glacial periods, European fauna was restricted to ice-free refuges, mainly in the southern Mediterranean peninsulas of Iberia, Italy and the Balkans, and expanded during the inter- and post-glacial periods (Hewitt, 2004; Schmitt, 2007). In addition, it seems that glacial refuges also existed in the Atlantic basin (Gómez & Lunt, 2006; Maggs *et al.*, 2008; McKeown *et al.*, 2010), contributing to the postglacial expansion of brown trout. In southern Europe, interglacial warming made some sections of the network of rivers unsuitable for brown trout and isolated populations to the upstream regions. Subsequently, the dispersal of freshwater species, such as brown trout, was the result of the confluence of the courses of rivers from hanging valleys in the lowlands due to falling sea levels, and through river capture events in mountainous regions (Bianco, 1990).

Bernatchez *et al.* (1992) identified five evolutionary lineages for the brown trout species complex: Adriatic – AD, Mediterranean – ME, Marmoratus – MA, Atlantic – AT and Danubian – DA, based on variation in the mitochondrial DNA (mtDNA) control region (CR). Extensive sampling and additional studies have described a sixth lineage that is restricted to the Duero River in the Iberian Peninsula (Duero lineage – DU, Vera *et al.*, 2010) and a seventh lineage in the Tigris River (Turkish), (Tigris lineage – TI, Sušnik *et al.*, 2005). In addition, two trout species, *Salmo obtusirostris* Heckel 1851 (soft-mouth trout) and *Salmo ohridanus* Steindachner 1982 (belvica), have been reclassified into the genus *Salmo* (Phillips *et al.*, 2000; Snoj *et al.*, 2002) and closely related to *S. trutta*. Molecular analyses of mitochondrial and nuclear sequences clearly support the classifications of these taxa as different species within the genus *Salmo* (Phillips *et al.*, 2000; Snoj *et al.*, 2002; 2008; Sušnik *et al.*, 2006; Pustovrh *et al.*, 2014), and they are often included in phylogenetic studies of the brown trout species complex for comparative purposes (Snoj *et al.*, 2009; Vera *et al.*, 2011; Hashemzadeh *et al.*, 2012; Berrebi *et al.*, 2013).

Together with the CR, various mitochondrial genes (cytochrome *b*, cytochrome *c* oxidase, ATPase, rRNA or NAD(P)H) have been used to clarify the classification of species within the genus *Salmo* and to perform phylogenetic studies (Marzano *et al.*, 2003; Sell & Spirskovski, 2004; Bardakci *et al.*, 2006; Sušnik *et al.*, 2006; Bouza *et al.*, 2007; Snoj *et al.*, 2008; Lo Brutto *et al.*, 2010; McKeown *et al.*, 2010) (Table 2.1). For instance, Crête-Lafrenière *et al.* (2012) used the cytochrome *b* and cytochrome *c* oxidase I gene sequences to distinguish five trout species among the 12 specimens analysed, *S. trutta*, *S. marmoratus*, *S. platycephalus*, *S. obtusirostris* and *S. ohridanus*. However, their results showed poor resolution of the phylogenetic relationships of species except for *S. ohridanus* and one specimen of *S. obtusirostris*, which formed a well-supported sister clade relative to other brown trout lineages.

Some phylogenetic studies of the genus *Salmo* have also involved nuclear genes, including single copy nuclear genes such as rRNA ITS region or transferrin (Phillips *et al.*, 2000; Antunes *et al.*, 2002; Presa *et al.*, 2002; Snoj *et al.*, 2002; Sušnik *et al.*, 2004), and repetitive DNA sequences – microsatellites – (Martínez *et al.*, 2007; Sušnik *et al.*, 2007a; b; Razpet *et al.*, 2007; Snoj *et al.*, 2010; Vera *et al.*, 2011; Hashemzadeh *et al.*, 2012; Kohout *et al.*, 2012; 2013; Berrebi *et al.*, 2013; Querci *et al.*, 2013). Among these nuclear genes, it is worth mentioning the protein coding gene *LDH-C* discovered through the first allozyme works (Hamilton *et al.*, 1989), for which the *LDH-C*90* allele is found exclusively in northern European populations of the Atlantic lineage. Based on the hypothesis of Hamilton *et al.* (1989), who suggest that the **90* allele arose in northwest Europe during or after the last glaciation period, the genotyping of this locus has traditionally been used as a phylogeographic marker to trace post-glacial colonization patterns. Subsequent studies (García-Marín *et al.*, 1999; Aurelle & Berrebi, 2001) have shown that both the **90* and the alternative **100* alleles were both found in ice-free areas, refuting the hypothesis of Hamilton *et al.* (1989) who suggested modern (*LDHC*90*) and ancestral (*LDH-C*100*) races. Currently, because most hatchery stocks originate from eggs or fry of northern Europe origin, the *LDH-C* locus is routinely genotyped to check for the presence of hatchery strains in natural brown trout populations (McMeel *et al.*, 2001).

Recently, some studies have reviewed the phylogeography and taxonomy of the genus *Salmo* based on a large set (22) of single-copy nuclear genes (Pustovrh *et al.*, 2011a; 2014; Gratton *et al.*, 2014). In addition to the ability of these markers to demonstrate hybridization between lineages that could not be detected by analysing haploid mtDNA, nuclear phylogenies mostly matched up with those based on mtDNA analyses. The few disagreements detected between the mitochondrial- and nuclear marker-based phylogenies were mainly confined to *S. obtusirostris* and the *S. trutta* Marmoratus lineage in the Western Balkans (Pustovrh *et al.*, 2014).

Despite all of the molecular studies cited above, which have resulted in an extended bibliography addressing the phylogeographic structure of brown trout, there are still several gaps in our understanding of its evolutionary history. Is this chapter, I review the molecular data of the brown trout species complex with the aim of providing a global perspective on this topic. I reconstructed the phylogeography of brown trout using published sequences of the mtDNA control region (CR) to shed light on the brown trout phylogeny. The results are discussed in comparison with the published phylogenetic data for this species.

Phylogeographic Review Based on the mtDNA Control Region (CR): Methods

The mtDNA-CR has been used in a large number of evolutionary studies on fishes because of its exceptionally high mutation rate, which in fishes is 2–5 times faster than that of mtDNA coding regions, and its exclusively uniparental inheritance pattern that avoids recombination and allows for the inference of matriarchal phylogenies and the dating of lineage divergence (Meyer, 1993). As with the rest of teleosts, the CR in brown trout is located between the tRNA^{Pro} and tRNA^{Phe} genes and is composed of a central, conserved domain flanked by two highly variable domains. Most of the initial phylogenetic studies on the *S. trutta* species complex were based only on the two most variable segments of the CR (Giuffra *et al.*, 1994; Bernatchez & Osinov, 1995; Apostolidis *et al.*, 1997). Cortey (2002) showed that the analysis of the complete sequence of the CR provided a better resolution of the evolutionary history in areas where previous studies, based on smaller mtDNA-CR fragments, had failed to detect any phylogeographic signal. McKeown *et al.* (2010) highlighted the importance of examining a large section of the mtDNA genome to infer phylogeographic structure because of the assumption that genealogical information in different segments of the mtDNA genome is additive rather than duplicated. Currently, many phylogenetic studies combine CR data with sequencing data from other regions of mitochondrial and nuclear genes. However, the mtDNA-CR is still considered effective for resolving brown trout phylogenies. In this species, this is also the molecular marker for which the most entries have been recorded in the GenBank database (Benson *et al.*, 2009) and therefore is the most represented in the published data. I therefore focused my phylogenetic review on this marker with the aim of covering data from the entire range over which the species complex is distributed (Figure 2.1).

In this review, CR sequences representative of the native range of the species, were compiled from GenBank to reconstruct the phylogeography of the brown trout (Table 2.2). Because the objective was to study a long segment of the entire CR (1015 *bp*), only sequences longer than 900 base pairs (*bp*) were considered. After excluding duplicate sequences, the remaining sequences were aligned in Genious R7 version 7.1.4 (http://www.geneious.com, Kearse *et al.*, 2012) thought the Genious alignment option, and 199 haplotypes were compiled. PolyT region of the CR was cut leaving a final alignment length of 900 *bp* that included 115 polymorphic sites (11 of them indels).

I then performed the best-fit evolution substitution model for these haplotypes based on the model selection by ML in MEGA v6 (Tamura *et al.*, 2013). According to the lowest Bayesian information criterion (BIC) scores, I found the most appropriate model was the

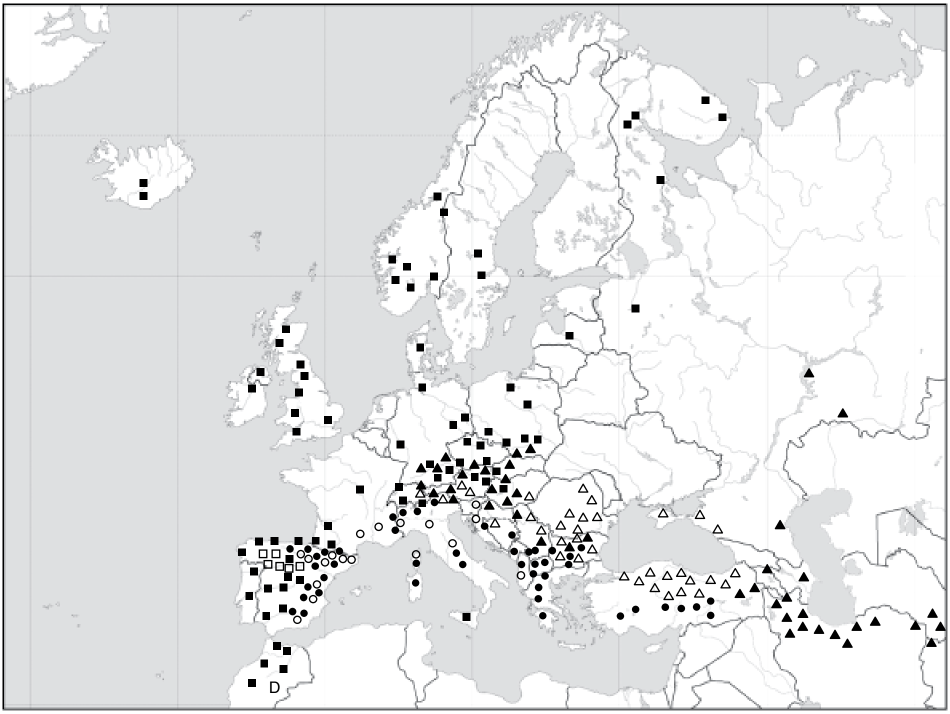

Figure 2.1 Aproximate geographical native distribution of the *S. trutta* species complex lineages, *S. obtusirostris* and *S. ohridanus*, based on the reported bibliography. ●: AD, ○: ME, *: MA, ■: AT, □: DU, DA: Dades, ▲: DA-ES, △: DA-BS, TI: Tigris, #: *S. obtusirostris*, +: *S. ohridanus*.

Table 2.2 Sequences used in this study with the GenBank Accession number. Source column include references of the authors of the Accession number (in bold) and all the studies where the same sequence was reported.

Haplotype	Lineage	Locality	Taxon	Accession number	Source
ADcs1	AD	Atlantic and West Mediterranean basin-Andalusia (Spain); Aegean basin (Balkans); Adriatic basin, Prespa (Albania, FYROM and Greece); Adige River (North Italy)	*S. trutta*, *S. carpio* *S. peristericus*, *S. platycephalus*	AY836330	**1**; 2; 3; 4; 5
ADcs2	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836331	**1**
ADcs3	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836332	**1**
ADcs4	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836333	**1**
ADcs5	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836334	**1**
ADcs6	AD	West Mediterranean basin- (Spain)	*S. trutta*	AY836335	**1**
ADcs7	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836336	**1**
ADcs8	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836337	**1**
ADcs9	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836338	**1**
ADcs10	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836339	**1**
ADcs11	AD	Adriatic basin (Greece; Albania; Montenegro, Serbia)	*S. trutta*, *S. dentex*	AY836340	**1**; 3; 6; 7
ADcs12	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836341	**1**
ADcs13	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836342	**1**
ADcs14	AD	Mediterranean basin (Corsica)	*S. trutta*	AY836343	**1**
ADcs15	AD	Mediterranean basin (Corsica)	*S. trutta*	AY836344	**1**
ADcs16	AD	Western Mediterranean basin (Spain)	*S. trutta*	AY836345	**1**
ADcs17	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836346	**1**
ADcs18	AD	Atlantic basin-Andalusia (Spain)	*S. trutta*	AY836347	**1**

(Continued)

Table 2.2 (Continued)

Haplotype	Lineage	Locality	Taxon	Accession number	Source
ADcs20	AD	Adriatic and Aegean basins (Bulgaria, Greece)	*S. trutta*	AY836349	**1**; 2
ADcs21	AD	West Mediterranean basin (Spain)	*S. trutta*	AY836350	**1**
cen02	AD	Adda River (North Italy)	*S. cenerinus*	KJ834852	**8**
AdAE1	AD	Aegean basin; Black Sea basin-Danube (Balkans)	*S. trutta*	GQ357908	**2**
AdAE2	AD	Aegean basin (Balkans)	*S. trutta*	GQ357909	**2**
AdAE3	AD	Aegean basin (Balkans)	*S. trutta*	GQ357910	**2**
ADTR1	AD	Turkey	*S. trutta*	JN543965	**9**
ADTR2	AD	Turkey	*S. trutta*	JN543966	**9**
ADTR4	AD	Turkey	*S. trutta*	JN543968	**9**
ADTR5	AD	Turkey	*S. trutta*	JN543969	**9**
ADTR8	AD	Turkey	*S. trutta*	JN543972	**9**
macros1	AD	Lake Posta Fibreno (Italy)	*S.t. macrostigma*, *S. fibreni*, *S. cettii*	JN807337	**10**; 11
and	AD	Neretva-AD basin (Bosnia-Herzegovina)	*S. trutta*, *S. dentex* *S. t. marmoratus* *S. obtusirostris*	DQ297172	**6**; 7, 12
AUA5	AD	Andalusian (Spain)	*S. trutta*	AF253551	**13**
M1	AD	AD basin-Zeta and Moraca rivers (Montenegro)	*S. trutta*	DQ381566	**6**; 7
ADC1	AD	AD basin-Zeta and Moraca river (Montenegro)	*S. trutta*	DQ381567	**6**
Let12	AD	Lake Ohrid (FYROM-Albania)	*S. letnica*	AY926570	**14**
Let13	AD	Lake Ohrid (FYROM-Albania)	*S. letnica*	AY926573	**14**
Let14	AD	Lake Ohrid; Drin River-AD basin (FYROM-Albania)	*S. letnica*	AY926571	3; **14**
Let15	AD	Lake Ohrid (FYROM-Albania)	*S. letnica*	AY926572	**14**
Let16	AD	Lake Ohrid (FYROM-Albania)	*S. letnica*	DQ381568	**6**
Let17	AD	Lake Ohrid (FYROM-Albania)	*S. letnica*	DQ381569	**6**
Let18	AD	Lake Ohrid (FYROM-Albania)	*S. letnica*	DQ381570	**6**
ADZ1	AD (MA)	AD basin-Zeta River(Montenegro)	*S. obtusirostris*	DQ381565	**6**; 7

Table 2.2 (Continued)

Haplotype	Lineage	Locality	Taxon	Accession number	Source
MEcs1	ME	Western ME basin (Spain). AD basin (Albania). Krka River (Croatia)	*S. trutta*	AY836350	**1**; 3; 15
MEcs3	ME	Western ME basin (Spain). Danube-Bistrica Ponto-Caspian basin (Slovenia)	*S. trutta*	AY836352	**1**
MEcs4	ME	Western ME basin (Spain).	*S. trutta*	AY836353	**1**
MEcs6	ME	Western ME basin (Spain).	*S. trutta*	AY836355	**1**
MEcs7	ME	Western ME basin (Spain).	*S. trutta*	AY836356	**1**
MEcs8	ME	Western ME basin (Spain).	*S. trutta*	AY836357	**1**
MEcs9	ME	Western ME basin (Spain).	*S. trutta*	AY836358	**1**
MEcs10	ME	Western ME basin (Spain).	*S. trutta*	AY836359	**1**
MEcs11	ME	Western ME basin (Spain).	*S. trutta*	AY836360	**1**
MEcs12	ME	Western ME basin (Spain).	*S. trutta*	AY836361	**1**
MEcs15	ME	Western ME basin (Spain).	*S. trutta*	AY836364	**1**
DU240	ME	Western ME basin (Spain).	*S. trutta*	AF253550	**13**
MAcs1	MA	Adriactic basin-Soca River (Slovenia); Adige and Po rivers (North Italy); Aegean basin (Greece)	*S. trutta*	AY836365	**1**; 2; 16
marm1	MA	Adda-Adige rivers (North Italy); Soca River (Slovenia)	*S. trutta*	KJ834770	**8**
MaK1	MA	Krka River (Croatia)	*S. trutta*	JX846931	**15**
Ma2a	MA	North Italy	*S. trutta*	DQ841189	5; **16**
Ma2b	MA	Adige River (North Italy)	*S. trutta*	DQ841190	5; **16**
MATR1	MA	Turkey	*S. trutta*	JN543996	**9**
Atcs1	AT	Denmark-Norway; Vistula, Elbe, Danube and Oder rivers (Central Europe); North Italy*	*S. trutta*	AF273086	5; 16; **17**; 18; 19; 20
Atcs3	AT	Denmark-Norway; Vistula, Elbe, Danube and Oder rivers (Central Europe); North Italy*	*S. trutta*	AF274574	5; 16; **17**; 18; 19; 20
ATcs4	AT	Denmark-Norway; Vistula, Elbe, Danube and Oder rivers (Central Europe); North Italy*	*S. trutta*	AF274575	5; 16; **17**; 18; 19; 20
ATcs5	AT	Denmark	*S. trutta*	AF274576	**17**
ATcs6	AT	Norway	*S. trutta*	AF274577	**17**

(Continued)

Table 2.2 (Continued)

Haplotype	Lineage	Locality	Taxon	Accession number	Source
ATcs11	AT	Beherobentako (South France); Duero River (Spain)	*S. trutta*	AY836327	**1**
Atcs12	AT	Beherobentako (South France); Elbe, Danube and Oder rivers (Central Europe)	*S. trutta*	AY836328	**1**; 18; 19; 20
ATcs13	AT	Beherobentako (South France)	*S. trutta*	AY836329	**1**
ATcs14	AT	Iceland	*S. trutta*	EF530476	**17**
ATcs15	AT	Garona River (Spain)	*S. trutta*	EF530477	**17**
ATcs16	AT	Cantabrian basin (Spain)	*S. trutta*	EF530478	**17**
ATcs17	AT	Cantabrian basin (Spain)	*S. trutta*	EF530479	**17**
ATcs18	AT	Cantabrian basin (Spain)	*S. trutta*	EF530480	**17**
ATcs19	AT	Cantabrian basin (Spain)	*S. trutta*	EF530481	**17**
ATcs20	AT	Vorobiev (Russian)	*S. trutta*	EF530482	**17**
ATcs22	AT	Beherobentako (South France)	*S. trutta*	EF530484	**17**
Atcs25	AT	Cantabrian basin (Spain); Atlantic basin (Morocco-North Africa)	*S. trutta*	EF530487	**17**; 21
ATcs26	AT	Duero River (Spain)	*S. trutta*	EF530488	**17**
ATcs27	AT	Duero River (Spain)	*S. trutta*	EF530489	**17**
ATcs28	AT	Tajo River (Spain)	*S. trutta*	EF530490	**17**
ATcs29	AT	Tajo River (Spain)	*S. trutta*	EF530491	**17**
ATcs31	AT	Tajo River (Spain)	*S. trutta*	EF530493	**17**
ATcs33	AT	Atlantic basin (Spain); Mediterranean basin (Morocco-North Africa and Sicily)	*S. trutta*	EF530495	**17**; 21; 22
ATcs37	AT	Atlantic basin (Spain)	*S. trutta*	EF530499	**17**
ATcs38	AT	Atlantic basin (Spain)	*S. trutta*	EF530500	**17**
ATcs41	AT	Duero River (Spain)	*S. trutta*	EF530502	**17**
ATcs42	AT	Duero River (Spain)	*S. trutta*	EF530503	**17**
ATcs43	AT	Duero River (Spain)	*S. trutta*	EF530504	**17**
ATcs45	AT	Iceland	*S. trutta*	EF530505	**17**
ATcs46	AT	Ireland	*S. trutta*	EF530506	**17**
ATcs48	AT	England (United Kingdom)	*S. trutta*	EF530508	**17**
ATcs49	AT	England (United Kingdom)	*S. trutta*	EF530509	**17**

Table 2.2 (Continued)

Haplotype	Lineage	Locality	Taxon	Accession number	Source
ATcs50	AT	England (United Kingdom)	*S. trutta*	EF530510	**17**
ATcs51	AT	Wales (United Kingdom)	*S. trutta*	EF530511	**17**
ATcs52	AT	Wales (United Kingdom)	*S. trutta*	EF530512	**17**
At11a	AT	Danube basin (Austria)	*S. trutta*	AY185578	**18**
At11b	AT	Danube basin (Austria)	*S. trutta*	AY185579	**18**
A5	AT	Elbe and Oder Rivers (Central Europe)	*S. trutta*	HQ848356	**20**
A7	AT	Elba, Oder, Vistula, Danube basin (Central Europe)	*S. trutta*	HQ848358	**20**
A8	AT	Danube basin (Central Europe)	*S. trutta*	HQ848359	**20**
A9	AT	Elba River (Central Europe)	*S. trutta*	HQ848360	**20**
A10	AT	Danube basin (Central Europe)	*S. trutta*	HQ848361	**20**
A11	AT	Danube basin (Central Europe)	*S. trutta*	HQ848362	**20**
A12	AT	Elba River (Central Europe)	*S. trutta*	HQ848363	**20**
A13	AT	Danube basin (Central Europe)	*S. trutta*	HQ848364	**20**
A18	AT	Elba River (Central Europe)	*S. trutta*	HQ848369	**20**
At1e	AT	Adige River (Northern Italy)*	*S. trutta*	DQ841192	**16**
ATSic	AT	Mediterranean basin (Sicily)	*S. trutta*	JF297974	**21**; 22
ATM1	AT	Atlantic basin (North-West Africa)	*S. trutta*	JF297978	**21**
ATM2	AT	Atlantic basin (North-West Africa)	*S. trutta*	JF297979	**21**
ATM3	AT	Atlantic basin (North-West Africa)	*S. trutta*	JF297980	**21**
JA387	AT	South Atlantic basin (Spain)	*S. trutta*	AF253553	**13**
T2	AT	South Atlantic basin (Spain)	*S. trutta*	AF253554	**13**
LM20	AT	South Atlantic basin (Spain)	*S. trutta*	AF253555	**13**

(Continued)

Table 2.2 (Continued)

Haplotype	Lineage	Locality	Taxon	Accession number	Source
STMAR2	AT	South Atlantic basin (Spain)	*S. trutta*	AF253556	**13**
PIG5	AT	South Atlantic basin (Spain)	*S. trutta*	AF253559	**13**
DUcs1	DU	Duero and Minho rivers (Spain)	*S. trutta*	EF530513	**17**
Ducs2	DU	Duero and Minho rivers (Spain)	*S. trutta*	AF273088	**17**
Ducs3	DU	Duero River (Spain)	*S. trutta*	AF274579	**17**
DUcs5	DU	Duero and Minho rivers (Spain)	*S. trutta*	EF530517	**17**
DUcs8	DU	Duero and Minho rivers (Spain)	*S. trutta*	EF530520	**17**
DUcs10	DU	Duero River (Spain)	*S. trutta*	EF530522	**17**
DUcs11	DU	Duero River (Spain)	*S. trutta*	EF530523	**17**
DUcs12	DU	Duero River (Spain)	*S. trutta*	EF530524	**17**
DUcs13	DU	Duero River (Spain)	*S. trutta*	EF530525	**17**
DUcs14	DU	Duero River (Spain)	*S. trutta*	EF530526	**17**
DUcs15	DU	Duero River (Spain)	*S. trutta*	EF530527	**17**
DUcs16	DU	Duero River (Spain)	*S. trutta*	EF530528	**17**
DUcs17	DU	Duero River (Spain)	*S. trutta*	EF530529	**17**
DUcs18	DU	Duero River (Spain)	*S. trutta*	EF530530	**17**
DUcs21	DU	Duero River (Spain)	*S. trutta*	EF530533	**17**
DUcs22	DU	Duero River (Spain)	*S. trutta*	EF530534	**17**
DUcs23	DU	Duero River (Spain)	*S. trutta*	EF530535	**17**
Dades	Dades	AT basin-Draa River (North-West Africa)	*S. trutta*	JF297974	**21**
Da1a	DA-ES	Danube and Vistula basins (Central Europe, Bulgaria, Serbia); Adige River (Northern Italy)	*S. trutta*	AY185568	2; 16; **18**; 19; 20
Da1b	DA-ES	Danube basin (Austria)	*S. trutta*	AY185569	**18**; 19
Da1c	DA-ES	Danube basin (Austria)	*S. trutta*	GQ284832	**19**
Da1d	DA-ES	Danube basin (Austria)	*S. trutta*	GQ284833	**19**
Da2a	DA-ES	Danube basin (Austria); Adige River (Northern Italy)	*S. trutta*	GQ284834	16; **19**
Da2b	DA-ES	Danube basin (Austria)	*S. trutta*	GQ284835	**19**
Da2c	DA-ES	Danube basin (Austria)	*S. trutta*	GQ284836	**19**

Table 2.2 (Continued)

Haplotype	Lineage	Locality	Taxon	Accession number	Source
Da9	DA-ES	Danube basin (Austria)	*S. trutta*	AY185572	**18**
Da9a	DA-ES	Plitvika river-Danube basin (Croatia)	*S. trutta*	GQ222380	**23**
Da22	DA-ES	Danube and Vistula basins (Central Europe). Balkans. Adige River (North Italy)	*S. trutta*	AY185573	**18**; 19; 20; 16
Da23a	DA-ES	Danube basin (Austria)	*S. trutta*	AY185574	**18**
Da23b	DA-ES	Danube basin (Austria)	*S. trutta*	AY185575	**18**
Da24	DA-BS	Danube basin (Austria)	*S. trutta*	AY185576	**18**
Da25	DA-BS	Danube basin (Austria)	*S. trutta*	GQ284837	**19**
Da26	DA-ES	Adige River (North Italy); Danube basin (Bulgaria)	*S. trutta*	DQ841194	2; **16**
D3	DA-ES	Danube basin (Central Europe)	*S. trutta*	HQ848371	**20**
D4	DA-ES	Danube and Vistula basins (Central Europe)	*S. trutta*	HQ848372	**20**
D7	DA-ES	Danube basin (Central Europe)	*S. trutta*	HQ848374	**20**
D8	DA-ES	Danube basin (Central Europe)	*S. trutta*	HQ848375	**20**
OxAFA2	DA-ES	Aral Sea basin (Afghanistan)	*S. trutta oxianus*	EU329720	**24**
OxAFE2	DA-ES	Aral Sea basin (Afghanistan)	*S. trutta oxianus*	EU329721	**24**
Orumieh2	DA-ES	Orumieh lake (North Iran)	*S. trutta*	JF276033	**25**
Iran7	DA-ES	Caspian Sea basin (North Iran)	*S. trutta*	JF276031	**25**
Iran8	DA-ES	Caspian Sea basin (North Iran)	*S. trutta*	JF276032	**25**
DATR20	DA-ES	Turkey	*S. trutta*	JN543992	**9**
DATR21	DA-ES	Turkey	*S. trutta*	JN543993	**9**
DATR22	DA-ES	Turkey	*S. trutta*	JN543994	**9**
DATR23	DA-ES	Turkey	*S. trutta*	JN543995	**9**
Iran1	DA-ES	Caspian Sea basin (North Iran)	*S. trutta*	HM237337	**27**
Iran2	DA-ES	Caspian Sea basin (North Iran)	*S. trutta*	HM237338	**27**
Iran5	DA-ES	Caspian Sea basin (North Iran)	*S. trutta*	HM237341	**27**

(Continued)

Table 2.2 (Continued)

Haplotype	Lineage	Locality	Taxon	Accession number	Source
DaDA1	DA-ES	Black Sea-Danube basin (Serbia)	*S. trutta*	GQ357906	**2**
DaDA2	DA-ES	Black Sea-Danube basin (Bulgaria)	*S. trutta*	GQ357907	**2**
IsDa21	DA-ES	Caspian Sea basin (North Iran)	*S. ischchan*	JF795537	**26**
DaBS1	DA-BS	Black Sea basin-Danube and non-Danube (Bulgaria); Turkey	*S. trutta*	GQ357897	**2**; 28
DaBS2	DA-BS	Black Sea-Danube basin (Rumania)	*S. trutta*	GQ357898	**2**
DaBS3	DA-BS	Black Sea-Danube basin (Bulgaria and Rumania)	*S. trutta*	GQ357899	**2**
DaBS4	DA-BS	Black Sea-Danube basin (Rumania)	*S. trutta*	GQ357900	**2**
DaBS5	DA-BS	Black Sea-Danube basin (Rumania)	*S. trutta*	GQ357901	**2**
DaBS6	DA-BS	Black-Sea basin non Danube (Turkey)	*S. trutta*	GQ357902	**2**
DaBS7	DA-BS	Black-Sea basin non Danube (Turkey)	*S. trutta*	GQ357903	**2**
DaBS8	DA-BS	Black-Sea basin non Danube (Turkey)	*S. trutta*	GQ357904	**2**
DaBS9	DA-BS	Black Sea-Danube basin (Serbia)	*S. trutta*	GQ357905	**2**
DATR3	DA-BS	Turkey	*S. trutta*	JN543975	**9**
DATR4	DA-BS	Turkey	*S. trutta*	JN543976	**9**
DATR6	DA-BS	Turkey	*S. trutta*	JN543978	**9**
DATR7	DA-BS	Turkey	*S. trutta*	JN543979	**9**
DATR8	DA-BS	Turkey	*S. trutta*	JN543980	**9**
DATR11	DA-BS	Turkey	*S. trutta*	JN543983	**9**
DATR14	DA-BS	Turkey	*S. trutta*	JN543986	**9**
DATR16	DA-BS	Turkey	*S. trutta*	JN543988	**9**
DATR17	DA-BS	Turkey	*S. trutta*	JN543989	**9**
DATR18	DA-BS	Turkey	*S. trutta*	JN543990	**9**
TITR1	TI	Tigris River-Euphrates basin. Persian Gulf drainage (Turkey)	*S. trutta*	JN543997	**9**; 28; 29

Table 2.2 (Continued)

Haplotype	Lineage	Locality	Taxon	Accession number	Source
Obtus1		Neretva River (Bosnia and Herzegovina)	*S. obtusirostris*	AF488535	**30**
Obtus2		Neretva River (Croatia)	*S. obtusirostris*	EF469832	**31**
Ohr1		Lake Ohrid (FYROM-Albania)	*S. ohridanus*	AY926564	**14**; 3
Ohr10		Lake Ohrid (FYROM-Albania)	*S. ohridanus*	AY926562	**14**
Ohr11		Lake Ohrid (FYROM-Albania)	*S. ohridanus*	AY926566	**14**
Ohr2		Lake Ohrid (FYROM-Albania)	*S. ohridanus*	AY926560	**14**
Ohr3		Lake Ohrid (FYROM-Albania)	*S. ohridanus*	AY926568	**14**
Ohr4		Lake Ohrid (FYROM-Albania)	*S. ohridanus*	AY926561	**14**; 3
Ohr5		Lake Ohrid (FYROM-Albania)	*S. ohridanus*	AY926569	**14**; 3
Ohr6		Lake Ohrid (FYROM-Albania)	*S. ohridanus*	AY926559	**14**; 3
Ohr7		Lake Ohrid (FYROM-Albania)	*S. ohridanus*	AY926563	**14**
Ohr8		Lake Ohrid (FYROM-Albania)	*S. ohridanus*	AY926567	**14**
S. salar			*S. salar*	U12143	**32**

1: Cortey *et al.* 2004; 2: Kohout *et al.* 2013; 3: Snoj *et al.* 2009; 4: Maric *et al.* 2006; 5: Meraner *et al.* 2013; 6: Sušnik *et al.* 2007; 7: Snoj *et al.* 2010; 8: Gratton *et al.* 2014; 9: Ozen & Bardakzi unpublished; 10: Querci *et al.* 2013; 11: Gratton *et al.* 2013; 12: Razpet *et al.* 2007; 13: Suárez *et al.* 2001; 14: Sušnik *et al.* 2006: 15: Jadan *et al.* 2015; 16: Meraner *et al.* 2007; 17: Cortey *et al.* 2009; 18: Duftner *et al.* 2003; 19: Baric *et al.* 2010; 20: Kohout *et al.* 2012; 21: Snoj *et al.* 2011; 22: Fruciano *et al.* 2014; 23: Jadan *et al.* 2009 unpublished; 24: Griffiths *et al.* 2009; 25: Hashemzadeh *et al.* 2012; 26: Osinov 2009; 27: Vera *et al.* 2011; 28: Bardakzi *et al.* 2006; 29: Sušnik *et al.* 2005; 30: Snoj *et al.* 2002; 31: Snoj *et al.* 2008; 32: Hurst *et al.* 1999.

Tamura 3-parameter (T92) (Tamura, 1992), with $\alpha = 0.61$, $i = 0.75$ and base frequencies of $A = 0.310$, $T = 0.310$, $C = 0.190$ and $G = 0.190$. Accordingly, I conducted phylogenetic analyses in MEGA v6 using a maximum likelihood (ML) method and the T92 model of nucleotide substitution. The robustness of tree nodes was assessed based on bootstrap analysis with 1000 replicates. Phylogenetic relationships were also determined via Bayesian inference using MrBayes v3.2.0 (Ronquist *et al.*, 2012). The general time-reversible (GTR) substitution model was chosen as it is the most similar model to the T92 model available in MrBayes. The GTR model had the lowest Akaike information criterion (AICc) value in MEGA v6. I conducted two replicate runs with four Markov chain

Monte Carlo (MCMC) chains. Runs were initiated by assuming a random starting tree and a GTR model with six categories for substitution rates, gamma-distributed rate variation across the sites and a proportion of invariable sites. Runs were continued until the value of the standard deviation of split frequencies fell below 0.01. The chain was sampled every 100 generations to obtain 20,000 sampled trees. The first 5,000 trees (25%) were discarded as the burn-in phase. A final consensus tree with branch lengths and clade credibility (posterior probability) values was constructed using the remaining 75% of the trees. In both ML and Bayesian phylogenetic reconstructions I used one sequence of *Salmo salar* (GenBank accession number U12143) as outgroup in unconstrained phylogenetic analysis. Based on the phylogenetic reconstruction, I estimated the net evolutionary divergence over sequence pairs between lineages using the T92 model (Tamura, 1992). Brown trout phylogeography was also represented based on the phylogenetic network of haplotypes generated using the median-joining algorithm with the Network 4.6.1.1 software package (Bandelt *et al.*, 1999).

Distribution and Phylogenetic Relationships of Brown Trout Lineages

The phylogenetic reconstructions based on the 199 sequences representative of the brown trout's native distribution were consistent between maximum-likelihood (ML) and Bayesian methods. Both approaches confirmed the basal (outgroup) position of the Atlantic salmon (*S. salar*) with respect to the brown trout haplotypes and revealed the same mtDNA lineages, with similar phylogenetic relationships (Figure 2.2). However, ML reconstruction resulted in a large polytomy at a high hierarchical level, which was partly resolved by the Bayesian approach. Moreover, this latter method achieved higher

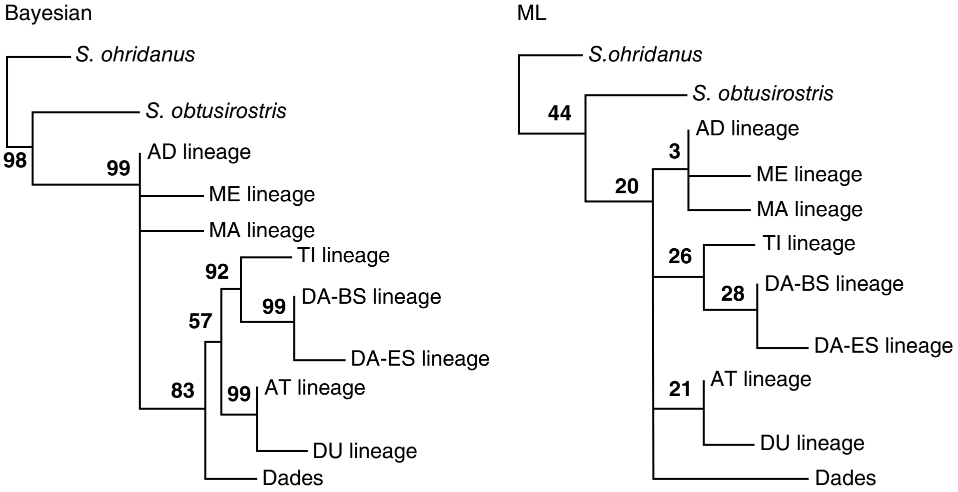

Figure 2.2 Phylogenetic relationships among *S. trutta* species complex lineages, *S. obtusirostris* and *S. ohridanus* inferred from the Bayesian inference and the maximum likelihood (ML) model. Posterior probabilities in the Bayesian tree and % of bootstrap values based on 1,000 replications in the ML tree are indicated.

posterior probabilities for all branch nodes (Figure 2.2; Figure 2.3). For the Bayesian reconstruction, the two independent runs converged to very similar likelihoods (−3,614.52, −3,610.62) after 8×10^6 generations.

Phylogenetic analyses confirmed the taxonomical positions of *S. ohridanus* and *S. obtusirostris* as two ancestral species that highly diverged from the brown trout species complex with support from high bootstrap and posterior probability values. In the brown trout species complex, haplotypes grouped into three 'major' lineages (Mediterranean, Danubian and Atlantic), and nine 'minor' lineages, all supported by high posterior probabilities (>90%), as follows: Adriatic (AD), Mediterranean (ME) and Marmoratus (MA) lineages within the Mediterranean 'major' lineage; Danubian-Black Sea (DA-BS) and Eastern Danubian (DA-ES) lineages within the 'major' Danubian lineage; and Atlantic (AT) and Duero (DU) lineages within the 'major' Atlantic lineage. In addition, two 'outlier' populations (Tigris-Turkey and Dades-North Africa) showed haplotypes that were highly divergent and were considered to be independent from the rest of the lineages, forming the Tigris (TI) and Dades lineages (Figure 2.3). The TI lineage was clearly within the Danubian 'major' lineage, but the phylogenetic position of the Dades lineage was not well-resolved. Further subdivisions within lineages were detected mainly in the AT, DA-BS and AD lineages. The ML phylogeny failed to resolve

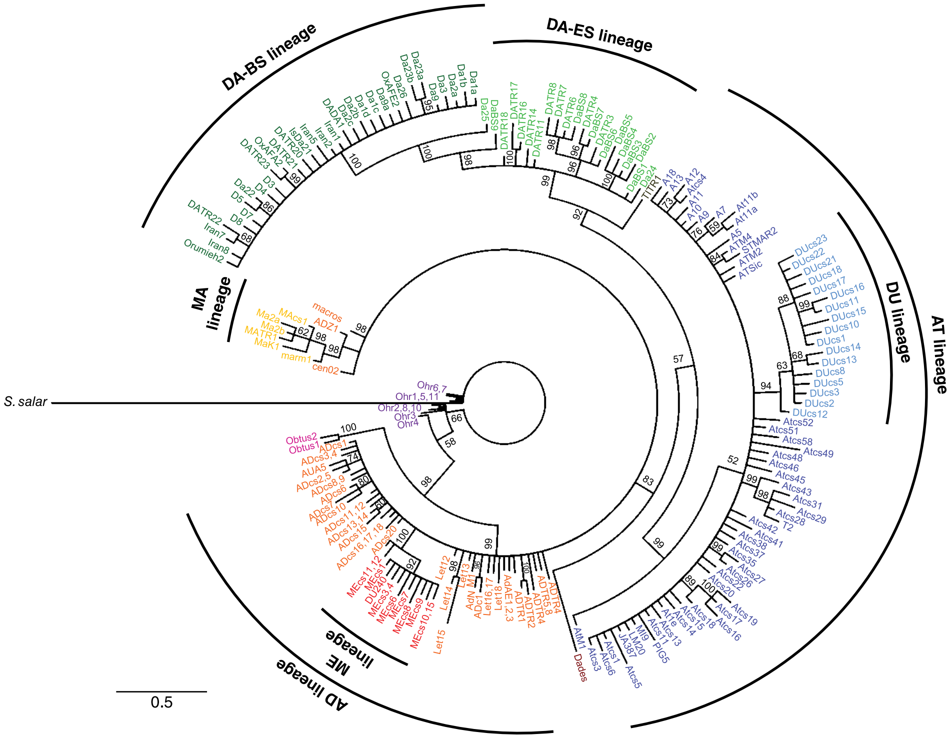

Figure 2.3 Phylogenetic tree of all compiled haplotypes of the *S. trutta* species complex, *S. obtusirostris* and *S. ohridanus* based on the Bayesian inference. Posterior probabilities higher than 50% are indicated at the main tree nodes. Tree is rooted with the out-group sequence from *S. salar*. Haplotype codes are detailed in Table 2.1.

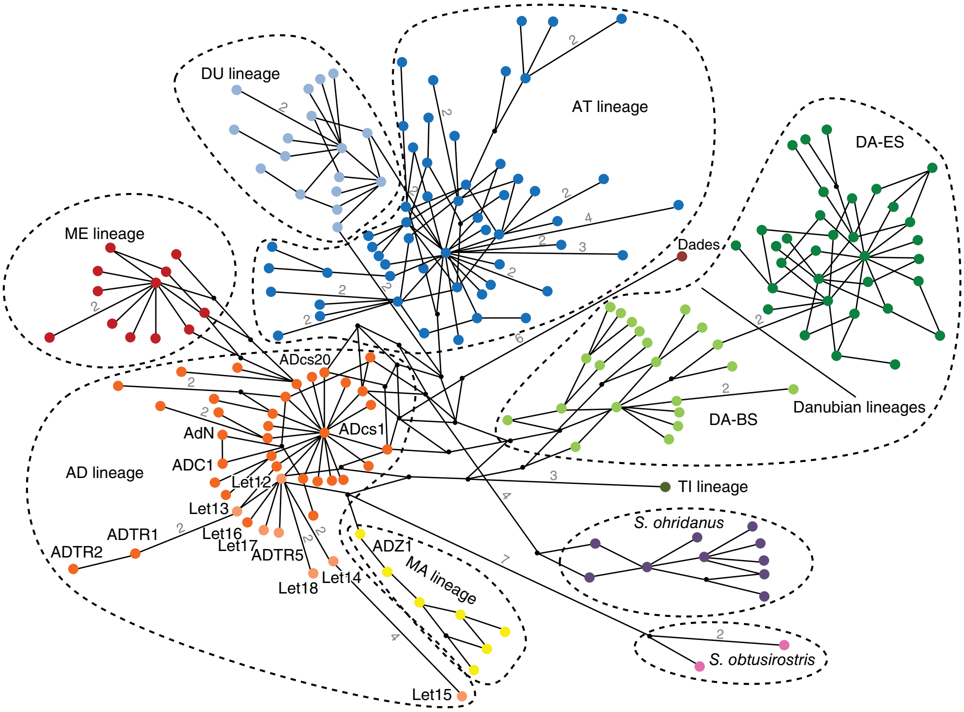

Figure 2.4 Median-joining network of compiled haplotypes of the *S. trutta* species complex, *S. obtusirostris* and *S. ohridanus*. The number of theoretical mutational steps (TMS) is indicated when it was more than 1. Small black dots represent median vectors. The length of branches is usually proportional to the number of TMS, but some have been slightly modified to give a better visualization. Haplotype codes are detailed in Table 2.1 but they were only indicated for those evolutionary relevant haplotypes specifically mentioned through the text.

tree topologies between the ‘major’ lineages. However, the Bayesian reconstruction indicated a basal position for the AD lineage with respect to the rest of brown trout lineages (Figure 2.2).

The median-joining network identified the same ‘major’ and ‘minor’ lineages (Figure 2.4). Connections among the major lineages were established via numerous theoretical mutational steps (TMSs) and several median vectors, whereas connections among minor lineages comprised a least two TMSs and zero or one median vector. For instance, the DU lineage was connected to the AT lineage by 2 TMSs, the two Danubian lineages were connected by 2 TMSs, and the ME and MA lineages were both connected to the AD lineage though two TMSs and one median vector. Star-like patterns of network structure explained by episodes of rapid expansion predominated within the AD and ME lineages, with some highly intricate connections observed mainly within the AT lineage but also in the DA-ES lineage. A highly structured network reflecting an ancient divergence characterized the patterns for *S. ohridanus* and *S. obtusirostris*, which were connected to the skeleton of the network by numerous TMSs and two median vectors.

Within the trout species complex, the recognized species *S. obtusirostris* and *S. ohridanus* have a highly restricted distribution. S. *obtusirostris* is endemic to a few rivers draining to the South Adriatic Sea whereas *S. ohridanus* is endemic to Lake Ohrid (shared between the former Yugoslav Republic of Macedonia – FYROM – and Albania) (Snoj *et al.*, 2002; Sušnik *et al.*, 2006). Brown trout lineages are distributed geographically, but many lineages overlap in their distribution in southern Europe, mainly in the Iberian, Balkan and Anatolian peninsulas (Figure 2.1).

Despite the fact that human activities and a warming climate have reduced the original distribution of most brown trout lineages, other lineages have extended their distribution via stocking of foreign lineages and translocation (Bernatchez, 2001). The best known example of this is the AT lineage, which is naturally distributed in the rivers of the Atlantic basin and is probably native to the upper Danube tributaries. This lineage has greatly expanded its range via stocking with hatchery fish of northern European origin obscuring, o explaining, present-day phylogeographic patterns (García-Marín *et al.*, 1999; Marzano *et al.*, 2003; Jug *et al.*, 2005; Simonović *et al.*, 2007; Meraner *et al.*, 2007; Kohout *et al.*, 2012; Gratton *et al.*, 2013). Based on literature reports, I tried to exclude anthropogenic distributions, mainly of the Atlantic lineage, from this review of native brown trout phylogeography.

Net evolutionary divergence between lineages ranged from 0.003 between the AD and ME lineages to 0.015 between the Dades and DA-ES lineages (Table 2.3). As expected, the highest evolutionary divergences were observed when *S. ohridanus* or *S. obtusirostris* were included in the comparisons (*S. ohridanus–S. trutta*: 0.008–0.016; *S. obtusirostris–S. trutta*: 0.008–0.018; *S. ohridanus–S. obtusirostris*: 0.010). Interestingly, the lowest and the highest evolutionary distances between *S. ohridanus* or *S. obtusirostris* with respect to *S. trutta* were obtained with the AD and Dades lineages, respectively.

I attempted to estimate divergence dates between lineages based on the molecular clock. Because secondary contacts among lineages and isolation episodes seem to be recurrent in the phylogeography of brown trout, molecular clock estimates based on evolutionary distance should be interpreted with caution (Rambaut & Bromham, 1998). In the genus Salmo, the CR appears to have evolved at a lower rate than some other regions of the mtDNA (Apostolidis *et al.*, 1997; Sušnik *et al.*, 2006). Based on the recommendations of Cortey *et al.* (2004), I assumed a molecular clock calibrated at the lower edge of the range commonly used for salmonids species (0.75% nucleotide divergence per 1 million years, Shedlock *et al.*, 1992) that was applied to evolutionary parameters (net evolutionary divergence) to obtain rough evolutionary dates. Accordingly, divergence times between *S. trutta* lineages ranged from 436,000 years, for the split between the AD and ME lineages, to almost 2 million years, for the split between the DA-ES and Dades lineages (Table 2.3). These estimates coincide with the early Pleistocene and upper Pliocene and largely encompass previously estimated dates (Bernatchez, 2001; Cortey *et al.*, 2004; Barkakci *et al.*, 2006; Snoj *et al.*, 2011; Gratton *et al.*, 2014; Pustovrh *et al.*, 2014).

S. ohridanus (Belvica Trout)

S. ohridanus is one of the 200 endemic species that inhabit Lake Ohrid, considered the oldest freshwater habitat in Europe. Phylogenetic analyses of mitochondrial and nuclear genes support the inclusion of *S. ohridanus* as a highly diverged member in the genus Salmo and a sister relationship of this species with *S. trutta* (Phillips *et al.*, 2000;

Table 2.3 Pairwise genetic differentiation and divergence times estimated between lineages. Below diagonal: Estimates of Net Evolutionary Divergence. Above diagonal: putative timing in kiloyears of divergence events according to the molecular clock rates of 0.75% per 1000 ky (Shedlock *et al.*, 1992).

	AD	**ME**	**MA**	**AT**	**DU**	**Dades**	**DA-ES**	**DA-BS**	**TI**	***S. obtusirostris***	***S. ohridanus***
AD		441	527	868	1 038	1 304	1 055	737	928	1 120	1 157
ME	0.0033		953	1 033	1 257	1 661	1 333	950	1 249	1 436	1 382
MA	0.0039	0.0071		1 323	1 524	1 746	1 373	1 195	1 160	1 371	1 668
AT	0.0065	0.0077	0.0099		501	1 526	1 250	887	1 157	1 185	1 498
DU	0.0078	0.0094	0.0114	0.0038		1 726	1 461	1 060	1 365	1 386	1 687
Dades	0.0097	0.0125	0.0131	0.0114	0.0129		1 938	1 542	1 846	2 495	2 117
DA-ES	0.0079	0.0100	0.0103	0.0094	0.0110	0.0145		591	797	1 867	1 891
DA-BS	0.0055	0.0071	0.0090	0.0066	0.0079	0.0116	0.0044		889	1 611	1 445
TI	0.0070	0.0094	0.0087	0.0087	0.0102	0.0138	0.0060	0.0067		1 685	1 790
S. obtusirostris	0.0084	0.0108	0.0103	0.0089	0.0104	0.0187	0.0140	0.0121	0.0126		1 333
S. ohridanus	0.0087	0.0104	0.0125	0.0112	0.0126	0.0158	0.0142	0.0108	0.0134	0.0100	

Sušnik *et al.*, 2006). It is believed that *S. ohridanus* split from a common ancestor of brown trout more than 4 million years ago (early Pliocene), overlapping with the estimates of the when Lake Ohrid formed. As a consequence, the most likely hypothesis is that Ohrid trout evolved '*in situ*' in Lake Ohrid by adapting to a resident deep water habitat (Sušnik *et al.*, 2006). The idea that *S. ohridanus* is a sister taxon to *S. obtusirostris* (Snoj *et al.*, 2002) suggests an alternative scenario for its origin that involves the past existence of a common ancestor of *S. ohridanus* and *S. obtusirostris* in the lake (Sušnik *et al.*, 2006). However, Berrebi *et al.*, 2013; Pustovrh *et al.* (2014) and this study (Figure 2.3) failed to detect a sister relationship between these two species and support the hypothesis of an ancestral and independent origin of Ohrid trout in the lake, that preceded divergence of *S. obtusirostris*.

A member of the *S. trutta* species complex, referred to by some authors as *S. letnica* (Kottelat & Freyhof, 2007) but belonging to the AD lineage of the *S. trutta* species complex (Snoj *et al.*, 2009), is sympatric with *S. ohridanus* in Lake Ohrid. It is thought that *S. trutta* colonized Lake Ohrid recently. Although successful artificial hybridization has been described between *S. trutta* and *S. ohridanus*, only rare hybridization events have been reported based on microsatellite markers, and no contemporary gene flow between taxa has been observed (Sušnik *et al.*, 2006).

S. obtusirostris **(Soft-Mouth Trout)**

S. obtusirostris is considered an old trout species endemic to a few South Adriatic Rivers. It was previously classified as a separate genus, but molecular data support a close relationship to *S. trutta* and its inclusion as a different species within genus *Salmo* (Snoj *et al.*, 2009). It is thought that this species evolved early in the Pliocene, approximately 2.5 million years ago (Crête-Lafrenière *et al.*, 2012; Pustovrh *et al.*, 2014).

Snoj *et al.* (2002) and Sušnik *et al.* (2006) proposed that *S. obtusirostris* and *S. ohridanus* formed a separate clade as brown trout sister taxa. The findings of the mito-nuclear study by Crête-Lafrenière *et al.* (2012) agree with this hypothesis but a much-reduced representation of brown trout diversity was included in this review. As indicated previously, the present study and the recent revision of Pustovrh *et al.* (2014) based on mitochondrial and nuclear markers, refutes the sister relationship between these species and suggests that *S. obtusirostris* is a sister taxon to the *S. trutta* complex, with *S. ohridanus* occupying a basal position.

The native range of *S. obtusirostris* is restricted to the Krka and Jadro rivers (Croatia), the Neretva and Vrljika Rivers (Neretva basin, Bosnia and Hercegovina and Croatia) and the Zeta River (Montenegro). However, mtDNA data has confirmed this species only in the River Neretva basin (Snoj *et al.*, 2008; 2009), where hybridization between *S. obtusirostris* and *S. trutta* has been detected based on microsatellite data (Razpet *et al.*, 2007). *S. obtusirostris* nuclear genotypes have been found in brown trout from the Jadro and Zeta Rivers fixed by mtDNA haplotypes of brown trout AD lineage, indicating natural ancient hybridization events between the ancestral nuclear lineage and the subsequent mitochondrial lineage by mtDNA capture events, probably during glacial periods (Sušnik *et al.*, 2007a; Pustovrh *et al.*, 2014). In these rivers, microsatellite loci analyses have confirmed *S. obtusirostris* to be living in sympatry with brown trout only in the Zeta River (Sušnik *et al.*, 2007a; b; Mrdak *et al.*, 2012).

S. trutta, Adriatic Lineage (AD)

The AD lineage of brown trout is distributed along southern Eurasia, from Turkish to Eastern Iberia, in rivers draining to the Mediterranean basin. It is a highly structured lineage with complex and reticulated distribution patterns for gene diversity and many instances of endemism (Bernatchez, 2001; Cortey *et al.*, 2004; Bardakci *et al.*, 2006; Gratton *et al.*, 2014).The reticulated structure within the AD lineage was undoubtedly favoured by climatic and environmental changes during Pleistocene glaciation periods that modified small-scale hydrographical connections and isolated brown trout populations to the headstreams during interglacial warm periods (Bianco, 1990; Giuffra *et al.*, 1994; Macklin *et al.*, 1995; Berrebi *et al.*, 2000; Sanz *et al.*, 2002; Bardakci *et al.*, 2006; Gratton *et al.*, 2014).

Secondary contact between lineages, associated with river captures common during the Pleistocene (Bănărescu, 2004), would explain the presence of the AD lineage in the southern Atlantic rivers of the Iberian Peninsula and probably also in the Danube basin (Sanz *et al.*, 2006; Kohout *et al.*, 2013).

Postglacial and more recent warming of the Mediterranean basin rivers has restricted trout populations to small areas in headstreams and increased isolation and genetic drift, promoting genetic singularities within the Adriatic lineage (Sanz *et al.*, 2002; Cortey *et al.*, 2004), a situation also described in other continental fish species in southern Europe (Durand *et al.*, 1999; Volckaert *et al.*, 2002; Seifertová *et al.*, 2012; DeFaveri *et al.*, 2012; Sanz *et al.*, 2015). *S. peristericus*, *S. platycephalus*, *S. macedonicus*, *S. pelagonicus*, *S. cetti*, *S. fibreni*, *S. cenerinus*, *S. carpio*, *S. dentex*, *S. macrostigma*, and *S. letnica* are some of the taxonomic units that have been morphologically identified in the Mediterranean-Adriatic region. However, classification of these taxa at the species level has been weakly supported by molecular data and they have all been reported to belong to the brown trout AD lineage (Sušnik *et al.*, 2004; 2006; Barkakci *et al.*, 2006; Lo Brutto *et al.*, 2010; Berrebi *et al.*, 2013; Querci *et al.*, 2013; Kohout *et al.*, 2013; Gratton *et al.*, 2013; 2014; Zaccara *et al.*, 2015). In spite of these taxonomic uncertainties, a few of the proposed taxonomic units certainly correspond to phylogenetic subdivisions within the AD lineage (Pustovrh *et al.*, 2014). In other cases, the proposed taxonomic units likely correspond to hybrids of ancient introgression between the AD and MA lineages (Gratton *et al.*, 2014) or between *S. trutta* and *S. obtusirostris* (Razpet *et al.*, 2007).

The high degree of endemism found within Adriatic trout is considered to be a consequence of ancient, allopatrically evolved populations with limited natural contact (Apostolidis *et al.*, 1997; Bernatchez, 2001; Cortey *et al.*, 2004; Bardakci *et al.*, 2006). For instance, haplotypes of AD lineage found in Lake Ohrid (*letnica*) have been considered a monophyletic lineage within the Adriatic trout that evolved in isolation in the lake. In the present review, *letnica* haplotypes formed a clear subcluster in the median-joining network (Figure 2.4), but this association was hardly reflected in the phylogenetic tree (Figure 2.3).

Sušnik *et al.* (2007b) suggested a Western Mediterranean origin of the AD lineage because the central, and presumably most ancestral, haplotype (ADcs1) was restricted to the Iberian Peninsula. However, subsequent studies have found ADcs1 haplotypes throughout the entire range of the AD lineage, including the Aegean and Adriatic basins (Cortey *et al.*, 2004; Marić *et al.*, 2006; Snoj *et al.*, 2009; Kohout *et al.*, 2013; Meraner *et al.*, 2013). This observation suggests an alternative hypothesis that considers an Adriatic-Balkan origin of the lineage that then expanded to the Iberian Peninsula via colonization by fish primarily with the ADcs1 haplotype. Interestingly, most of the Iberian Peninsula haplotypes occupied a radial and end position derived from the most common haplotype (ADcs1) in the median-joining network (Figure 2.4). The remaining haplotypes, found outside of the Iberian region, in the Adriatic, Tyrrhenian, Ionian and Aegean sub-basins, are not connected to the central ADcs1 haplotype through the Iberian haplotypes and are located in more distant and derived positions. In addition, AD letnica brown trout coexist with *S. ohridanus* in the most ancient European lake (Lake Ohrid), and their haplotypes are linked to the MA lineage and the ancestral species *S. obtusirostris* (Figure 2.4). Molecular studies have observed particularly high levels of diversity and endemism in the Adriatic basin, with ancestral and independent evolutionary histories in many Adriatic–Balkan populations (Marić *et al.*, 2006; Sušnik *et al.*, 2007b; Razpet *et al.*, 2007; Snoj *et al.*, 2009; 2010; Apostolidis *et al.*, 2011; Gratton *et al.*, 2014; Jadan *et al.*, 2015), which supports this region as the main centre where the Adriatic lineage evolved. Alternatively, Sušnik *et al.* (2004), Bardakci *et al.* (2006) and Arslan & Bardakci (2010) studied brown trout from the Anatolian peninsula and proposed Turkey as an important focus for the diversification of the Adriatic lineage.

Wherever the origin of the AD lineage occurred, all of the above observations agree with an ancestral pre-Pleistocene origin of this lineage (Bardakci *et al.*, 2006). Cortey *et al.* (2004) estimated the separation of Atlantic and Mediterranean 'major' lineages during the period of Pliocene-Pleistocene climatic cooling (1 million years ago). The main expansion of the Adriatic lineage has been estimated to have occurred 150,000–200,000 years ago, before the last glacial cycle (Cortey *et al.*, 2004; Sušnik *et al.*, 2007b). Nevertheless, the high diversity of brown trout in the entire Adriatic drainage has been explained by successive colonization events. Ancient colonization waves, independent of the main expansion, probably explain the occurrence of Adriatic Ohrid brown trout (Sušnik *et al.*, 2007b; Pustovrh *et al.*, 2014). Razpet *et al.* (2007) related the lack of intermediate haplotypes found in the Neretva River (AdN) to relict single arrivals of the lineage into the Neretva basin (Bosnia-Herzegovina) during the initial phase of the formation of the Adriatic lineage. The same wave of colonization would have involved the AD-C1 divergent haplotype in the Zeta River (Montenegro, Sušnik *et al.*, 2007b) and the Ad*Prz haplotype found in the Tripušnica and Drin river basin (Serbia and Albania, Marić *et al.*, 2006; Snoj *et al.*, 2009), which are closely related to the ADN haplotype (Marić *et al.*, 2006; Razpet *et al.*, 2007, Figure 2.4 in this study). Similarly, Adriatic haplotypes found in Albania are not closely related to the rest of the Adriatic lineage, suggesting an independent colonization of this region (Snoj *et al.*, 2009).

***S. trutta*, Marmoratus Lineage (MA)**

Marmoratus trout (i.e., marble trout) is an endemic salmonid of the Southern Alpine watersheds draining to the North Adriatic (North Italy, Slovenia and Croatia) and is also found in the Balkan Peninsula (Albania and Greece). This group was firstly defined as a phenotypically and ecologically distinct species (marble trout), mostly confined to the alpine region of the Pô River basin in Northern Italy and the Soca River system in Slovenia (Bernatchez, 2001; Berrebi *et al.*, 2000; Snoj *et al.*, 2000). Bernatchez *et al.* (1992) and Giuffra *et al.* (1994; 1996) reported the first molecular data that confirmed a distinct monophyletic origin of marble trout (MA lineage) within the *S. trutta* complex, which may have originated in the North Adriatic.

The geographic range of marble trout overlaps with that of the AD, ME and Danubian lineages (Giuffra *et al.*, 1994; Marzano *et al.*, 2003; Meraner *et al.*, 2007). However, a recent study by Meraner *et al.* (2013) failed to find a significant presence of the AD and ME lineages in the northern Adriatic region and questioned the autochthony of the AD lineage in this area. The natural hybridization of marble trout with all of these lineages, and even with *S. obtusirostris*, has been reported (Snoj *et al.*, 2000; Razpet *et al.*, 2007; Jadan *et al.*, 2015). It is thought that selection would prevent the complete mixture of the gene pools (Giuffra *et al.*, 1996; Gratton *et al.*, 2013); however, extensive hybridization between brown and marble trout, promoted by massive stocking, threatens the conservation of pure populations of native marble trout, to the point that trout with a morphologically typical marbled phenotype are currently rare (Berrebi *et al.*, 2000; Fumagalli *et al.*, 2002; Jug *et al.*, 2005; Pujolar *et al.*, 2011). Present climate conditions, overfishing and intense poaching are also thought to contribute to the possible extinction of this trout and the isolation of the remaining populations.

Phylogenetic studies have suggested a very ancient divergence between *S. trutta* and *S. marmoratus*, approximately 500,000–2 million years ago (Giuffra *et al.*, 1994; 1996; Bernatchez, 2001), which roughly coincided with the divergence dates estimated here (Table 2.3). Subsequent secondary contacts during inter-glacial and even post-glacial periods must be responsible for the natural hybridization between lineages (Cortey *et al.*, 2004; Gratton *et al.*, 2014). Alternatively, based on the distribution of MA and Mediterranean (AD and ME) lineages in northern Italian basins, Berrebi *et al.* (2000) proposed that brown trout were the first colonizers and that the subsequent invasion of the MA lineage led to the total disappearance of the original colonizers and natural hybridization.

Marble trout are also considered native in the South Adriatic (Albania) (Snoj *et al.*, 2009) and in Greek populations draining to the Ionian Sea but have likely been introduced in Greek rivers draining to the Aegean Sea (Apostolidis *et al.*, 2008; Kohout *et al.*, 2013). MA haplotypes have also been found in trout inhabiting in the Krka (Croatia) (Jadan *et al.*, 2015) and Neretva (Bosnia-Herzegovina) (Razpet *et al.*, 2007) rivers and in Central Italy (Splendiani *et al.*, 2006). In all these regions, despite the presence of the MA mitochondrial lineage, no marbled phenotypes have been found, suggesting that there is no correlation between the marbled phenotype and lineage outside the Italian-Slovenian region (Apostolidis *et al.*, 1997; 2008; Snoj *et al.*, 2009; Jadan *et al.*, 2015). Interestingly, MA haplotypes found in Central Italy and in the Krka river are genetically close to those from Albania and western Greece (South Adriatic-Ionian populations), suggesting a recent and natural history of dispersion of trout between the two coasts of the Adriatic Sea (Splendiani *et al.*, 2006; Jadan *et al.*, 2015). In addition, Adriatic haplotypes have been found in individual phenotypically marble trout in the Zeta and Cijevna Rivers (Montenegro) (Sušnik *et al.*, 2007b) and in the Neretva River basin (Bosnia-Herzegovina) (Razpet *et al.*, 2007). Similarly, and unexpectedly, the marbled phenotype has been observed in brown trout inhabiting the Otra River in Norway (Skaala & Solberg, 1997), but that group obviously not monophyletic with the MA lineage (Delling, 2000). All of these observations support the hypothesis that similar colour patterns could have evolved independently via adaptive selection in some coding-genes.

Based on the above observations, some authors suggest that marble trout from the North and South Adriatic could represent divergent evolutionary lineages (Razpet *et al.*, 2007; Snoj *et al.*, 2009; Jadan *et al.*, 2015). Pustovrh *et al.* (2011b; 2014) suggested that northern and southern Adriatic marble trout form a monophyletic group that diverged in the early Pleistocene. The phylogenetic reconstruction in my study grouped all MA haplotypes in a well-supported cluster that included the ADZ1 haplotype found by Sušnik *et al.* (2007b) in the Zeta River (Figure 2.3; Figure 2.4). Curiously, the ADZ1 haplotype was found in trout with soft-mouth phenotype (Sušnik *et al.*, 2007b; Snoj *et al.*, 2010), in spite of the fact that brown, marble and soft-mouth trout have been observed in this river (Mrdak *et al.*, 2012). Sušnik *et al.* (2007b) included the ADZ1 haplotype in the AD lineage, but they based its phylogenetic reconstruction on only 563 bp of the 5'-end of the CR and did not include reference haplotypes from the MA lineage in their analyses. Our phylogenetic reconstruction, which is based on the complete sequence of the CR and includes other MA haplotypes, clearly includes the ADZ1 haplotype within the MA lineage. Indeed, the entire MA lineage connects to the AD lineage through this ADZ1 haplotype, which in turn links to the AD haplotypes from Lake Ohrid (letnica) and to the ancestral species *S. obtusirostris* (Figure 2.4). These observations support the hypothesis of a common origin for all MA haplotypes and of a very early divergence of the MA lineage, prior to the main expansion of the AD lineage, probably from an ancestral form of the AD lineage. Based on mitochondrial and nuclear loci, Gratton *et al.* (2014) and Pustovrh *et al.* (2011b; 2014) suggested a very early divergence of the MA lineage (0.6–1.7 million years ago) that occurred before the diversification of the AD lineage in Italy. Gratton *et al.* (2014) suggest hybridization between AD and MA lineages as a consequence of natural recent gene flow of the Adriatic haplotypes into the ancestral MA gene pool. Similarly, natural hybridization of marble trout with *S. obtusirostris*, has been reported (Razpet *et al.*, 2007).

Because of the extensive distribution of the MA mtDNA lineage and the fact that phenotypically marble trout were found in North Italy, previous works have considered this region as the origin of this lineage (Giuffra *et al.*, 1996; Bernatchez, 2001). Alternatively, this lineage could have originated from the ancestral AD lineage in the Balkan region and then expanded towards the North Adriatic with a main expansion event in that region, where the marbled phenotype may have appeared via the process of selection. In this case, genetically singular haplotypes found in the southern Adriatic and Balkan Peninsula could represent relicts of the route of colonization of the MA lineage from the Balkans to the North Adriatic. These southern populations represent, in turn, the southern geographical limit of the MA lineage and could be very sensitive to stochastic events, genetic drift, and bottlenecks, which may have been particularly intense in the Balkan Peninsula during the Pleistocene (Snoj *et al.*, 2009).

Finally, Pustovrh *et al.* (2014) suggest the classification of the marble trout as a distinct species, which would be a sister taxon to the brown trout species complex, based on its basal position and the high phylogenetic divergence reported for this trout in their nuclear DNA. However, their work covered only the western Balkans, and the sampling of trout from the MA and AD lineages was restricted to Slovenian and the Balkans, respectively. Therefore, their conclusions about global phylogenetic reconstructions may be biased because of a poor representation of both these lineages. For instance, mitochondrial MA haplotypes from the southern Adriatic and Italian populations of the AD lineage were not included in this review. Therefore, missing (non-sampled) haplotype and genotype intermediates between the MA and AD lineages seems a plausible explanation for these observations.

S. trutta, Mediterranean Lineage (ME)

The Mediterranean lineage is mostly distributed in the rivers of the Iberian Peninsula and southern France draining to the western Mediterranean Sea (Cortey *et al.*, 2004; Bernatchez, 2001). It has occasionally been found in Central Italy (Splendiani *et al.*, 2006), Corsica (Berrebi, 2015), the Krka River (Croatia) (Jadan *et al.*, 2015), Albania (Snoj *et al.*, 2009), the Aegean basin (Apostollidis *et al.*, 1997), and even in the Danube drainage (Slovenia) (Cortey *et al.*, 2004). The predominance of this lineage in the Iberian Peninsula suggests that it originated in this region (Cortey *et al.*, 2004). The expansion of Mediterranean haplotypes out of the Iberian Peninsula could be explained by the natural dispersal of the Mediterranean lineages to the eastern Mediterranean during the last Pleistocene glaciation period (Cortey *et al.*, 2004; Snoj *et al.*, 2009; Jadan *et al.*, 2015). The phylogeographic distribution of this lineage resembles that described for the MA lineage and may be explained by a similar evolutionary history. However, in contrast to the scenario described for the MA lineage, all of the scattered ME haplotypes found outside of the Iberian Peninsula have also been found in Iberian brown trout populations. This fact reinforces the idea of an Iberian origin for all haplotypes of the ME lineage.

Over most of their range, ME haplotypes coexist in sympatry with AD lineage haplotypes (Figure 2.1). Intergradation among different lineages in the Iberian region has also been revealed based on analyses of nuclear allozyme loci (Sanz *et al.*, 2002). In Corsica, Berrebi (2015) considered the AD haplotypes to be the ancestral lineage primarily inhabiting the southern half of the island, with the Mediterranean lineage (ME) invading northern regions of Corsica after the last glacial maximum. In the Iberian Peninsula, both lineages show a patchy distribution without any evident hydrographical pattern, but the ME haplotypes are more frequently found in the northern regions (Cortey *et al.*, 2004; Sanz *et al.*, 2006). Stochastic events appear to have been particularly intense in the southern European peninsulas during the Pleistocene and genetic drift probably contributed to the present mosaic distribution of the AD and ME lineages (Sanz *et al.*, 2002; Cortey *et al.*, 2004; Jadan *et al.*, 2015).

Recurrent founder events and secondary intergradations in the Mediterranean region have surely eroded the molecular signals of older evolutionary events, which make it particularly difficult to infer divergence dates and phylogeographic histories. Cortey *et al.* (2004) suggested a mid-Pleistocene parapatric divergence of the ME lineage from the AD lineage. These authors estimated the divergence date at approximately 500,000–600,000 years ago, which fits with molecular clock estimates of this and previous studies (Sanz *et al.*, 2002; Snoj *et al.*, 2009). The main expansion of the ME lineage likely took place 190,000 years ago (Cortey *et al.*, 2004). The star-like structure of the Mediterranean mtDNA haplotypes in the median-joining network (Figure 2.4) supports the hypothesis of a rapid population expansion. Curiously, ME haplotypes connect to the AD lineage through one median vector and the ADcs20 haplotype, which has been found in Greece (Adriatic and Aegean basins). This haplotype network pattern resembles those observed in the Adriatic haplotypes of the Neretva and Zeta rivers, which were explained by an independent ancestral colonization from the ancestral AD lineage (Razpet *et al.*, 2007).

Similarly, Mediterranean haplotypes could have originated from an ancestral Adriatic form that colonized the western Mediterranean, diverged and then expanded into the Iberian Peninsula.

***S. trutta*, Danubian Lineages (DA-BS, DA-ES and TI)**

Danubian haplotypes have an extended geographical distribution as they are found from Central Europe and eastwards to the Afghanistan Rivers draining to the Aral Sea and up to the northern Russian rivers draining to the Caspian Sea (Figure 2.1). The Danubian major lineage was originally described in rivers draining to the Danubian basin (Bernatchez *et al.*, 1992). Subsequent studies detected Danubian haplotypes in rivers draining to the Black Sea, even outside of the Danubian drainage (Kohout *et al.*, 2013), and in rivers draining to the Caspian and Aral Seas (Griffiths *et al.*, 2009; Hashemzadeh *et al.*, 2012). In addition, Danubian haplotypes have occasionally been found in the upper Vistula, which drains to the Atlantic Sea, probably as a consequence of secondary post-glacial contact between the upper tributaries of the Vistula and the Danube Rivers (Kohout *et al.*, 2012). The rerouting of the north-flowing rivers from large ice-dam lakes that discharged southward was common during the Quaternary glaciations that affected northern Russia (Mangerud *et al.*, 2004). Similarly, Danubian haplotypes are found in the Adige and in the upper Neretva Rivers, draining to the Adriatic Sea, probably due to secondary connections via river captures between Danubian tributaries and these rivers during the Pleistocene (Meraner *et al.*, 2007; Razpet *et al.*, 2007). In addition, the anthropogenic introduction of Danubian trout cannot be completely discarded in the Adige River (Meraner *et al.*, 2007).

Sušnik *et al.* (2005) revealed the existence of a new, highly divergent haplotype in the upper Tigris (Euphrates River system of the Persian Gulf basin), which grouped with the Danubian lineage with low bootstrap support. Based on mtDNA-RFLP analyses, Bardakci *et al.* (2006) confirmed this highly divergent lineage in the Tigris River, but they did not resolve the position of this lineage with respect to the AD and Danube lineages. According to my phylogenetic reconstruction (Figure 2.3; Figure 2.4), the TI lineage groups with the rest of the Danubian lineages with high bootstrap support and occupies a basal position in the Danubian group. Based on the comparison of the Tigris sequence with other published Danubian haplotypes, Sušnik *et al.* (2005) estimated that the isolation of TI lineage took place 1–2 million years ago, predating the estimated age of expansion for the major lineages (154,000–309,000 years ago according to Bernatchez (2001)). The geological history of this area provides evidence that the Tigris River reached the Persian Gulf through headwater captures between the Black Sea and the Tigris Euphrates basin during the late Pliocene, when the regions of the Black, Caspian and Aral Seas were interconnected (Sušnik *et al.*, 2005; Bardakci *et al.*, 2006). Presumably, Pliocene orogeny isolated the upper reaches of the Euphrates from the Black Sea basin. Subsequent extreme periods of desiccation in this area in the Quaternary period likely led to adaptations that contributed to the unique and highly divergent population in the upper Tigris (Sušnik *et al.*, 2005). Unexpectedly, analyses of microsatellite data clustered the Tigris River brown trout population, in which the highly divergent mtDNA TI haplotype is found, with other brown trout from the Euphrates River of the AD mtDNA lineage (Arlsan *et al.*, 2010). Convergence of microsatellite alleles could explain the above observation. However, a comparison of the results from the mtDNA and microsatellite data suggests an ancient origin of this population but recent secondary contact between brown trout of the Mediterranean and Euphrates basins (Bardakci *et al.*, 2006; Arslan & Bardakci, 2010).

Bernatchez (2001) detected genetic divergences within the Danubian major lineage and suggested different evolutionary units for each sea basin (Black and Caspian-Aral Seas). Bardakci *et al.* (2006) also reported the distribution of Danubian haplotypes in some rivers draining to the Aegean Sea and defined different sublineages in the Black/Marmara Seas, Aegean Sea and Caspian Seas within the Danubian major lineage. Based the CR sequencing data, Kohout *et al.* (2013) revealed new haplotypes in the Danube River basin and the southern Black Sea Rivers that were clearly divergent from the rest of the DA haplotypes found in some rivers of the Danube basin and in rivers draining to the Caspian and Aral Seas. These authors related the most frequent Black Sea haplotype (DaBS1) to the mtDNA-RFLP BM12 haplotype that has been identified across the Turkish regions of the Black/Marmara Sea basins by Barkakci *et al.* (2006). I tested this similarity via sequence alignment and found that the DaBS1 haplotype was identical to the Turkish haplotype DATR15 (Ozen and Bardakzi, unpublished). Kohout *et al.* (2013) considered these two groups representative of two sympatric species of brown trout described in eastern Anatolia and suggested a separate evolution of these lineages. The inclusion of the unpublished sequences from Ozen & Bardakzi from Turkish brown trout in my phylogenetic review clearly confirms the existence of these two lineages (DA-BS and DA-ES) within the Danube group, which corresponds with those already proposed by Bernatchez (2001) and Kohout *et al.* (2013).

Based on the first trout fossils recorded in the Caucasus and inferences from phylogenetic reconstructions, Bernatchez (2001) suggested that the Danubian major lineage originated in Black Sea drainages. This hypothesis fits well with the phylogenetic position of the DA-BS lineage ancestral to the DA-ES, observed by Kohout *et al.* (2013) and in this study (Figure 2.3; Figure 2.4). Bardakzi *et al.* (2006) estimated that the Black/Marmara Sea and Caspian lineages diverged in the early Pleistocene, generally coinciding with the demographic expansion of the Danubian lineage (Bernatchez, 2001) and the time estimated for the divergence of the DA-BS and DA-ES lineages (Table 2.3). The isolation of the Black and Caspian basins during the early and middle Pleistocene should have favoured the allopatric divergence of the lineages that expanded westward and eastward, respectively. More recent secondary contacts are necessary to explain the distribution of both lineages in the Balkan Peninsula and in the upper Danube. These episodes seem to have been particularly important after the last glacial maximum in this area and to have occurred as a consequence of super floods caused by the extensive melting of glaciers, with water bodies reported to extend from the Aral to the Marmara Seas (Chepalyga, 2007). In Central Europe, Lerceteau-Köhler *et al.* (2013) revealed pure Danube-lineage populations that were practically restricted to previously glaciated regions. These authors suggest that this lineage colonized the upper Danube postglacially, before the expansion of the Atlantic lineage, and became isolated in these headwaters. It is then quite probable that both the DA-BS and DA-ES lineages reached Central Europe after the last glacial maximum. Similarly, several Danubian lineages that expanded postglacially have been described in other freshwater fish species. For instance, Durand *et al.* (1999) revealed two eastern and western Danubian lineages involved in the postglacial dispersion of *Leuciscus cephalus*, which came into contact in the Elbe River. Culling *et al.* (2006) also identified two refuges of *Cobitis taenia* in the

Ponto-Caspian area that recolonized Europe, one of them spreading north before moving west. For the anadromous cyprinid *Rutilus frisii*, Kotlík *et al.* (2008) suggested an ancient Pleistocene divergence between the Black Sea and Caspian Sea populations, with separate glacial refuges that came into contact during the period of glacial melting.

***S. trutta*, Atlantic Lineage (AT)**

The brown trout of the AT lineage have the most extended latitudinal and longitudinal distribution, from Northern Europe to North African and from Western Europe to Western Asia (Bernatchez *et al.*, 1992). In addition, the distribution of the AT lineage has expanded as a consequence of fishery management because a long tradition of stocking commercial hatchery fish of Atlantic origin exists in many countries (García-Marín *et al.*, 1991; Giuffra *et al.*, 1996; Berrebi *et al.*, 2000; Hansen *et al.*, 2000; Mezzera & Largiadèr, 2001; Duftner *et al.*, 2003; Jug *et al.*, 2005; Marić *et al.*, 2006; Kohout *et al.*, 2012; Meraner *et al.*, 2013). The anthropogenic distribution of the Atlantic lineages has often made it difficult to discern if natural colonization or stocking might have taken place in contact zones (Weiss *et al.*, 2001; Baric *et al.*, 2010; Lerceteau-Köhler *et al.*, 2013; Schenekar *et al.*, 2014).

Bernatchez (2001) suggested that the most ancient separation among brown trout subdivisions was when the Atlantic lineage split from the rest of the eastern brown trout via allopatric fragmentation approximately 700,000 years ago. The centre of origin of this lineage would have obviously been the Atlantic basin. A review based on the analysis of multiple nuclear loci (Pustovrh *et al.*, 2014) supports the hypothesis that the Atlantic lineage was the first to split off, a conclusion also corroborated by an ITS nuclear gene analysis (Presa *et al.*, 2002). Alternatively, later studies based on mtDNA analyses suggest that the Danubian major lineage could be the oldest one and have revealed a sister relationship between the Atlantic and Mediterranean lineages (Cortey *et al.*, 2009). Weiss *et al.* (2001) and Snoj *et al.* (2009) suggest that the AT lineage split from a common ancestor after the isolation of the Mediterranean lineages and spread north early in the Pleistocene or late in the Pliocene. This last hypothesis is also supported by the present phylogenetic reconstruction (Figure 2.2), in spite of the fact that the paraphyly observed in the ML reconstruction among the major phylogenetic lineages does not allow for the hypothesis of a simultaneous, allopatric divergence of lineages to be refuted.

For the AT lineage, it is particularly difficult to infer ancient evolutionary histories because Quaternary cold periods heavily influenced its distribution. The extinction of many ancestral AT populations during Quaternary glaciations and the rapid post-glacial expansion of brown trout from glacial refuges characterize the phylogeographic history of this lineage (reviewed in Cortey *et al.*, 2009). Several studies have focused on defining the post-glacial colonization routes and the putative glacial refuges for brown trout in the margins of the ice sheets (Hamilton *et al.*, 1989; Hynes *et al.*, 1996; GarcíaMarín *et al.*, 1999; Weiss *et al.*, 2000; Bernatchez, 2001). Bernatchez (2001) proposed a model of three refuges, in the Iberian Peninsula, north-eastern Europe and west-central Europe, involved in the recolonization processes. However, Pyrenees were an important barrier for freshwater fish species, even during glaciations, and this region acted more as a cradle for fish endemism than as a source for northward colonization (Gómez & Hunt, 2006). Accordingly, subsequent studies have recognized the Iberian glacial refuge but have failed to support the contribution of Iberian trout to the post-glacial colonization, and have located the probable origin of the postglacial expansion northwards in Southern France (Weiss *et al.*, 2000; 2001; Cortey *et al.*, 2009). Aurelle & Berrebi (2001) revealed the existence of two genetically well-differentiated groups of Atlantic brown trout in the south-west region of France that corresponded to the classical modern (**90*) and ancestral (**100*) races proposed by Hamilton *et al.* (1989) based on alleles at the *LDH-C* locus. Aurelle & Berrebi (2001) refuted the hypothesis of Hamilton *et al.* (1989) and suggested that both groups diverged independently during the early-middle Pleistocene in Southern France and in the northern Iberian region (Pays Basque), respectively. Therefore, only the northern-most lineage (characterized by the *LCH-C *90* allele) likely contributed to the post-glacial northward expansion.

The review by Cortey *et al.* (2009) showed a mixed distribution of at least two Atlantic clades in glaciated areas, suggesting that different evolutionary groups contributed to several waves of post-glacial colonization. Based on a PCR-RFLP analysis of four mitochondrial genes, McKeown *et al.* (2010) reviewed the phylogeographic structure of brown trout populations in Britain and Ireland and suggested that at least five potential freshwater and marine glacial refuges (Southern England and Western France, north-eastern regions including the Baltic and White Seas, Western Ireland, the North Sea and the Celtic Sea) contributed to the postglacial colonization of these regions. The so-called 'Southern refuge' was probably represented by brown trout lineages found in Southern France. These authors also showed that sympatric, reproductively isolated brown trout populations in Lough Melvin (Ireland) (Ferguson & Taggart, 1991) corresponded to independent colonization waves from two distinct Atlantic lineages. The high frequency of AT haplotypes in the unglaciated regions of Central Europe, as well as the occurrence of some AT haplotypes found exclusively in the Danube River, supports the existence of a north-eastern genetic refuge that expanded to Central Europe post-glacially (Osinov & Bernatchez, 1996; Bernatchez, 2001; Weiss *et al.*, 2001; Kohout *et al.*, 2012; Lerceteau-Köhler *et al.*, 2013; Schenekar *et al.*, 2014).

These multiple waves of colonization from distant genetic refuges, are likely why many studies have revealed the existence of divergent evolutionary units within the AT lineage (Suárez *et al.*, 2001; Cortey *et al.*, 2009; McKeown *et al.*, 2010). However, the patchy distribution of the genetic units identified, which is also reflected in the present phylogenetic reconstruction (Figure 2.3; Figure 2.4), makes it difficult to recognize distinct phylogeographic subdivisions. In Britain, McKeown *et al.* (2010) related the mosaic distribution of divergent Atlantic lineages to the migratory capabilities of anadromous *S. trutta* from different glacial refuges and the lack of barriers to moving around the coasts through the marine environment. These authors suggest that this behaviour promotes a greater degree of clade intermixing in island regions than in continental regions. Interestingly, a similar situation is found in the AT clade's distribution in the Cantabrian and South Atlantic coastal rivers of the Iberian Peninsula (Cortey *et al.*, 2009), where anadromous trout are currently present. In contrast, Atlantic brown trout clades are highly structured in the upper regions of the main Atlantic rivers of the peninsula (Tajo and Duero basins), indicating a long evolutionary history of brown trout isolation in these basins (Sanz *et al.*, 2000; Cortey *et al.*, 2009, Figure 2.5 in this study).

Although the southern limit of anadromous brown trout is presently located around the 42°N parallel, it is accepted that in the past, before the last glacial period and during the Pleistocene, anadromous trout was presumably present even in the Mediterranean

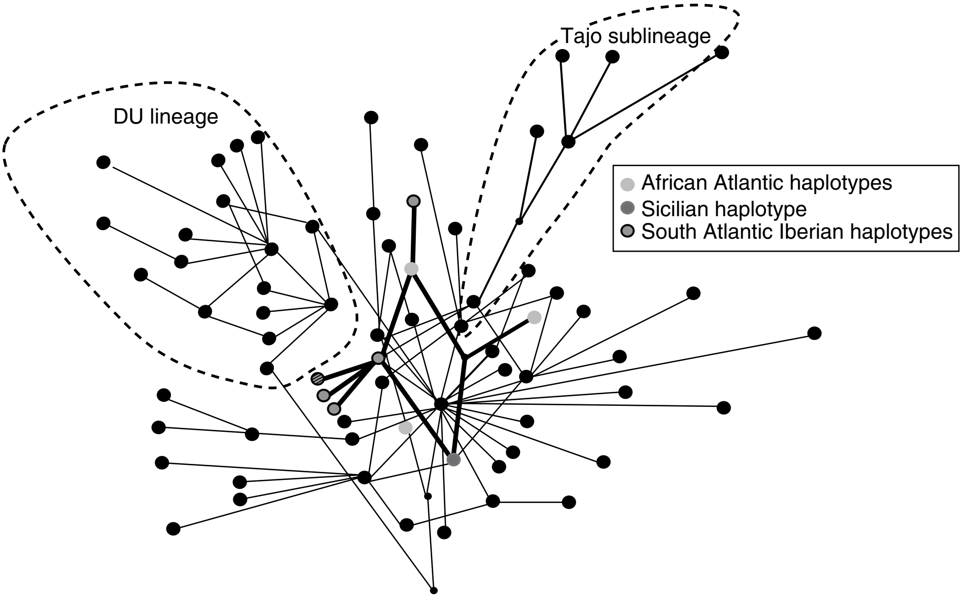

Figure 2.5 Extended view of the median-joining network of haplotypes from the AT lineage. Phylogenetic relationships among Iberian, Sicilian and North-African haplotypes is highlighted.

Sea (Bouza *et al.*, 1999). This could explain the distribution of coastal Iberian AT haplotypes up to Sicily and in North African rivers (Snoj *et al.*, 2009; Figure 2.1; Figure 2.5 in this study). Is seems that the southern groups of the AT lineage colonized the Atlantic and Mediterranean rivers in Morocco and expanded eastwards along the NorthWest African coast up to Sicily (Schöffmann *et al.*, 2007; Snoj *et al.*, 2011; Fruciano *et al.*, 2014). Snoj *et al.* (2011) suggested that this wave of colonization by the AT lineage arrived at Morocco in the Middle Pleistocene, 100,000–200,000 years ago, as a consequence of the expansion and contraction of the Atlantic trout distribution during the glacial and inter-glacial periods. It is interesting to note that, in an opposite manner to how it occurred in the northern regions, brown trout in the southernmost regions were restricted in their distribution to higher altitudes during the warm interglacial periods and expanded southwards during periods of glacial cooling. As a consequence, in the southern region of the AT lineage's distribution, some areas acted as interglacial refuges for the preservation of cold and temperate biota during warm interglacial periods (Cortey *et al.*, 2009). For instance, it appears that the coastal rivers of the Iberian Peninsula and Southern France may have served as a centre for the northern expansion of the AT lineage during interglacial warming and a centre for its southward expansion during glacial cooling (Cortey *et al.*, 2009).

Apart from the haplotypes of Iberian origin, another divergent AT haplotype has been found in North African rivers (ATM1) that evolved 400,000 years ago (Snoj *et al.*, 2011). Interestingly, this haplotype occupies a basal, well-supported position in the phylogeny of the AT lineage (Snoj *et al.*, 2011, Figure 2.3 in this study). This observation fits with the hypothesis of Bernatchez (2001) that situates the centre of origin of the Atlantic lineage at its southernmost distribution, the Iberian Peninsula, or even further southward, in North Africa, although this author estimated an earlier divergence time.

S. trutta, Duero Lineage

The Duero lineage is distributed in the Spanish region of the Duero basin (García-Marín & Pla, 1996; Sanz *et al.*, 2000; Vera *et al.*, 2010; 2015) and represents the unique brown trout subdivision within the Atlantic group that has been recognized as a distinct lineage.

The first genetic analyses based on allozymes already identified a different evolutionary unit in the upper Duero River that extended northwards to the Sil, a tributary of the Miño River (Sanz *et al.*, 2000). Based on an mtDNA-CR analysis, Suárez *et al.* (2001) identified and endemic group in the Duero basin, which was subsequently confirmed by Cortey *et al.* (2009). Vera *et al.* (2010) proposed a new and distinct brown trout lineage (Duero, DU) endemic to the inner of Duero and dated the divergence between the AT and DU lineages at 574,000 years ago, agreeing with the date estimated based on allozyme variation (Bouza *et al.*, 2001) and roughly agreeing with the present estimate (Table 2.3). The results from an analysis of the nuclear ITS1 locus related the Duero trout to an ancient Mediterranean group that colonized southern Iberia (Presa *et al.*, 2002). Vera *et al.* (2010) suggested that Duero brown trout could represent an ancestral colonization of the Iberian Peninsula, predating the expansion not only of the AT lineage but also of all other brown trout lineages found in the Peninsula (AT, ME and AD). Interestingly, although the Bayesian tree and median-joining network both indicate the AT lineage as the one genetically closest to the DU lineage, the median-joining network also connects the DU haplotypes to the AD lineage through two TMSs and three median vectors (Figure 2.4).

Bouza *et al.* (2007) confirmed the presence of DU haplotype fixed in several isolated populations from the upper course of the Miño River and its main tributary, the Sil River. It is thought that Pleistocene glaciations could have contributed to contacts between the Esla River (Duero) and the nearby Sil River (Miño) and could be responsible for the fact that the DU lineage is found in the Sil River and in other tributaries in the inner Miño basin (Vera *et al.*, 2015). Similarly, DU haplotypes and nuclear Duero alleles found in some tributaries of the Tajo River and AT haplotypes found in some headstream tributaries of the Duero river are thought to be the consequence of Quaternary hydrographic captures occurring upstream of these rivers (Sanz *et al.*, 2000; Cortey *et al.*, 2009).

The endemism demonstrated by the Duero lineage resembles that of the MA lineage. However, marble trout is threatened by high levels of hybridization with other brown trout lineages (Jug *et al.*, 2005; Gratton *et al.*, 2014). In contrast, it seems that strong isolation in the inner regions of the Duero and Miño basins and selective processes related to regional temperatures have limited hybridization and favoured pure Duero brown trout (Martínez *et al.*, 2007; Vera *et al.*, 2010).

S. trutta, Dades Lineage

As occurred with the TI lineage, the Dades lineage is represented by a single, highly divergent haplotype, which is found exclusively in the Draa River of the High Atlas (Morocco) (Snoj *et al.*, 2011). However, in contrast to the TI lineage, the phylogenetic position of the Dades lineage was not fully resolved in the present study. According to the Bayesian reconstruction (Figure 2.3), this haplotype had a basal position with respect to the Atlantic and Danubian haplotypes, but neither the basal position of the Dades lineage nor the grouping with the Atlantic and Danubian haplotypes were well-supported (Figure 2.3). Alternatively, the Dades haplotype shared a large polytomy with the rest of the major mitochondrial lineages in the ML reconstruction (Figure 2.2). A similar controversy in the phylogenetic position of the Dades haplotype based on ML and maximum parsimony (MP) reconstructions was reported by Snoj *et al.* (2011). It seems that the Dades lineage became isolated more than 1 million years ago (Snoj *et al.*, 2011, Table 2.3 in this study), and may correspond to a very old and relict trout lineage with an independent evolutionary history that justifies its designation as a separate lineage. It is thought that the Dades trout could represent the first established brown trout in Morocco and probably diverged from the ancestor before all the other trout lineages (Snoj *et al.*, 2011).

Neither the large number of previously published studies dealing with brown trout phylogeography nor the present review has been able to fully resolve the complex evolutionary history of the brown trout species complex. Currently, three well-recognized species are supported: *S. ohridanus*, *S. obtusirostris* and the *S. trutta* species complex, which comprises nine mtDNA lineages, two of them represented by a single haplotype (TI and Dades). Several sublineages have been reported within the AD, AT, DU and DA-ES lineages, and the number of these sublineages increases as more studies focus on specific geographical regions (see for instance McKeown *et al.*, 2010). In addition, genetic divergences have arisen at the microgeographical level among local populations occupying different hydrographic basins. Such local divergences are considered a consequence of recent isolation and genetic drift occurring after the last glacial maximum (Sanz *et al.*, 2002; Gratton *et al.*, 2014), and these trends will presumably be favoured by the present warming of the climate and by environmental degradation (Snoj *et al.*, 2011).

According to Bernatchez (2001), the three major brown trout lineages (Atlantic, Danubian and Mediterranean) diverged allopatrically in the late Pliocene and early Pleistocene, probably in association with geological events that separated main river systems draining to different basins. Several biogeographical models have been proposed to explain the ancient diversity and distribution of freshwater fishes in the Eurasian continent, and most of these models have considered an eastern (Asiatic) origin of the ancestral European fish species (Bianco, 1990; Durand *et al.*, 2003). According to Bianco (1990), the first freshwater fish colonized Europe from eastern Asia during the Miocene as a result of the decrease in the salinity of the Paratethys Sea and at the time (5 million years ago) when the hyper salinity of the Mediterranean Sea prevented the dispersion of any freshwater species. Subsequently, the Mediterranean basin was colonized from the Paratethys Sea during the freshwater Lago Mare period that promoted a high radiation of all aquatic fauna. Accordingly, Pérès (1985) suggested that warm climatic conditions in the Mediterranean Sea likely prevented the expansion of salmonids until the Pliocene. In concordance with this hypothesis, Crête-Lafrenière *et al.* (2012) estimated that intraspecific divergence in the *S. trutta* species complex occurred during the Pliocene, 2.5–5 million years (MY) ago, associated with the cooling climate of the Northern hemisphere. This time frame and the biogeographical model of Bianco (1990) completely fit with the divergence of *S. ohridanus* in Lake Ohrid (4 million years ago, Sušnik *et al.*, 2006) and of S. *obtusirostris* in the headwaters of some Adriatic basin rivers (2.5 million years ago, Pustovrh *et al.*, 2014).

Based on nuclear and mitochondrial genetic variation in Danubian and Atlantic brown trout, Osinov & Bernatchez (1996) suggested the Black, Caspian and Aral Sea basins as the origin of the brown trout species complex. The earliest brown trout fossils found in the Caucasus and dated to the upper Pliocene (Vladimirov, 1948) support this hypothesis, which is also sustained by the studies of Antunes *et al.* (2002), Cortey (2005) and Griffiths *et al.* (2009). Alternatively, based on a phylogenetic reconstruction from nuclear loci, Giuffra *et al.* (1994) and Presa *et al.* (2002) suggested that the Atlantic brown trout occupies the most basal position. In contrast to these previous hypotheses and based on an extended review of the variation described in the mtDNA control region, my phylogenetic reconstruction suggests that the AD lineage occupies the basal position (Figure 2.3). This was also observed by Snoj *et al.* (2011) and Berrebi *et al.* (2013), although their studies focused on North-West African trout and Prespa trout, respectively, more than reviewing the brown trout phylogeny. Interestingly, only these last studies included S. *ohridanus* in their phylogenetic reconstruction.

Several findings are worth mentioning that support the hypothesis of the Adriatic brown trout as the most ancestral origin for the brown trout species complex. It appears well-supported that the Adriatic major lineage originated in the Balkan region, where brown trout populations show particular high levels of genetic variation and ancestral endemism (Apostolidis *et al.*, 1997, 2008; Marić *et al.*, 2006; Razpet *et al.*, 2007; Sušnik *et al.*, 2007; Kohout *et al.*, 2013). In addition, this region harbours five (AD, ME, MA, DA-BS, DA-ES) of the nine lineages described within the brown trout species complex and all three brown trout species (*S. trutta*, *S. obtusirostris* and *S. ohridanus*). *S. ohridanus* and *S. obtusirostris* are appropriately considered the closest ancestor of the *S. trutta* complex and the fact that they originated in this region is unquestionable. According to the net evolutionary distance, the AD lineage is the closest to the ancestral species *S. obtusirostris*, in spite of the fact that a similar distance was found between the AT lineage and this ancestral species (Table 2.3). Finally, the MA lineage is genetically close to the AD lineage, and several studies have pointed to a very early divergence of this lineage (0.6–1.7 million years ago) that occurred before the diversification of the Adriatic brown trout.

Based on the points discussed above, it seems reasonable to suggest that a large proportion of the ancient brown trout diversity originated in the Balkans. Alternatively, Bardakci *et al.* (2006) suggested a pre-Pleistocene isolation of the Turkish brown trout and provides evidence of Anatolia as a centre of diversification for the DA, AD and TI lineages. These authors showed that all of these lineages were in the Tigris-Euphrates river system and suggested that they may have originated from Anatolia, probably in association with contact between the Middle East and the proto-Black and proto-Caspian Seas via the proto-Euphrates River. In favour of this hypothesis is the basal position of the Turkish haplotypes (ADTR and DATR) within both the AD and DA lineages in the phylogenetic reconstruction (Figure 2.3) and the ancient divergence time estimated for the TI lineage (1–2 million years ago), which predates the estimated age of expansion for the major lineages. Because the Southern Balkans have been considered a 'hot spot' for brown trout diversity (Sušnik *et al.*, 2007; Apostolidis *et al.*, 2008; Snoj *et al.*, 2009) and for other aquatic fauna (Bănărescu, 2004), many brown trout studies have focused on this region. In contrast, little information exists about brown trout in the Anatolia region, in spite of the fact that it has been considered a centre of speciation for other freshwater species (Durand *et al.*, 2002).

Since the evolutionary history of freshwater organisms is closely related to the biogeographical evolution of the region, it is expected that many freshwater fauna share common phylogeographic histories and similar radiation events. Durand *et al.* (2000; 2003) suggested a model with two radiation events in the phylogeography of the cyprinid genera Chondrostoma and Leuciscus. The first one occurred 5–4 million years ago and was probably associated with the Lago Mare theory of Bianco (1990). The second radiation is suggested to have taken place 1–2 million years ago from ancestral populations in Mesopotamia that entered Europe though the Anatolia inland lake and reached up to the Danube region. A large radiation event would have been promoted by the isolation of numerous Turkish river systems as a result of the Anatolian surface uplift in the Plio-Quaternary period (Durand *et al.*, 2002). Similarly, an evolutionary history based on two ancient pre-Pleistocene waves of colonization-radiation could well explain the origin of the major Adriatic and Danubian brown trout lineages. The first colonization wave associated with the Lago Mare phase of the Mediterranean would have allowed the ancestral Adriatic brown trout to spread southward to the Balkan region and western Turkey, where it could have then expanded and diversified along the Mediterranean basin, moving into Italy, France and the Iberian Peninsula. The movement of fish across the Mediterranean Sea was probably facilitated by the reduction in salinity, lowered sea temperatures and drop in sea level characteristic of the quaternary Mediterranean Sea (Bianco, 1990). The MA lineage could have diverged early in this wave of colonization and prior to the separation of the AD and ME lineages. Tentatively, this same south-eastern wave of colonization could have reached up to North Africa, where the Dades lineage would be a relic of this event that survived the climate warming of the Pleistocene in the High Atlas. Interestingly, the AD brown trout was the closest one to the Dades lineage (eight TMSs and two median vectors) in the median-joining network and was connected to the AD lineage through haplotypes found exclusively in the Turkish and the Aegean basin populations (Figure 2.4). The second wave of colonization would have come from the Middle East, radiating into the Anatolina Peninsula through Mesopotamian and expanding to the northwest up to the Balkan Peninsula and the Danube, resulting in the origin of the major Danubian lineage. This lineage could have subsequently diversified and extended into the western regions (Caspian-Aral Seas) during the Pleistocene. According to this hypothesis, western Turkey and the Balkan Peninsula would have been the contact zones between the first ancestral waves of colonization, which would explain the high diversity and phylogenetic complexity of the brown trout populations in these areas.

When and how the ancestral AT lineage originated is unclear. In spite of the fact that the ancestral evolutionary history of Atlantic brown trout has been diluted by an overlapping pattern of postglacial colonization, it seems likely that the ancestral Atlantic lineage diverged early, possibly at the same time as the rest of the major brown trout lineages or even earlier (Osinov & Bernatchez, 1996; Bernatchez, 2001; Cortey *et al.*, 2009). Assuming the ancestor of the brown trout arrived in the Paratethys Sea during the Pliocene, an independent wave of colonization would have expanded to the Atlantic region. As previously suggested for other freshwater fishes (Durand *et al.*, 1999; Englbrecht *et al.*, 2000), Cortey (2005) proposed a possible route from the Black Sea towards the north that allowed fish to disperse through the Baltic coasts, and suggested that the colonization of the major European Atlantic river systems likely took place via routes along the coastlines. This author also proposed an alternative route of colonization that involved a pre-Pleistocene expansion from the Danube basin to southern

Europe through the Rhine-Elba River systems, as suggested by the phylogeography of *Thymallus thymallus* (Weiss *et al.*, 2002).

Aurelle & Berrebi (2001) suggested two ancestral Atlantic forms (corresponding to the **90* and **100* alleles at the *LDH-C* locus) that diverged in the late Pliocene, 2.2 million years ago. Consequently, it is also possible that several ancestral colonization waves reached the Atlantic basin. Tentatively, brown trout from the Danube basin may correspond to the ancestral *LDH-C*100* form that crossed Europe from east to west via a continental route and reached the Iberian Peninsula and probably into North Africa, and the ancestral *LDH-C*90* brown trout may have arrived in Southern France along the northern coastline. The extinction of freshwater fish during glacial periods may have removed evidence of these ancestral colonization pathways, as has been suggested for the three-spined stickleback (Sanz *et al.*, 2015). The ancestral lineage characterized by the *LDH-C*100* allele has been maintained only in Southern France, the Iberian Peninsula and North Africa, but did not contribute significantly to the northern postglacial expansion. The ancestral *LDH-C*90* form would have survived in Southern France and in most of the northern glacial refuges that expanded during the post glacial period.

Brown Trout Phylogeographic Complexity and the Definition of Conservation Units

Climatic oscillations during the Quaternary period had important effects on the distribution of species, mainly in northern and temperate regions (Hewitt, 2004). Nevertheless, the effects were not restricted to glacial regions but were also noticeable in the coastal areas of southern peninsulas where the rising and lowering of sea levels altered connections between river basins (Bianco, 1990). The consequences of Quaternary events on changes in the distribution of species largely depended on the migratory capability and adaptability of each species (Hewitt, 2004). In brown trout, the anadromous behaviour surely promoted numerous events of secondary intergradation between lineages, even between geographically distant regions, that blurred their allopatric origin and makes it difficult to infer evolutionary timelines and histories. Apart from the secondary contacts described between ancestral brown trout lineages, the existence of multiple waves of post-glacial colonization from multiple glacial refuges adds further complexity to the phylogeographic pattern of brown trout in glaciated regions. The complex and uncertain phylogenetic relationships among haplotypes can be observed in the phylogenetic trees, as the clustered haplotypes within lineages were not resolved in most cases (Cortey *et al.*, 2004; Sušnik *et al.*, 2007a, Snoj *et al.*, 2009; Hashemzadeh *et al.*, 2012; this study). Overlapping connections among haplotypes are observed mainly within the AT lineage, which was obviously the most affected by glaciations, and are also observed within the DA-ES lineage, which expanded into Central Europe postglacially (Figure 2.4; Figure 2.5). The phylogeographic complexity of the European brown trout is then evidenced by many cases of minimal phylogeographic structure in the patterns of haplotype distribution, which makes it difficult to define conservation units of evolutionary significance.

All of the above described episodes of colonization and secondary contacts have resulted in large genetic differences within lineages and in many endemic populations that are not necessarily represented by a unique mtDNA lineage. These 'naturally admixed' populations represent unique gene pools that have adapted for thousands or millions of years and the conservation of these gene pools is difficult, even in a management strategy based on mtDNA lineages (Lercerteau-Köhler *et al.*, 2013). Concerns about the design of suitable conservation strategies associated with complex phylogeographic patterns have been broadly documented in the southernmost regions of the brown trout's distribution (Antunes *et al.*, 2001; Sanz *et al.*, 2002, Sušnik *et al.*, 2006; 2007a; Snoj *et al.*, 2010; Berrebi *et al.*, 2013; Kohout *et al.*, 2013). In the Balkan region, Pustovrh *et al.* (2014) suggested that some phylogenetic subdivisions within lineages supported maintaining taxonomic nomenclature at a species level (for instance for the Adriatic brown trout from Lake Ohrid, *S. letnica*). The increase in the number of new 'species' is considered a strategy that may promote conservation because this increases the number of species that meet the IUCN Red List criteria for being threatened (Garnet & Christidis, 2007). However, the concordance between species and phylogenetic subdivisions is not clear in many cases, and this strategy does not resolve the problem of defining conservation units for those populations that are naturally admixed. In addition, this situation is not exclusive to the southernmost regions that survived during the glacial periods because highly divergent lineages coexisting as a single population (McKeown *et al.*, 2010) or as cryptic sympatric populations (Palmé *et al.*, 2013) also occur in in the Atlantic basin.

Based on the complex phylogeography of *Thymallus thymallus*, Weiss *et al.* (2013) addressed the problem of defining conservation units for a widely distributed organism, particularly in the Europe continent. These authors outlined serious problems in the conservation of unique gene pools following a management strategy based exclusively on mtDNA lineages. In contrast to the traditional and most widely used top-down hierarchical structure used to define conservation units, these authors used a bottom-up prioritization based on a population perspective of management that considers genetic structures even at microgeographical scales. Considering the complex evolutionary history of the brown trout, the present distribution of genetic variability and the high level of physical and genetic fragmentation among populations, the definition of conservation units based on assessments at the population level is strongly recommended in the brown trout species complex.

Future Directions

Including the present review, more than one hundred papers have studied phylogenetic relationships in the brown trout species complex. Nevertheless, its phylogeographic reconstruction has still some gaps which provide challenges for future research. First, anthropogenic movements of fish through stocking, translocation or artificial river connections confound historical lineage distributions and obscure subsequent interpretation of phylogeographic analyses. It is fairly easy to discriminate between native and exogenous distribution when stocking records and data from stocking hatcheries are available. If they are not, or when translocations are suspected, this is a difficult task. In these cases, better sampling is necessary to recognize natural versus anthropogenic distribution, especially in areas where natural and human-mediated introgression has occurred or is suspected. For instance, the broad study by Lerceteau-Köhler *et al.* (2013)

revealed natural introgression of the Atlantic lineage into the Danubian gene pools in the contact zone of Central Europe, in spite of extensive stocking with hatchery Atlantic fish taking place in this region.

Another important question to deal with is the unresolved politomies at high hierarchical levels in the brown trout phylogeny. Some recent studies (Gratton *et al.*, 2014; Pustovrh *et al.*, 2014) attempted to clarify these phylogenies using a set of nuclear genes. Obviously, nuclear markers overcome mtDNA limitations, because they may assess putative hybridization among lineages, but nuclear DNA phylogenies fairly matched with those inferred from mtDNA (Pustovrh *et al.,* 2014). Alternatively, increasing the number of populations as well as the number of individuals per population in some understudied geographical areas can be the key to find intermediate or very ancestral haplotypes and subsequently clarify obscure aspects of the phylogeny. In this sense, sampling and research effort should be directed towards some hotspot regions studied only in a few works, as the Anatolian peninsula (Bardakci *et al.,* 2006).

Interestingly, understanding the phylogeography provides a platform for further research on the evolutionary forces determining phylogenetic relationships. For instance, life-history variation among lineages and populations is an important factor for its distribution. Also, selective processes can explain lineage distribution, as it seems to occur in the marble trout, and patterns of structure within lineages. Therefore, ecological data and population dynamics can help to elucidate some biogeographical patterns, and landscape genetics can evaluate the effects of environmental variables on evolutionary processes such as gene flow or natural selection (Manel & Holderegger, 2013).

Finally, Next Generation Sequencing (NGS) has made whole genome datasets available, to provide a solid framework of the evolutionary relationship in the brown trout species complex. Fully assembled genomes have been used to generate highly resolved phylogenetic trees that clarify discordances among single gene phylogenies (Snel *et al.*, 1999). A SNP-array technology to genotype 15,225 loci have been developed for *S. salar*, and a panel of 39 SNPs is currently used in the genetic characterization of *S. trutta* from the Baltic Sea (Drywa *et al.,* 2013). This study demonstrated the applicability of the Salmon SNP-chip on brown trout populations, a feature worth exploring in future research.

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3

Genetics of the Genus *Salmo* in Italy: Evolutionary History, Population Structure, Molecular Ecology and Conservation

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Introduction

The Mediterranean region constitutes a hotspot in terms of European salmonid biodiversity. Numerous morphologically (e.g. Kottelat & Freyhof, 2007) and/or genetically (e.g. Gratton *et al.*, 2014) distinct taxa are present. While trout are not known to migrate to the sea in the Mediterranean basin (Kottelat & Freyhof, 2007), complex life-histories have evolved in distinct freshwater habitats, with Mediterranean salmonid populations mainly clustering into riverine and lacustrine forms. Within the latter, river-running populations are to be distinguished from those populations, which spend their entire life-cycle, including reproduction, within the lacustrine habitat. This is the case for Lake Garda's *Salmo carpio*.

Within the Mediterranean basin, the Italian peninsula plays a decisive role in terms of salmonid biodiversity. The central and likewise exposed position of the peninsula, the remoteness from Central European water courses caused by the Alpine massif and the diversity and magnitude of aquatic habitats are likely triggers forming (and preserving) salmonid biodiversity.

Thus, the Italian peninsula harbours a complex arrangement of native salmonid taxa, moulded by complex colonisation routes, palaeo-hydrology and ecological adaptation. In addition, this diversity has massively been altered by anthropogenic translocation of non-native trout, thus promoting biotic homogenisation and introgressive hybridisation. In this chapter, we first summarise the knowledge on relevant colonisation hypotheses, which are useful to explain the present native salmonid biodiversity of Italian freshwater habitats. We thus start reconstructing evolutionary history and highlight likely colonisation paths, which might have led to the present-day distribution of salmonids.

We then point to the major bifurcation of genetic lineages as the uppermost hierarchical genetic level grouping Italian salmonid biodiversity. This arrangement of two major lineages is then progressively apportioned, by describing a series of distinct metapopulations, including riverine and lacustrine ecotypes. We exemplify this diversity

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herein by highlighting aspects of the molecular ecology of two prominent Italian trout, these being marble trout (*Salmo marmoratus*) and Lake Garda's carpione (*Salmo carpio*).

In addition, we focus on the problem of exotic brown trout in Italy, including biotic homogenisation and introgressive hybridisation as the negative consequences of this invasion. We reconstruct origins and distribution patterns of exotic brown trout in Italy and highlight that exotic Atlantic brown trout are nowadays distributed all over the Italian peninsula, with differing consequences for the native salmonid biodiversity. Finally, we merge the genetic results presented in this chapter and propose an attempt towards the definition of management units (MUs) fundamental for conservation of native salmonid biodiversity in Italy. We highlight that within the 'marble' and the 'peninsular' lineages – as the uppermost genetic entities of the genus *Salmo* in Italy – a series of management units persist, on which future concrete conservation actions have to build on, in order to halt the additional loss of native salmonid biodiversity in Italy.

From East, from West or *in situ*? On Origins and Colonisation Scenarios of the Genus *Salmo* in Italy

Despite the wealth of studies including genetic information, the evolutionary history of the genus *Salmo* in the Mediterranean region is still poorly resolved. Gratton *et al.* (2014) noted that this knowledge gap might be attributable to at least two key-factors. First, taxonomy and evolutionary models are still based on a high number of disconnected and mainly microgeographic studies. Each work undoubtedly addresses consequential tasks in terms of the evolutionary history. However, broadscale surveys covering the entire Mediterranean area are lacking and the deduction of general evolutionary paths by merging research results from different surveys is hindered by taxonomic confusion and by the plenitude of alternative, not comparable molecular methodologies applied. Second, the evolutionary history of Mediterranean trout is inherently complex and shaped by the interaction of subsequent colonisation waves, adaptation to local ecological conditions and secondary contact, either natural or human-mediated.

However, despite these limitations, some general paths underlying the present-day distribution and organisation of Mediterranean salmonid biodiversity may firmly be outlined.

A first general evolutionary principle concerns the macrogeographic origin of the genus *Salmo* in the Mediterranean area. In a broad context, Bianco (1990) hypothesised the advent of Mediterranean freshwater fishes from eastern refuges, positioned in or close to the Ponto-Caspian area, vaguely correlating with the present-day Black-Sea region. There, during the Middle Miocene (15 Myr ago), the former Paratethys basin became progressively an arrangement of freshwater watersheds, since the emergence of Central-Eastern mountain chains (e.g. Alps, Dinarides and Pontic) diverged most European river basins into east. Thus, the Paratethys was a dilution basin, while the Mediterranean basin was (and is) an evaporation basin. This repeatedly allowed the influx of freshwater into the Mediterranean area and enabled westward dispersal of freshwater biota. Accordingly, a primary east to west colonisation trend seems to constitute a key factor explaining the dispersal routes of freshwater fish taxa in the Mediterranean and is more likely than a dispersal by river captures between Northern and Southern Europe, as suggested by Banarescu (1992). According to Bianco (1990), a first penetration of freshwater fishes into the peri-Mediterranean districts should have occurred as soon as during the 'Messinian' (5 Myr ago) lacustrine 'Lago Mare' phase of the Mediterranean from freshwater refuges in the Ponto-Caspian area. Successive colonisation waves are likely to have followed. For instance during the Pleistocene, when climatic conditions determined cooler sea water temperatures, reduced salinity and extended palaeo-river basins might have enhanced freshwater fish dispersal throughout the Mediterranean. Migration between freshwater fish populations of adjacent river basins was finally disrupted and population divergence was therefore enhanced only after the re-rise of the Mediterranean Sea level, following the last glaciation and the recovery of full strength salinity.

The proposed general westward directed colonisation path is also plausible for the genus *Salmo* in the Mediterranean area (Figure 3.1). Interestingly, the most ancient salmonids natively present in peri-Mediterranean waters are known from Eastern Adriatic habitats and thus geographically close to the supposed origin of the genus in the Ponto-Caspian refuge. In fact, *Salmo ohridanus* (Ohrid belvica; Phillips *et al.*, 2000) is supposed to have diverged from a common brown trout ancestor during early Pliocene some 4 Myr ago (Pustovrh *et al.*, 2011). This species is one out of a plenitude of endemics found in Lake Ohrid, which is considered Europe's oldest permanent body of freshwater and should have directly originated between 4 to 10 Myr ago from the draining of the Paratethys Sea (Hsü, 1978) as a consequence of tectonic shifts (Banarescu, 1992). Adriatic salmonid biodiversity is further enriched by the occurrence of deeply divergent *Salmo obtusirostris* (softmouth trout; Snoj *et al.*, 2002a), inhabiting Eastern Adriatic watercourses, and *Salmo marmoratus* (marble trout), positioned in the Central Adriatic zone. Both taxa are thought to have derived during early Pleistocene from a common brown trout ancestor prior to the fragmentation of the *Salmo trutta* complex. Altogether the presence of phylogenetically highly divergent taxa of the genus *Salmo* in the Adriatic led Sušnik *et al.* (2007) to consider the Adriatic drainage as a unique, or even primary, centre for radiation of the genus *Salmo*. Finally, Mediterranean salmonid biodiversity was further augmented by allopatric fragmentation of the *Salmo trutta* complex into major evolutionary clades, such as the Danubian, the Atlantic and the Mediterranean/Adriatic lineages. Favourable climatic conditions during the late Pleistocene might have allowed the dispersal of the *Salmo trutta* complex from Ponto Caspian westwards into the Mediterranean, thus enabling allopatric fragmentation of this species complex and the emergence of Mediterranean matrilineal clusters, such as the Mediterranean and the Adriatic clades (Bernatchez, 2001). Recent studies confirmed the present-day weak geographical sorting and mosaic distribution of the latter mitochondrial clades (e.g. Cortey *et al.*, 2004). Likewise, a shallow genetic differentiation among Italian trout from freshwater habitats draining into distinct seas (*Salmo cettii vs. Salmo cenerinus* confined to the Tyrrhenian and Adriatic basins, respectively) was disclosed (Gratton *et al.*, 2014). Altogether, these results indicated the pronounced dispersal of salmonids either directly across the Mediterranean or through a stepwise migration, by using broad freshwater pathways formed by extended palaeo-river drainages in peri-Mediterranean regions. Significant and long-distance dispersal of salmonids in the Mediterranean was only interrupted after the last glacial maximum, thus fuelling intraspecific population divergence.

Albeit east to west dispersal is likely to represent the 'rule' in the evolutionary history of Mediterranean trout, at least one exception with particular emphasis on Italian salmonid biodiversity is visible. In fact, Schöffmann *et al.* (2007) and more extensively Fruciano

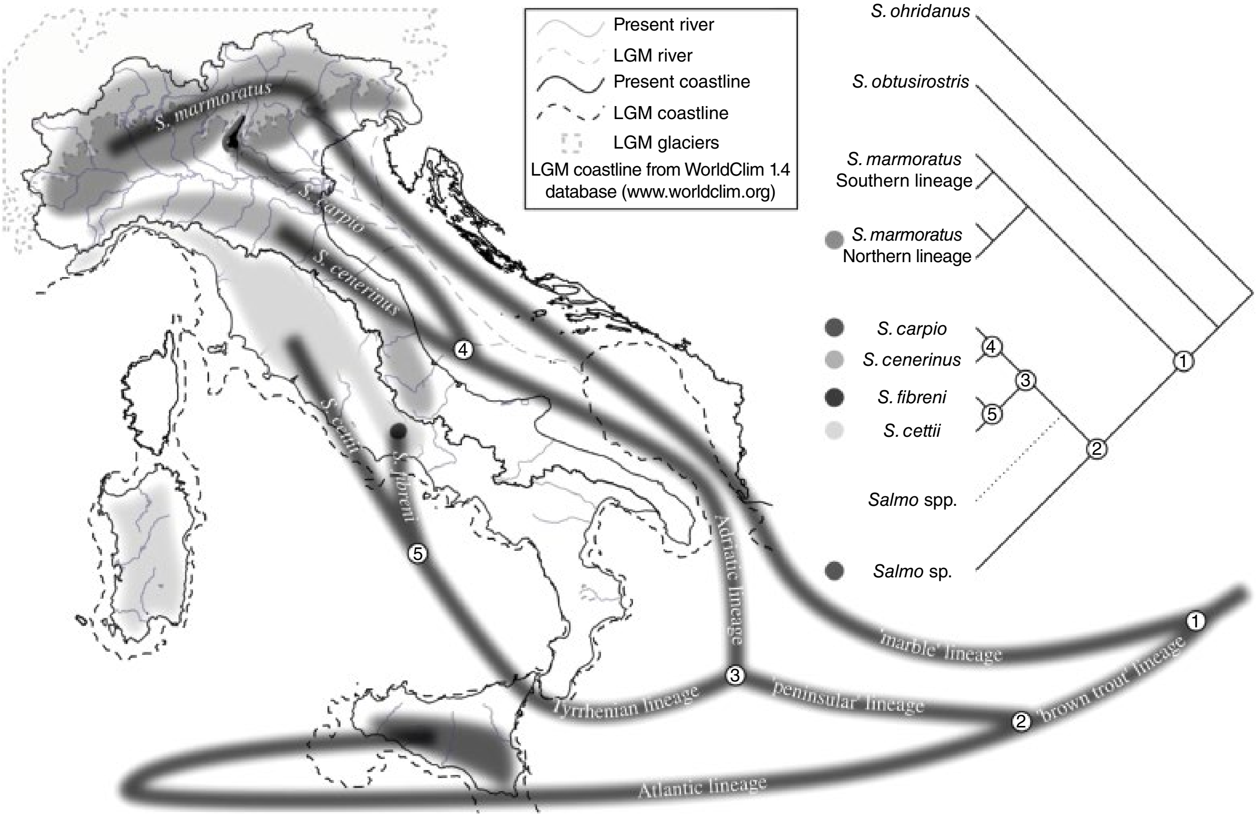

Figure 3.1 A plausible overview upon colonisation scenarios of major evolutionary lineages of the genus *Salmo* into the Italian peninsula, by taking into account inferred phylogenetic relationships and relative time of separation between them: ① split between 'marble' and 'brown trout' lineages; ② split between 'peninsular' and Atlantic lineages; ③ split between Adriatic and Thyrrenian lineages; ④ split between *S. cenerinus* and *S. carpio*; ⑤ split between *S. cettii* and *S. fibreni*. Albeit the general pattern of east to west dispersal from the supposed origin of the genus in Ponto-Caspian refuge, Sicilian brown trout populations are likely to originate from Pleistocene west to east colonisation events from the North African Atlantic brown trout lineage, expanding back into the Central-Eastern Mediterranean.

et al. (2014) studied brown trout inhabiting small brooks in South-Eastern Sicily. Interestingly, Fruciano *et al.* (2014) depicted an astounding diversity of 58 mitochondrial haplotypes from 194 analysed specimens sampled from only four minor brooks in Sicily. All genetic variants clustered in the Atlantic mitochondrial lineage of the *Salmo trutta* complex. These haplotypes were closely related to those encountered in Southern Atlantic populations from North Africa, Portugal and Spain, thus pointing to a natural, and not hatchery-mediated, origin of Sicilian trout. Indeed, it seems very plausible that these Sicilian populations represent a remnant of a Pleistocene colonisation process of the Atlantic brown trout lineage deep into Central-Eastern Mediterranean waters.

Native Salmonid Biodiversity in Italy: The 'Peninsular' and 'Marble' Lineages

The evolutionary history of the genus *Salmo* in its southern distribution range is still sparsely resolved. The limited knowledge in terms of evolutionary relationships and the non-interaction of these with classical taxonomic endeavours provoke scientific uncertainty (see Table 3.1), disenabling concerted conservation and hindering efficient management actions.

On the one hand, classical taxonomy recognises as much as 20 Mediterranean *Salmo* species mainly defined upon non-private morphological characters or upon rarely unique life-history traits (Kottelat & Freyhof, 2007). Given the particularly pronounced plasticity of the genus *Salmo* and the elevated and rapid adaptive potential of populations to mutated environmental conditions, taxonomic classifications without genetic considerations seem to be unreasonable. On the other hand, genetic classification of the genus *Salmo* based traditionally on major mitochondrial lineages, such as Atlantic, Danubian, Adriatic, Mediterranean or after associated phenotypes, such as in the case of the Marmoratus lineage (Bernatchez *et al.*, 1992; Giuffra *et al.*, 1994). It is clear today that depicting evolutionary relationships by the inference on mtDNA haplogroups alone is not scientifically sound and is often misleading in terms of biodiversity conservation. In fact, single gene trees not necessarily resemble species trees and thus mtDNA genealogies have not to be consistent with nuclear genetic or morphological variation (e.g., Ballard and Whitlock, 2004). In addition, evolutionary relationships based upon mtDNA genealogies tend to underestimate the 'real' evolutionary complexity, especially when processes of ecological speciation or secondary contact are involved. In this context, a closer look at the native salmonid biodiversity in Italy illustrates the non-exclusiveness of either classical taxonomic- or molecular-based classification schemes, especially when conservation issues and, in practical terms, management units have to be deducted.

Recently, Kottelat & Freyhof (2007) presented a taxonomic framework of Italian salmonid biodiversity and listed five species, namely *S. marmoratus*, *S. cenerinus*, *S. cettii*, *S. carpio and S. fibreni* (Table 3.1). *S. marmoratus* (marble trout) is placed in parapatry to *S. cenerinus* ('Northern Italian brown trout') within the Alpine slope of the Adriatic drainage basin, while the latter species is considered as the sole native salmonid occupying the Apenninic slope of the Adriatic basin. The corresponding counterpart for the Tyrrhenian drainage is classified as *S. cettii* (Kottelat & Freyhof, 2007). While *S. carpio* is endemic to Lake Garda in Northern Italy (Adriatic drainage), *S. fibreni*

Table 3.1 Alternative taxonomic classification of native trout in Italy, and respective natural distribution areas, as proposed by different authors. =: the same species name and the same natural distribution area are proposed by different authors; ≠: the species name is not accepted by different authors.

		Natural distribution area		
Scientific name	**Common name**	**Kottelat & Freyhof, 2007**	**AIIAD, 2013**	**Bianco, 2014**
S. marmoratus Cuvier, 1829	Marble trout	Alpine slope of the Adriatic drainage basin	=	=
S. carpio Linnaeus, 1758	Carpione del Garda	Lake Garda	=	=
S. cettii Rafinesque, 1810	Mediterranean trout	Tyrrhenian Basin (including Sardinia and Sicily)	Sardinia and Sicily, Posta Fibreno and Ninfa lakes and few Tyrrhenian watercourses	Tyrrhenian Basin (including Sardinia and Sicily)
S. cenerinus Chiereghin 1847	Northern Italian brook trout	Adriatic Basin	≠	≠
S. ghigii Pomini, 1941	Apenninic or Adriatic trout	≠	Apenine slopes of the Adriatic and Tyrrhenian drainage basins	≠
S. farioides Karaman, 1938	Adriatic brown trout	≠	≠	Western Alpine Po drainage (headwaters) and Apennine Adriatic slope rivers, to the Aterno-Pescara River southward (Meso-Adriatic ditch, during the last glacial maximum)
S. fibreni Zerunian & Gandolfi, 1990	Fibreno trout (Carpione del Fibreno)	Lake Posta Fibreno	=	=

inhabits the lacustrine habitat of Lake Posta Fibreno in Central Italy (Tyrrhenian basin). Partially different taxonomic entities and native distribution areas were recently proposed by different authors (AIIAD, 2013; Bianco, 2014; Table 3.1), not basing however on novel and more convincing data.

By formally starting from Kottelat & Freyhof (2007) taxonomic arrangement, Gratton *et al.* (2014) proposed a molecular classification scheme for native Italian trout, by analysing microsatellite and SNP datasets by means of assignment tests and Approximate Bayesian Computation approaches. As a synthesis, the authors propose a primary bifurcation among Italian trout taxa, by disentangling the 'peninsular' from the 'marble' evolutionary lineage.

The '**peninsular**' lineage represents the uppermost genetic hierarchy of phenotypic brown trout native to Italy, encompassing all samples of *S. cenerinus*, *S. cettii*, *S. fibreni* and, in a broader context, *S. carpio* as well, thus irrespective of the Adriatic or Tyrrhenian origin of the different taxa. Divergence among taxonomic entities within the 'peninsular' lineage is most likely very recent, probably starting not earlier than the last glacial maximum, around 18,000 years ago. Gratton *et al.* (2014) point to evidence that such a scenario of recent genetic divergence is in line with the weak geographical sorting and thus mosaic distribution of mtDNA haplotypes in the Mediterranean region (e.g. Cortey *et al.,* 2004; Splendiani *et al.*, 2006; Snoj *et al.*, 2009). Altogether, these results suggest the dispersal of trout along the Mediterranean coastlines during recent geological periods, possibly facilitated by lower salinity and/or cooler temperature regimes of the Mediterranean Sea. Consequently, any supposed speciation process within the 'peninsular' lineage, leading to taxonomic units with neither strict morphological or life-history distinctness such as *S. cenerinus* (Adriatic) and *S. cettii* (Tyrrhenian), should stem from very recent population divergence. Molecular data suggest that the underlying genetic divergence (e.g. *S. cettii* vs. *S. cenerinus*) is shallow and comparable to the divergence level that separates intraspecific marble trout metapopulations inhabiting distinct river basins. Aside the allopatric arrangement of 'peninsular' taxa into Adriatic (*S. cenerinus*) and Tyrrhenian (*S. cettii*) demes, a sympatric taxa pair is present within the Tyrrhenian area as well. Both *S. cettii* and *S. fibreni* cluster within the 'peninsular' lineage and naturally occur in Tyrrhenian habitats (Gratton *et al.*, 2013). *S. cettii* constitutes the riverine brown trout with a broad distribution area, originally thought to cover the whole Tyrrhenian slope of the Apennine in Central-Southern Italy, with the possible exception of Sicilian watersheds (Fruciano *et al.*, 2014). In contrast, *S. fibreni* is endemic to Lake Posta Fibreno (lake surface around 0.30 km^2) and is strictly reliant on karstic lacustrine pools for spawning (Zerunian & Gandolfi, 1986, 1990; Gandolfi *et al.*, 1991; D'Orsi & Seminara, 2010). The distribution area of both 'peninsular' Tyrrhenian taxa is overlying in the Lake Posta Fibreno catchment area, where *S. cettii* dominates in the Lake's tributaries, while *S. fibreni* inhabits the lacustrine habitat (Zerunian & Gandolfi, 1986). Interestingly, while genetic introgression is rare in typical riverine and lacustrine sites, a hybrid zone (with genetic introgression beyond the F1 level) exists in zones of intermediate environmental conditions (Gratton *et al.*, 2013). An interplay of spawning site selection, philopatry and natural selection might explain the observed temporal stability of this sympatric co-occurrence (Gratton *et al.*, 2013). Whether *S. fibreni* evolved in sympatry through ecological adaptation to the lacustrine habitat of Lake Posta Fibreno or it is the result of allopatric speciation, thus assuming *S. cettii* to have colonised Lake Posta Fibreno catchment later on, is still controversially discussed (Gratton *et al.*, 2014). Anyhow, adaptation of *S. fibreni* to the lacustrine habitat of Lake Posta Fibreni, and especially karstic-spring spawning, are the key factors responsible for either the origin and/or the maintenance of *S. fibreni*'s unique gene pool.

A comparable situation of sympatric 'peninsular' taxa is unknown for the Adriatic drainage basin in Italy. Here, 'peninsular' entities are strictly allopatric, since *S. cenerinus* is confined to the Apenninic slope and generally missing in the Alpine catchment of the Adriatic, where marble trout is dominating. Accordingly, *S. cenerinus* is not interacting with Lake Garda's carpione (*S. carpio*). *S. carpio*, completing the entire life-cycle in the lacustrine habitat, is best seen genetically as originating from the 'peninsular' lineage, but with a possible, limited, genetic contribution from the 'marble' lineage through natural secondary contact (Gratton *et al.*, 2014). Comparably to the *S. fibreni – S. cettii* species pair example, *S. carpio* has either achieved or is at least preserving its genetic integrity and isolation (from marble trout and exotic brown trout) through a potent prezygotic isolation factor, which is the ecological adaptation to the lacustrine environment of Lake Garda and especially *in situ*, deep water spawning.

The '**marble**' lineage, taxonomically classified as *S. marmoratus*, represents the second important evolutionary entity present in Italy. While *S. marmoratus* was traditionally associated to a well-defined mitochondrial clade, the MA clade (Giuffra *et al.*, 1994; Bernatchez, 2001), recent studies highlighted the non-accordance of gene- and species trees in this case (Pustovrh *et al.*, 2014; Gratton *et al.*; 2014). In fact, Pustovrh *et al.* (2014) highlighted that marble trout in southern regions, such as the Neretva and Skadar drainages, do not carry MA mitochondrial haplotypes, but are associated to Adriatic (AD) mitochondrial haplotypes. Thus, although the marble trout is monophylethic on a nuclear genetic basis, the mtDNA MA clade is not fixed in marble trout throughout its entire distribution range. On the other hand, mtDNA haplotypes of the MA clade are not private for marble trout, indicated by the occurrence of MA haplotypes in Mediterranean brown trout from Greece (Apostolidis *et al.*, 1997), Dalmatia (Bernatchez, 2001), Central Italy (Splendiani *et al.*, 2006), Albania (Snoj *et al.*, 2009) and Corsica (Lerceteau-Köhler *et al.*, 2013), for which no recent contact with *S. marmoratus* seems plausible. Gratton *et al.* (2014) compared divergence time estimates between 'Atlantic/Adriatic' and 'marble' trout entities when basing separately on mitochondrial and nuclear genetic data. Mitochondrial data suggest a more recent divergence of the marble trout clade, dated at ca. 0.4 Myr ago, compared to the 'marble' lineage divergence time estimate based on nuclear genetic data, dated at ca. 1.2 Myr ago. Thus, the 'marble' lineage, *S. marmoratus*, had already established long before divergence within the *S. trutta* complex into major mitochondrial clades (including MA) begun. This latter divergence led to the formation of distinct entities within the *S. trutta* complex, such as the 'peninsular' lineage, for which both nuclear and mitochondrial data indicate concordant divergence time estimates ranging between 0.2 and 0.6 Myr ago. The mtDNA clade MA should thus be not private to marble trout, but evolved independently in a Mediterranean brown trout ancestor and was acquired by Northern marble trout through secondary contact with brown trout. Low effective population size and subsequent genetic drift then might have favoured the fixation of the MA haplogroup in Northern marble trout.

Genetic diversity within the 'marble' lineage is structured in a series of metapopulations of distinct river basins. In fact, Gratton *et al.* (2014) addressed genetic divergence among *S. marmoratus* populations inhabiting the Po, the Adige as well as the Soca River drainages. Population divergence was found to be significant, with divergence time estimates indicating a recent population differentiation, started after the last glacial maximum.

To sum up, native salmonid biodiversity of the Italian peninsula can be split into two evolutionary units, being the '**peninsular**' and the '**marble**' lineages. The 'peninsular' lineage is best seen as a deme within the *S. trutta* complex, diverged from other evolutionary lineages within this species complex, e.g. the 'atlantic' lineage, between 0.2 and 0.6 Myr ago. While traditionally classified into four distinct species (*S. cenerinus*, *S. cettii*, *S. carpio* and *S. fibreni*) genetic divergence within the 'peninsular' lineage is most likely very recent and of postglacial origin. On the other hand, the origin of the 'marble' lineage predates that of the 'peninsular' lineage by far and the 'marble' lineage is likely to have independently evolved since around 1.2 Myr ago. Pronounced population differentiation is detectable within the 'marble' lineage, confined to metapopulations inhabiting distinct Adriatic river drainages and, likewise to the situation found for the 'peninsular' lineage, of recent postglacial origin. Since the origin of the 'marble' lineage predates that of formation of the mtDNA MA clade, the latter should have been acquired '*a posteriori*' through secondary contact with a Mediterranean brown trout ancestor.

Italian *Salmo* 'Brand-Marks': Molecular Ecology of Marble Trout (*Salmo marmoratus*) and Lake Garda's Carpione (*Salmo carpio*)

Beyond the uppermost genetic bifurcation of native Italian trout into 'peninsular' and 'marble' lineages, indigenous taxa cluster in a vast array of distinct metapopulations (Meraner *et al.*, 2010; Pujolar *et al.*, 2011a). Most of these trout are adapted to riverine habitats (e.g. marble trout, peninsular brown trout), while some others are lacustrine and strictly endemic to single watersheds (e.g. Lake Garda's carpione, carpione del Fibreno). Spanning the last two decades, genetic studies have explored several of the cited taxa, allowing novel insights into evolutionary history, population structure, genetic variability, life-history as well as anthropogenic hybridisation and introgression (Giuffra *et al.*, 1994, 1996; Nonnis Marzano *et al.*, 2003; Meraner *et al.*, 2007, 2010, 2013a; Pujolar *et al.*, 2011a; Splendiani *et al.*, 2006, 2013; Querci *et al.*, 2013; Gratton *et al.*, 2013, 2014; Fruciano *et al.*, 2014; Zaccara *et al.*, 2015).

In the following section we review the scientific literature concerning two prominent Italian trout, being marble trout (*Salmo marmoratus*) and Lake Garda's carpione (*Salmo carpio*). Alternative strategies in habitat choice and life-history greatly conditioned molecular ecology of these species. Distinct, in part opposing, responses in terms of population structure, gene flow and genetic integrity in the context of biological invasions are reported and serve here to illustrate a substantial bandwidth of heterogeneity within the genus *Salmo* in Italy.

Marble Trout (*Salmo marmoratus*)

The marble trout, *Salmo marmoratus*, is an endemism of the North to South-Eastern Adriatic drainage system in Northern Italy, Southern Switzerland, Slovenia, Bosnia-Herzegovina and Montenegro. The species distribution range covers the orographic left tributaries of the palaeo-Po River system, which formed a macrogeographic drainage basin given by sea level regressions of the Adriatic Sea at the end of the last glacial maximum (Bianco, 1990). Although likewise colour patterns have been observed in unrelated trout from Norway (Delling, 2002) and from Spain (Schöffmann, 2015), marble trout still appears to be morphologically unique, due to the combination of the pronounced marbled colour pattern in adult fish and diagnostic meristic characters (Delling, 2002). The marbled colour pattern is formed by an irregular arrangement of white to yellow lines, which tend to anastomose, thus giving a reticulate, marbled appearance. The skin background colouration strongly depends from the hydrogeology of the home river, and reaches from light grey to dark grey, olive green, brownish to almost black. *S. marmoratus* represents a large European salmonid of running waters and might have reached up to 140 cm in length, exceeding 20 kg in weight (Gridelli, 1936). At present, trophy size rarely exceeds 90 to 100 cm in length and 8 to 10 kg in weight. Life-history of the species strongly resembles that of brown trout, but a pronounced tendency towards piscivory is observable in later age classes (Gandolfi *et al.*, 1991). In addition, the typical home range of the marble trout is associated to lowland rivers, rather than to high alpine brooks, preferentially occupied by brown trout (Giuffra *et al.*, 1994). This longitudinal distribution pattern is typical for marble trout populations inhabiting Central-Northern water courses in the Adriatic drainage basin (Southern alpine slopes in Northern Italy). In contrast, stable populations in small, secluded high-alpine brooks in karstic hydrogeological circumstances are reported for marble trout in the Balkans, such as the Soca River basin in Slovenia (Fumagalli *et al.*, 2002; Jug *et al.*, 2005; Sušnik Bajec *et al.*, 2015). Consistent migratory populations of marble trout are unknown at present, but it seems highly likely that populations inhabiting tributaries of lakes, such as the major subalpine lakes in Northern Italy, Lake Garda, L. Maggiore, L. Lugano and L. Como, developed stream-resident and lake-dwelling forms. In fact, the few available historical photographs of 'lacustrine trout' of subalpine lakes in Italy, remind the typical colour pattern of marble trout. Nowadays, lacustrine phenotypes of the subalpine lakes in Northern Italy are predominated by Atlantic strains, with marble trout genetic signatures rarely occurring (Gratton *et al.*, 2014). Sea-running marble trout populations are unknown, notwithstanding rare by-catches of trout showing the typical marble trout colour pattern are documented.

Due to its morphological distinctness, the critical conservation status and its elevated importance for recreational angling, marble trout was studied exhaustively in the course of projects with conservation genetics content. These studies, distributed over more than the last two decades, aimed at resolving tasks of population structure, stocking induced hybridisation and genetic introgression as well as the conservation status of the species (Giuffra *et al.*, 1994, 1996; Fumagalli *et al.*, 2002; Jug *et al.*, 2005; Meraner *et al.*, 2007, 2010; Pujolar *et al.*, 2011a; Gratton *et al.*, 2014; Pustovrh *et al.*, 2011, 2014; Sušnik Bajec *et al.*, 2015). The most striking results are summarised in the following paragraphs.

Population Structure

In sharp contrast to the situation of panmixia observed in *S. carpio* (see below), the marble trout is constituted by a complex aggregation of distinct metapopulations, organised at least at three hierarchical genetic levels.

The uppermost genetic bifurcation within monophyletic *S. marmoratus* comprises 'northern' (Italy and Slovenia) versus 'southern' (Bosnia-Herzegovina and Montenegro) population clusters. The southern group encloses marble trout populations from Neretva (Bosnia-Herzegovina) and Skadar River (Montenegro) basins and appear to be a sister group to northern marble trout (Pustovrh *et al.*, 2011). Notably, although being phenotypically and genetically (nuclear genetic setup; Pustovrh *et al.*, 2011) closely related to northern marble trout, southern populations harbour mtDNA signatures of the AD lineage, generally associated with brown trout populations from Central-Eastern Mediterranean populations. MtDNA genetic profiles of the MA lineage are completely missing in these southern populations, thus contrasting with the traditional view of *S. marmoratus* and the mtDNA MA clade being inseparably associated and the latter being diagnostic for marble trout identification. The approximate timing of the major split of *S. marmoratus* in southern versus northern populations was investigated in

Pustovrh *et al.* (2014) based on nuclear DNA single nucleotide polymorphism (SNP) analyses. These authors indicated that the major bifurcation within marble trout should have occurred as early as 0.84 Myr ago, in a similar period when divergence between Danubian and Adriatic + Mediterranean genetic lineages of *S. trutta* has started (Pustovrh *et al.*, 2014).

With focus on northern marble trout, periodical sea-level oscillations of the Adriatic Sea most likely caused a second important step of population structuring. In fact, glacial maxima during the Pleistocene enabled the formation of a palaeo-Po River basin, into which nowadays isolated drainage basins as those of rivers Po, Adige and Soca discharged. This hydrological situation allowed genetic exchange and counteracted early population differentiation at the macrogeographic scale in the Northern Adriatic basin (Pujolar *et al.*, 2011a; Gratton *et al.*, 2014). The situation dramatically changed with the disruption of the palaeo-Po system after the last glacial maximum around 18,000 years ago, when rivers and consequently trout populations of basins such as the Po, the Adige and the Soca definitively split because of a pronounced sea-level rise of the Adriatic Sea. Genetic data support this biographical scenario. In fact, Gratton *et al.* (2014), using microsatellite and SNP datasets in conjunction with an Approximate Bayesian Computation (ABC) approach, found greatest statistical support for a comparably recent population isolation of marble trout from Rivers Adda (Northern Italy; Po Basin), Adige (Northern Italy) and Soca (Slovenia). In detail, genetic data suggested a recent origin of population divergence of marble trout from nowadays isolated rivers in the Northern Adriatic, dated after the last glacial maximum, while the alternative scenario of an earlier population divergence was statistically rejected. Likewise, Pujolar *et al.* (2011a) analysed Italian and Slovenian marble trout populations, inhabiting Northern Adriatic waters from the Western Po Basin to the Soca Basin in the East. These authors identified a significant genetic differentiation between marble populations, gradually augmenting with an increase in hydrological distances between sites, thus fulfilling the criteria of an Isolation-By-Distance pattern (Pujolar *et al.*, 2011a).

Population structure within *S. marmoratus* is pronounced also at the microgeographic level. To this effect, marble trout inhabiting small, secluded headwaters in the Upper Soca basin in Slovenia stand out as special. Fumagalli *et al.* (2002) pointed to exceptionally high genetic differentiation among neighbouring samples, with pairwise genetic differentiation reaching F_{ST} values up to 0.79 between populations separated by less than 15 km of waterway distance. Long term physical isolation in combination with exceptionally low intrapopulation variability and small effective population sizes, due to restricted habitat availability and stochastic hydrological events (floods and landslides), caused extreme genetic differentiation in this headwater habitats (Fumagalli *et al.*, 2002; Pujolar *et al.*, 2011b). More moderate, but significant, microgeographic differentiation is observable also in Italian marble trout. For instance, significant genetic differentiation is present between samples of the same river basin, separated by no more than 15 km of waterway distance (Pujolar *et al.*, 2011a). However, this small-scale genetic differentiation was remarkably lower among Italian than among Slovenian neighbouring populations (Pujolar *et al.*, 2011a). Likewise, shallow, but often significant, genetic differentiation characterises marble trout populations in the Upper Adige Basin in South Tyrol, Northern Italy (Meraner *et al.*, 2010). There, genetic heterogeneity between mainstream, e.g. Adige River, and headwaters, e.g. Passirio River, was detected based on a microsatellite marker set and used to deduce practical conservation guidelines (Meraner *et al.*, 2010).

While more pronounced intrapopulation variability and geneflow between neighbouring populations are slowing down interpopulation divergence at the microgeographic scale for marble trout in Northern Italy, opposing mechanisms seem to act on Slovenian populations. Low genetic variability within single populations, due to the concurrence of bottleneck effects and reduced long-term effective population sizes, as well as missing geneflow are causing extreme genetic differentiation at the interpopulation level.

Hybridisation and Genetic Introgression

Stocking-induced genetic introgression with exotic brown trout represents a primary stressor for marble trout throughout the species distribution range (Giuffra *et al.*, 1994, 1996; Fumagalli *et al.*, 2002; Jug *et al.*, 2005; Meraner *et al.*, 2007, 2010; Pujolar *et al.*, 2011a; Sušnik Bajec *et al.*, 2015). Brown trout of Atlantic origin have widely been introduced in the Adriatic region at least since the advent of the 19th century, in order to compensate for population declines of wild trout.

Due to hybridisation, the intrusion of brown trout genetic signatures into marble trout`s genepool was a direct consequence of brown trout stocking throughout the Northern Adriatic basin.

Recently, Sušnik Bajec *et al.* (2015) provided an extensive genetic survey of trout populations of the Soca basin in Slovenia. Importantly, the authors endorsed former genetic results (Fumagalli *et al.*, 2002; Jug *et al.*, 2005) and pointed to eight genetically pure marble trout populations in tributaries of the Soca and the Idrjica Rivers. These remote sites still represent pristine marble trout populations, without any sign of genetic introgression. In contrast, genetic introgression is widespread but highly variable throughout the hybridisation zone. Introgression frequencies generally follow an altitudinal gradient. In the Upper Soca, marble trout populations exhibit comparably low introgression rates (<20%) and purebred marble trout are still visible at these sites. Higher introgression rates and fewer pure marble trout specimens persist downstream in the Soca basin as well as in the Idrijca basin, where marble trout genetic profiles predominated at three of ten sites only (Sušnik Bajec *et al.*, 2015).

Interestingly, marble trout in the Soca basin also occupies small headwaters and it is there, where purebred populations persisted. This is an important difference to the situation in Southern Alpine headwaters in Italy, where the species dominates in the middle and lower stretches of the rivers, but is generally missing in the upper and middle stretches of the headwaters, widely occupied by brown trout (Sušnik Bajec *et al.* 2015; Archive of the Fisheries Department of Bolzano/Italy). This longitudinal dispersal pattern is important in the context of genetic introgression in Southern Alpine populations in Italy, which is summarised in Figure 3.2. In fact, pristine marble trout populations are unknown from Northern Italian sites. This seems directly related to the confinement of marble trout in the Southern Alps to lower altitudinal belts, thus easily accessible for fisheries management and stocking measures. A consequence is that within this zone marble trout is in either case accompanied by exotic brown trout and/or hybrid specimens. Unlike the Slovenian situation, genetic introgression among Italian populations does not follow an altitudinal cline, but shows an unpredictable, mosaic distribution. Variance in the magnitude of genetic introgression most likely resembles differing ‘immigration rates’ (*sensu* Hansen, 2002) and depends upon the ratio of stocking input, i.e. stocking number and periodicity of exotic brown trout, and

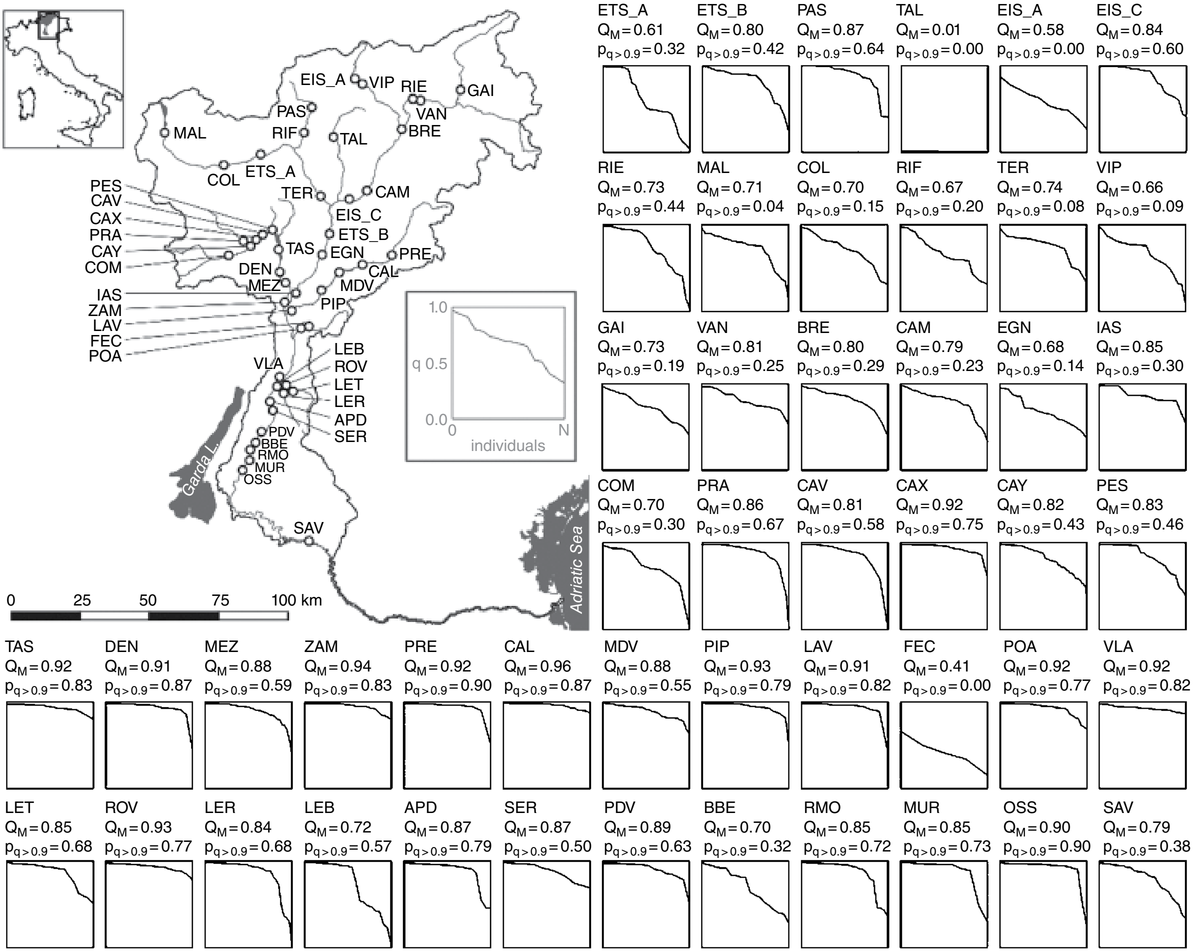

Figure 3.2 Patterns of genetic introgression of marble and exotic brown trout in the Adige River Basin (data from Baraldi *et al.*, 2010 and Meraner *et al.*, 2010). The data are relative to phenotypically defined marble trout and hybrid individuals, found in sympatry with brown trout in the original studies. For each sampling site, the individual introgression pattern resulting from admixture analysis (STRUCTURE, Pritchard *et al.*, 2000) and basing on microsatellite datasets of 10 (Baraldi *et al.*, 2010) and 12 (Meraner *et al.*, 2010) loci is presented. Admixture values (q) are sorted from highest to lowest, with q = 1 indicating pure marble trout and q = 0 pure exotic brown trout. The population level average of estimated marble trout ancestry (Q_M), and the proportion of individuals with $q > 0.9$ ($p_{q>0.9}$), thus indicating the 'pure' marble trout proportion at each site, are shown. Only in three cases out of 48 sampling sites (TAL, EIS-A and FEC) no single individual has reached a q value > 0.9, thus indicating absence of marble trout at these three sites.

standing stock, i.e. the abundance and wealth of the wild population at each single location. In fact, exceptionally high introgression rates and the almost complete decline of marble trout in some localities of the Upper Adige River basin (Province of Bolzano; Northern Italy) seems to be a result of low initial population size of the native species thus already outcompeted by moderate numbers of stocked fish (Meraner *et al.*, 2010). The fact that genetic introgression is visible at each site has not to be confounded with genetic profiles at the individual level. In analogy to the situation in the Upper Soca basin, purebred marble trout specimens were detected within introgressed populations in the majority of Italian sites, potentially as a result of prezygotic isolation mechanisms (Meraner *et al.*, 2010). While in-stream experiments performed by Meldgaard *et al.* (2007) did not provide evidence for reproductive barriers between marble and brown trout, Meraner *et al.* (2010) hypothesised that temporal differences in the spawning period of both species, overlapping only marginally at the end of November, might present an (incomplete) prezygotic isolation mechanism. This might slow down genetic introgression and delay hybrid swarm formation (Epifanio & Philipp, 2001).

Conservation Status and Population Management

At present, marble trout is considered 'least concern' in the IUCN red-list (Crivelli, 2006a). This classification primarily bases on the expert assessment of the species in Slovenia. There, the marble trout seems to be demographically, through around 10,000 specimens estimated, and genetically, through protected isolated, purebred populations, safeguarded. Management actions, which officially started in 1996 in the frame of the national marble trout rehabilitation plan (Povž *et al.*, 1996), included fisheries actions, such as the legal prohibition of brown trout stocking, protection and care of remnant purebred populations, safeguarding of these genepool populations by translocating them into neighbouring streams and the selection of purebred specimens from hybridised populations for supportive/captive breeding actions (Povž *et al.*, 1996; Vincenzi *et al.*, 2012; Sušnik Bajec *et al.*, 2015). Thus, marble trout conservation seems to be on the right path in Slovenia and should gradually decrease genetic introgression, if management actions will be continued on the long run.

Marble trout conservation seems not be in such an advanced state in Italy. A limitation to marble trout conservation in Italy is given by its decentralised fashion, since conservation actions are mainly planned and financed by meritorious, private fisheries associations or local fisheries authorities. An area-wide long-term management plan, an analogue of the 'Slovenian marble trout rehabilitation plan', aiming at merging all interest groups at a significant macrogeographic level, the river basin, and defining basic conservation conventions is still completely missing. This implies that key-aspects of marble trout conservation greatly vary even between adjacent fisheries districts and are rarely agreed, not even if concerning adjacent stretches of one and the same river. However, some promising marble trout conservation perspectives seem to develop in Northern Italy. First, fisheries regulations of the various districts in Northern Italy increasingly acknowledge the detrimental effect stocking of exotic brown trout had on wild marble trout. As a legal consequence, brown trout stocking is widely prohibited at least in lowland rivers, typically inhabited by marble trout (e.g. Fisheries Department of the Autonomous Province of Bolzano, personal communication). Second, genetics appears now not only in scientific studies, but also enters applied conservation programmes.

Traditionally, suitable marble trout spawners were selected upon morphological characters, mainly patterns of skin colouration. Although skin colour patterns and genetic set-up significantly correlate in marble trout (see Figure 3.3 for details), an accurate discrimination of purebred marble trout from hybrid specimens necessitates genotyping based on multiple neutral markers. Since purebred populations are not available in Italy and fish to be included in breeding programs must be selected from hybridised populations, genetic tools are of central importance. A major challenge in this regard consists in high-throughput genetic screening of potential spawners, which enables for the rapid selection of wild fish, thus getting captive breeding strains dispensable and strengthening supportive breeding actions. In addition, given the pronounced population structure of marble trout even at the microgeographic level (see above), genetics plays a central role also for the definition of management units (MU; Moritz, 1994), on which conservation plans are to be oriented. Third, there is growing awareness that sustainable salmonid conservation is not achievable with restocking programmes only. Today, marble trout waters suffer from multiple anthropogenic pressures and habitat restoration measures have undoubtedly to play the primary role. However, since this objective is not achievable in the mid-term and it is moreover hard to reach ever in heavily modified watercourses, restocking efforts through supportive breeding will remain important for marble trout conservation. Therein, genetic tools surely constitute an integrant component.

Lake Garda's Carpione (*Salmo carpio*)

Salmo carpio is an endemic trout of Northern Italy, inhabiting exclusively Lake Garda as the primary lacustrine watershed in Italy (surface area = 368 km^2). The history of Lake Garda is relatively recent, dating back to the retreat of Southern Alpine glaciers at the end of the Pleistocene some 15,000 to 18,000 years BP. The carpione is thought to have originated within Lake Garda from an ancestral 'peninsular' brown trout and rapidly adapted to this lacustrine environment. Some adaptations, such as silvery-grey body colouration and bentho-planctonic feeding behaviour are commonly reported within the genus *Salmo* and most likely reflect the substantial phenotypical and ecological plasticity, generally associated to polytypic brown trout. Other peculiarities, including pronounced schooling behaviour extended to entire life-span, but most importantly the expression of a double reproductive period (either at the population or the individual level; Melotto & Alessio, 1990), one more extended period peaking in winter months (between December and February) and one short-time period peaking in summer (from July to August), seem to be unique within the genus *Salmo*. In sharp contrast to most lacustrine brown trout morphs studied so far, reproduction of *S. carpio* seems not to involve running waters (lake inflows or outlets), but should strictly occur *in situ*, deposing the eggs on submerged gravel ridges of Lake Garda, at estimated depths between around 50 and 200 meters (Lunelli *et al.*, 2012). Early growth (until stage 2+) was found to resemble that of other lacustrine brown trout forms (and also that of anadromous lacustrine brown trout of Lake Garda; Merlo, 1955, 1956). In contrast, growth at later life stages is less pronounced in *S. carpio*, probably as a direct consequence of bentho-planktonic feeding and the absence or sparseness of piscivory, thus leading to maximum fork lengths of 500 mm and 1 kg of weight (Melotto & Oppi, 1987).

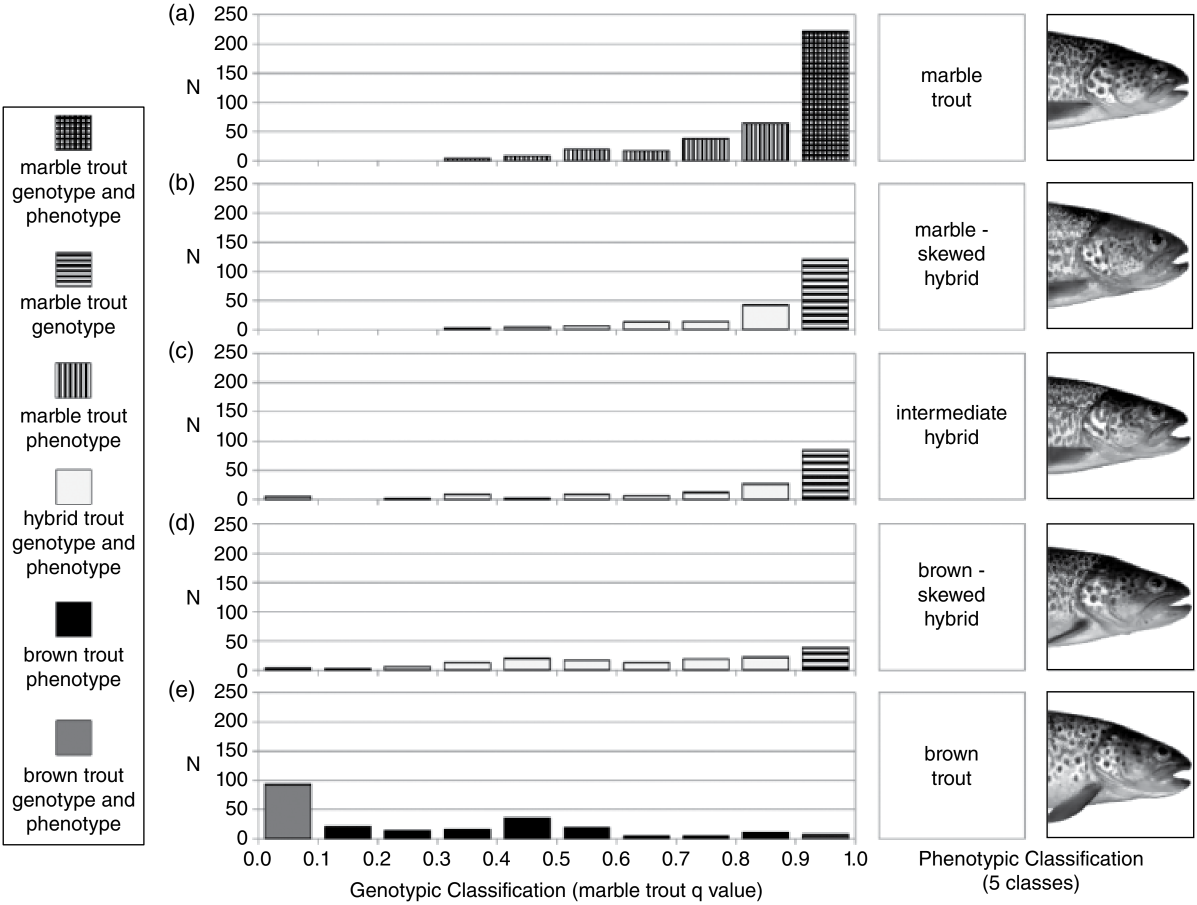

Figure 3.3 Phenotypic versus genotypic classification of marble trout (1103 individuals, data from Baraldi *et al*., 2010). Each individual was assigned (i) to one of five phenotypic classes (a: marble trout, b: marble-skewed hybrid, c: intermediate hybrid, d: brown-skewed hybrid, e: brown trout) based on morphology; and (ii) to one of ten genotypic classes based on the individual coefficient of admixture (q) between marble trout ($q = 1$) and exotic brown trout ($q = 0$) estimated from the analysis of ten microsatellite markers (STRUCTURE, Pritchard *et al*., 2000). Despite the general trend of concordance between phenotypic and genotypic assignment, a significant number of discordant classification cases are highlighted. Two cases are of particular relevance: (i) genetically hybrid individuals (vertical lines bars; $0.3 < q \leq 0.9$) are classified as marble trout on a phenotypic basis and would therefore be included in a phenotypically based supportive breeding program. This possibly fuels genetic introgression in natural populations; (ii) genetically 'pure' marble trout individuals (horizontal lines bars, $0.9 < q \leq 1$) are classified as hybrids on a phenotypic basis and would therefore be excluded from the group of marble trout spawning candidates in a phenotypically based supportive breeding program, thus possibly resulting in the loss of genetic diversity.

Interestingly, longevity seems not to occur in *S. carpio*, as age classes > 5+ have not been reported in literature so far (Merlo, 1955; Alessio *et al.*, 1990).

Already recognised and described since the mid 16th century (Belon, 1553; Rondelet, 1555; Salviani, 1557), the Lake Garda's carpione has been investigated at the molecular level since the last two decades, exploring aspects of evolutionary history, population structure, genetic introgression and conservation status (Giuffra *et al.*, 1994, 1996; Gratton *et al.*, 2014).

The ***evolutionary history*** of this endemic salmonid was firstly investigated in Giuffra *et al.* (1994, 1996) on the basis of mtDNA sequence, RFLP and nuclear protein electrophoresis data. *S. carpio* was not associated with a single phylogenetic distinct branching, but harboured instead four mtDNA lineages, being Adriatic (AD), Marmoratus (MA), Mediterranean (ME) and domestic Atlantic (AT). This result was interpreted as evidence for the recent, postglacial origin of *S. carpio*, probably occurring within Lake Garda after the retreat of Southern Alpine glaciers. Thus, analysis of nuclear genetic data, with *S. carpio* occupying an intermediate (between Adriatic brown trout and marble trout) position in phylogenetic reconstructions, led Giuffra *et al.* (1996) to hypothesise a hybrid origin of the carpione. Thus, *S. carpio* should have originated from postglacial hybridisation between marble trout and Adriatic brown trout and should have diverged from these taxa through selection (i.e. for the lacustrine habitat) and/or genetic drift (i.e. genetic bottlenecks).

Almost two decades later, Gratton *et al.* (2014) re-focused on the evolutionary history of *S. carpio* by exploring mtDNA, microsatellite and nuclear DNA sequence data and by adopting a hierarchical Approximate Bayesian Computation (ABC) approach. These authors found greatest statistical support for an evolutionary scenario, where *S. carpio* directly derives from an ancestral 'peninsular' brown trout and diverged from the latter within Lake Garda after the last glacial maximum. Genetic contribution (i.e. hybridisation) from marble trout was not ruled out, but should have been marginal and thus genetic introgression highly asymmetric (Gratton *et al.*, 2014). Alternatively, the presence of both Adriatic and Marmoratus mtDNA haplotypes within *S. carpio*'s genepool could be the result of original mtDNA diversity within 'peninsular' brown trout, thus pointing to the non-private character of marmoratus mtDNA haplotypes for the marble trout taxon.

In the absence of spatial isolation, the evolution of intraspecific heterogeneity and ***population substructure*** depends on ecological adaptation and subsequent reproductive isolation. Prominent salmonid examples include Scottish lacustrine brown trout (*S. ferox* in Kottelat & Freyhof, 2007; see Duguid *et al.*, 2006) and whitefish species flocks, evolving in sympatry (e.g. Hudson *et al.*, 2011). Local adaptation seems to be a potent evolutionary force, promoting reproductive isolation and leading, at the end, to ecological speciation. In *S. carpio*, a double reproductive period ('winter' spawning near to Lake Garda's western bank; 'summer' spawning near the eastern bank) has been reported by several Italian ichthyologists since Malfer (1927), potentially indicating intraspecific heterogeneity and population structure. Two hypotheses were reported regarding the bi-annual reproductive period of *S. carpio*. First, summer and winter spawning could be related to intraspecific heterogeneity within *S. carpio* and point to cryptic population structure of the species within Lake Garda. Such a scenario was tentatively supported by some authors, indicating that adult females hold ripe eggs either in winter or summer month, thus opposing a double reproductive behaviour at the individual level (D'Ancona & Merlo, 1959; Tortonese, 1970).

Contrarily, other ichthyologists found oocytes within single ovaries at different stages of vitellogenesis, thus supporting a bi-annual spawning behaviour at the individual level (Malfer, 1927; Melotto & Alessio, 1990). The population structure of *S. carpio* was investigated in Gratton *et al.* (2014) by adopting Bayesian statistics and by combining mtDNA and ncDNA sequence, as well as microsatellite data. These authors found no substructure within *S. carpio* genotypes, thus pointing to a single, panmictic carpione population within Lake Garda. Since shallow genetic substructuring could have been overlooked due to the study's macrogeographic setup, we re-analysed the carpione dataset presented in Gratton *et al.* (2014) (present study). We sorted the dataset according to sampling locality and grouped samples from the western lake bank ('winter spawning site', WSC) and samples from the eastern bank ('summer spawning sites', ESC) (see Figure 3.4 for details). We then applied Bayesian assignment tests (STRUCTURE; Pritchard *et al.*, 2000) and tested for statistical significance of population substructuring within the carpione's metapopulation (see Figure 3.5). We reconstructed the most likely sibship arrangement of the carpione sample-set by using COLONY software 2.0 (Jones & Wang, 2010). We thus calculated the number of family groups, as well as full- and half-siblings represented by the entire carpione dataset, by explicitly evaluating the hypothesis of population substructuring within *S. carpio*. To this end, we tested for a significant difference in the proportion of sibship relationships within and among samples caught at 'winter' and 'summer' spawning sites (see Table 3.2).

Neither Bayesian assignment tests nor sibship reconstruction supported the hypothesis of (even shallow) population structuring within *S. carpio*, therefore validating the scenario of panmixia proposed by former studies (Nümann, 1953; Merlo, 1954, 1955; Melotto & Alessio, 1990).

Anthropogenic ***genetic introgression*** due to stocking and translocation of non-native conspecifics is exceptionally widespread within salmonids, heavily impacting the overwhelming majority of genetic entities within the genus *Salmo* throughout their distribution range (e.g. Meraner *et al.*, 2010; Caudron *et al.*, 2012; Sušnik Bajec *et al.*, 2015). While empirical examples of partial (i.e. occurrence of both pure parental and hybrid genotypes) and complete (i.e. hybrid swarm) genetic introgression are found in the scientific literature, case studies pointing to the absence of genetic introgression after strong secondary contact are very rare or absent in salmonids. Here, *S. carpio* stands out from the salmonid crowd as special.

While Giuffra *et al.* (1994, 1996) reported evidence of genetic introgression of Atlantic mtDNA haplotypes in phylogenetic analyses of carpione samples, Gratton *et al.* (2014) could not detect any foreign Atlantic haplotype within *S. carpio*. This result was further corroborated by microsatellite data and Bayesian assignment tests, which virtually excluded any genetic contribution of exotic Atlantic genes into *S. carpio*. The discrepancy between the two studies might be due to the erroneous inclusion of Atlantic brown trout into the carpione sample set of the first one, since sample sizes analysed in Gratton *et al.* (2014) were much larger than those presented in Giuffra *et al.* (1994, 1996), thus limiting the possibility of overlooking exotic brown trout. Here, we additionally extended the *S. carpio* sample set and re-performed phylogenetic analyses based on mtDNA sequence data as well as Bayesian assignment tests based on multilocus microsatellite data (see Figure 3.5 for details; present study). None of these led to hypothesise the presence of exotic brown trout genetic profiles in *S. carpio*.

Figure 3.4 Map of sampling locations for individuals included in the Bayesian clustering analysis (see Figure 3.5: Lake Garda's carpione (WSC, *S. carpio* from the western lake bank and ESC, *S. carpio* from the eastern bank, Gratton *et al*., 2014), stream resident brown trout (ALB, Albola River, Meraner *et al*., 2013a), lake dwelling trout (GAL, lacustrine trout from Lake Garda and SAL, lacustrine trout from River Sarca, Gratton *et al*., 2014), and reference populations (MAR, marble trout, SVE, Tyrrhenian brown trout and HAT, hatchery brown trout of Atlantic origin; Meraner *et al*., 2013a).

Additional simulation data (present study) indicated that Bayesian assignment efficiency was quite high, allowing the detection of potential later generation backcrosses (carpione × Atlantic brown trout) under an extreme scenario of highly asymmetric geneflow at least to the forth hybrid generation (see Figure 3.6). Thus, *S. carpio* seems still completely isolated from domestic Atlantic genepools even after decades of

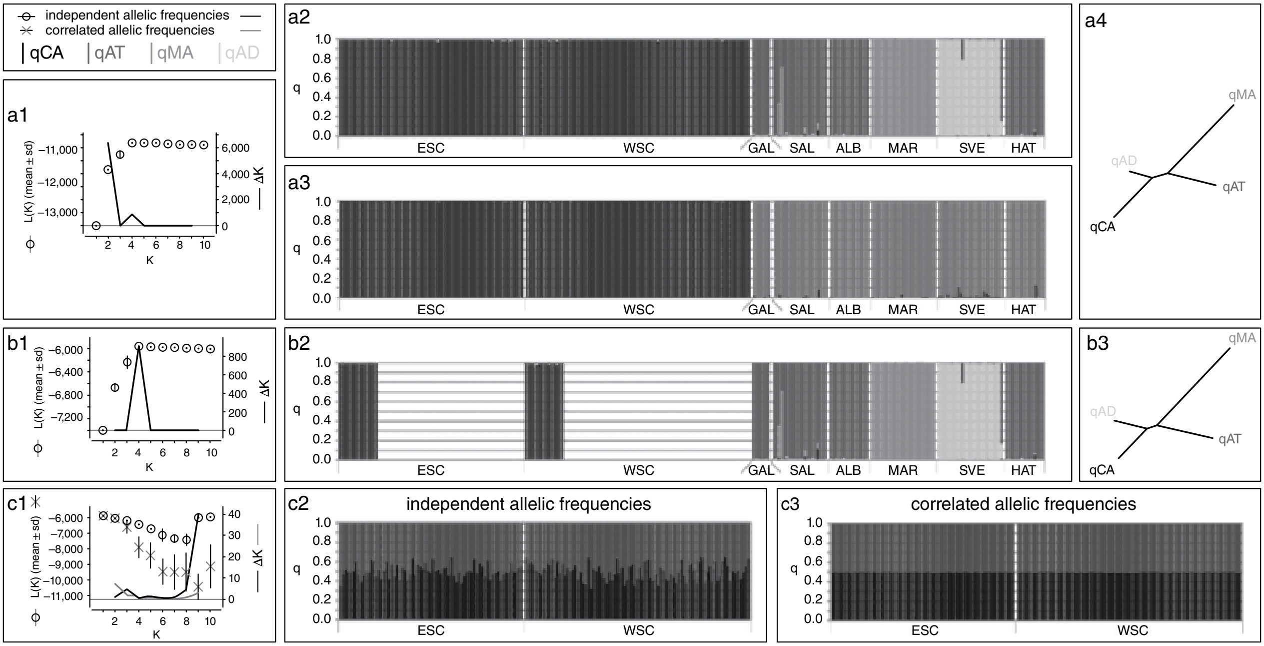

Figure 3.5 Results of a hierarchical Bayesian clustering analysis by STRUCTURE (Pritchard *et al*., 2000) on the Lake Garda's carpione (12 microsatellite markers, data from Gratton *et al*., 2014) and new reference samples (Meraner *et al*., 2013a) (see Figure 3.4). a1. Mean of the estimated ln probability of data (± sd) and ΔK statistics (Evanno *et al*., 2005) as a function of the different tested number of genetic clusters (1 ≤ K ≤ 10, 10 replicate runs for each K value). a2. The most likely number of genetically homogeneous clusters (K) is four, differentiating a single *S. carpio* metapopulation (ESC and WSC), marble trout (MAR), Tyrrhenian brown trout (SVE) and an exotic Atlantic brown trout cluster including hatchery individuals (HAT) as well as lacustrine (GAL and SAL) and stream resident (ALB) trout from the Sarca-Garda Basin. a3. An alternative solution, with K = 2 (*S. carpio* metapopulation versus other trout) was offered by the ΔK statistics, possibly due to a numeric overrepresentation of *S. carpio* in the dataset. b1 and b2. The analysis was thus repeated by only including a random subsample of *S. carpio* and by pointing to the same solution presented in Figure a2. c1–c3. The entire *S. carpio* sample set, independently analysed, offered no evidence of genetic substructuring within the *S. carpio* metapopulation, with both of the allelic frequency models (c2, independent allelic frequencies; c3, correlated allelic frequencies) implemented in the analysis.

Table 3.2 Sibship arrangement of the *S. carpio* sample-set (Gratton *et al*., 2014) by using COLONY analysis (Jones & Wang, 2010). By implementing full-pedigree likelihood methods, COLONY uses multilocus genotypic data to cluster offspring specimens into either full-siblings (FS, sharing both parents), half-siblings (HS, sharing father or mother) or unrelated individuals. Here, the entire *S. carpio* dataset (ESC + WSC, see Figure 3.4) was analysed under the full likelihood method assuming a polygamous mating scheme for both genders, setting the 'sibship complexity prior' which reduces the possibility of erroneously misclassifying unrelated or loosely related specimens as half-siblings, as advised in the context of weak family structure, polygamy and limited genotypic resolution power (J. Wang, personal communication). Three independent models were run (Model 1, 2 and 3). For each model, the number (N) and the proportion (Prop.), over the number of possible pairs, of individual pairs assigned to half-siblings (HS, sharing father or mother) and full-siblings (FS, sharing both parents) classes (either all cases or only cases with estimated $p \geq 0.95$) were thus calculated within sampling sites (ESC and WSC), within the overall carpione population (ESC + WSC) and between sampling sites (ESC vs. WSC). To test for significant difference in the proportion of sibship groups within and between sampling sites a subsampling approach was adopted. To obtain independent estimates of the proportion of HS and FS within and between sampling sites, the overall carpione population (ESC + WSC) was divided into two subpopulations A and B of equal size ($N = (71 + 87)/2 = 79$), by randomly assigning each individual to either A or B. Population A was used to estimate the within-population sibling rates; population B for the between-population rates. This was done for each of the three models tested in COLONY, and performed 10,000 times. For each division, the difference between the proportion of HS and FS relationships measured within sites and the proportion measured between sites was calculated. Finally, the distribution of the differences was used to assess a possible deviation from the null hypothesis of no difference. No significant difference in the proportion of sibship relationships within and between sampling sites was found, suggesting that HS and FS individuals can be found with equal probability within and between sampling sites and reinforcing the scenario of panmixia, suggested for *S. carpio* by means of individual assignment tests (Figure 3.5).

		Within WSC	Within ESC	Within overall	Between WSC and ESC	Total
	N of individuals	71	87			158
	N of pairs	2,485	3,741	6,226	6,177	12,403
Model 1	N HS_{all}	68	97	165	160	325
	N $HS_{p\geq0.95}$	51	66	117	115	232
	N FS_{all}	12	17	29	21	50
	N $FS_{p\geq0.95}$	8	13	21	14	35
	Prop. HS_{all}	0.027	0.026	0.027	0.026	0.026
	Prop. $HS_{p\geq0.95}$	0.021	0.018	0.019	0.019	0.019
	Prop. FS_{all}	0.005	0.005	0.005	0.003	0.004
	Prop. $FS_{p\geq0.95}$	0.003	0.003	0.003	0.002	0.003
Model 2	N HS_{all}	73	49	173	175	348
	N $HS_{p\geq0.95}$	58	42	143	138	281
	N FS_{all}	19	30	49	29	78
	N $FS_{p\geq0.95}$	10	18	28	15	43
	Prop. HS_{all}	0.029	0.013	0.028	0.028	0.028
	Prop. $HS_{p\geq0.95}$	0.023	0.011	0.023	0.022	0.023
	Prop. FS_{all}	0.008	0.008	0.008	0.005	0.006
	Prop. $FS_{p\geq0.95}$	0.004	0.005	0.004	0.002	0.003

(Continued)

Table 3.2 (Continued)

		Within WSC	**Within ESC**	**Within overall**	**Between WSC and ESC**	**Total**
Model 3	N HS_{all}	51	82	133	130	263
	N $HS_{p\geq0.95}$	34	50	84	79	163
	N FS_{all}	7	10	17	10	27
	N $FS_{p\geq0.95}$	4	6	10	5	15
	Prop. HS_{all}	0.020	0.022	0.021	0.021	0.021
	Prop. $HS_{p\geq0.95}$	0.014	0.013	0.013	0.013	0.013
	Prop. FS_{all}	0.003	0.003	0.003	0.002	0.002
	Prop. $FS_{p\geq0.95}$	0.002	0.002	0.002	0.001	0.001

Model 1: Excluded Maternal Sibship based on mtDNA haplotype information; allelic dropout rate = 0.05; other error rate = 0.05.
Model 2: No Excluded Maternal Sibship based on mtDNA haplotype information; allelic dropout rate = 0.05; other error rate = 0.05.
Model 3: Excluded Maternal Sibship based on mtDNA haplotype information; allelic dropout rate = 0.00; other error rate = 0.00.

sympatry with exotic lacustrine brown trout in Lake Garda. The latter, most likely introduced around 1900 in Lake Garda with increasing population densities in the last decades, is spawning in River Sarca (major tributary of Lake Garda) and is supported through local breeding programmes. Today, lacustrine brown trout with increasing population densities in the last decades represent an important target for professional fisheries and especially for recreational angling. The peculiar life-history of *S. carpio*, especially deep-water, lake spawning, is acting as a powerful pre-zygotic isolation mechanism, completely protecting *S. carpio*'s genepools from any genetic introgression so far.

While the genetic integrity of *S. carpio's* genepool seems still to be in an original state, ***conservation status*** of the species is alarming. International red lists register the species as a Critically Endangered taxon (Crivelli, 2006b), given the pronounced population declines observed during the last decades. Associated catch rates dropped from 20–40 tons, regularly reported since the end of the nineteenth century (Melotto & Oppi, 1987) to only few kilograms currently, thus reflecting severe population decline of the species. Although the exact causes of this population decline are still a matter of debate and hopefully exhaustively investigated in the near future, environmental degradation (e.g. deterioration of spawning grounds), overfishing and especially interspecific competition with introduced whitefish (*Coregonus* ssp.) seem to be primary threat factors.

Supportive breeding programs, started as early as in 1880 (Bernardi, 1956), were only occasionally interrupted mainly during the two World Wars and finally ceased in 1970 because considered ineffective in halting population decline (Melotto & Oppi, 1987). More recently, captive breeding programmes have been initiated in order to halt further population loss (Ciutti *et al.*, 2010; Parati *et al.*, 2013). Such management actions are to be planned and executed thoroughly, since the strong pre-zygotic isolation barriers found in the wild could be surmounted in the hatchery environment, e.g. when mislead

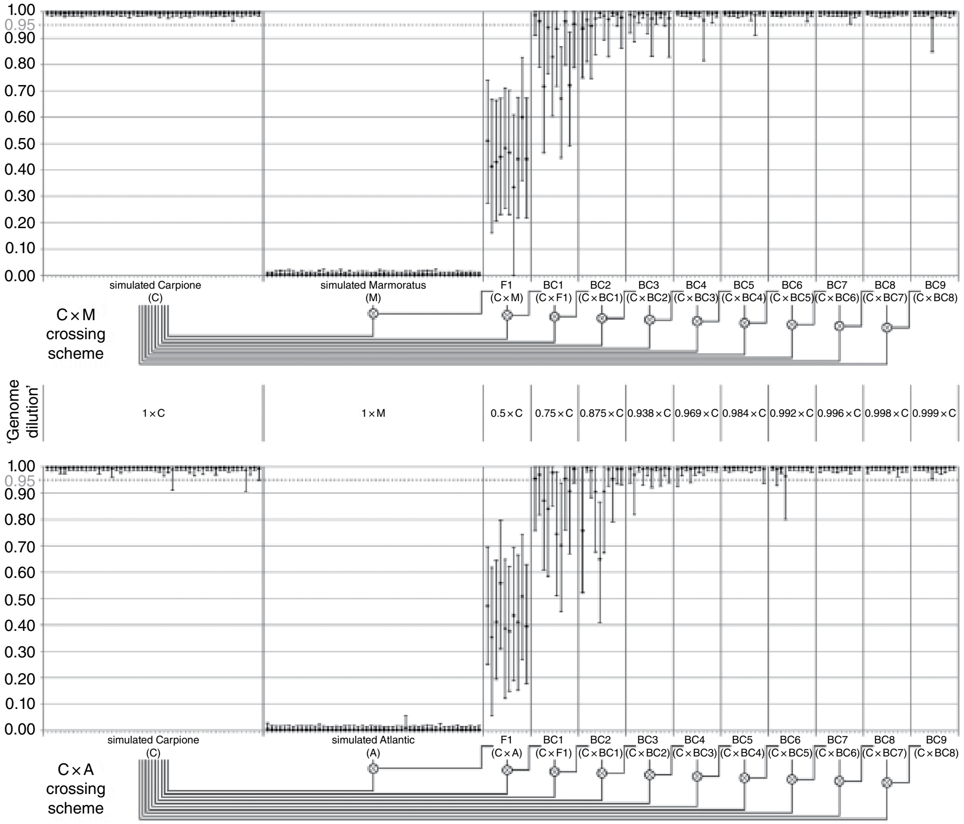

Figure 3.6 In order to evaluate the performance of STRUCTURE to discriminate between purebred and different hybrid classes within the *S. carpio* dataset from Gratton *et al.* (2014), simulated datasets were generated with Hybridlab 1.0 (e.g Nielsen *et al.*, 2006). Three new purebred populations (N = 500 each) were generated for carpione (C), marble trout (M) and Atlantic brown trout (A), by randomly self-crossing the observed multilocus genotypes from the ESC + WSC, MAR and HAT sampling sites, respectively (see Figures 3.4 and 3.5). The simulated purebred population C was then independently crossed with populations M and A, thus generating two first generation hybrid classes (F1 (C×M), N = 500 and F1 (C×A), N = 500). Each F1 class was then backcrossed to purebred C, and each newly generated backcross generation (BC1 (C×M), deriving from C×F1 (C×M), N = 500 and BC1 (C×A), deriving from C×F1 (C×A), N = 500) was again backcrossed to purebred C. The last step was repeated for each newly generated backcross generation, up to the ninth backcross class, i.e. the tenth admixed generation. Two new datasets (C×M and C×A) were finally created by randomly selecting 100 individuals from both the purebred parental classes (C and M for C×M, and C and A for C×A) and 10 individuals from each of the hybrid classes, summing up to N = 200 each. The number of individuals included from hybrid classes was limited, as an increased proportion of hybrids in the sample clearly have a detrimental effect on the efficiency of hybrid identification (see Vähä & Primmer, 2006). The two new datasets were then analysed with Structure (Pritchard *et al.*, 2000), settings K = 2, to estimate individual admixture proportions (q-values) and the respective 90% credibility intervals.

forced matings between carpione and lacustrine brown trout lead to unnoticed hybrid formation. The stocking of such hatchery-derived hybrids within Lake Garda could relax pre-zygotic isolation mechanisms and finally lead to the intrusion of foreign genome portions into *S. carpio*'s unique genepool.

Exotic Brown Trout in Italy: Origins, Distribution and Genetic Interference with Indigenous Trout Taxa

Introductions of non-native species, either accidentally or intentionally, constitute a major driver for the biodiversity decline worldwide (Ribeiro & Leunda, 2012). This is particularly evident for the Mediterranean biodiversity and for Italian freshwater fish biota therein, massively and irreversibly altered by exotic taxa (Bianco & Ketmaier, 2001). In Italy, several exotic freshwater fish introductions including the appropriate ecological consequences are relatively new, and have emerged during the last few decades only (Bianco, 2014). This is the case for several exotic cyprinid taxa, as well as catfish and pikeperch, which, although of late arrival, now dominate fish communities in entire large Italian river systems, such as the Po River system (Bianco & Ketmaier, 2001; Meraner *et al.*, 2013b). In contrast to these novel exotics, other non-native freshwater fish species entered Italian waters much earlier, with salmonids being of particular importance.

First, spatially restricted, salmonid translocations are likely to have occupied alpine waters in Italy as soon as around 1500 from Northern Alpine source populations. The Austrian monarch, Maximilian I (1486–1519) is known to have conducted salmonid stocking in alpine waters originally free of fish (Pechlaner, 1984; Weiss *et al.*, 2001), likely including also transalpine, southwards directed, salmonid transport from Austrian (Danubian drainage) to Northern Italian (Adriatic drainage) waters (Meraner *et al.*, 2007, 2014; Meraner & Gandolfi, 2012). These first salmonid transalpine stockings are thought to have involved beside Alpine charr *(Salvelinus umbla*) and potentially European grayling (*Thymallus thymallus*) mostly brown trout from Danubian waters (Meraner *et al.*, 2007). Supposed limited relicts of the latter translocations persist in brown trout populations from the Upper Adige River (Northern Italy, Southern Alpine slope), where molecular traces of 'Danubian clade' brown trout are still visible at the mtDNA haplotype level (Meraner *et al.*, 2007) (Figure 3.7).

In contrast to spatially restricted historical translocations, exotic brown trout stocking triggered by commercial aquaculture trade routes had massive macrogeographic effects. Due to their elevated importance in aquaculture and thereafter sport fisheries, exotic *S. trutta* stocks have been transported across the Alps at the latest since around the end of the nineteenth century via aquaculture trade channels (Canestrini, 1914; Ketmaier & Bianco, 2004; Pontalti, 2011). This second, Italian-wide stocking wave is supposed to have included mostly or exclusively brown trout of Atlantic genetic origin. This is supported by historical trading and advertising documents, indicating even stocking of 'Scottish brown trout' in Northern Italian waters around 1900 and the long tradition of intensive salmonid aquaculture in Central Europe in conjunction with known trade relationships to Italian fish-farmers (Pontalti, 2011). Genetic evidence of a predominant 'Atlantic' genetic setup of stocked brown trout comes from surveys involving acclimatised trout populations. In fact, most if not all acclimatised brown trout populations, known to derive from stocking, genetically cluster with 'Atlantic' hatchery stocks. This is the case for brown trout populations inhabiting formerly fish-free secluded brooks in the Southern Alps (Meraner *et al.*, 2013a) as well as for introduced, lake-dwelling forms populating subalpine lakes in Northern Italy, such as Lake Garda (Gratton *et al.*, 2014).

Italian fish farms, which imported non-native brown trout from Central European aquaculture facilities to Italy, acted as 'stocking-multipliers', in that foreign trout were

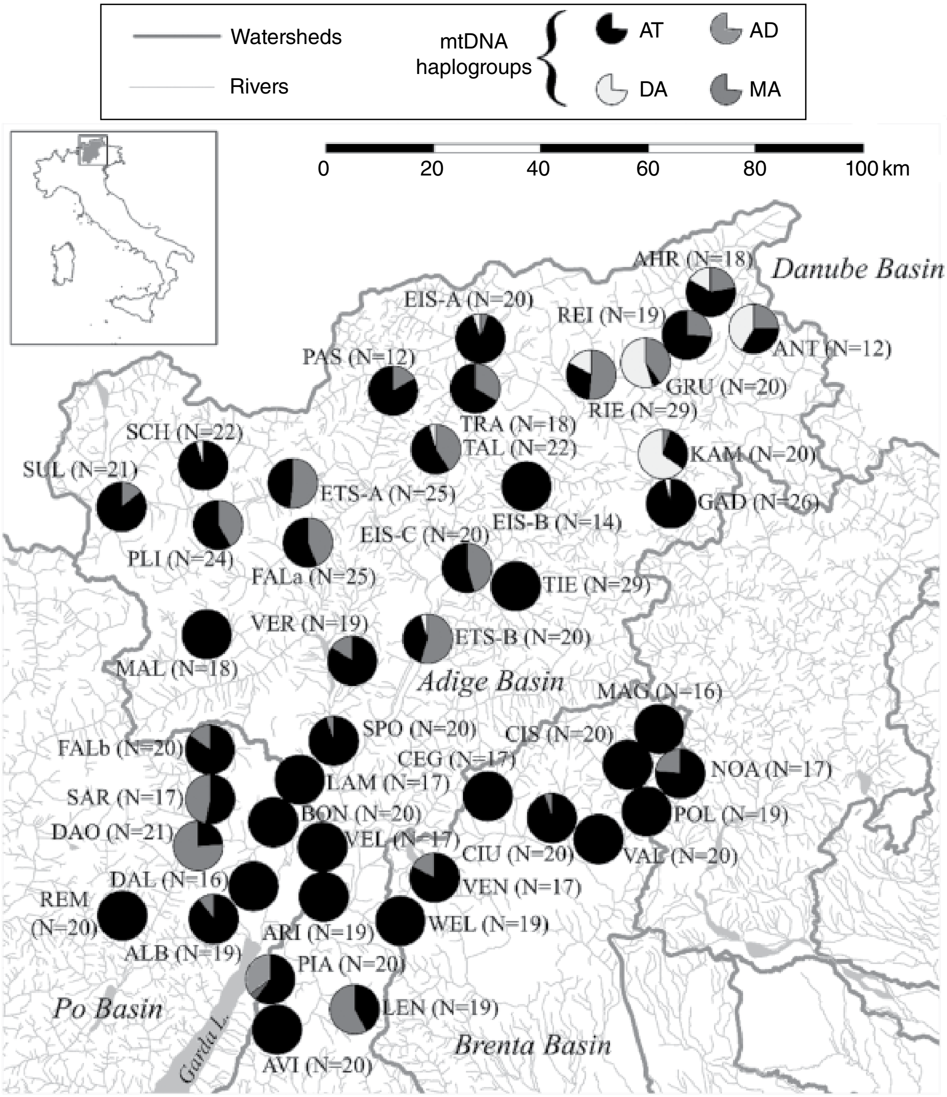

Figure 3.7 Map of the River Adige Basin (Northern Italy) indicating brown trout sampling sites investigated in Meraner *et al.* (2007, 2013a). For each site a pie chart is provided which displays the population frequency of major mtDNA control region lineages (AT, Atlantic; AD, Adriatic; DA, Danubian; MA, Marmoratus).

not only imported and directly stocked in Italian waters, but also held and bred locally. Thus, local Italian fish farms propagated and disseminated brown trout throughout the Italian peninsula, irrespective of the exotic, Atlantic, origin of these hatchery strains. Brown trout of native, ‘peninsular’ origin are still only exceptionally found in breeding strains of Italian fish farmers. Thus, beside some efforts to exclude specimens of exotic origin from supportive breeding programmes through genetic-marker assisted selection (Meraner *et al.*, 2008), stocking of exotic brown trout seems still to be more rule than exception in Italy.

The present-day distribution of exotic brown trout in Italy is highly alarming. Genetic imprints of 'Atlantic' brown trout were present in the overwhelming majority of genetic surveys dealing with Italian brown trout, with genetic fixation of exotic alleles having been observed in several sampling sites across Italian salmonid waters (see Figure 3.8 and Table 3.3). Most genetic studies pointed to a prevalence of allochthonous genetic variability in most analysed trout populations, with native genetic profiles being rare or

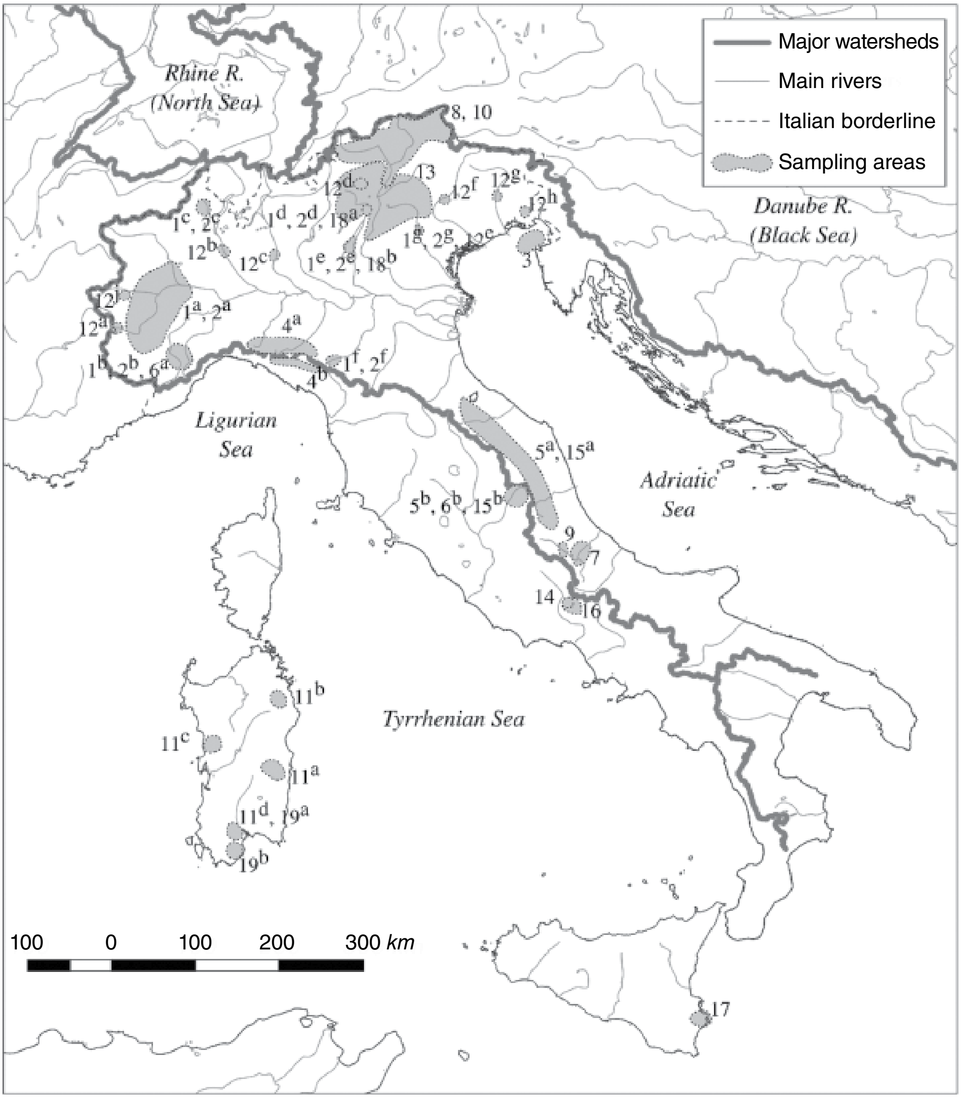

Figure 3.8 Geographical locations of genetic studies focusing on populations of the *Salmo* genus in Italy and offering a picture of anthropogenic genetic introgression from exotic brown trout of Atlantic origin (see Table 3.3 for main outcomes of the studies). Numbers refer to the molecular studies, while areas shaded in grey indicate the approximate spatial distribution of respective sampling sites. Major watersheds are evidenced by thick grey lines.

Table 3.3 Overview upon genetic studies focusing on the *Salmo* genus in Italy and investigating the anthropogenic genetic introgression from exotic brown trout of Atlantic origin on native taxa. References are presented together with the type of molecular marker used, sampling areas (see Figure 3.8 for locations), number of individuals and sampling sites included in the area, and percentages of exotic genetic contribution estimated with mitochondrial and nuclear markers.

	Genetic markers			**N of individuals (sites)***		**Exotic proportions**		
Reference	**mtDNA**	**ncDNA**	**Sampling sites**	**mtDNA**	**ncDNA**	**% Atlantic (mtDNA)**	**% Atlantic (ncDNA)**	**Code[§]**
Giuffra *et al.*, 1994	CR[a], cytb[b], ATPase[c]		Upper Po tributaries	83 (7)		9.64		1a
			Tanaro R.	47 (3)		2.13		1b
			Toce R.	10 (1)		0.00		1c
			Sarca R.	8 (1)		0.00		1d
			Garda L.	16 (1)		6.25		1e
			Panaro R.	27 (2)		40.74		1f
			Brenta R.	12 (1)		33.33		1 g
Giuffra *et al.*, 1996		allozymes	Upper Po tributaries		82 (7)		10.95	2a
			Tanaro R.		47 (3)		3.67	2b
			Toce R.		9 (1)		4.33	2c
			Sarca R.		8 (1)		31.33	2d
			Garda L.		15 (1)		0.00	2e
			Panaro R.		27 (2)		47.67	2f
			Brenta R.		10 (1)		3.33	2 g
Snoj *et al.*, 2002b	CR	LDH[d]	Piran and Coper Bay, Gulf of Trieste (Croatia/Italy)	11	11	100.00	86.36	3

(Continued)

Table 3.3 (Continued)

	Genetic markers			N of individuals (sites)*		Exotic proportions		
Reference	**mtDNA**	**ncDNA**	**Sampling sites**	**mtDNA**	**ncDNA**	**% Atlantic (mtDNA)**	**% Atlantic (ncDNA)**	**Code[§]**
Nonnis-Marzano *et al.*, 2003	16S[e]	LDH	Nure, Enza, Taro, Trebbia Rivers (Adriatic)	193 (12)	132 (9)	59.85	81.87	4a
			Magra, Vara, Serchio Rivers (Tyrrenian)	33 (4)	51 (6)	3.92	30.30	4b
Caputo *et al.*, 2004; Splendiani *et al.*, 2006	ND1, ND-3/4 and ND-5/6[f]	LDH	Marecchia R., Metauro R., Cesano R., Esino R., Chienti R., Tenna R. (Adriatic)	193 (15)	200 (15)	72.02	71.50	5a
			Nera R. (Tyrrhenian)	14 (1)	11 (1)	14.29	18.18	5b
Lucentini *et al.*, 2006		LDH	Stura di Demonte (Adriatic)		35 (1)		11.43	6a
			Monterivoso R., Nera R.(Tyrrhenian)		73 (2)		8.22	6b
Marconato *et al.*, 2006	cytb, 16S	LDH	Aterno, Pescara Rivers (including tributaries) (Adriatic)	103 (9)	103 (9)	7.77	26.70	7
Meraner *et al.*, 2007	CR		Adige River (including tributaries) (Trentino-Alto Adige)	672 (20)		47.9 (+10.4% DA)		8
Gratton *et al.*, 2007	CR	SSR[g], LDH	Aterno, Pescara Rivers (Abruzzo)	24 (1)	24 (1)	0.00	15.1 (SSR) −22.9 (LDH)	9
Meraner *et al.*, 2010		SSR	Adige River (including tributaries) (Trentino-Alto Adige)		328 (9)		mean Q missing	10

Sabatini *et al.*, 2011[#]	CR	LDH	Flumendosa R.	46 (2)		26.09% exotic and 69.56% hybrid		11a
			Posada R.	7 (1)		0% exotic and 71.43% hybrid		11b
			Scano Montiferru R.	5 (1)		20.00% exotic and 60.00 hybrid		11c
			Cixerri R.	46 (3)		0% exotic and 0% hybrid		11d
Pujolar *et al.*, 2011a	CR	SSR	Pellice R.	59 (1)	59 (1)	0	3.3	12a
			Ticino R.	39 (1)	39 (1)	7.69 (+23.08% DA)	18.5	12b
			Adda R.	11 (1)	11 (1)	9.09 (+45.45% DA)	33	12c
			Adige R.	102 (2)	102 (2)	0.98	5.1	12d
			Brenta R.	26 (1)	26 (1)	7.69	14.9	12e
			Piave R.	93 (1)	93 (1)	1.08	7.5	12f
			Tagliamento R.	50 (1)	50 (1)	(4.00% DA)	12.4	12g
			Isonzo R.	45 (1)	45 (1)	11.11	12.9	12h
			Chisone R.	23 (1)	23 (1)	100	99.5	12j
Meraner *et al.*, 2013a	CR	SSR	Adige, Brenta, Sarca, Chiese Rivers (Trentino-Alto Adige)	467 (25)	61 (3)	87	99	13
Querci *et al.*, 2013	CR	SSR, LDH	Fibreno River	81 (1)	74 (1)	0	1	14
Splendiani *et al.*, 2013	ND-5/6	LDH	Marecchia R., Metauro R., Esino R., Potenza R., Chienti R., Tenna R., Aso R., Tronto R. (Adriatic)	674 (35)	783 (35)	59.64	63	15a
			Nera R. (Tyrrhenian)	38 (1)	46 (1)	18.42	24	15b
Gratton *et al.*, 2013	CR	SSR, LDH	Posta Fibreno L. and Fibreno R.	48 (5)	105 (5)	0	9 (LDH) −2.8 (SSR)	16

(Continued)

Table 3.3 (Continued)

	Genetic markers			N of individuals (sites)*		Exotic proportions		
Reference	mtDNA	ncDNA	Sampling sites	mtDNA	ncDNA	% Atlantic (mtDNA)	% Atlantic (ncDNA)	Code[§]
Fruciano *et al.*, 2014	CR	LDH	Anapo R., Cassibile R., San Marco R., Tellesimo R.	100 (4)	188 (4)	5	22.87	17
Gratton *et al.*, 2014	CR	SSR, LDH	Sarca R., Garda L.	9 (1)	28 (1)	100	almost 100% exotic	18a
			Garda L. (S. carpio)	49 (1)	149 (1)	0	0	18b
Zaccara *et al.*, 2015	CR	LDH	Cixerri R.	201 (5)	206 (5)	0	0	19a
			Pula R.	44 (2)	47 (2)	0	0	19b

[*] Number of trout analysed in the respective genetic study. Values within brackets indicate number of sampling sites.

[§] see Figure 3.8.

[#] mtDNA and ncDNA data results cumulatively presented in the reference source.

[a] CR = Control region (D-loop)

[b] cytb = Cytochrome b gene

[c] ATPase = ATPase subunit VI gene

[d] LDH = LDH-C1 gene

[e] 16S = 16S rDNA gene

[f] ND1, ND-3/4 and ND-5/6 = NADH-dehydrogenase gene(s)

[g] SSR = Short sequence repeats; microsatellite marker(s)

even absent in lots of populations (see graphical overview for details). This is true for the Adriatic drainage basin in Northern and Central Italy. Within this macro-area, exotic Atlantic genetic imprints routinely appear in almost all salmonid waters, thus affecting both endemic marble trout populations in Southern Alpine waters, as well as in native brown trout, *S. cenerinus*, populations in Apenninic water courses.

The situation is comparably worrying in salmonid waters of the Tyrrhenian drainage basin, comprising the Italian peninsular as well as major islands, Sardegna and Sicily. In fact, available genetic surveys point to a widespread presence of 'Atlantic' hatchery brown trout alleles in riverine and lacustrine habitats, thus bringing into contact exotic hatchery trout with native species, such as *S. cettii* and *S. fibreni*.

Genetic consequences of stocking induced secondary contact of exotic hatchery and native wild trout can theoretically reach from scenarios of no genetic interaction, to limited hybridisation and, finally, to widespread genetic introgression and the formation of hybrid swarms. In the context of the interaction between exotic and native trout, empirical case studies for all these theoretical scenarios are described in the recent literature dealing with Italian trouts. Case studies of complete genetic isolation after stocking induced secondary contact are rare and mainly confined to lacustrine forms, i.e. *S. fibreni* from Lake Posta Fibreno (Central Italy; Tyrrhenian drainage) and *S. carpio* from Lake Garda (Northern Italy; Adriatic drainage).

Particularly strong selection regimes, resulting from adaptation to the lacustrine habitat and acting against genetic introgression, have to be assumed. Adaptation of spawning behaviour to the lacustrine habitat, deep water spawning for *S. carpio* and karstic spring spawning for *S. fibreni*, seem to act as potent prezygotic isolation mechanisms, completely preventing the intrusion of exotic alleles via genetic introgression.

Limited genetic introgression constitutes a frequent result of secondary contact among trout in Italy. It is the case for most analysed marble trout populations analysed so far, with varying introgression rates and exotic, hybrid and native trout being found within single water courses. Introgression clines are likely to resemble varying relative stocking pressure (i.e. the ratio between stocking rate and wild stock; *sensu* Hansen, 2002). In addition, environmental factors, such as hydrological conditions, can trigger levels of genetic introgression in Central Italian brown trout populations (Splendiani *et al.*, 2013).

Limited introgression could be a stable situation (i.e. hybrid zone) or represent a transitional state, which finally leads to complete genetic introgression and hybrid swarm formation. In the context of exotic brown trout, future long-term genetic monitoring is needed to disentangle both scenarios, but at least for marble trout incomplete isolation mechanisms seem to act against complete genomic extinction.

Finally, scenarios of complete replacement of native by exotic trout are commonplace, but probably underestimated in genetic surveys, since these generally do not focus on strongly impacted populations, but centre on 'conservable' populations, given mostly time- and resource limited project frameworks.

From Genetics to Practice: Deducting Management Units for Sustainable Conservation Planning

Native salmonid biodiversity on the Italian peninsula is extraordinarily complex, moulded by the interacting impacts of colonisation history, secondary contact and local adaptation. We extensively endorsed this statement in the preceding paragraphs of this chapter and highlighted that beyond the uppermost genetic bifurcation of the genus *Salmo* in Italy, given by ‘marble’ and ‘peninsular’ lineages, salmonid biodiversity is arranged by a complex interplay of metapopulations. This poses a particular challenge for future conservation planning, if we presume that sustainable conservation efforts have to target on the entire magnitude of genetic heterogeneity beyond taxonomic frameworks. Following Ehrlich’s (1988) statement that the loss of genetically distinct populations within species is as important a problem as the loss of the entire species, a conservation perspective limited to general taxonomic classifications is clearly insufficient for encompassing the entire salmonid biodiversity in Italy.

To that purpose, a purely taxonomic approach, as is generally the case for international, national and local red lists, is applicable only on two out of five taxonomic demes of *Salmo* in Italy, namely on *S. carpio* and *S. fibreni*; both taxa are endemic to single lake basins, being Lake Garda and Lake Posta Fibreno, respectively. The genetic results summarised in this chapter have convincingly proven that both species consist each of a single panmictic (meta)population, without further subpopulation structure (Gratton *et al.*, 2013, 2014; present work). Thus, each of these species represents one enlarged management unit and genetic endeavours in the frame of conservation plans, such as supportive breeding actions, are relatively straightforward.

The situation becomes considerably more complicated in the context of riverine salmonids in Italy. At present, all Italian marble trout populations traditionally group into a single taxonomic unit, being *S. marmoratus*. The genetic data extensively reviewed within this chapter clearly indicate, that a complex arrangement of metapopulations is present beyond monophylethic *S. marmoratus*. At least three hierarchical layers appear at the intraspecific level, accommodating for the distinction between Northern (Italy-Slovenia) and Southern (Bosnia-Montenegro) clusters, then metapopulations of major river drainages, separated since the last glaciation event and, finally, the distinction of differentiated population demes within single river drainages.

In this context, the presence of highly differentiated populations at the intra-drainage level present a particular challenge for conservation plans. Genetic studies have indeed indicated that even neighbouring populations, separated by less than 15 km of waterway distance (Pujolar *et al.*, 2011a) or between mainstream and headwater (Meraner *et al.*, 2010) are genetically highly divergent. Misguided rehabilitation measures, as supportive breeding not involving marker assisted selection, might erode the original genetic distinctness of locally adapted populations and artificially homogenise marble trout population diversity. Microgeographic population heterogeneity stems from allopatric fragmentation in the case of physically isolated populations, but likely also results from local adaptation and the evolution of sympatric isolation mechanisms, such as spawning site fidelity. In this view, the definition of microgeographic management units, based on high-resolution genotyping, is mandatory for preserving the full genetic heterogeneity and adaptive potential of the species.

Likewise, the dispersal of ‘peninsular’ brown trout population demes across numerous distinct river drainages from the Central to Southern Italian peninsula, must be underestimated by the two taxonomic units defined so far, being *S. cenerinus* and *S cettii*. In analogy to the considerations made for marble trout, future conservation plans concerning native Italian brown trout have to be based on microgeographic management units. As most of these brown trout populations inhabit mainly secluded headwaters, population differentiation should be even more pronounced than for marble trout, mostly confined to contiguous lowland rivers in Northern Italy.

However, a comprehensive genetic survey, encompassing ‘peninsular’ brown trout population diversity on a macrogeographic scale and indispensable as the scientific basis future conservation programs could be based on, is still completely lacking.

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4

Understanding the Brown Trout Population Genetic Structure in the Iberian Peninsula

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Origin and Phylogeographic Relations among Iberian Trout Populations

In the Iberian Peninsula, the brown trout (*Salmo trutta*) is currently restricted to freshwater systems and inhabits headwater streams, but an extension of the downstream distribution occurred during the glacial periods (Muñoz & Casadevall, 1997). Although apparently marginal, trout populations in these areas harbor a significant legacy of the species' genetic diversity (Garcia-Marin & Pla, 1996; Antunes *et al.*, 2002; Presa *et al.*, 2002; Vera *et al.*, 2010a). Because freshwater fish populations survived glacial periods in the southern European region, the Iberian Peninsula (as with the Balkan region) represents a reservoir of diversity in brown trout and related *Salmo* species (Suarez *et al.*, 2001; Snoj *et al.*, 2002; Susnik *et al.*, 2007). Many populations in these territories are likely the result of complex evolutionary histories and processes involving secondary contacts between ancient lineages and local adaptations (Antunes *et al.*, 2002, Sanz *et al.*, 2002; Snoj *et al.*, 2008; Vera *et al.*, 2010a). The high degree of brown trout genetic diversity in the Iberian Peninsula agrees with the persisting viability of the species in these river basins.

Salmo trutta and other phylogenetically-related *Salmo* species hypothetically colonized and diverged in Europe following the Pliocene–Pleistocene climatic cooling of the region (Shedko *et al.*, 2012). Nevertheless, salmonids are absent from tertiary fish fossil strata, including those from the Pliocene period, that were collected in the Iberian Peninsula (De la Peña, 1995). Until now, the older *Salmo* remains in the Iberian Peninsula consist of teeth dated in Middle Pleistocene (400 Kya) and collected in the Sima de los Huesos site at Atapuerca, Spain (Cuenca-Bescos *et al.*, 2001).

Disentangling the phylogenetic relationships and biogeography of brown trout throughout all its native range has been and continues to be a major focus of scientific inquiry and debate (Bernatchez, 2001; Presa *et al.*, 2002; Cortey *et al.*, 2004; 2009; Lerceteau-Köhler *et al.*, 2013; Vera *et al.*, 2010a; 2015). A recent review on European

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trout suggests splitting the species *S. trutta* into a large number of morphologically differentiated taxa (Kottelat & Freyhof, 2007). According to some authors, *S. trutta* species would be circumscribed in the Iberian Peninsula to the rivers of the Cantabrian coast and Galicia, and the European Mediterranean lineages could consider separate, yet undescribed, species (Freyhoff & Brooks, 2011). Allozyme variation by fixed-allele distinction at the *LDH-C** locus clearly distinguishes southern European trout populations from those inhabiting postglacially colonized areas (Hamilton *et al.*, 1989), but the worldwide acceptable primary source of molecular divergence of current trout lineages has been the phylogenetic architecture and diversity expressed by deep mitochondrial DNA patterns of variation (mtDNA, reviewed in Chapter 3). Four mitochondrial lineages - Mediterranean (ME), Adriatic (AD), Atlantic (AT), and Duero (DU) – are present in native Iberian populations (Suarez *et al.*, 2001; Cortey *et al.*, 2004, 2009; Vera *et al.*, 2010a), whereas the AT and DU lineages are mainly found in Atlantic Iberian rivers and the ME and AD are found in the Mediterranean basin.

In the Atlantic Iberian basins, the AT and DU lineages exhibit phylogeographic boundaries that are associated with major drainage systems (Figure 4.1), with the AT lineage predominating most of these basins. In the Duero River basin (98,160 km^2), two ichthyological areas have been defined. The Portuguese portion of the basin is characterized by the presence of anadromous fish species, and the Spanish Duero Valley is characterized by the presence of resident ones (Doadrio *et al.*, 1991). The DU lineage was first described from trout collected in the inner Spanish tributaries of the Duero River basin (Vera *et al.*, 2010a). The Duero brown trout also shows genetic distinction at protein-coding loci, with differences in alleles that are nearly fixed at the *sMDH-B1,2**, *βGLUA** and *PEPLT** loci (Sanz *et al.*, 2000; Bouza *et al.*, 2001), and displays spatial heterogeneity at microsatellite loci (Martinez *et al.*, 2007). Morphological differentiation suggesting adaptations to particular feeding and flow regimes of the Duero brown trout has also been described (Hermida *et al.*, 2008). Analyses of the ribosomal DNA ITS1 locus have shown the Duero lineage is related most closely to a Mediterranean group (rMEDA) that colonized the southern rivers of the Iberian Peninsula (Figure 4.1). According to the pattern of diversity displayed by this nuclear marker, the DU lineage is phylogenetically close to the Danubian and marbled trout, *S. marmoratus* (Presa *et al.*, 2002; Martinez *et al.*, 2009). The rMEDA group is also detected in samples collected from the Guadalquivir River and Eastern Pyrenean Rivers; however, the mitochondrial lineages AD and ME predominate in these basins. Thus, the above evidence suggests, but does not confirm, that the Duero brown trout could be the vestige of an ancestral brown trout colonization of the Iberian Peninsula, pre-dating the expansion of the currently more abundant AT (in the Atlantic) and AD and ME (in the Mediterranean) brown trout lineages (see Chapter 3). The replacement of older trout colonizers by more recent expansions has also been shown by evolutionary changes and the distribution of the transferrin gene alleles (Antunes *et al.*, 2002). These authors considered an Asian origin of the species and a first trout expansion favoring colonization of the Danube River and arriving eastward through the Mediterranean basin until reaching the Iberian Peninsula. A second trout expansion involved the colonization of the Atlantic Iberian Rivers through long-distance dispersal from the Adriatic region. Finally, a third expansion, once again from within the Mediterranean basin, affected most of the current European range but with lesser penetration in previously well-established populations of the South European basins. It is yet unclear how the above scenarios depicted by transferrin alleles are consistent with the

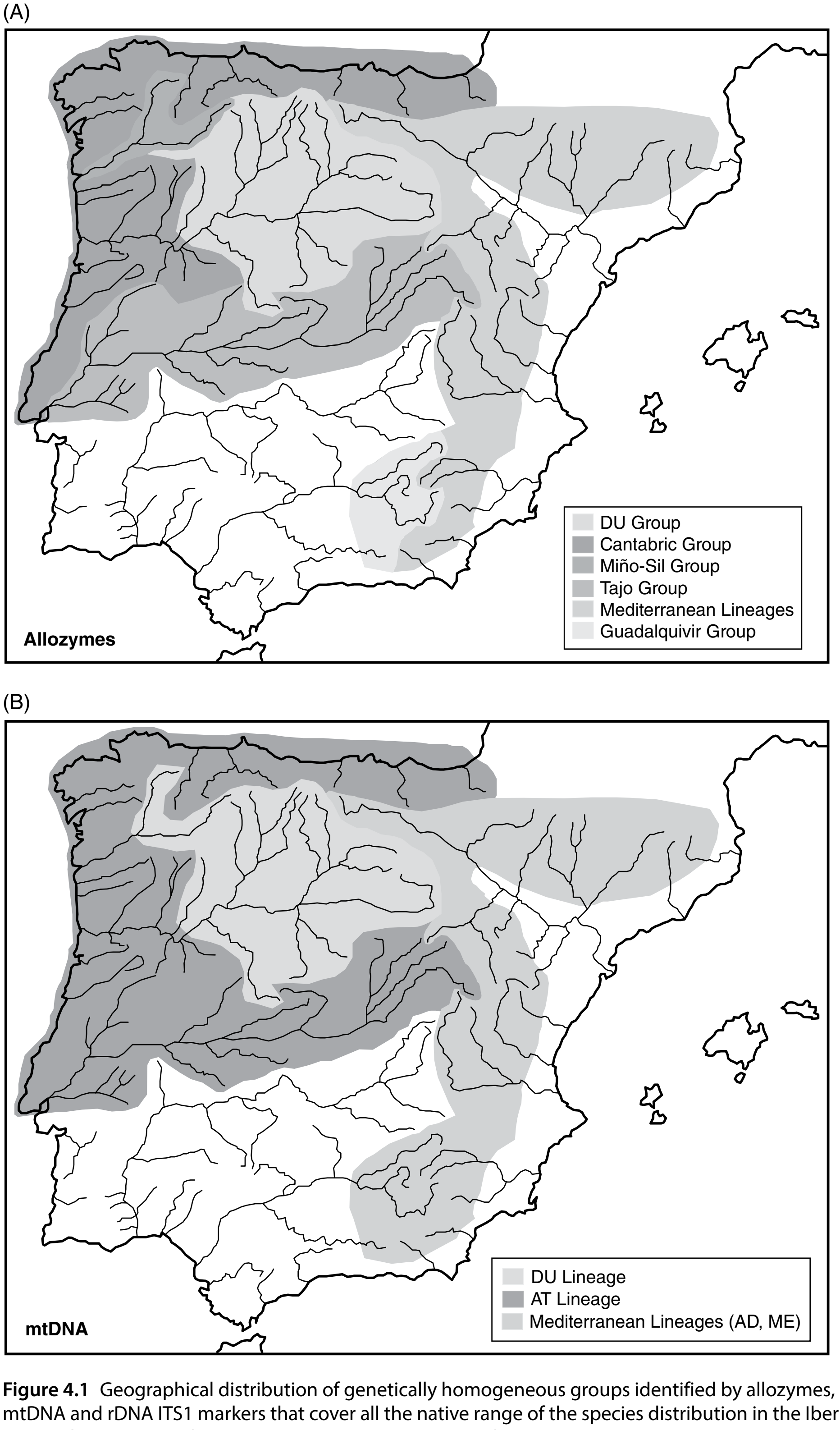
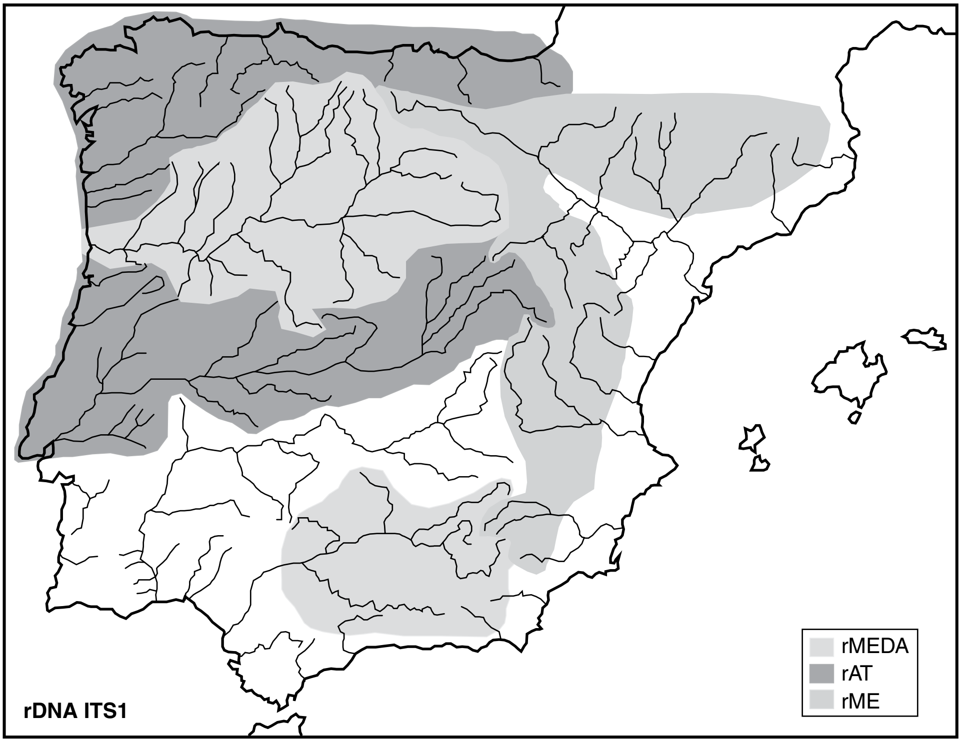


Figure 4.1 Geographical distribution of genetically homogeneous groups identified by allozymes, mtDNA and rDNA ITS1 markers that cover all the native range of the species distribution in the Iberian Peninsula. A: Sanz *et al*., 2000; B: Cortey, 2005; C: Presa *et al*., 2002.

(C)



A From Sanz et al. 2000
B From Cortey 2005
C From Presa et al. 2002

Figure 4.1 (Continued)

current distribution of mtDNA lineages. Differentiated modes of evolution and transmission among marker sets may confuse congruence between the nuclear and mitochondrial phylogeographic patterns. For example, because mtDNA is haploid and maternally transmitted, it is expected to exhibit a fourfold lower effective population size (Ne) than autosomal nuclear loci (Birky *et al.*, 1989). Lower Ne should lead to higher rates of mtDNA lineage sorting divergence (Hoelzer, 1997).

The time of divergence of the AT and DU groups was dated to the mid-Pleistocene at 574 Kya (Vera *et al.*, 2010a). However, current populations of the native brown trout with the AT lineage, which have been observed in the Portuguese part of the Duero River basin and in the Tajo River basin, probably originated from a glacial trout expansion at the beginning of the Würm glacial period 115 Kya. Native AT lineages observed in the Cantabrian and Galician River basins were the results of an older southward expansion of European trout populations that likely occurred during the Riss glacial period, 200 Kya (Cortey *et al.*, 2009). Recent analyses have detected isolated populations in the upper course of the River Miño basin (Galicia, NW Iberian Peninsula) where the DU haplotypes are fixed (Bouza *et al.*, 2008; Vera *et al.*, 2015), indicating a wider distribution of the DU lineage in the past. The segregation of the Atlantic and Duero trout at the outlet and in the inner sections of the Miño-Sil River, respectively, had previously been indicated with allozymes (Sanz *et al.*, 2000) and greatly resembled observations made in the Duero River (Vera *et al.*, 2010a). In addition, the DU haplotypes in this basin likely resulted from an older trout expansion pre-dating those of the AT lineage. In fact, the most frequent DU-Galician haplotypes are absent in the Duero drainage and are thus endemic to the Galician drainages. The divergence time between these Galician DU haplotypes and the ancestral DU group detected in the Duero River was estimated as 110–120 Kya, suggesting isolation since the interglacial period before the present one (Vera *et al.*, 2015). This time of divergence is a bit older than the population expansion that is related to the presence of the native AT haplotypes in these basins (Cortey *et al.*, 2009), supporting the long-time presence of the DU lineage in some Galician drainages. The Duero brown trout have avoided hybridization, both with the AT lineage that currently occupies the lower course of the Duero River (Bouza *et al.*, 2001) and with hatchery stocks (Almodóvar *et al.*, 2006). A sharp variation in the allele frequencies has been observed between the two groups in the contact zone inside the basins (Bouza *et al.*, 2001; Martinez *et al.*, 2007, 2009), and selection processes favoring the DU lineage in the inner part of the basins could explain the longtime persistence of this lineage in these Iberian rivers (Martinez *et al.*, 2007; 2009; Vera *et al.*, 2010a).

The mitochondrial AD lineage was found in Iberian rivers from the Mediterranean basin and coexists with the ME lineage (Cortey *et al.*, 2004). The AD lineage predominated among the trout populations of South Iberia, even in the Guadalquivir River, which flows into the Atlantic (Machordom *et al.*, 1999; Sanz *et al.*, 2006). This lineage likely expanded throughout the Mediterranean 170 Kya ago, somewhat parallel to the expansion of the ME lineage. These AD and ME lineage expansions originated, respectively, from the eastern and western Mediterranean basins, and extensive secondary contact between the lineages occurred in most of the Mediterranean rivers of the Iberian Peninsula (Cortey *et al.*, 2004). Nevertheless, the presence of the ancient rMEDA group of the ribosomal DNA ITS1 in the Andalusian river basins (including the Guadalquivir River) and in some Pyrenean basins (Figure 4.1) confirmed the presence of brown trout in the Iberian Mediterranean river basins since older colonizations, likely in parallel to the establishment of an ancestral trout that colonized the Duero River basin.

Brown Trout (*Salmo trutta*) Population Structure Among and Within Iberian Rivers

As indicated above, at least four evolutionary brown trout lineages naturally colonized the Iberian rivers and expanded their distributions across the Iberian Peninsula in a complex pattern that resulted from drainage isolation, secondary contacts between trout lineages, and recent historical releases of foreign stocks (Sanz *et al.*, 2006). Meanwhile, single clades of the AT lineage colonized most of the Atlantic rivers; ancestral populations of DU lineage are present inland in a few of these rivers (Figure 4.1). Otherwise, the Mediterranean and southern Iberian basins were colonized by the AD and ME lineages. However, the pattern of genetic relatedness among the Mediterranean populations does not follow the hierarchical structure of the haplotype genealogy and the reciprocal monophyly expected from allopatric models of lineage isolation.

The observed population structure in these basins shows better agreement with populations that recently expanded during the last glacial period (Cortey *et al.*, 2004). Early studies on population structure that were undertaken 20 years ago using allozyme variation already detected high levels of population differentiation among Iberian brown trout populations ($F_{ST} > 0.600$, Table 4.1); these levels of population differentiation are

Table 4.1 Patterns of population structure at broad Iberian and some regional scales depicted in the Iberian Peninsula by distinct molecular markers (Allozyme, mtDNA RFLPs, mtDNA Control Region sequences, and microsatellites). N Loc: Number of localities analyzed, ST: proportion of population differentiation (F_{ST} or ϕ_{ST}).

Region	Marker	N Loc.	ST	Source
Iberian	Allozyme	4	0.615	1
Iberian	Allozyme	24	0.640	2
Iberian	mtDNA RFLPs	58	0.795	3
Atlantic basins	mtDNA CR seq	56	0.900	4
Atlantic basins	Allozyme	23	0.645	5
Atlantic (Portugal)	mtDNA CR seq	7	0.350	6
Cantabrian Rivers	Allozyme	18	0.215	7
Cantabrian Rivers	Allozyme	3	0.604	5
Galician Rivers	Allozyme	41	0.268	8
Galician Rivers	msats	30	0.173	9
Galician Rivers	msats	6	0.048	10
Duero River	Allozyme	62	0.455	11
Duero River	msats	16	0.348	12
Duero River	mtDNA CR seq	21	0.788	13
Duero River (inner)	Allozyme	5	0.150	14
Duero River (inner)	Allozyme	9	0.062	5
Tagus River	Allozyme	8	0.228	14
Tagus River	Allozyme	7	0.398	5
Southern basins	Allozyme	8	0.528	15
Southern basins	mtDNA CR seq	8	0.948	15
Mediterranean basins	Allozyme	36	0.615	16
Mediterranean basins	mtDNA CR seq	30	0.723	17
Eastern Pyrenean	Allozyme	13	0.396	18
Eastern Pyrenean	msats	13	0.281	19
Eastern Pyrenean	mtDNA CR seq	41	0.635	20

1: García-Marín *et al.*, 1991; 2: García-Marín & Pla, 1996; 3: Machordom *et al.*, 2000; 4: Cortey *et al.*, 2009; 5: Sanz *et al.*, 2000; 6: Weiss *et al.*, 2000; 7: Moran *et al.*, 1995; 8: Bouza *et al.*, 1999; 9: Vilas *et al.*, 2010; 10: Campos *et al.*, 2007; 11: Bouza *et al.*, 2001; 12: Martínez *et al.*, 2007; 13: Vera *et al.*, 2010; 14: Machordom *et al.*, 1999; 15: Sanz *et al.*, 2006; 16: Sanz *et al.*, 2002; 17: Cortey *et al.*, 2004; 18: Araguas *et al.*, 2004; 19: Fernández-Cebrián *et al.*, 2014; 20: Vera, 2006.

the largest reported for the species within a European country (revised in Garcia-Marin *et al.*, 1999a). The distinct nature of the current lineages inhabiting the Atlantic and Mediterranean rivers mostly contributes to such divergence (García-Marín & Pla, 1996; Machordom *et al.*, 2000). However, large population divergence within these two major watersheds also contributes significantly to the amount of total diversity (Table 4.1). Interestingly, the distribution of genetic diversity within these two major Iberian watersheds resulted in contrasting patterns of population structure at a macrogeographic scale, despite showing similar levels of total diversity ($H_T = 0.072$, Table 4.1). In the Atlantic watershed, a higher proportion of divergence was detected between (61%) than within the river basins (39%) (Sanz *et al.*, 2000). Alternatively, the proportion of divergence within river basins (~51%) was significantly higher than the divergence among the river basins in the Mediterranean watershed (Sanz *et al.*, 2002).

In the Atlantic, greater opportunities for fish exchange among the rivers including large anadromous populations since historical times have resulted in a model of isolation by distance in the Cantabrian and Galician rivers (Moran *et al.*, 1995; Bouza *et al.*, 1999; Ayllón *et al.*, 2006). Nevertheless, even at a microgeographic scale, substantial divergence has been reported among resident trout populations inhabiting the Atlantic rivers flowing to the Cantabrian Sea (Table 4.1). This pattern is consistent with the maintenance of isolated relict populations resulting from successive waves of colonization by distinct clades of the AT lineage during the southward expansions of trout populations during the quaternary glaciation (Cortey *et al.*, 2009). Beyond the large genetic differences observed between geographical close population in the contact zone of DU and AT lineages, low divergence is observed among Spanish populations located in the inner part of the Duero river basin (Machordom *et al.*, 1999; Sanz *et al.*, 2000) or among the Portuguese populations (Antunes *et al.*, 2001). In the Tajo River, several successive hydrographic captures during the Pleistocene have altered the basin (Scotti *et al.*, 2014; Giachetta *et al.*, 2015), and have affected the distribution of its fish fauna (e.g., Carmona *et al.*, 2002; Filipe *et al.*, 2009). Most of the trout populations in this basin resulted from the colonization by a singular cluster of AT lineage during the last glacial period, but in some of the Tajo River tributaries, hydrographical captures of Duero River streams introduced the DU lineage (Cortey *et al.*, 2009). Despite the common origin of the present trout populations in the Tajo basin, the large F_{ST} values observed between populations suggest strong isolation as observed in the southern Iberian and Mediterranean rivers (Table 4.1).

In contrast to the general pattern of population structure observed in the Atlantic rivers, in the Mediterranean ones, even within close populations, large genetic differences are explained by the isolation of local populations and the patchy random distribution of major trout lineages (Cortey *et al.*, 2004). Pure and admixed populations of the ME and AD lineages were observed within all the river basins, resulting in a pattern of population relatedness associated with the ancestry of the haplotypes found within each location, rather than with the hydrological network system (Sanz *et al.*, 2002). This pattern is extremely marked among populations in the Pyrenees, where the better Mediterranean trout populations of the Iberian Peninsula are preserved (Almodovar *et al.*, 2012). In this area, low water levels in the rivers during the summer period reduce gene flow between populations along river basins, resulting in increased genetic differentiation between neighboring populations (Cortey *et al.*, 2004, Araguas *et al.*, 2004, Vera *et al.*, 2010b, Fernández-Cebrián *et al.*, 2014). A kin-biased spatial distribution, which implies a very limited dispersal of related fish, has been indicated in a demographic study of Mediterranean brown trout (Sanz *et al.*, 2011). The local geographical structure of Mediterranean trout is therefore supported by small populations that occasionally exchange individuals. Such exchanges between neighboring demes are essential for preserving diversity levels and limiting the effects of the drift expected in isolated small populations. Each deme is distributed over a few kilometers within the river streams and is connected to neighboring ones by the greater tendency of individuals to disperse with age (Vera *et al.*, 2010b; Sanz *et al.*, 2011). A similar situation has been reported among northern European brown trout suffering similar conditions (Oestergaard *et al.*, 2003). In a similar way, reduced populations of anadromous trout in some Iberian Atlantic rivers are maintained through individuals migrating from neighboring rivers each year, and such migrants also stabilize the local genetic composition (Ayllón *et al.*, 2006).

Current Factors Disturbing the Regional Population Structure

Several worldwide threats to freshwater ecosystems such us Global Climatic Change, watershed modifications, habitat loss, and the transfer of alien stocks are currently modifying the historical local and regional patterns of population structure among Iberian trout populations. The southern and Mediterranean Iberian basins are mostly affected by the large interannual variability in precipitation and river flow regimes, with large disparities existing between wet and dry years (Trigo *et al.*, 2004). This variability generates extreme conditions in the habitat that threaten the integrity and persistence of trout populations (Sanz *et al.*, 2006; 2011; Almodovar *et al.*, 2012; Vera *et al.*, 2013) and currently restrict trout populations to upstream locations in southern and Mediterranean basins. In Iberian populations, trout recruitment densities are often below the carrying capacity of the streams (Nicola *et al.*, 2008, 2009), and spawning periods are longer in the southernmost populations permitting offspring emergences during optimal seasonal environmental conditions (Górtazar *et al.*, 2007, Larios-López *et al.*, 2015). Extremely low effective population sizes, ranging from 5 to 32 individuals, have been estimated in many Mediterranean streams with high environmental instability (Sanz *et al.*, 2011). Climate change scenarios developed for the Iberian Peninsula point to a general increase in the risk of summer droughts with increasing variability in water supplies (Ragab & Prudhomme, 2002; Gibelin & Deque, 2003; Sumner *et al.*, 2003). Within Iberian rivers, the ongoing climate change will impede the connectivity between populations dramatically, stressing their isolation, which in turn will lead to a greater risk for local extirpations during this century (Almodovar *et al.*, 2012). Even prediction models that consider the adaptive response of brown trout toward climate change indicate a high probability of extinction for the Mediterranean populations (Ayllon *et al.*, 2016).

Natural barriers that restrict gene flow and further increase genetic divergence between trout populations have been described elsewhere in the Iberian Peninsula (Bouza *et al.*, 1999; Campos *et al.*, 2006). Similarly, dams contribute to river fragmentation and promote isolation among fish populations, with an asymmetric model of migration favoring downstream connectivity (e.g., Blanchet *et al.*, 2010). As a result, upstream populations lose their genetic diversity and the overall population relationships within basins are disrupted in long-term dammed drainages (Horreo *et al.*, 2011). Nevertheless, other factors such as natural, stepwise, upstream, river colonization may explain the above patterns of genetic diversity (Paz-Vinas *et al.*, 2015). The restoration of natural connectivity along the river should reestablish natural patterns of genetic diversity in brown trout as observed in salmon populations (Perrier *et al.*, 2014). Nevertheless, the restitution of connectivity may be detrimental to remnant native populations isolated upstream by favoring upstream dispersal of alien stocks or invasive species (Rahel, 2007). Homogenization of fish communities upstream and downstream after dam removal may prove an unintended outcome warranting attention and appropriate preventative actions (Kornis *et al.*, 2015).

Finally, trout populations in the Iberian Peninsula have suffered introgressive hybridization with divergent alien hatchery stocks of central European origin commonly used to reinforce wild populations until recent times (García-Marín *et al.*, 1999; Aparicio *et al.*, 2005; Almodovar *et al.*, 2006). The availability of diagnostic genetic markers to differentiate between northern European brown trout stocks and the native Iberian populations has allowed monitoring of the genetic impact of fish releases involving these foreign stocks (e.g., Garcia-Marin *et al.*, 1991; Martinez *et al.*, 1993; Arias *et al.*, 1995). These markers have demonstrated that released hatchery fish have successfully spawned with native fish, and a variable degree of hybridization has been detected in many of the affected populations, particularly when hatchery fish are not stressed by fishing shortly after their release (García-Marín *et al.*, 1998). In addition, other abiotic factors contribute to the survival and admixture of released hatchery fish in Iberian basins, and introgression tends to be higher in stocked localities with fertile waters and stable discharge (Almodovar *et al.*, 2006). Despite the large amount of hatchery releases in all the Iberian rivers, genetic markers showed little contribution of hatchery individuals in the rivers flowing into the Atlantic (Moran *et al.*, 1991; Antunes *et al.*, 1999, 2001; Arias *et al.*, 1995; Madeira *et al.*, 2005; Almodovar *et al.*, 2006; Santos *et al.*, 2006), but significant introgression was observed among many of the Mediterranean populations (García-Marín *et al.*, 1998; Araguas *et al.*, 2004; Sanz *et al.*, 2000; 2002; 2006). Genetic changes produced by hatchery fish include incremental changes in local diversity levels by the introduction of foreign alleles and the homogenization of gene pools between populations (Figure 4.2), which alters phylogeographic integrity among native populations (Araguas *et al.*, 2004). Perpetuation of such practices would lead to the whole replacement of the native population structure that is currently related to the natural hydrographical hierarchy (Machordom *et al.*, 1999; Fernández-Cebrián *et al.*, 2014).

Management and Conservation of Iberian Trout

Due to the brown trout's important socioeconomic value for recreational fisheries (García de Jalón & Schmidt, 1995) in Iberian and other European countries, the primary management strategy to maintain or improve degraded wild trout populations to support fisheries has been the extensive release of fish from cultured stocks. Until recently, most of the Spanish hatchery stocks had a common source of eggs and fry imported from central Europe (mostly Denmark and Germany) long ago, and hence, these stocks belong to a genetically different trout linage (Garcia-Marin *et al.*, 1991; Martinez *et al.*,

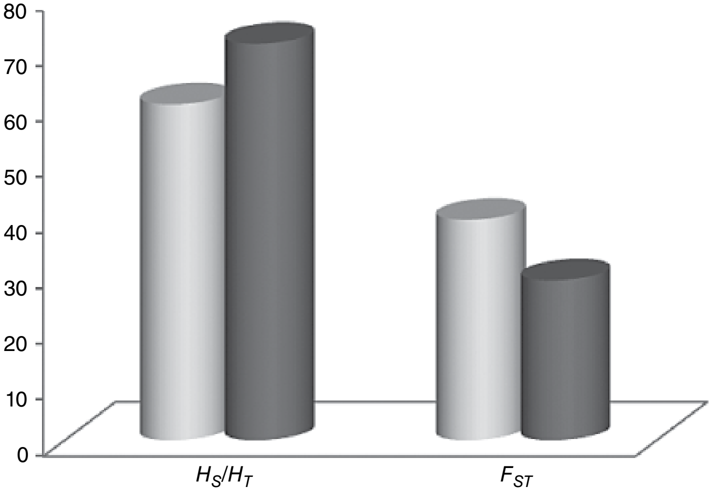


Figure 4.2 Percentage of the gene diversity within (H_S/H_T) and between (F_{ST}) populations, estimated from Pyrenean brown trout in1993 (light grey) and in 1999 (dark grey).

1993; Machordom *et al.*, 2000). Several negative consequences on native populations have been reported from such stock transfers, including the reduction of effective population size in wild populations and the loss of local genetic diversity, which lead, in some cases, to the complete replacement of local native populations (Araguas *et al.*, 2004; 2017; Sanz *et al.*, 2006). These problems are shared with other salmonid species and countries (Brown and Day 2002; Arlinghaus & Mehner, 2005; Laikre *et al.*, 2008; Baric *et al.*, 2010; Cowx *et al.*, 2010), where for several decades, hatchery-reared fish have either escaped or have been released deliberately into wild populations (Allendorf *et al.*, 2001; Valiquette *et al.*, 2014). These reared individuals represent a major threat to the preservation of local genetic diversity, which is crucial to conserve the evolutionary potential of the species (Ryman *et al.*, 1995a; Hurt & Hedrick 2004; Utter, 2004).

Different studies provide evidence of the erosion of native populations due to the introduction of hatchery non-native individuals in the Iberian rivers. In the Asma River in northwestern Iberia (Arias *et al.*, 1995) and in the Irati River in the western Pyrenees (Blanco *et al.*, 1998), the introgression rate of exogenous genomes into the native gene pool was estimated to be as great as 5% per year. Similar results were obtained at the Riutort Creek, a small tributary of the Llobregat River in the eastern Pyrenees (García-Marín *et al.*, 1999b). However, Araguas *et al.* (2004) screened 13 sites in the eastern Pyrenees and detected an introgression rate of 1% per year at a regional scale. In addition, hatchery releases have directly or indirectly resulted in the introgression of native populations in heavily fished or in protected areas. For instance, in a survey along the Noguera de Tor River (in the Ebro River basin), García-Marín *et al.* (1998) detected hatchery alleles in all sampled locations, although the most introgressed locations were in the streams inside the *Aigüestortes i Estany de Sant Maurici* National Park, an unstocked area, which has been protected since 1955. Such observation suggests that released hatchery trout in locations sustaining recreational fisheries may disperse to adjacent protected areas, with the protected areas operating then as a reservoir of hatchery genes (Araguas *et al.*, 2004). Similar results were observed in the never-stocked Riutort Creek, a tributary of the Llobregat River (García-Marín *et al.*, 1999), which undergoes extensive yearly stocking. Irrespective of its rate, introgression leads to the homogenization of wild populations, as observed in central Spain, where the ancestral pattern of genetic variation that distinguishes Tajo and Duero trout is being blurred (Machordom *et al.*, 1999). Similarly, in the southern Iberian Peninsula, the native pattern of the relation between the Atlantic and Mediterranean brown trout is threatened by hybridization with hatchery stocks (Sanz *et al.*, 2006). Disappointingly, the *LDH-C*90* allele, fixed in hatchery stocks but absent in undisturbed Iberian wild populations, is now almost fixed in some Mediterranean trout populations (Madeira *et al.*, 2005; Araguas *et al.*, 2008; Vera *et al.*, 2013; Araguas *et al.*, 2017) indicating a near complete replacement of ancestral lineages with introduced or introgressed stocks.

On the other hand, in spite of the extensive stocking along Iberian rivers, the genetic impact of these releases varied at local and regional scales, often in an unpredictable way. For instance, limited introgression has been observed in some stocked Atlantic Rivers (Moran *et al.*, 1991, Antunes *et al.*, 1999; 2001, Santos *et al.*, 2006). Differences in the amount of introgression have been related to environmental conditions and ecological interactions at local and regional scales (Almodóvar *et al.*, 2001; Madeira *et al.*, 2005; Almodóvar *et al.*, 2006; Santos *et al.*, 2006; Vera *et al.*, 2013). Because trout recruitment densities are often below the carrying capacity of the Spanish streams (Nicola *et al.*, 2008, 2009), releases could be more successful in years of low natural recruitment density. In addition, hybridization between stocked and wild trout also seems to occur more frequently in resident populations than in anadromous ones (Ruzzante *et al.*, 2004; Utter, 2004), a fact that could somewhat explain the low impact of stocking in North Iberian Atlantic rivers where anadromous trout occur. Local management and angling pressure also contribute to introgression differences at a regional level because hatchery trout reportedly are more vulnerable to angling than native fish (García-Marín *et al.*, 1998; Mezzera & Largiader, 2001; Baer *et al.*, 2007; Harkonen *et al.*, 2014).

Overall, current stocking strategies and practices have failed to provide a beneficial long-term effect (i.e., sustained viability) on the restoration of overexploited trout populations, and the continuous need for hatchery releases provides the strongest evidence for this failure (Araguas *et al.*, 2009). Based on the above reported negative consequences of stocking and taking into account the economic importance of brown trout as recreational fisheries promoting local tourism, the authorities responsible for its management in Spain are developing several new management approaches that will balance the harvest and conservation of wild genetic resources, such as creation of genetic refuges; supplementation with native stocks; and release of sterile triploid trout.

Genetic Refuges

Since 1997, to improve native trout populations, the Autonomous Government of Catalonia created genetic refuges in the headwaters of some rivers in the eastern Pyrenees, where the brown trout displayed reduced or no evidence of introgression of hatchery alleles (Figure 4.3). In the genetic refuges, hatchery releases were completely banned, but pre-existing recreational fishing activities were permitted. Allowance of fishing activities distinguishes these refuges from the genetic sanctuaries defined by

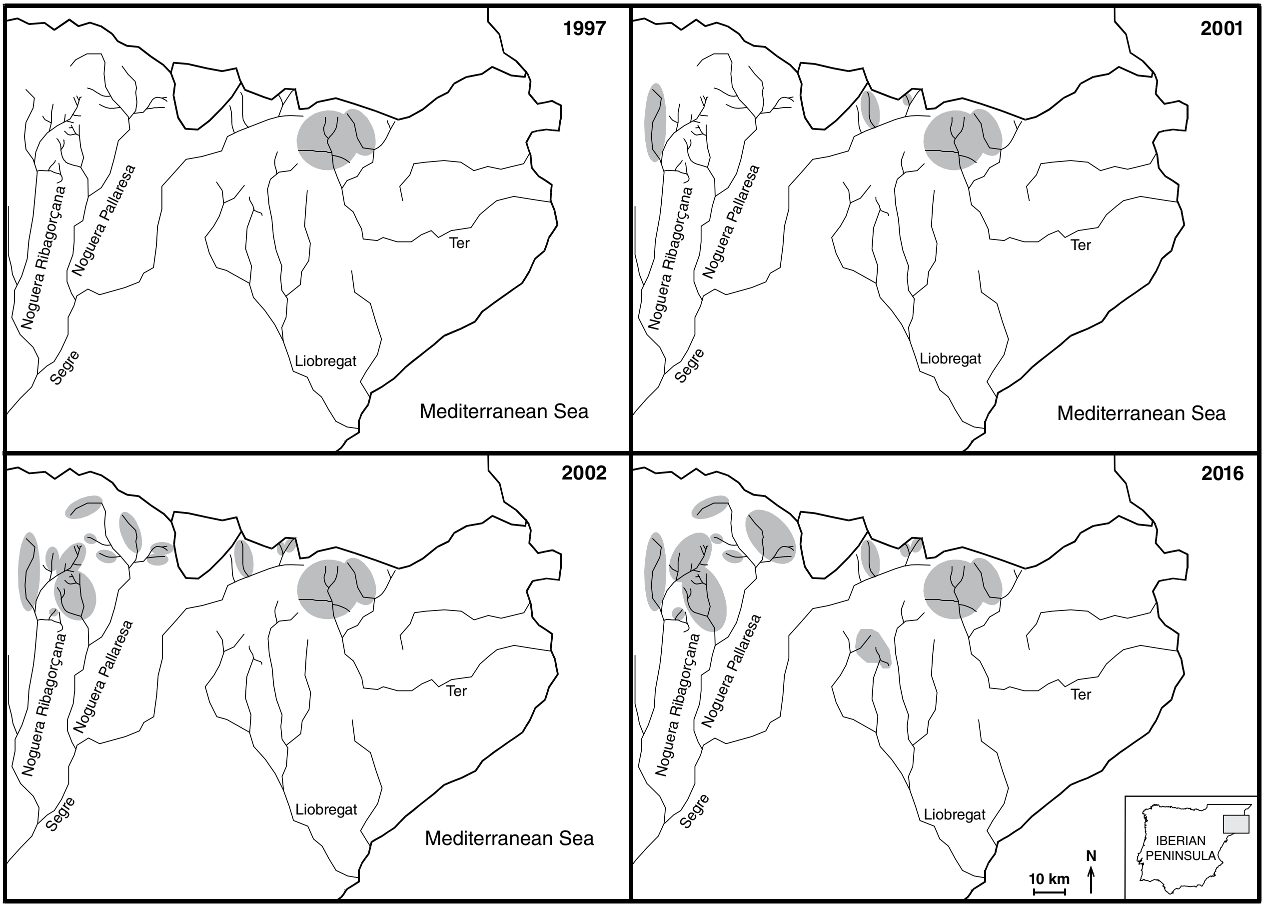


Figure 4.3 Genetic refuges created in Catalonia (Iberian Peninsula) from 1997 to 2016.

Poteaux & Berrebi (1997) in French rivers, where neither stocking nor fishing is permitted. In addition, the stocking ban has been accompanied with global measures to promote recruitment in self-sustaining fisheries; these measures include a daily harvest limit, an increase in minimum length, and the transformation of some river stretches into 'catch-and-release only' areas (Araguas *et al.*, 2008; 2009).

The efficiency of genetic refuges to preserve or recover the native integrity of wild trout populations has been assessed through genetic surveys separated by short periods. These surveys indicated that the establishment of the genetic refuges did not reduce the average regional abundance of the foreign stock alleles, although this policy of genetic refuges stopped the increase of the regional amount of introgression observed before its implementation. At the same time, the creation of genetic refuges in all basins maintained major trends in the native pattern of population structure (Araguas *et al.*, 2008; 2009; 2017). Similar results were detected in trout populations in France, where the policy of genetic refuges was established later (Caudron *et al.*, 2011; 2012). In these French trout populations, translocation of native fish to the genetic refuge areas has been used to more quickly achieve the restitution of native gene pools in some locations (Gil *et al.*, 2016).

Unfortunately, the recovery of ancestral patterns of diversity has not been achieved uniformly across the brown trouts range. Changes in the genetic composition at a local scale resulted in the recovery of native gene pools in some locations, but the abundance of hatchery alleles increased in other stretches (Araguas *et al.*, 2008, 2017). An increase of hatchery alleles in some refuges could be the result of upstream migration of admixed or released hatchery fish from nonrefuge areas, as previously reported by García-Marín *et al.* (1998) in the protected area of the *Aigüestortes i Estany de Sant Maurici* National Park. To prevent such situations, Araguas *et al.* (2009) proposed the establishment of unstocked fishing areas between the genetic refuges and the stocked area. This interposed fishing area should act as 'buffering river segments' to the migration of released fishes because, as previously stated, stocked trout could selectively be removed by anglers in these areas.

The possibility for the dispersal of released fish along rivers also suggested that genetic monitoring based on a few reference locations can give a rough impression of the average status of brown trout populations at large regional scales, but they lack sufficient precision at the local level (Fernández-Cebrián *et al.*, 2014). For instance, Araguas *et al.* (2017) detected a naturalized exogenous population at a location within one of the first genetic refuges established in 1997. This location has never been genetically studied before. Thus, genetic surveys on a large number of locations along the river basins are necessary to accurately evaluate the success of genetic refuge areas and to design future strategies of management (Araguas *et al.*, 2017).

Supplementation with Native Stocks

Recent Spanish legislation on the conservation of biodiversity (Article 52.2, Law 42/2007 of Natural Heritage and Biodiversity) has forbidden releases of foreign stocks into freshwater ecosystems inhabited by native trout. Consequently, several trout fishery administrations around Spain are selectively replacing foreign stocks with native ones derived from regional or local sources or are promoting translocations of wild native individuals to sustain captures in exploited rivers (Fernández-Cebrián *et al.*, 2014). Native stock reinforcement following habitat recovery is an accepted measure within the European Inland Fisheries Advisory Commission (EIFAC) code of practice for recreational fisheries (FAO, 2008; see also Epifanio & Waples, 2016, for some cautionary tales). Such practices need, as a first step, a correct identification of genetically differentiated units to be supplemented to avoid the loss of local adaptation that results from releases of nonlocal fish (Laikre *et al.*, 2010). Therefore, management based on native stocks implies the maintenance of native stocks for each genetically differentiated population present on the rivers. Due to the amount of total diversity and complex population structure among Iberian brown trout populations, particularly in the Mediterranean basins, this would demand substantial commitments of time, personnel, and hatchery infrastructure for implementation and monitoring (Araguas *et al.*, 2009). In addition, released fish from native stocks and their wild progeny often exhibited decreased performance compared to wild populations (Araki *et al.*, 2008). For instance, genetic changes in the steelhead (*Oncorhynchus mykiss*) occurring during a single generation of hatchery culture resulted in maladaptation to the wild (Christie *et al.*, 2012). In addition, a large number of founder individuals are necessary to avoid problems of inbreeding and loss of genetic variability (Ryman & Laikre, 1991; Ryman, 1994; Ryman *et al.*, 1995b; Hansen *et al.*, 2000; Wang & Ryman, 2001; Machado-Schiaffino *et al.*, 2007), which would compromise the general long-term viability of this management option.

Native stocks founded with autochthonous trout have been performed in some Spanish hatcheries. For instance, based on information from mitochondrial lineages, the Government of Aragon has maintained several autochthonous brown trout stocks in two hatcheries to supplement regional populations (Mitjana, 2010). In the hatchery of Brieva de Cameros (La Rioja), a mixed stock that originated in 2003 from autochthonous adults collected in several rivers of the region was used for releases without consideration for the relevant local adaptive differences. Native individuals were also used in 2006 to create two native stocks in the Galician hatchery of Veral (Lugo), which are still maintained but no longer used (J. Latas, Responsible for the Veral Fish Hatchery, personal communication). In Asturias, hatchery stocks presented a mixed gene pool of native and non-native trout, and only one stock, which was founded in 2006 with wild adult individuals from upstream areas, was free of the non-native *LDH-C**90 allele (Horreo *et al.*, 2015). Unfortunately, no scientific studies have assessed the effectiveness of these native Iberian stocks regarding the question of the global capacity of supplementation, the genetic changes induced in the stocks by culture in hatchery installations, and the effects of these changes on preserving native diversity at regional and local scales. Stocking with native stocks in the French Alps recovered Mediterranean alleles in highly introgressed populations (Gil *et al.*, 2016). A simulated supplementation program using native brown trout stocks predicted the recovery of native alleles in populations highly impacted by releases of a foreign hatchery stock, but at the same time, this simulation indicated substantial losses in regional divergences (Fernández-Cebrián *et al.*, 2014). More often, managers consider that any stock generated with native individuals can be widely used in all the rivers under its jurisdiction, without realizing the potential value that local genetic distinctions might have for maintaining native fish in the long term. To avoid the risk of genetic homogenization of wild populations with a single native hatchery stock, some European countries have limited the releases of native trout stocks to local source populations (Laikre *et al.*, 2010).

The supplementation of wild populations with native individuals also can be performed through supportive breeding, in which, a proportion of each generation of native wild spawners are captured and transported to the hatchery for breeding (Ryman & Laikre, 1991; Hansen *et al.*, 2000; Wang & Ryman, 2001). Again, no scientific assessment of such practices has been conducted on Iberian trout populations; however, in northern Iberia, supportive breeding has been used in populations of *Salmo salar* since 1992 as an alternative to stocking with foreign fish (Horreo *et al.*, 2008). Genetic surveys reported significantly lower allelic richness in juveniles released in the rivers for supportive breeding efforts than has been observed in the wild stocks (Machado-Schiaffino *et al.*, 2007). Horreo *et al.* (2012) also found that hatchery-reared Atlantic salmon have problems with straying, so supportive breeding has induced changes at the population level in terms of genetic variability and structure. In spite of that, supportive breeding from native spawners could be used as a periodic tool to recover fish abundance or to restore genetic integrity in depressed populations.

Supplementation with Triploid Individuals

To achieve a sustainable fishery in wild populations while also preventing the introduction of exogenous genes, some authors have suggested fishery reinforcements performed with sterile triploid individuals (Chatterji *et al.*, 2008; Piferrer *et al.*, 2009). Triploid production, involving either physical treatment (temperature or pressure shocks) or the application of chemicals, is simple and cheap (Thresher *et al.*, 2014), and a protocol for the optimization and production of triploid *S. trutta* has recently been described (Preston *et al.*, 2013). However, only triploid females are potentially 100% sterile because their ovaries fail to develop normally, whereas triploid males can produce functional spermatozoa and attempt to spawn with females, competing with wild males (Piferrer *et al.*, 2009; Fjelldal *et al.*, 2014).

Although studies about the usefulness of triploid individuals in commercial fish farming (Benfey, 2001) and recreational fishing (Kozfkay *et al.*, 2006) exist, little information is available on the impact of released triploid individuals on wild populations (Chatterji *et al.*, 2008). Some evidence suggests similar performance and behavior of stocked diploid and triploid individuals (Budy *et al.*, 2012). Nevertheless, due to the density-dependent mortality described in some brown trout populations (Lobón-Cerviá, 2012; Richard *et al.*, 2015), releases would be expected to disturb wild populations in any case. Sterile fish might have additional negative consequences for native populations through indirect processes such as competition, disease introduction, or reduction of the effective size of the recipient wild population (Kozfkay *et al.*, 2006). For instance, large triploid trout stocked in the rivers of Southern England quickly became piscivorous and, consequently, threatened the smallest fish (Riley *et al.*, 2013). Some attempts have been made to obtain triploid trout from hatchery foreign stocks in Catalonian hatcheries (R. Marsol, responsible for the Pont de Suert Hatchery, personal communication), but the resulting fish have not been released, and scientific studies to evaluate this management strategy have not yet been conducted.

A long-term sustainable exploitation of populations should be based on the natural reproduction of wild individuals. Thus, stocking practices, either using native stocks or sterile individuals, should be not used as a way to maintain put-and-take-based fisheries on usually overexploited populations. Otherwise, conservation actions aimed to increase population sizes through the improvement and recovery of the brown trout habitat should receive priority. Genetic refuges and additional measures to promote self-sustaining fisheries (e.g., restrictions on the bag limit per day or an increase in the minimum size of the captures) could be a way to balance the harvest and conservation of wild genetic resources. However, a change in social attitudes that favors a reduction in the exploitation at levels sustained by natural reproduction is a key element in brown trout conservation. In this context, catch and release is a fishing modality voluntarily practiced by many salmonid recreational anglers. The extension of this practice to all fishing areas would be desirable and would mitigate the pressure for hatchery releases (Araguas *et al.*, 2009). For that, educational and social programs, involving the participation of local stakeholders, is necessary to raise an awareness of the importance of maintaining brown trout genetic diversity to assure the long-term conservation of their wild populations, and hence fishing activities.

Conclusions

In the Iberian Peninsula, brown trout diversity occurs within a reduced area in a mainly continental context, and limited to headwater streams in the Mediterranean and in South Iberian basins. Nevertheless, this species complex displays a high level of gene diversity, with four mtDNA lineages distributed along main river basins and pronounced patterns of populations structure revealed by nuclear (microsatellite) markers, even at a microgeographical scale. This high level of diversity in a quite reduced geographical region is the result of the brown trout survival along Quaternay glaciations, and natural processes (e.g. post-glacial recolonization and hydrology modication during glacial-interglacial periods) that modeled lineage distribution and often resulted in intrincated patterns of genetic structure. As well, anthropogenic disturbances (including management based on stocking, translocations and modifications of the hydrographic network) have altered native distribution of the brown trout gene diversity in the Peninsula. Conservation and restoration of the remaining native gene diversity will rely on ever-improving strategies accompanied by scientific monitoring, and evaluation with sensitive techniques and methods that permit assess consequences of management and to design future strategies for brown trout conservation.

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5

Understanding Brown Trout Population Genetic Structure: A Northern-European Perspective

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Introduction

The freshwater landscape is complex, constituted by water masses varying in size, structure and connectivity. This physical landscape, and its highly variable geological history, moulds the organisms living there into highly variable entities due to limitation of dispersal and gene flow and highly divergent selection pressures. Freshwater organisms living in such complex environments diverge through time because of a number of evolutionary processes, both directional and stochastic (Hewitt, 1996).

During the last glaciation Northern Europe was completely glaciated and the sea level was substantially lower than present. Freshwater fish species such as the brown trout *Salmo trutta* were thus restricted to glacial refugia to the south or east (Hewitt, 1996, Bernatchez, 2001, Hewitt, 2004, Costedoat and Gilles, 2009, Jonsson and Jonsson, 2016). It is still discussed where the brown trout refugia were located and which dispersal corridors were used when dispersing into Northern Europe. There is still no complete agreement as to how the *Salmo trutta* species is to be defined.

Following the advent of modern genetic methods, a large number of phylogeographic papers on the '*Salmo trutta* species complex' have been published. The complex is often considered to be composed of five major evolutionary lineages: the Atlantic, Danubian, Adriatic, Mediterranean, and the *Salmo marmoratus* lineage (Bernatchez, 2001). This classification is based on studies of the distribution of mitochondrial DNA (mtDNA) haplotypes. However, there is still confusion and disagreement regarding the evolutionary status of the different mtDNA lineages, how many lineages there are, and if the different lineages should be awarded species or sub-species status. Recent investigations using other genetic markers and methods clearly show that the lineages are not clearly differentiated, and that a purely phylogeographic analysis based on mtDNA fails to describe the evolutionary history of the taxa (Lerceteau-Kohler *et al.*, 2013). The various populations and taxa may be mixtures or mosaics of different lineages, indicating complex dispersal and admixture processes (McKeown *et al.*, 2010, Lerceteau-Kohler *et al.*, 2013, Gratton *et al.*, 2014).

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

It is therefore uncertain how many 'brown trout' species there are. One particular position is taken by Kottelat and Freyhof (2007), who identified many species within the '*Salmo trutta* species complex' in Europe. One classical issue (of several) has been the taxonomic status of several locally identifiable morphotypes of brown trout in the British Isles – called respectively ferox, gillaroo and sonaghen (Ferguson and Mason, 1981, Ferguson and Taggart, 1991). A review of the species complex was briefly given by Jonsson and Jonsson (2011), who also presented a comprehensive table summarizing the various species and subspecies names attributed to populations within the complex. They take the position that there is one highly polymorphic species of *Salmo trutta* in North Europe. Phenotypically diverse trout individuals are thus members of more or less reproductively isolated populations, and the phenotypic differences are then either due to plastic or evolutionary responses to local selection pressures. There is an obvious need for a thorough revision of the genus as there is a confusing mixture of species concepts used in the literature, as well as some misunderstanding of evolutionary processes. This is however not the place to take on this discussion; I will therefore focus on the Atlantic lineage as presented by Bernatchez (2001), and treat all populations as members of the *Salmo trutta* species.

The brown trout is known to be one of the most phenotypically diverse freshwater species, exhibiting a wide range of life-history tactics and morphologies. One daunting task has been to try to understand the drivers of that variation, being it environmental (through plastic responses to varying environmental factors) or genetic (through differences in evolutionary processes such as mutation, selection, gene flow and genetic drift). The brown trout can survive and thrive under very different environmental conditions (Elliott, 1994, Jonsson and Jonsson, 2011), and it has been introduced into most parts of the world (Budy *et al.*, 2013). Thus the environmental contexts where trout are encountered during parts of the life-cycle vary from alpine hyper-oligotrophic lakes to highly productive marine environments. There is even some evidence that brown trout can successfully spawn in brackish water (Landergren and Vallin, 1998). This may lead to large variation in type and strength of selection pressures, as well as large variation in population size. Thus, we can expect large variation in effective population size and also level of genetic variation. On top of local scale processes determining level of genetic variation, we can also expect genetic signatures based on processes at different temporal and spatial scales, such as effects of post-glacial dispersal from glacial refugia, genetic bottlenecks and founder events.

Such variation in genetic structure and variability can be expected to have an impact on population resilience and the ability to respond to new and emerging selection pressures (such as climate change). However, the evidence is still limited (Merilä, 2012).

Here, I have summarized data on the genetic population structure of brown trout in Northern Europe, and use analysis of these data to try to elucidate factors important for population differentiation. A large number of studies have used analysis of putatively neutral genetic markers to estimate genetic diversity metrics (heterozygosity, allelic richness, effective population size) and level of genetic differentiation among populations. I first describe the data used, and then present and discuss the observations at different spatial scales. I have tried to only use data on wild trout, and avoid the effect of human interventions. However, such interventions are unavoidable for a species such as the brown trout, one of the world's most invasive species (Budy *et al.*, 2013).

The Data and their Analysis

The first studies investigating the genetic population structure of the brown trout appeared in the 1970s. Since then the type and number of markers, spatial and temporal extent of sampling and complexity of the study systems has increased. The first studies were performed in small Swedish lakes, using a limited number of allozyme loci to test for the existence of reproductive isolation between trout spawning in different tributaries (Allendorf *et al.*, 1976, Allendorf *et al.*, 1977, Ryman *et al.*, 1979). Since these first pioneering studies a number of new techniques have been developed, ranging from microsatellites, to single nucleotide polymorphisms and full genome sequencing using next generation sequencing techniques. The advent of what is still called next generation sequencing technologies has changed the way researchers think about population genetic studies, leading the way into the area of population genomics. However, up until now no population genomic studies have been conducted on the brown trout. A large number of studies have also used mitochondrial DNA as substrate for analyses. Studies of variation in mtDNA are particularly useful for understanding divergence at large temporal scales, and for estimating female effective size. Here, however, I focus on nuclear DNA markers that are sex independent and assumed to be neutral.

Using web-based searches (Web of Science) I identified 75 publications (see Appendix for data; available at https://www.researchgate.net/project/Understanding-brown-trout-population-structure-a-Northern-European-perspective) that could be used to extract information on standard population genetic metrics such as allelic richness (n = 389), observed heterozygosity (n = 461), expected heterozygosity (n = 506), effective population size (N_e, n = 104) or pairwise population differentiation (F_{ST}, n = 1112). The effective population size is defined as the number of individuals in a theoretical population having the same extent of genetic drift as the actual population (Hartl and Clark, 1997). N_e is impacted by a number of factors in addition to population size itself. The main factors are unequal sex ratio, skewed family size and variation in population size. In addition, most methods developed for estimating N_e assume unrealistic conditions such as no overlapping generations as well as require some hard-to-access data (see discussion by Serbezov *et al.*, 2012a, Serbezov *et al.*, 2012b). This explains the relatively limited number of estimates of N_e. Allelic richness is the total number of alleles in a population, estimated per locus. This means that allelic richness may differ strongly among marker types with the allele numbers being much lower for allozymes and SNPs than for microsatellites. In most, but not all, studies the allelic richness is estimated using a rarefaction procedure (Kalinowski, 2004). Thus the estimates of allelic richness presented here are not directly comparable, and must be treated with some caution.

In addition to the various metrics describing genetic variation, it was possible to extract a standard metric of population differentiation. The most commonly used metric for such comparisons is the fixation index (F_{ST}) (Hartl and Clark, 1997). A total of 1112 pairwise between-population estimates of F_{ST} were extracted from a total of 27 studies. For a limited number of these studies, it was also possible to extract a metric for pairwise geographic distance between samples (n = 122). Most of these metrics have been used to test for an isolation-by-distance genetic structure (Wright, 1943). It was also possible to identify whether impassable waterfalls were acting as barriers to upstream gene flow separating the various pairs of populations. Such barriers reduce connectivity in dendritic stream networks, and may lead to unique genetic clusters above these waterfalls (see for example Kelson *et al.*, 2015). Further, I classified the spatial scale used in the comparison into three categories: (i) within watershed; (ii) among watersheds at a regional scale; and (iii) among locations at national or larger scales.

The number of studies found and used herein is probably not exhaustive, as estimates of genetic diversity may be found in studies having variable research foci. However, the studies used here are probably representative for the overall picture. The studies used cover the time interval from 1979 to 2015, and comprise research endeavours in 13 Northern European countries (Table 5.1). A few of the estimates are temporal replicates from the same population(s). However, the number of replicated estimates is very low and I treat them all as independent observations. The countries included in this study are countries bordering to the Baltic Sea and the North Sea. This means that I have excluded studies from countries where other than the Atlantic lineage of the brown trout can be expected to occur. Most studies are from the Nordic countries (Norway, Sweden and Denmark). Further, only studies including putatively natural populations are included, thus excluding populations where supplementary stocking and introduction of non-native individuals has been deemed as important. However, trout stocking and translocations are very common today and have been so historically (Elliott, 1994, Budy *et al.*, 2013), so it is very difficult to be certain that no stocking or translocations have happened. This has to be kept in mind. Other kinds of human encroachments in the river systems have not been evaluated.

Most studies are based on microsatellites (n = 409) and allozymes (n = 240), whereas very few estimates are based on amplified fragment length polymorphisms (AFLP; n = 11) or single nucleotide polymorphisms (SNP; n = 11). Allozymes were the first

Table 5.1 Number of estimates of genetic diversity per country or region (sorted according to number of total estimates).

Country/Region	H_o	H_e	AR	N_e	F_{ST}
Norway	140	193	110	27	328
England	37	37	42	5	322
Sweden	77	50	30	11	246
Russia	6	18	29	2	120
Denmark	112	127	81	46	18
Finland	0	38	54	0	0
Scotland	19	0	0	0	2
Baltic region	0	0	5	0	36
Northern Ireland	34	0	0	0	0
Ireland	9	16	13	7	39
Estonia	19	19	19	3	0
Poland	7	7	5	2	1
Lithuania	1	1	1	1	0

H_o = observed heterozygosity, H_e = expected heterozygosity, AR = allelic richness, N_e = effective population size, F_{ST} = fixation index, level of genetic differentiation between pairs of populations.

genetic markers used, and studies using allozyme markers have been published throughout the whole period covered by the data. However, microsatellites quickly became popular for population genetic studies in the late 1990s and seem to have been the marker of choice since then. Following the development of the new high-throughput sequencing technologies the use of SNP-based analyses is expected to be more and more popular in the future (see also Cuéllar-Pinzón *et al.*, 2016). AFLP, on the other hand, was a technique that had a short period of popularity and quickly faded out.

Overview of the Data

A general description of the data shows that observed and expected heterozygosity varies enormously, covering the range from close to zero to almost unity (Figure 5.1; Table 5.1). Overall these two metrics are strongly correlated (Spearman's $\rho = 0.937$, $n = 334$). There were more estimates of H_e ($n = 506$) than there were of H_o ($n = 461$). As evidenced from Figure 5.1 there is a strong curvilinear relationship between heterozygosity and allelic richness (AR). The strong curvilinear effect is particularly driven by the low H_e and AR estimates from the allozyme, SNP and AFLP markers. A closer look at the H_o and H_e distributions indicates a bimodal distribution (Figure 5.2). The two peaks seem directly linked to the use of different markers (Figure 5.3), with heterozygosity being in general much higher for microsatellite markers than for the other markers (ANOVA; H_e: $F_{3,502} = 866.3$, $P < 0.001$, H_o: $F_{2,458} = 1679.0$ $P < 0.001$). This was also the case for allelic richness ($F_{2,386} = 86.9$, $P < 0.001$). Based on this evaluation I will

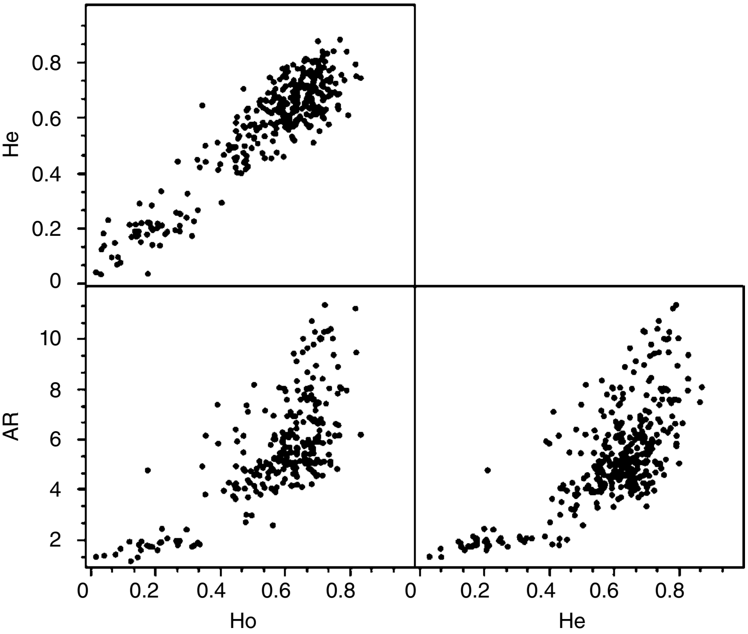

Figure 5.1 Scatterplots showing the relationships between observed heterozygosity (H_o), expected heterozygosity (H_e) and allelic richness (AR) for brown trout in North Europe.

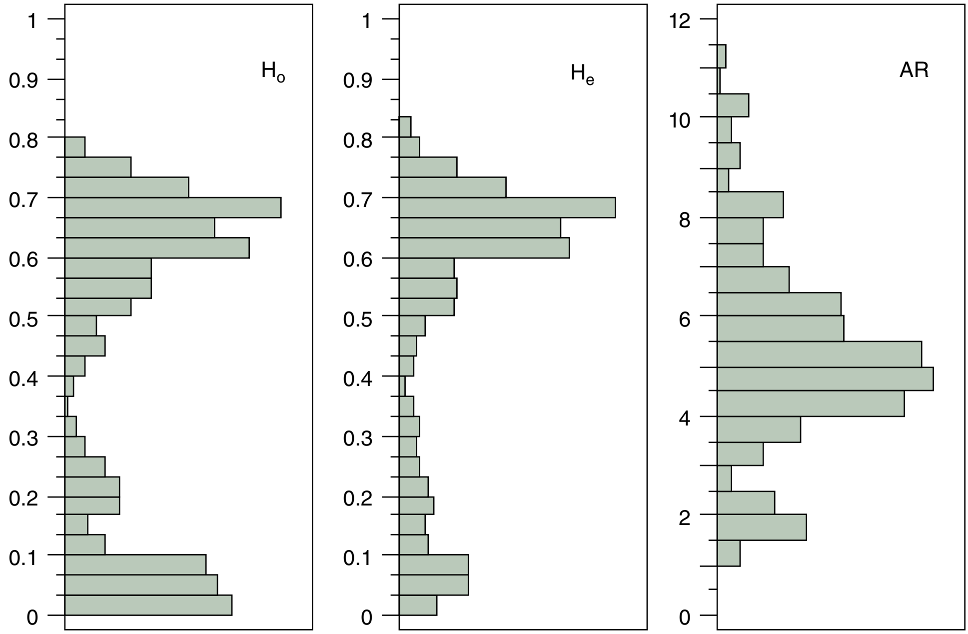

Figure 5.2 Distributions of observed heterozygosity (H_o), expected heterozygosity (H_e) and allelic richness (AR) for brown trout in North Europe.

focus on variation in H_e in the further analyses, and where appropriate use marker type as a random effect in the statistical evaluation of the data.

H_e did decrease marginally depending on the number of individuals ($r^2 = 0.01$, $P = 0.031$, $n = 464$) and the number of markers ($r^2 = 0.01$, $P = 0.065$, $n = 487$) used in the analyses. However, the effect sizes were very low. On the other hand, estimates became significantly larger over time ($r^2 = 0.50$, $P < 0.001$, $n = 506$).

Effective population size (N_e) was estimated in relatively few cases ($n = 104$). Estimates ranged widely, from a low of 8.6 to a high of 4235 individuals. The distribution was highly skewed to the left (Figure 5.4), with a median of 145.5 individuals. The estimates did not differ depending on marker type (ANOVA, $F_{2,101} = 0.742$, $P = 0.479$), number of markers used ($r^2 < 0.001$, $P = 0.960$, $n = 104$), number of individuals genotyped ($r^2 = 0.004$, $P = 0.521$, $n = 104$) or year of publication ($r^2 = 0.003$, $P = 0.259$, $n = 104$).

A total of 1112 estimates of pairwise F_{ST} values were extracted. The distribution of F_{ST}-values was strongly skewed towards low values, with a mean of 0.078 and a median of 0.052 (range 0.0 to 0.648). The mean estimates did not differ depending on marker type used ($F_{2,1112} = 1.077$, $P = 0.341$). However when accounting for unequal variances in the estimates (Levene test, $F_{2,1109} = 2.61$, $P = 0.004$; standard deviation was significantly larger for microsatellites than for allozymes and SNPs) it was weak evidence for SNP-estimates being larger than estimates based on allozymes and microsatellites (Welch ANOVA, $F = _{2,58.5} = 4.89$, $P = 0.011$). Further, there was a weak negative relationship between F_{ST} and number of markers used in the analyses ($r^2 = 0.004$, $P = 0.031$, $n = 1112$) and year of publication (Figure 5.5; $r^2 = 0.004$, $P = 0.036$, $n = 1112$). There was also overall a weak tendency for the use of a higher number of markers with time ($r^2 = 0.068$, $P < 0.001$, $n = 1112$).

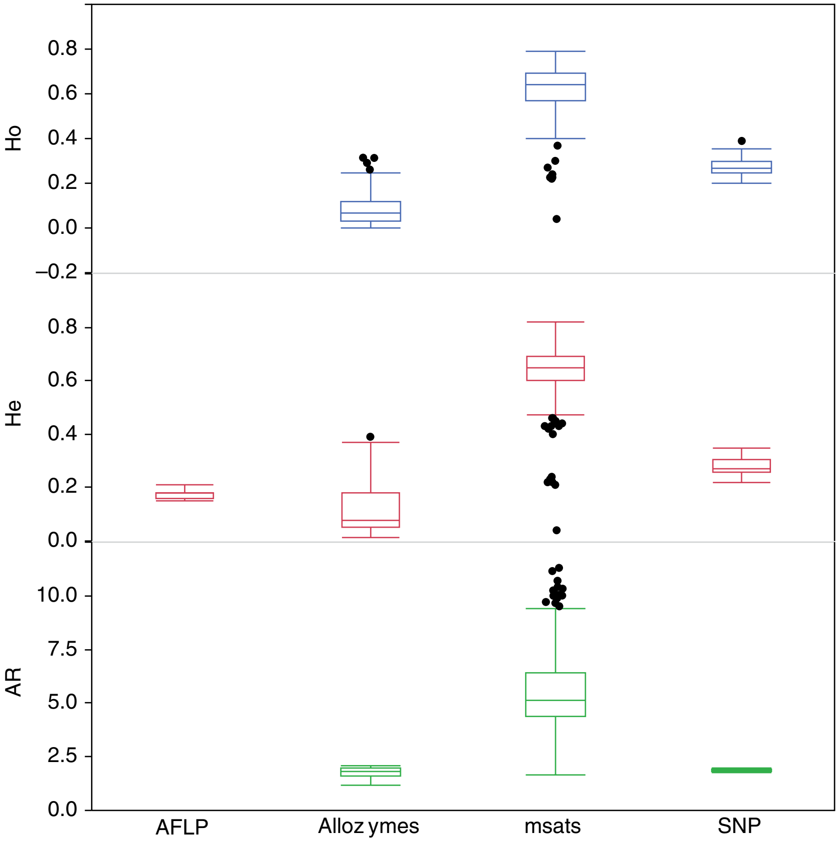

Figure 5.3 Boxplot showing observed heterozygosity (H_o), expected heterozygosity (H_e) and allelic richness (AR) for brown trout in North Europe estimated based on AFLPs, allozymes, microsatellites or SNP-markers.

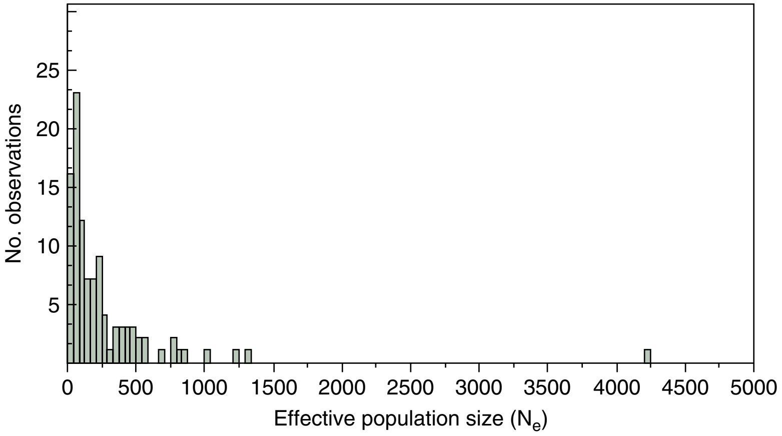

Figure 5.4 Distribution of estimates of effective population size for brown trout in North Europe.

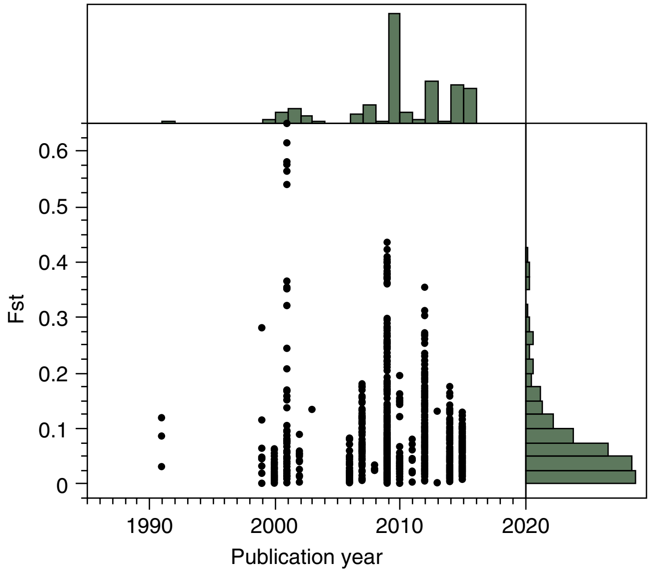

Figure 5.5 Relationship between estimated pairwise F_{ST} and publication year for brown trout from North Europe. Along the borders: distribution of observations.

For the pairwise F_{ST}-estimates I also downloaded 122 estimates of geographic distance between populations (shortest waterway distance). The mean distance was 44 km, ranging from 0 to 141.5 km.

Genetic Variation

The level of neutral genetic variability is usually assumed to be important for understanding demographic history and adaptive evolution. As shown in Figure 5.1 there is large variation in within-populations heterozygosity in brown trout. In an early study of genetic diversity among marine, freshwater and anadromous fish species, higher levels of within-population diversity were found in the marine species (Ward *et al.*, 1994). Anadromous species were assumed to be intermediate between freshwater and marine species. Detailed population-genetic studies on various salmonid fishes over large spatial scales also show this pattern. Recent examples are the comparison between anadromous steelhead and freshwater resident rainbow trout *Oncorhynchus mykiss* (Van Doornik and Berejikian, 2015) and between freshwater resident and anadromus Dolly Varden *Salvelinus malma* (Harris *et al.*, 2015). I therefore classified the populations of brown trout into anadromous and freshwater resident populations, and tested for differences in H_e between these two groups using a linear mixed effects model. Marker type was used as a random effect in the model, and year of publication was used as a covariate. The average H_e was significantly higher for the anadromous (mean ± se; 0.345 ± 0.105) than for the freshwater resident populations (0.266 ± 0.105) ($F_{1,\,500} = 105.6$, $P < 0.001$). These results clearly indicate that the large opportunity for gene flow among anadromous populations leads to increased genetic diversity. A metapopulation perspective (Schtickzelle and Quinn, 2007) should therefore probably be used when discussion conservation and management of in particular the anadromous trout populations.

The estimate of H_e increased significantly with year of publication (slope 0.007 ± 0.001; $F_{1,\,502} = 67.7$, $P < 0.001$). To test if this could be due to the already described temporal changes in the use of different molecular markers, and the fact that H_e-estimates differ among the marker types, I included marker type as a random effect in the statistical model. There was a highly significant interaction effect ($F_{1,\,5.6} = 11.51$, $P = 0.011$). This indicates that some of the temporal effect is due to methodological changes through time.

Most brown trout live in dendritic landscapes consisting of multiple nodes and branches. The arrangement of the landscape clearly influences genetic variation through its effect on dispersal probabilities and thus effective gene flow. In dendritic freshwater landscapes, with or without barriers to upstream migration, gene flow will tend to be asymmetric in a downstream direction (Morrissey and de Kerckhove, 2009). This leads to loss of diversity upstream, particularly above impassable waterfalls, and potentially an overall loss of genetic diversity within the meta-population over time. However, the dendritic organization of sub-populations potentially leads to quasi-independent development of different branches in the meta-population (see discussion on meta-population structure in salmonid fishes: Schtickzelle and Quinn, 2007) leading to an elevated level of genetic variation relative to other models of geographical population structure (Morrissey and de Kerckhove, 2009). This points to the importance of the small headwater populations when it comes to conserving overall diversity in trout populations, as recently discussed for the brook trout *Salvelinus fontinalis* (Kelson *et al.*, 2015). In the same way that conserving sub-populations with divergent numerical dynamics may elevate overall productivity and resilience (the portfolio concept: Schindler *et al.*, 2010, Anderson *et al.*, 2014, Schindler *et al.*, 2015), a diversity of independent sub-population may lead to long-term conservation of genetic diversity at larger scales.

Effective Population Size

It is usually assumed that the adaptive potential of a population is reduced in small and isolated populations, such as brown trout populations isolated in headwaters or small lakes. This assumption is among other things based on the premise that genetic variation is lost through genetic drift and inbreeding in small populations (Lande, 1988, Frankham, 1996, Wood *et al.*, 2015). The relevant metric for quantifying population size in this context is the effective population size (N_e), because N_e reflects the proportion of individuals that contribute genetically to the next generation (see Waples, 2004). There were few estimates of effective population size available for the brown trout ($n = 104$), and the estimates were highly skewed towards smaller values (Figure 5.4). I tested for variation in N_e between freshwater resident and anadromous populations using a generalized linear model with a Poisson distribution and a log link. Average N_e was significantly higher in anadromous (354 ± 62, $n = 56$) than in freshwater resident populations (167 ± 67, $n = 48$) ($\chi^2 = 3509$, $P < 0.001$). There was one significant outlier in the data (Blykobbe River, Bornholm, Denmark, sampled in 1950; Fraser *et al.*, 2007). Removing that estimate ($N_e = 4235$) decreased the average N_e for anadromous trout to 283 ± 34 individuals, but the average was still significantly larger than that for freshwater resident trout ($\chi^2 = 1547$, $P < 0.001$). As expected, there was a positive correlation between estimated N_e and H_e (Spearman's $\rho = 0.383$, $P < 0.001$).

It was not possible to extract data on census population size, or size of available habitat for a given population. However, the samples of freshwater resident trout could be classified as coming from a river/stream environment or from a lake habitat. I used the same generalized linear model as before to test for differences among habitat types. Average heterozygosity ($n = 289$) did not differ between trout from these two habitat types (lake: 0.311 ± 0.122; river/stream: 0.316 ± 0.123), but there was a significant tendency for N_e ($n = 48$) being larger for trout sampled in rivers (178 ± 50) than in lakes (159 ± 43) ($\chi^2 = 24.4$, $P < 0.001$). To test if this result could have a methodological explanation I included marker type as a factor in the analysis. There was a significant effect of marker type ($\chi^2 = 8.91$, $P = 0.003$), but the effect of habitat was retained ($\chi^2 = 16.4$, $P < 0.001$). It is not evident what the reasons for this observation might be. The summary data collected for this analysis does not include information about the size of available habitat or census size. A careful evaluation of such biological factors as well as careful consideration of the sampling strategies used in the different studies are needed in order to fully understand if this result is biologically relevant or a sample artefact.

Effective population size (N_e) is assumed to be correlated with census population size (N). However, this assumption is not always tested, and if tested not really validated (Wood *et al.*, 2015). Further, N_e is notoriously difficult to estimate with high precision in species with long reproductive life, overlapping generations, strong reproductive skew and alternative reproductive tactics such as for trout (Waples, 2004). Many of the models used to estimate N_e make strong assumptions associated with these issues, assumptions that are difficult to meet. We evaluated a number of these factors in a small stream-living population of trout showing the importance of adequate sampling, quantification of life-history parameters, gene flow estimation, and using this information for estimation of N_e (Serbezov *et al.*, 2012b, Serbezov *et al.*, 2012a). The conclusion from these, and numerous other, studies show that with appropriate sampling designs it is possible to acquire good estimates of effective population size; hopefully many more such studies will be performed in the future.

Population Structure: Spatial Scales and Landscape Structure

A classic way of describing population structure is by estimating among-population genetic differentiation using F_{ST}. I extracted a total of 1112 pairwise F_{ST} estimates, and tested if among-population differentiation increased with larger spatial scales. I did this by classifying geographic scale into three categories (1: within watershed; 2: among watersheds within region; 3: larger scales). In general, the level of genetic differentiation was larger at larger scales (Figure 5.6) ($F_{2,\,1109} = 32.1$, $P < 0.001$). It is, however, worth noting that very large genetic differentiation can be found also at the smallest scale studies here. Level of differentiation did not differ between the two larger spatial scales. This indicates that the potential for gene flow is low at the two larger scales, meaning that different evolutionary processes are important on the small and large scale.

Focusing on the within-watershed scale, it was evident that the level of differentiation was significantly larger when a putative dispersal barrier was present between the two populations (F_{ST}; with barriers: 0.099 ± 0.005, $n = 201$; without barriers: 0.043 ± 0.003, $n = 471$) ($t_{670} = 9.58$, $P < 0.001$). This is to be expected since in such systems the gene flow

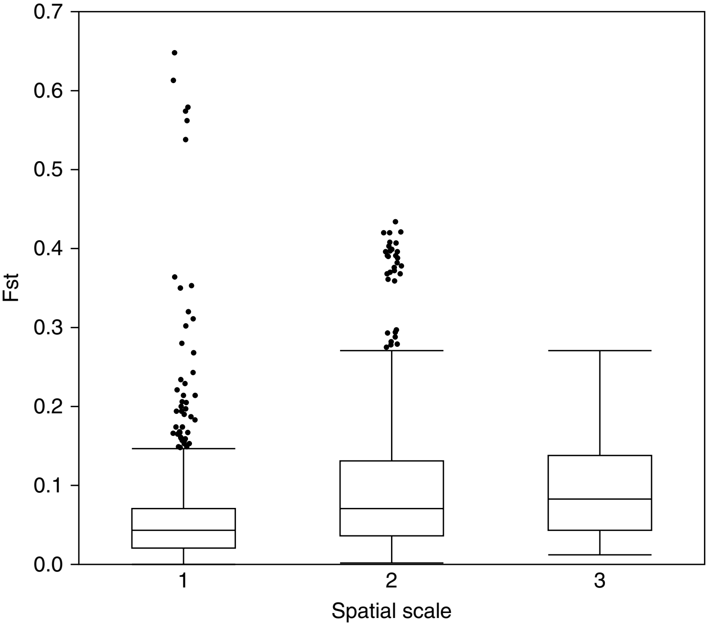

Figure 5.6 Box plot showing pairwise F_{ST} estimates for brown trout in North Europe at different spatial scales (1: within watershed; 2: between watershed; 3: between regions and larger scales).

will be asymmetric in the downstream direction, and in particular since populations situated above dispersal barriers in different branches in a river network will develop independently. Downstream populations may develop under the influence of gene flow from several isolated upstream branches. This leads to a fine scale and complex genetic structure in these dendritic networks (Morrissey and de Kerckhove, 2009, Kelson *et al.*, 2015).

When dispersal among populations is possible the level of gene flow is usually correlated with geographic distance, producing an isolation-by-distance (IBD) genetic signature (Wright, 1943). I investigated the generality of this by focusing on all F_{ST} estimates extracted from within watersheds where no migration barriers were present. Based on 103 available observations there was a highly significant isolation by distance signature ($r^2 = 0.329$, $P < 0.001$) (Figure 5.7). More unexpectedly there was also significant correlation between F_{ST} and geographic distance when barriers to migration were present ($r^2 = 0.390$, $n = 19$, $P = 0.004$). Actually, the slopes of the F_{ST} – distance relationship did not differ ($P = 0.770$), neither did the elevations ($P = 0.454$). This clearly shows that downstream gene flow is very important even in systems with barriers to upstream migration. There are also other explanations to the last observations. One potential reason is transport of fish among locations such as transport of fish from below a barrier to upstream the barrier. Such activity is known to occur in many systems, even if it is not a part of a management plan and thus unknown to management authorities. Anthropochore upstream transport and natural downstream dispersal will clearly produce an IBD-signal similar to what is observed in systems without barriers.

Looking at the scatterplot in Figure 5.7 it is evident that level of differentiation can be relatively large also at short distances, even when there is no obvious barrier to migration. This has been investigated in some detail by several authors.

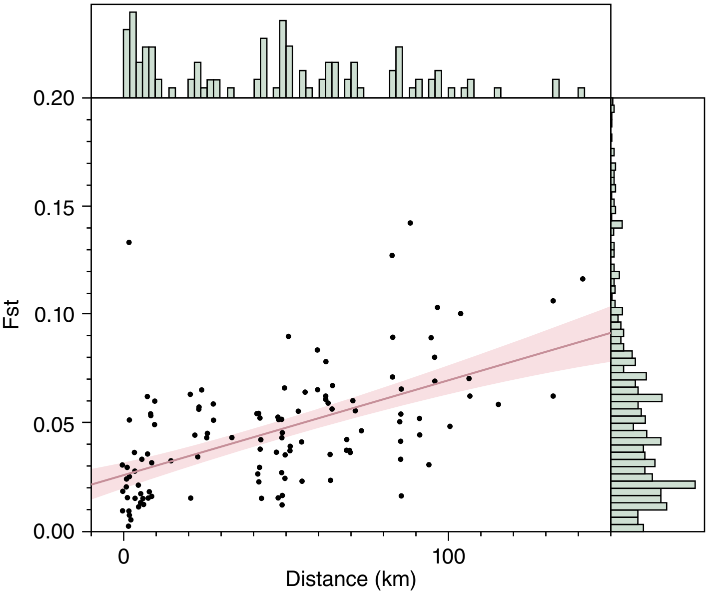

Figure 5.7 Relationship (regression line with confidence limit envelope) between estimated pairwise F_{ST} and geographic distance for brown trout from North Europe. Along the borders: distribution of observations.

The results indicate that limited dispersal and philopatry are important factors driving the level of local scale genetic differentiation (Carlsson *et al.*, 1999, Carlsson and Nilsson, 2000, Vøllestad *et al.*, 2012). In a detailed study of genetic structure in a small stream I recently showed significant isolation by distance signatures even at scales smaller than 1.4 km (Vøllestad *et al.*, 2012). However, the signature depended on sampling strategy in that the signature was significant when analysed for the younger age classes but the signal decayed with increasing age of the fish used in the analysis. This probably shows that dispersal is a continuously on-going process, and that such a random and on-going dispersal process (both up- and downstream) will reduce the importance of the structure. Thus, at small scales the isolation-by-distance structure may be due to the sampling of related individuals, a problem that has been discussed previously (Hansen *et al.*, 1997). A careful sampling strategy is clearly warranted.

Genetic differentiation between populations is driven by differences in genetic drift (and thus N_e) and level of gene flow. It is assumed that there is a balance between genetic drift and gene flow (Hartl and Clark, 1997), such that:

$$N_e m = \frac{\frac{1}{F_{ST}} - 1}{4},$$

where m is the gene flow from other populations. The number $N_e m$ is the number of immigrants per generation. After excluding three values with very low F_{ST} values (≈0) and therefore very high $N_e m$ values, the overall average $N_e m$ was 9.16 ± 0.62 ($n = 1098$) individuals per generation. The number of effective migrants was much higher between populations without barriers than between populations with barriers (as expected;

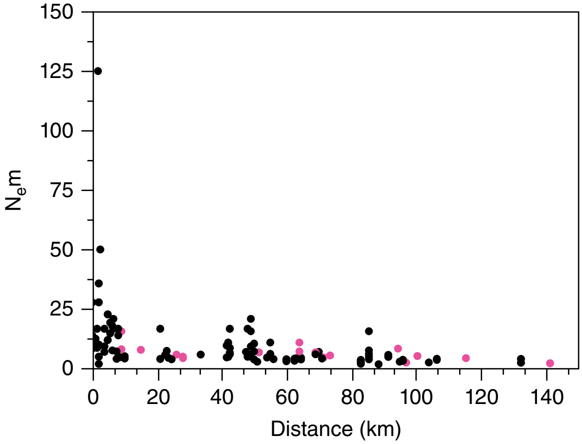

Figure 5.8 Relationship between estimated effective number of migrants per generation (N_em) and geographic distance for brown trout from North Europe. Black dots: no barriers to migration; pink dots: barriers.

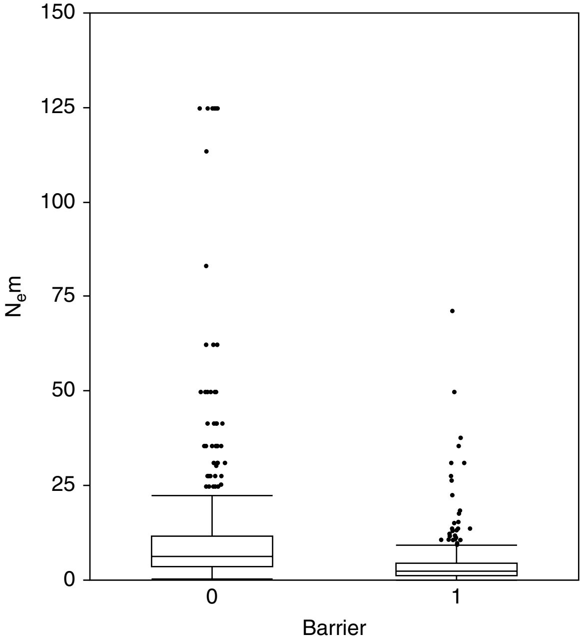

Figure 5.9 Box plot showing estimated effective number of migrants per generation (N_em) for brown trout from North Europe depending on if barriers to upstream migration is present (1) or not (0).

Figures 5.8 and 5.9). And there was a strong negative relationship between number of migrants and spatial distance between pairs of populations, both with and without barriers to migration. In conservation biology it has since long been discussed the optimal number of effective migrants per generation that is necessary to minimize loss of diversity while allowing divergence among these populations. A rule of thumb of allowing a minimum of 1 and a maximum of 10 migrants per generation has been advocated (Mills and Allendorf, 1996). The optimal number of effective migrants will depend on, among other things, the number of populations that exchange migrants (Hendry *et al.*, 2004).

This leads on to the question about the relationship between population divergence and local adaptation.

Local Adaptation: What it is and What we Know

Population divergence is a prerequisite for population diversification to happen. If the diversification leads to differences in fitness-related traits we can talk about local adaptation. Locally adapted genotypes will have reduced fitness in alternative environments. Documentation of significant differentiation is not, however, documentation of local adaptation – it only indicates the potential for local adaptation. Under certain conditions adaptation (i.e. response to selection) may be stronger than genetic drift and gene flow, but documentation that this may be the case is actually rare in the literature. The reason is evident; evidence for local adaptation requires hard work by performing reciprocal transplant experiments or raising individuals under common environment conditions (common garden experiments) (Stearns, 1992, Roff, 2002). A particularly powerful tool is to study the phenotypic expression of traits across environments and quantify the genotype–environment interaction. This norm of reaction approach quantifies the phenotypic plasticity, and at the same time tests for genetically based difference in the reaction norms (Schlichting and Pigliucci, 1998, Hutchings, 2011, Oomen and Hutchings, 2015).

Very few studies on the brown trout have used these approaches. Some examples are a common garden study on the genetic variation in early life-history traits in Danish trout (Jensen *et al.*, 2008, Meier *et al.*, 2014), indicating local adaptation in some of the traits. In contrast, a large-scale common garden experiment on Swedish and Norwegian trout did not find any differences in thermal growth performance (Forseth *et al.*, 2009). Overall, there is a large number of studies showing phenotypic differences in many traits among populations, but for many of these there is no direct evidence that the differences are genetically based and thus due to adaptation. An interesting behaviour that has been shown to be adaptive is the differential response to water current of juvenile trout whose parents were spawning either in the inlet or the outlet river of a large Norwegian lake (Jonsson *et al.*, 1994). Clearly, more such studies are needed.

Of particular importance is to investigate the level of gene flow that a population can experience and still maintain its locally adapted genotype. Low levels of gene flow can facilitate adaptation given that the population is reasonably large, whereas high levels of gene flow may dilute specialized adaptive genetic combinations and lead to loss of fitness (Sexton *et al.*, 2014). Recent studies on guppies, *Poecilia reticulate*, do show that local adaptation can be maintained in the face of high gene flow given strong selection (Fitzpatrick *et al.*, 2015). The same has been suggested for grayling, *Thymallus thymallus* (Kavanagh *et al.*, 2010, Junge *et al.*, 2011). This point is of utmost importance given the high intensity of stocking and transportation of trout among watersheds. To what degree such activity is breaking down local adaptations is controversial, but most evidence suggests that it is negative for the native gene pools (Hindar *et al.*, 1991, Garcia de Leaniz *et al.*, 2007, Jonsson and Jonsson, 2011, Hutchings, 2014). One common effect is the homogenization of gene pools across the landscape, and a potential loss of genetic variability at larger spatial scales. Unfortunately, the effects of translocations and stocking on the native populations are rarely evaluated (see a summary for Norway: Vøllestad and Hesthagen, 2001).

Some Concluding Remarks

As mentioned in the introduction, the brown trout is impacted by a number of human interventions at many different scales. Of particular interest is the effect of disruption of connectivity through the building of dams, culverts etc. The main effect of such encroachments is the reduction in population size (both census and effective size) leading to increased genetic drift. This may over time lead to reduced genetic variability and potentially loss of adaptive ability.

In this chapter I have summarized information on genetic diversity and diversification in brown trout based on 75 publications from Northern Europe. From these I extracted estimates of hetereozygosity, allelic richness, effective population size and pairwise estimates of population differentiation. The main results were:

- Large among-population variation in heterozygosity, some of which were due to the use of different genetic markers.
- Heterozygosity and effective population size was larger for anadromous than for freshwater resident populations.
- Effective population size was larger for riverine than for lake-living populations, for unknown reasons.
- There was significant isolation-by-distance signals both with and without barriers to migration in the systems.

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Section 2

Reproductive Traits and Early Ontogeny

6

The Velocity of Love. The Role of Female Choice in Salmonine Reproduction

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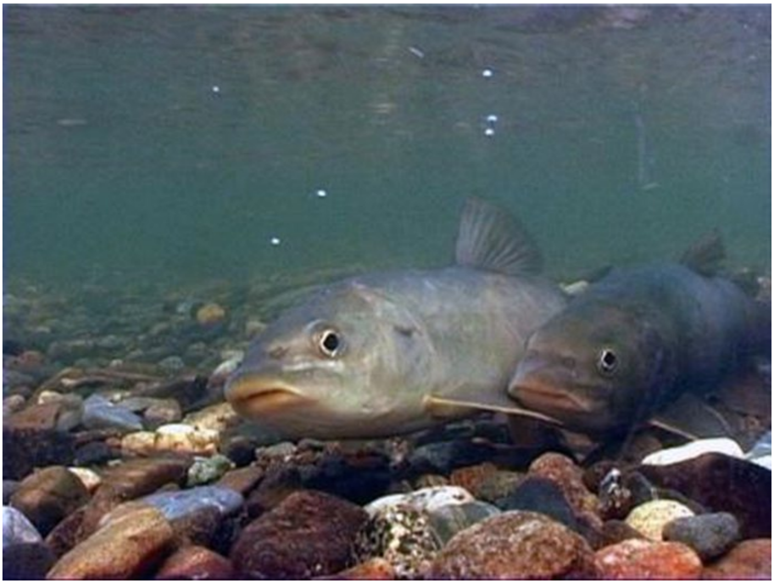

A pair of lenoks, (*Brachymystax lenok*), during spawning (Esteve & McLennan, 2008).

Introduction

Every year during late fall and early winter, on the thousands of rivers where salmon and trout live, one of the most extraordinary wild shows takes place. Males fight until their final strength in a struggle that for many species is their once in a lifetime reproductive event: spawning. Darwin (1859) described the battles that male salmon

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

tirelessly pursue on the spawning grounds. Since then, researchers' fascination with the male's role in salmon reproduction is evident in the bulk of literature addressing it. Traditionally, however, the scientific community has assumed that females play a passive role in the spawning process (Fleming and Gross, 1994; Quinn and Foote, 1994; Petersson *et al.*, 1999). According to this view, females always end up mating with the male who wins the battles taking place around them and therefore their ability to choose a mate is very limited. The use of remote underwater cameras in a long-term project studying the evolution of reproductive behaviour in the Salmoninae subfamily (*Brachymystax*, *Salmothymus*, *Hucho*, *Salmo*, *Parahucho Salvelinus* and *Oncorhynchus*) has allowed us to reconsider this view. In the following pages I will combine my published and unpublished observations (over a 15-year period with various co-authors) of 23 salmonine species belonging to seven genera with previous work by other authors to formulate a hypothesis addressing the female's role in salmonine reproduction. I will begin with a brief general picture of Salmoninae spawning behaviour. I will then explain how female behaviour affects male reproductive success. After that I will evaluate the relative importance of female choice versus male competition based on (a) data from an experiment in which female choice was artificially removed from a natural salmon population; and (b) the spawning behaviour of two 'non-nest building' salmonid species. As a separate block-text I will include an evolutionary view about female choice and male competition in the Salmoninae group by delineating the transition from rivers to still waters of a hypothetical fish population. I will conclude recommending future research that may or may not support the main idea of this chapter, that is, *the velocity by which salmonine females build their nest is an indicator of their choice.* One note here: this chapter is included in a book about brown trout, but many salmonine species are discussed. It is important to point out that most of the conclusions presented herein are valid for brown trout; indeed, all observations with brown trout during spawning not only support the main hypothesis of this chapter but have been decisive in order to reach it.

Salmoninae Spawning Behaviour

Salmonines spawn in clean, cold, well-oxygenated waters with gravel bottoms free of silt (Groot 1996). Some species, or sub-populations of species, spawn in still waters in gravel or rock beds on shoals or along lake shores provided there is good intergravel flow to irrigate embryos (Groot, 1996; Wilson, 1997; Quinn, 2005). During spawning females built a series of nests in the gravel to successively lay their eggs (Figures 6.1–6.4). Males do not participate in nest building; they fight ferociously to gain access to nesting females (Figure 6.5). The winner then occupies his time courting the female and preventing other males from approaching her (reviewed by Esteve, 2005b). A general description of spawning behaviour follows a sequence from nest site selection to nest completion with subsequent oviposition (Figure 6.6), egg covering and, in some species, nest defence by the female until her death (Table 6.1).

Figure 6.1 A marble trout (*Salmo marmoratus*) female digging her nest at the Soča River, Slovenia.

Figure 6.2 A lenok (*Brachymystax* lenok) female digs her nest in the Uur River, Mongolia (Esteve & McLennan, 2008b).

Figure 6.3 A Danube huchen female digging her nest (see Esteve *et al.*, 2013).

Figure 6.4 Female softmouth trout probing substrate with her anal fin during nest construction. Neretva River, Bosnia and Herzegovina (see Esteve *et al.*, 2014).

Figure 6.5 Sakhalin taimen males fighting at Karibetsu River, Hokkaido, Japan (Esteve *et al.*, 2009b).

Figure 6.6 Pair of white spotted charr (*Salvelinus leucomaenis*) during the spawning act. Tokimae River, Hokkaido, Japan (see Esteve *et al.*, 2011a).

Table 6.1 Phases of salmonine spawning behaviour (the change from a phase to the next one is gradual, and very often a particular phase would present behaviours from the anterior or next phase). For detailed descriptions of each behaviour see (Esteve, 2005a).

Phase	**Timing**	**Behaviours**		**Particularities**
		Females	Males	
(1) Nest selection	From the female arrival on the spawning grounds until the first 3 nest building diggings.	*Exploring* *Exploratory diggings* *Building diggings*	*Tastings* *Quiverings* *Fights* and *displays*	Females in crowded density areas wait in holding places for nesting spaces to become free.
(2) Nest building	From the first 3 nest building diggings until the first 3 probings	*Building diggings* *Weaving* *Probings*	*Quiverings* *Tastings* *Fights and displays* *Crossovers*	Normally after a digging event females return to their nests by circling. During nest building females travel relatively less than during exploratory diggings.
(3) Nest probing	From the first 3 probings until the first false spawning	*Probings* *Building diggings* *Weaving* *Resting*	*Quiverings* *Crossovers* *Fights* and *displays*	Respiratory frequency increases. Emission of bubbles occurs. Usually after a digging episode females return to the nest by letting the current carry them back.
(4) Nest completion	From the first false spawning to real spawning	*Probing, gaping & vibrating* *False spawning* *Spawning*	*Quivering* *Gaping* *Spawning*	*Multiple paternity* spawning events are very common.
(5) Nest covering	From real spawning to total nest covering	*Covering diggings* *Resting* *Defending*	*Staying* *Leaving the redd*	Covering diggings have fewer tail beats per bout. Iteroparous species do not defend the redd.

Fixed Behavioural Patterns

Based on the work of early ethologists, we know that fixed behaviours, as for example the expulsion of eggs, occur when a certain physiological threshold is exceeded (Lorenz 1932, 1935 & 1940; Tinbergen, 1939, 1942, 1948 & 1951; Fabricius, 1950). This threshold is variable over time, and depends on a continual feedback between the individual's internal motivation and external stimuli. In most salmonines, the motivation for spawning depends on the female's state of maturation. The external stimuli come mainly from three sources:

1) The environment (temperature, flow and water velocity, photoperiod, etc).
2) The courting male (morphology, size, colouration and behaviour).
3) The progress of nest construction (depth and shape).

The female, obviously, has no way of modifying the environment or the characteristics of the courting male; she only has control over the nest shape (every time she is digging she is changing it and consequently modifying the stimulus the nest provides). This point is critical because, as we will discuss below, nest depth has proven to be the key stimulus necessary for egg release.

The Critical Depth

Tautz & Groot (1975) built a depression in the gravel simulating a nest in an artificial channel on Vancouver Island (Canada). When they placed a mature chum salmon female (*Oncorhynchus keta*) on this false nest they found that the number of diggings she performed before spawning with the male courting her was significantly lower than the average number a female needs to build a nest from the beginning (75 vs. 225). This experiment thus identified nest depth as the key stimulus to induce oviposition. Studies on Atlantic salmon in rivers and experimental channels in Norway by Fleming (1996) later revealed the tremendous variation in time females spent nest building, ranging from a few hours to even days. Given that a female does not spawn until the nest is finished, it follows that the rate at which a female digs is correlated with her motivation to spawn. So, all other factors being equal, does a female vary the frequency of her nest building digs depending on the quality of the male accompanying her?

The Index of Choice

The index of choice (Esteve, 2005a) is an indirect measurement of a female's urge to spawn with the male who accompanies her and can be defined as:

$$I = b/T$$

where b is the number of female nest diggings and T is the time. A female with a greater urge to mate with the male courting her will dig her nest at a faster rate, while a female that is not attracted to her courting male will delay nest building, increasing the chances that a new male will eventually defeat and replace the current one. It is important to notice that the index of choice formulated as it is, is only a measurement of how the female likes her mate partner. It does not tell if her choice is due to any particular male character (size, coloration, morphology, behaviour). Also, it should be clarified that when 'I' is compared among several females, in order for it to be an accurate measurement it should be used only with females having a similar internal motivation. Comparing females at different stages of maturation will lead to misinterpretations. Table 6.1 divides the spawning process in different phases according to the nest progress. An experienced researcher can assign a female to a particular phase based upon her behaviour although, as noted, there might be some overlap between adjacent phases (Esteve, 2005a); and consequently use only females at the same stage to study I.

The equation can now be normalized between 0 and 1 according to the following conversion:

$$In = [(b/T) - I\,min)]/(I\,max - I\,min)$$

Values close to 0 indicate no interest whatsoever while values close to 1 indicate that the mating desire is maximum.

Figure 6.7 is based on data from 20 different pairs of sockeye salmon spawning in rivers of Washington and British Columbia (Esteve, 2005a). In all cases females were in the nest-completion spawning phase. The observation time for each pair was an hour. The chart indicates that females vary in nest digging speed depending on the male courting them.

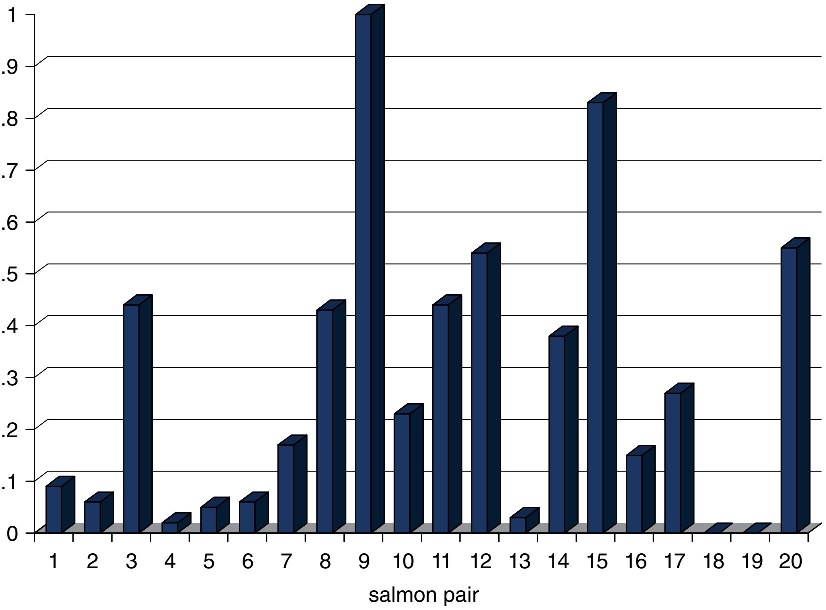

Figure 6.7 Normalized Index of Choice based on 20 pairs of sockeye salmon (*Oncorhynchus nerka*). All females were in the probing size and all pairs contained fish of similar relative size.

Female behaviour is influenced by a variety of male traits. If we want to study a particular male trait we theoretically could eliminate the other traits by choosing only pairs with males having those other traits which are similar. For instance, if we want to study the influence of courtship in female choice (in salmonines courtship manifests as 'quiverings', high frequency and low amplitude vibrations performed by the male along the female's body); we should compare only pairs with similar relative sizes. Ideally we should also control for morphology by choosing pairs whose males have similarly developed sexual characters. We then could introduce the effects of quiverings (or in fact any other trait) by modifying the preceding equation:

$$\mathrm{In} = [(\mathrm{b}/\mathrm{qT}) - \mathrm{I\ min})]/(\mathrm{I\ max} - \mathrm{I\ min})$$

q being the number of quiverings by the courting male.

So far I have suggested that females, by accelerating or slowing their nest building velocity, choose, in an indirect way, their mating partner. But if this is true, based on what characteristics do they make their choice? And more importantly, what guarantees do they have they are making a wise choice? To answer these questions it is necessary to go back in time to two of the great architects of the theory of sexual selection proposed by Darwin (1871): The English mathematician Ronald Fisher and the Israeli ethologist Amotz Zahavi.

Fisher, Zahavi and the Salmon Female

The 'Runaway Selection' proposed by Fisher (1930) and the 'handicap principle' proposed by Zahavi (1975) have been used as alternative mechanisms of sexual selection through female choice. Fisher proposed that females choose a male based on aesthetic characters that are not necessarily correlated with the genetic quality of their carriers. His model assumes that there is heritable variation for both the male characters and the female preferences. Once, for arbitrary reasons, females begin to express preferences for a particular character, the male and female progeny inherit the character and preference; but only the males express the character while the females express the preference. In the model of the handicap principle, however, the choice of the female it is based on indicators of genetic quality. Zahavi reasoned that an extravagant character involves a high cost to the wearer and can therefore be used by females as a reliable indicator of genetic quality simply because males of inferior quality cannot incur such a cost.

Theoretically, in the case of salmonines (and probably in other groups of animals as well) either of these models by itself could present some problems (but see Grafen 1990). Fisherian runaway selection for a particular trait is susceptible to being invaded and interrupted by a similar runaway selection process for another character (a runaway selection process for a developing the male jaw upwards could for instance be invaded by another selection process for developing the jaw downwards). On the other hand, for a Zahavian character to be selected, a previous mechanism responsible for the development of such a character had to exist (extravagant characters are not available to females all of a sudden). With this regard, when integrated together both models can explain the formation of exaggerated male characters through female choice. A female who, for instance, has chosen a male with a prominent hump (Figure 6.8) is choosing an

Figure 6.8 The big hump on this pink salmon (*Oncorhynchus gorbuscha*) male is a disadvantage in shallow rivers with predators present (Skykomish River, WA, US).

individual who has survived despite having this disadvantage (a big hump reduces hydrodynamics plus makes the wearer more conspicuous to predators). However, an exaggerated hump may not appear suddenly in the male population. Fisher's model solves this problem (males inherit their father's hump which is slightly greater than the average and females inherit the desire for mating with larger than the average hump males). Provided there is a minimum disagreement between both parameters (females prefer males with humps higher than the average of the population) the process of 'building' humps which are increasingly bulky continues on an accelerated basis with limits imposed only by natural selection. If the combination of the two models is true, salmonids will constitute a clear example of species in which females have driven the males to handicap themselves in exchange for sex. But for the males, even having survived carrying a big handicap is not enough. Females have a second way to guarantee they are choosing good males: 'make' them fight.

The Males' Response

A salmonid male is an individual competing for sex. In many cases it is a fair competition that follows the rules by which females make their choice: the biggest and most powerful male wins the fights and gets the genetic transmission award. Such males decrease their chances of survival by spending more years in the feeding areas (oceans and lakes) and returning to the breeding sites at formidable sizes. However, the advantage of being big decreases when your competitors are also big; a problem that has been solved by the evolution of alternative male mating strategies. The relative success of each strategy depends on what the others are doing (Gross, 1984; Myers, 1986, Fleming, 1996 & 1998; Foote *et al.*, 1997). Some males, for instance, mature more quickly and

Figure 6.9 Masu salmon (*Oncorhynchus masou*) adult male close to precocious males (Sanru River, Hokkaido, Japan (see Esteve *et al.*, 2011b).

return to the river at a younger age and smaller size. They wait near the nest vicinity adopting a subdominant role. At the moment of spawning, they dart towards the female and emit sperm. The success of this male depends on his proximity to the female at the time of egg release (Mjølnerød *et al.*, 1998), so even subdominant males have to fight among themselves to maintain the tactical position immediately behind the dominant male (Healey and Prince, 1998). Some other males never fight.

These are individuals that resemble females in morphology and coloration (Schroder, 1981), which helps them remain close to females without being attacked by the dominant male. In this complex and evolving system there is still room for more strategies; there are males that never go to the feeding and growing areas. Instead, they mature sexually before growing. These are called precocious parrs (12 to 16 cm) that hide in the gravel awaiting the opportunity to mate with adult females returning from the feeding areas (Figure 6.9). Interestingly, when adults are not present the precocious parr fight among themselves and exhibit dominant/subdominant and submissive roles over the nesting territory similar to the adult males (García de Leániz, 1990; Esteve *et al.*, 2011b). Is this variety in male strategies a consequence of females choosing their mates? We can begin to answer this question by artificially removing female choice in a natural population and see what happens.

Better be Friends

At the UW Fisheries School we built a salmon female decoy using as a template a real chinook salmon (*Oncorhynchus tschawytscha*) we bought at the Seattle Market. Our dummy with the name of Messalina mimicked the posture (arched body and gaping

Figure 6.10 Messalina impatiently waiting for the males' arrival (Cedar River, WA, US).

jaws exaggerated) females have few seconds before spawning (Esteve, 2007; Figure 6.10). Messalina also had (i) a silent submarine vibrator inside her belly that made her constantly vibrate at 150 Hz (no perceptible amplitude); and (ii) a line attached to her tail that made the lower mid-section of her body tremble at amplitude of approximately 5 cm (4–7 Hz). Messalina was placed over a gravel area in the Cedar River, WA (USA) to which wild sockeye salmon had free access. Each time a male (regardless of his size and physical condition) came close we made Messalina vibrate using the line attached to her tail (mimicking the stimuli females provide just before spawning). A female providing any male those stimuli, independent of his size and physical condition, is thus a female that exhibits 'no choice'. The vibratory and trembling movements of Messalina elicited a total of 45 sperm emissions by five different males during the two one-hour trials (Figure 6.11). Similar results using dummies were already reported in the literature (Sato *et al.*, 1987, 1991 & 1994; Taukechi *et al.*, 1987) however, our study differed in that was performed in the wild without controlling male access. On the first trial, Messalina was surrounded by five males; on the second trial by at least by nine males. During the two hours of observation in both trials we did not record a single male fight. This non-aggressive behaviour persisted during the seconds before and after sperm emissions, contrasting with observations from all the other salmonine river spawning species observed to date (Esteve, 2005a). Before and between spawnings the males swam around Messalina, occasionally brushing their bodies along her body. On several occasions they performed quiverings. Frequently two, three or more males were present close to Messalina a few seconds before she initiated spawning. At no time did they show any indication of hostility against each other. A male courting a real female, on the contrary, courts and guards her in the seconds prior spawning.

Figure 6.11 Night is falling in the Cedar River, WA. Messalina keeps mating with any male approaching her regardless of his morphology and condition.

Any approach from another male at those times invariably results in a launching attack (Esteve, 2005a). The unusual results provoked in these trials allowed us to propose that males only fight because females discriminate whom to mate with. That is, if females did not discriminate against males, as in the Messalina case, males would be peaceful as there would be no reason to fight. According to this reasoning, male fighting may be the result of highly sexually motivated males not receiving the appropriate spawning stimuli from a female and consequently turning their sexual urges into aggression. Research on a number of species has identified that the line separating sexual and aggressive behaviours is a slim one and often both behaviours get triggered (Tinbergen, 1952). This explanation is weakened somewhat by the fact that Messalina, being a dummy, cannot mimic a real female's entire behavioural repertoire. A different way to test this hypothesis then would be to observe salmonine species that have no apparent female choice. Two such species are lake trout (*Salvelinus namaycush*) and whitefish (*Coregonus lavaretus*).

Lake trout spawn over gravel areas along lake shores; they swim slowly circling such areas accompanied by a variable number of males and release batches of eggs intermittently (Gunn, 1995). Only a few detailed studies describing lake trout spawning behaviour exist in the literature (Esteve *et al.*, 2008; Muir *et al.*, 2012, Binder *et al.*, 2015). No male–male fighting displays or actual attacks were reported in any of them (although Binder *et al.*, 2015 suggested some kind of choice may occur before reaching the spawning grounds). Whitefish, *Coregonus lavaretus*, are salmonids from the Coregoninae subfamily, known to spawn in promiscuity. There is only one paper in the English literature (to the best of my knowledge) describing in detail the actual behaviours leading to gamete release (Fabricius, 1954).

The following paragraph regarding the males' behaviour is from that paper:

> *They never showed any fighting, nipping, chasing, threatening or other aggressive behaviour. Actually, the whitefish seem to be the most peaceful species of fish we have ever watched (pp. 107).*

In both species, thus, the apparent absence of female choice is associated with peaceful males. Interestingly, both species spawn in still waters without building nests, which brings about the question of how the type of habitat has influenced sexual selection in salmonines.

The Velocity of Hate

Females of a hypothetical ancestral salmonid fish population spawning in a river could maximize their reproductive success by burying their eggs deep inside the gravel (build a nest) where they would be protected from predators and currents. There is, however, a cost to this behaviour. Firstly, the female needs to build a good nest, (i.e., minimum depth and shape), which takes time and energy (225–350 digging bouts Esteve, 2005a; Tautz & Groot, 1975). Secondly, given that building a nest is costly, it is logical that the female should lay the maximum number of eggs in one nest rather than laying a few eggs in multiple nests. This of course increases the risk that the female will lose all, or a large part of, her offspring in an accidental event (major floods, severe droughts, and predation). So the cost of nest building includes energy plus time consumption plus a high risk of losing progeny (compared to distributing the eggs across many sites). Numerous extant salmonine species build their nests in fast waters, indicating that the benefits outweigh the costs in many cases. As noted previously, salmonine males are individuals (usually) competing for sex. A male will monopolize as many females as he can so long as the costs of acquiring one more mate do not incur a decrease in his final number of offspring. Yet, a nesting female cannot be mated until she has finished her nest. This creates a time conflict because, unlike the female, males are not time limited but always ready for mating (Esteve *et al.*, 2009b). Furthermore, the success of a male depends on his proximity to the female at the time of egg release (Mjølnerød *et al.*, 1998); the male nearest male the female will fertilize more eggs. So males not only have to wait while the female digs her nest, but they have to fight to win and maintain the best position close to her. This is the dramatic history of the river spawning salmonids we have discussed in most of this chapter.

Let's turn now to our hypothetical fish population. Let's suppose that some of the fish have become trapped in a lake (land locked) and are able to live and spawn there. Given that there are no flowing currents in the lake, females who do not build nests will be favoured, as will females who spread the eggs intermittently across various locations because this minimizes the risks associated of having them together. Males seeking to mate with these females will now have to follow them. Males that fight instead of following itinerant females will lose reproductive opportunities. This is the actual history of lake trout spawning (Gunn, 1995) and may let us to infer the following: With the movement from running to still waters, intersexual sexual selection in salmonines was relaxed because the males now had to be constantly moving, tracking the female. This relaxation was reflected in the loss of characters involved in male aggression and female choice (bright colors, developed jaws and humps, etc.). Once male sexual characters disappeared, there was no selection against fish spawning during night time (reducing predation of diurnal species). This description matches lake trout and whitefish spawning behaviour (Gunn, 1995; Fabricius, 1954); which further allow us to infer that female movement prior to spawning is negatively correlated, at least in salmonids (and probably in other species), with the intensity of sexual selection. Itinerant females are followed by non-aggressive males. Static females generate male aggression.

Conclusions and Future Research

Several studies have highlighted the importance of female choice in salmonine reproduction (Schroder, 1981; Foote, 1989; Berejikian *et al.*, 2000; Gaudemar *et al.*, 2000; Petersson & Järvi, 2015). None of them, however, have made a connection between such choice and the females nest building velocity, nor have any of them balanced the relative importance of the two main components of sexual selection (choice and competition) as proposed herein. The observations with Messalina show that, in the absence of female choice, salmonine males do not fight, implying that fighting occurs because females discriminate the males they are mating with. By choosing partners, females incite males to fight, which, in turn, eliminates weaker individuals and thus guarantees that females make an accurate choice. The absence of male aggression in two salmonids known to spawn promiscuously (no obvious female choice) further supports this idea. One way to study this hypothesis is to place a brook trout (*Salvelinus fontinalis*) female (builds a nest, shows choice behaviour: Blanchfield, 1998) with several lake trout males (males follow non-nest building females). Hybridization between these two species occurs in nature (Berst *et al.*, 1981). The question to answer is whether there will be attacks between the lake trout males when placed with a gravid female that remains static over a nest without providing the sperm release stimuli to all males. The alternate pairing (brook trout males with a mobile, non-nesting lake trout female) can also provide useful information. Another very valid way to test this hypothesis will be to compare the spawning behaviour of populations within species that have adapted to lake spawning with river spawning populations.

For instance, female sockeye salmon (*Oncorhynchus nerka*) from populations spawning along lake shores (Quinn, 2005) apparently spread the eggs over the gravel without making nests (anonymous, pers. comm.). Do males compete with each other for access to these females? My hypothesis would predict that they do not fight. In fact, this hypothesis can be examined in any species in which males compete for access to females.

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7

Observations of Male Choice in Brown Trout (*Salmo trutta*) from Lar National Park, Iran

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Introduction

Male competition and female choice have been identified as the two major forces driving sexual selection (Andersson 1994). Numerous studies of both components have been reported in salmonines (Fleming & Reynolds 2004; Petersson & Järvi 2015). Considerably fewer studies have also described sexual selection in salmonines the other way around: male choice and female competition. Regarding male choice, there is selection for males choosing bigger females since fecundity is related to female size (Gaudemar 1998) and bigger females produce bigger eggs and dig deeper nests (Crisp & Carling 1989). However, in a system were the males can only inseminate one female at a time, female size is not the most important factor. Males can, in fact, optimize their potential reproductive success by courting females closer to egg release. Several works have demonstrated that males chose to court those females more actively involved in nest activities independently of their size (Schroder 1982 for chum salmon; Foote 1988 for sockeye salmon; Beall & Gaudemar 1999 for Atlantic salmon). Studies of female–female competition have also been described. Normally, females will compete for the best nesting territories and frequently will fight among themselves to occupy the best nesting sites (Esteve 2005). Alternatively, females have been described stealing nests from other females: female nest replacement (Van Den Berghe & Gross 1989). Here we will report for the first time, a different case of sexual selection in salmonines. We will describe recorded observations of male choice throughout intrasexual competition; that is a brown trout (*Salmo trutta*) male attacking one female chasing her away of her nest and 'choosing' to court another one. To do so, we will first introduce the status of

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brown trout in Iran making particular emphasis on the situation in Lar National Park. We will then describe the methods for recording the trout in the wild, write the results and discuss their significance.

Study Area and Methods

Brown Trout in Iran

In Iran, there are three basins hosting native brown trout populations, namely the Caspian Sea, the Urumieh Salt Lake, and the Namak Lake basins (Hashemzadeh *et al.* 2012). Brown trout is restricted to the southern Caspian Sea basin. Its populations in Iran are locally vulnerable and they had been exposed to restocking activities since 1983 (Abdoli 2000). The threats to the sustainability of the species in Iran are dam construction, pollution, rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) farming, habitat degradation, and overfishing.

In the Southern Caspian Sea basin, the Lar National Park (LNP) system including the Lar Lake, Dalichy, Absefid, Elarm, Kamardasht, Khoshkehrud and Lar Rivers provide a unique habitat for the brown trout (Figures 7.1–7.6). LNP is located in the North of Iran between Tehran and Mazandaran Provinces. Since the water resources of the park are exploited to supply the drinking water for the Tehran city, and due to the protected nature of the park, no industrial or agro-aquaculture activities are permitted in the area. Due to the noted reasons, wildlife and especially brown trout populations have a good portion of habitat, which is hard to find in other parts of the Caspian basin. The brown trout populations of the park had not been exposed to restocking activities before; hence they can be considered wild. The brown trout inhabiting the LNP have two forms of resident and lake run forms. The lake run forms migrate to the lake and return to the natal rivers as adults for spawning (unpublished data). The lake run individuals are phenotypically distinguishable from the resident ones. They are larger in size with fewer red spots, darker coloration, and more frequent star like black spots.

Filming the Trout

Recordings took place at the LNP during 26–29th November. Four GoPro cams were used to record the mating activities of different brown trout pairs at the Elarm, the Khoshkehrud and the Kamardasht Rivers. Based on distinct morphology, stream and lake residents were distinguished and in some cases spawning aggregations contained both types of trout (Figures 7.7 and 7.8). The following method was employed to film the fish: two groups of two people silently walked along the river bank; once a possible nesting female was located, the observers waited until they could confirm at least three *digging* episodes (female turns into one side and beats vigorously the gravel with her tail). Then one person entered the water and located the camera approximately 50–30 cm from the nest. After leaving the camera, the two people moved away from the area and returned two hours later to change the camera batteries. Here we will include only the results of one pair recorded at the Kamardasht River on November 29th during the period 13:19–14:24 local time (65 minutes). Other pairs recorded at the Elarm and the Khoshkehrud Rivers are only included as descriptive pictures as we failed to record the mating act and had problems related to camera failures.

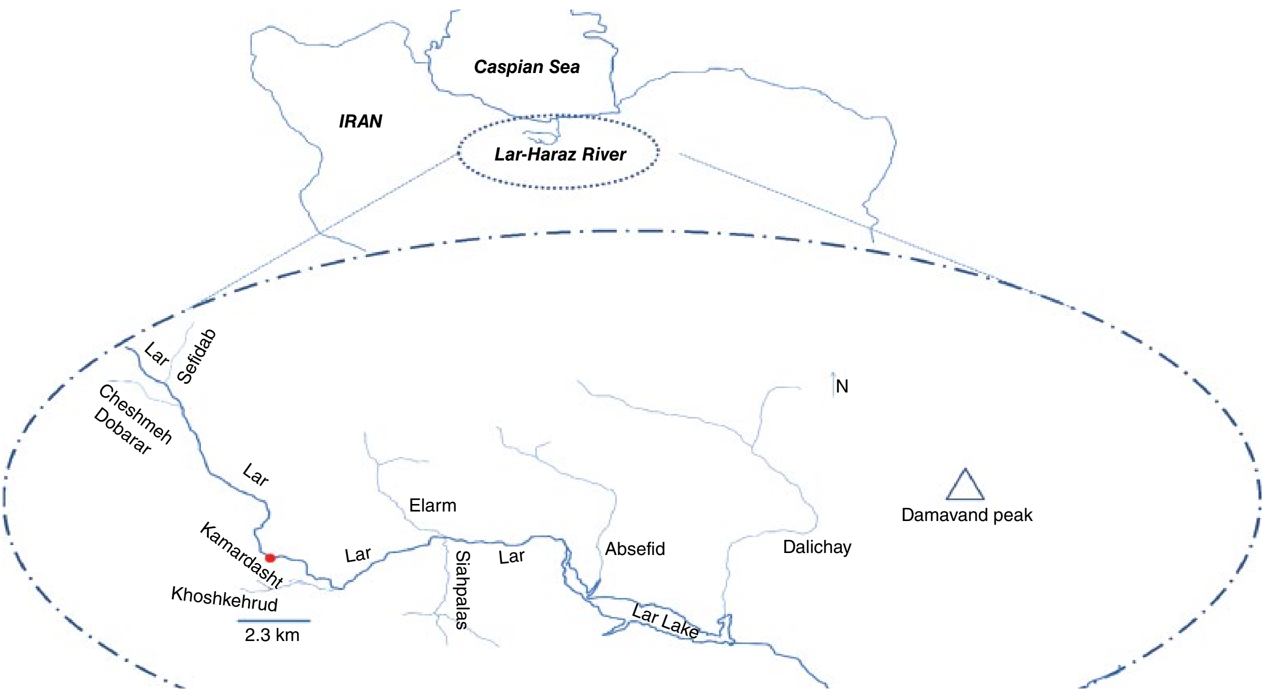

Figure 7.1 Map showing the study area.

Figure 7.2 Khoshkehrud River (LNP).

Figure 7.3 Elarm River (LNP).

Results and Discussion

The camera was positioned at the nest place at 13:15 (local time) and both fishes moved away upriver beyond sighting. Four minutes later the pair returned and resumed their spawning activities. For clarity purposes time will be set at this starting point as 00:00 (minutes: seconds); additionally to distinguish the fish, any pair consisting of a nesting female and a guarding and courting male will be named F (for female) and M (for male) followed by a number corresponding to the order of appearance on the screen (i.e. F1, F2...). The ethogram for the entire recording period is graphically represented in Figure 7.9.

Figure 7.4 Elarm River is a fabulous trout reproduction habitat with plenty of suitable spawning grounds. We witnessed several nesting females on November 26th.

Figure 7.5 Kamardasht River (LNP).

At 00:00 F1 and M1 (Figure 7.10), returned to the nest and resumed their spawning activities. F1 was approximately 20 cm in length and M1 14 cm (judged by the view of two independent observers). M1 was slightly darker than F1 and presented more spots along his body, but both fish were considered by the observers to be resident type. From 0:00 to 3:14 F1 performed five digging episodes. During this time interval M1 continually courted and guarded F1. To court her he performed continuous quiverings and crossover episodes and to guard her he performed fighting displays and actual attacks to any male approaching F1 (for a detailed description of courting and fighting displays see Esteve 2005).

Figure 7.6 Spawning grounds at Khoshkehrud River a few meters away from its spring source.

Figure 7.7 Details of resident brown trout pigmentation at LNP (Kamardasht River).

Figure 7.8 Details of lake brown trout pigmentation at LNP (Elarm River top, Kamardasht River bottom).

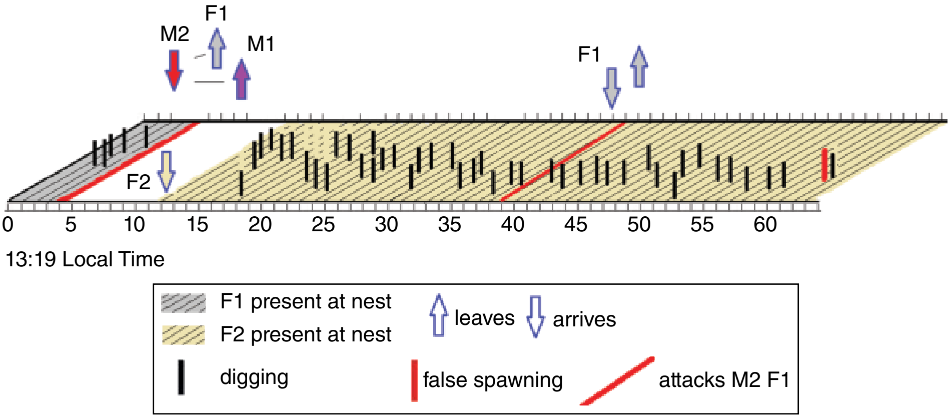

Figure 7.9 Ethogram showing recording history of the F1M1 and F2M2 spawning pairs at Kamardasht River; only attacks between M2 and F1 are included.

Figure 7.10 The F1–M1 pair.

Figure 7.11 M2 in parallel display with F1.

Overall, in this time interval a total of four other males approached the nest. Two of them were slightly smaller than M1 and were forced out by several fighting displays and by an actual attack from M1 to one of the males. The other two were juveniles in the parr stage that remained with their bodies pressed to the gravel and both M1 and F1 ignored both of them for most of the time. At 3:32 a new male M2 approximately 19 cm in length, came and place himself alongside F1 while maintaining the typical frontal display posture (Figure 7.11). Three seconds later, M1 managed to position himself between F1 and M2, but he was rapidly expelled from this position by a violent chase from M2. For the following 20 seconds M2 maintained a lateral display threat position to F1 and moved up and down with her, with both fish frequently appearing and disappearing off the screen. M1 remained during these seconds in a backward position and progressed from time to time to interchanged fighting displays with M2. One of those displays ended in a violent launching attack (a bite from M2 to M1) that resulted in all the fish moving away from the nest. Up to that moment, the displays performed by M2 towards M1 and F1 were apparently identical and in both cases seem to have an aggressive effect. At 5:40 M2 returned alone to the nest, establishing possession (Figure 7.9). During the following 6 minutes M2 interchanged periods of stay and absence of the nest.

During this time interval a few other males came to the nest and were chased away by M2. At 11:36 while being M2 on the nest a new female F2 arrived and occupied the nest (Figure 7.12). F2 was approximately the same size as M2 (19 cm length). She was slightly lighter and with fewer spots than M2 but again both fish appeared to be resident type. During the first 90 seconds F2 tested the nest suitability by using her senses of view and touch; she noticeably looked at the bottom with her body pointing downwards and she used her lower jaw against the substrate, possibly to feel the intergravel flow (Groot 1996). This exploratory behaviour probably indicated that the nest was not hers, meaning that she had not excavated in this nest before. At 13:15 she performed her first digging episode. At 17:02 M1 came and interchanged some lateral displays with M2 and both males bit eachother. The fight ended at 18.27 when M1 was finally expulsed by a launching attack with a bite (Figures 7.13 and 7.14). At 25:25 F2 performed her first

Figure 7.12 F2.

Figure 7.13 M1 bites M2.

Figure 7.14 M2 bites M1.

Figure 7.15 F2 digging, M2 on the background.

probing behaviour (the female presses her body to the bottom rising her tail and forcing her anal fin into the gravel; probing is indicative that spawning is close; Groot 1996).

From this point in time to the end of our observations F2 continually repeated the probing behaviour, normally followed by digging episodes (Figure 7.15). At 38:50 F1 came back to the nest. M2 rapidly positioned himself in parallel display with F1 and at 38:57 he bit F1 (Figures 7.16–7.18). For the following 10 seconds he repeated biting her until forcing her away of the nest. F1 was never seen again; for the next 22 minutes the M2 F2 pair resumed their courting and nest building behaviours respectively. At 61:23 both F2 and M2 remained pressed to the gravel while trembling their bodies and agaping their jaws in what is the typical spawning act description (Figure 7.19; Jones & Ball 1954). This behaviour lasted for two seconds and a sperm cloud was clearly visible on the screen. However, the fact that after this behaviour F2 remained in a probing position instead of performing the usual covering diggings, made us to think that we

Figure 7.16 M2 with F1.

Figure 7.17 F2, M2 and F1.

Figure 7.18 M2 bites F1.

Figure 7.19 F2 and M2 during the false spawning act recorded.

witnessed a *false spawning* (female mimics real spawning by agaping her jaw and trembling her body while maintaining a probing position, however she does not release eggs: Esteve 2007). False spawnings occur when at the last moment the female does not receive enough stimuli to reach a physiological threshold inducing *egg release*. This lack of stimuli can come from either the substrate (depth and shape: Tautz & Groot 1975) or from the courting male (Esteve 2007). The fact that at 61:39, F2 performed another building digging reinforces us to think that we witnessed a false spawning.

For the following 5 minutes the rate of male competition increased significantly and this prevented F2 to remain at the nest continually. Unfortunately, at 65:54 the camera battery died and we failed to observe the complete spawning process. Yet, our observations allow us to highlight several facts that have not been discussed before elsewhere. We have described for first time a coordinated male–female nest replacement. Regarding the male, M2 was observed twice attacking and forcing F1 away from her nest. For a male, attacking a female only makes sense if such a female is somehow preventing his immediate reproduction. Our results reinforce this idea. From 11:36 to the recording's end, F2 performed 43 digging episodes; if we assume that a nest needs on average 300 digging episodes to be completed (Esteve, Chapter 6, this volume) it means that F2 did only 14.3% of the nest building work (43/300). These numbers raise the question of why the nest stealing behaviour perpetrated by dominant males is not more common in salmonines, something that up to this day has not been fully investigated.

Esteve (Chapter 6) suggested that female choice in salmonines overrules male-male competition. Here we have recuperated the male's importance in salmonine reproduction by describing a new case of sexual selection. Our observations have indeed described for the first time a male–female cooperation in competition. Probably the relative importance of these two views is somewhere in between, and always changing subject to particular selection pressures. In any case, we hope that our study may lead other scientists to report similar cases in salmonines or in other species, as well to continue the growth of the sexual selection theory. Finally, today, as we are already well into the 21st century, and with a biodiversity crisis of unprecedented magnitude challenging our planet, we want to close this manuscript by highlighting the necessity of preserving areas as the majestic and pristine LNP and all its water bodies.

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8

Energetic Trade-Offs Faced by Brown Trout During Ontogeny and Reproduction

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Introduction

The life of higher organisms is divided into two parts. The first part is centred about procuring resources from birth to the approach of maturation for survival, growth and ultimately towards future reproduction. The second part is the reproductive period, centred on allocation of resources to achieve reproductive success, including resources necessary for initial survival of offspring. For iteroparous fishes, like brown trout, there is also the trade-off between present and future reproductive allocations that involve survival and growth between reproductive events. Living organisms can be seen as systems that convert energy into progeny (Wootton, 1998). Provided sufficient food consumption, energy can be used for maintenance and eventual surplus energy can be used for growth (energy storage or fat, growth of tissues) and reproductive investment (Sloat *et al.*, 2014). There is, however, also a clear cost of increased individual size as total metabolic energy requirements increase with body size (e.g. Elliott, 1994).

An individual's fitness can be measured by the number of surviving offspring in the next generation. The optimal energy allocation to reproduction at any given time therefore depends on the trade-off between the benefit in terms of number of offspring produced in the present and the cost in terms of survival to, and potential success in future breeding attempts (Williams, 1966; Stearns, 1992; Sloat *et al.*, 2014; Wootton & Smith, 2015). Two basic decisions are thus faced in regards to this trade-off: (1) At what age shall the individual brown trout mature? And (2) if an individual decides to reproduce, what proportion of available resources should be allocated to the reproductive attempt and to each individual offspring. There is a multitude of factors, each with its set of trade-offs (Figure 8.1), that determines the individual response to these questions.

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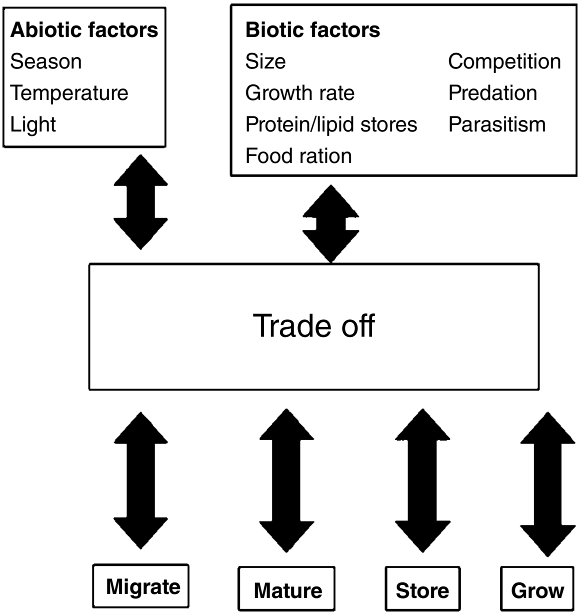

Figure 8.1 Overview of external factors affecting energy allocation into different purposes during the life of a brown trout. The factors interact in the individual use of energy into different processes.

The most energetically demanding period of life for many organisms is the reproductive period. In the pre-reproductive period, resources are diverted into metabolism and structural tissue. In the reproductive period, resources are diverted into necessary tasks for breeding, including the allocation of energy to breeding behaviour and sexual characters. Energy used in current reproduction detracts energy that that could be used to maintain the individual. The allocation of resources to current reproduction is therefore associated with residual life span (Williams, 1966; Hendry & Stearns, 2004; Sloat *et al.*, 2014). As each individual has a limited amount of total energy available, there are trade-offs in the allocation of resources between the different components associated with reproduction (Figure 8.2). The optimal solution to these trade-offs depends on a number of central biological characteristics of an individual, such as sex, size, age, condition, energy stores, reproductive system of the species, as well as timing of reproduction and the physical characteristics of the breeding site (e.g. Wootton, 1998; Jonsson & Jonsson, 2011; Sloat *et al.*, 2014; Barson *et al.*, 2015; Wootton & Smith, 2015). The interaction between conditional strategies, seasonality and genetics leading to maturation (e.g. Wootton & Smith, 2015) resembles the regulation of anadromy or residency in salmonid fishes (Dodson *et al.*, 2013; Kendall *et al.*, 2015) and there are many similarities. Brown trout are nearly related to many other species of fish and many aspects of brown trout energetics are shared by near related species. It is most closely related to Atlantic salmon (*Salmo salar*). These two species make up the genus *Salmo* (Webb *et al.*, 2007), one of several genera (e.g. *Oncorhynchus* (Pacific salmonids); *Salvelinus* (Char); *Coregonus* (Whitefish); *Thymallus* (Grayling)) in the family Salmonidae, which are a distinct group in cold freshwaters of northern areas (e.g. Jonsson & Jonsson, 2011). Because many genes and features are similar between these species a review of brown trout energetics must have a comparative perspective.

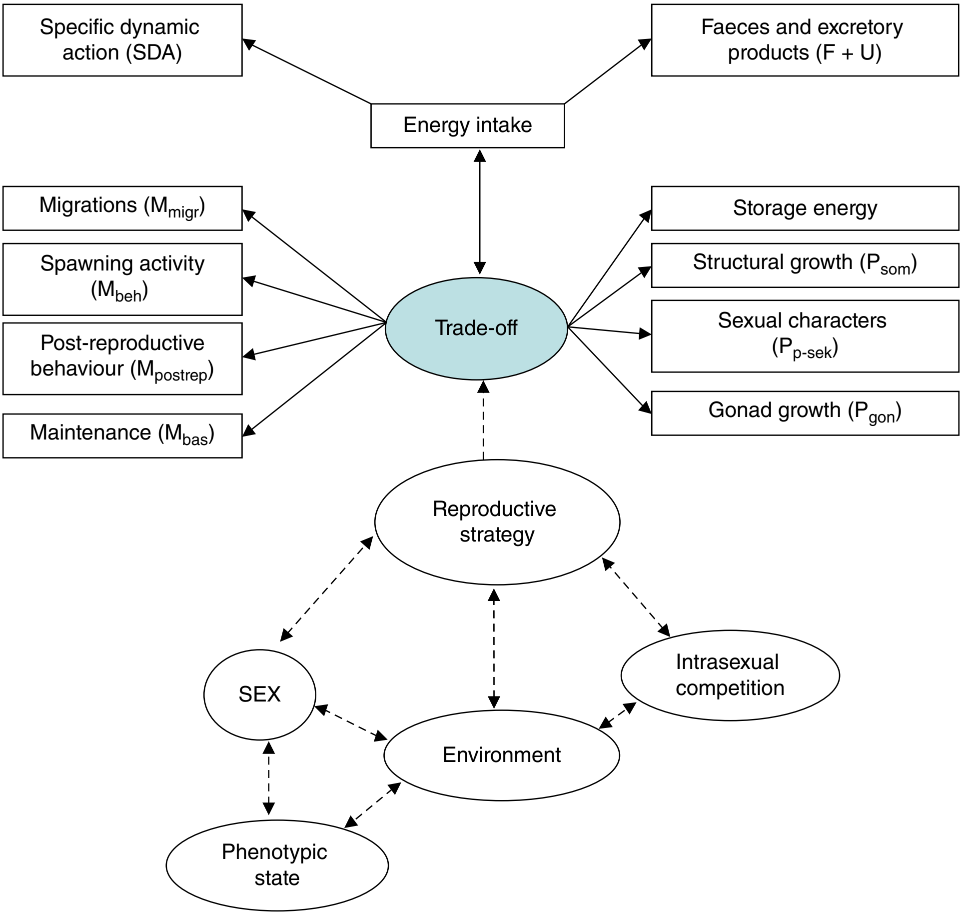

Figure 8.2 The limited energy available to the individual through food intake has to be allocated towards different tasks (solid lines) associated with both maintenance and growth. The trade-off between different allocation patterns is governed (stippled lines) by the reproductive strategy. The optimal trade-off between the different energy compartments depends on both the sex of the individual, various environmental characteristics and intrasexual competition for the access to partners as well as interactions between these factors. The phenotypic state compartment covers individual state like energy stores and growth rate.

The natural distribution of brown trout in the temperate zone is characterized by pronounced seasonal variation, with a marked summer and winter contrast in both abiotic and biotic conditions. Such temperate freshwater fishes are constrained by an upper lethal temperature limit and may also face challenges from the low water temperatures during long winter periods. For instance, the northward distribution of brown trout appears constrained by low temperature, low food availability and competition with Arctic char *Salvellinus alpinus* (Finstad *et al.*, 2011; Ulvan *et al.*, 2012). Within its core distribution area, brown trout experience marked seasonal variation in water temperatures that affects bioenergetic efficiency (Budy *et al.*, 2013) and they must therefore have a corresponding span in their temperature-dependent metabolic adaptations.

Bioenergetics provides a functional framework with a standardised, common energetic currency (kJg^{-1}) and balanced equations, suited to link physiological, evolutionary and ecological theory. In this chapter, we will focus mainly on the patterns of energy allocation associated with brown trout, although the modelling tools are universal (e.g. Elliott, 1994; Jonsson & Jonsson, 2011; Wooton & Smith, 2015). Our approach here is based on the framework of optimization models in the context of life-history theory, and how the optimal allocation pattern is influenced by various environmental factors and individual and population states. We start by outlining the basic principles of bioenergetics and how the energy budget of the reproductive expenditure may be modelled, before we discuss what factors affect these trade-offs.

Essential Bioenergetics

Bioenergetic studies involve the examination of energy gains and losses and transfer of energy within the organism or organ system (e.g. gonadal energy investment). Ingested energy is partitioned into the major physiological components according to the universal energy budget equation:

$$C = F + P + M + U$$

Of the energy consumed as food (C) some is lost in faeces (*F*), some is invested into the growth of somatic tissue and gametes (*P*), some is expended in providing energy for a range of metabolic processes, both basic metabolic rates and metabolic costs associated with activity and digestion of food (*M*). Production of new tissues includes both somatic growth, but also change in energy density. Changing energy density may influence somatic growth (see e.g. Canale & Breck, 2013) and may seriously affect the relationship between consumption (C) of energy and growth. Metabolism results in production of nitrogenous (largely ammonia) waste products in urine (*U*) (e.g. Wootton, 1998; McCormick *et al.*, 2013).

The different compartments of the original energy budget can be partitioned into different subunits. Under circumstances with no (negligible) nutritional intake and given no investment in structural somatic tissue as in brown trout, the total energy resources allocated to reproduction can be simplified:

$$P_{gon} + P_{sek} + M_{bas} + M_{migr} + M_{beh} + M_{postrep}$$

The energy invested in growth of reproductive tissue is divided into gametes (P_{gon}) and secondary sexual characteristics (P_{sek}). In addition to the basic metabolic demands during the reproductive period (M_{bas}), behavioural components associated with reproduction lead to increased metabolic costs associated with migration to breeding sites ($M_{mig\mathrm{r}}$), and reproductive behaviour once there, including defending of territories, courtship and mating (M_{beh}). Finally, there can also be increased metabolic costs associated with post-reproductive behaviour ($M_{postrep}$), such as parental care or nest defence. With no or insignificant nutritional intake, the energy invested into reproduction is reallocated from tissue stores of energy into somatic tissue or gametes. The costs of reproduction equal the difference in body energy content before ($E_{tot\ pre}$) and after ($E_{tot\ post}$) spawning.

$$E_{tot\,pre} - E_{tot\,post} = P_{gon} + P_{sek} + M_{bas} + M_{migr} + M_{beh} + M_{postrep}$$

When nutritional intake is considerable during the reproductive season, it in addition to stored somatic resources are used for reproduction

$$E_{net\,energy intake} + \left(E_{tot\ pre} - E_{tot\ post}\right) = P_{gon} + P_{s-sek} + M_{bas} + M_{migr} + M_{beh} + M_{postrep}$$

Energy has the benefit that it is given in a universal currency (1 cal = 4.2 J), where fat is assigned an energetic content of 39 $\mathrm{kJg^{-1}}$ (Jobling, 1983; 1994; 1995). This value is not precise, because energy content varies slightly between different lipid classes (Tocher, 2003), and a value of e.g. 36.4 $\mathrm{kJg^{-1}}$ has also been used. The highest lipid energy value is for saturated animal lipids and appropriate for trout, while the latter value is more appropriate for unsaturated lipids (Higgs *et al.*, 1995; Tocher, 2003). Freshwater trout will largely feed on terrestrial and freshwater lipid sources whereas anadromous trout will acquire lipids from marine sources with a higher content of unsaturated lipids (Tocher, 2003). Lipid stores can be assessed as either reversible lipid stores (largely non-polar lipids) or as total lipids including cellular membranes and nervous tissue. Membranes and nervous tissue are lipid-rich systems, where lipid stores are considered more or less irreversible. Protein is usually assigned an energy content of 24 $\mathrm{kJg^{-1}}$. It must be noted that this value is related to *dry* protein, whereas living fat-free tissue has a dry protein content of only 15%, with the rest being water. During starvation, the use of muscle protein thus provides less than 3.6 $\mathrm{kJg^{-1}}$, or less than a tenth of the energy available in fat stores.

Since there are limited resources to be invested into the different purposes, there is a trade-off in allocation of resources to the different parts of the energy budget. Energy budgeting during spawning has been examined for a number of species of salmonids. These species often rely completely on stored energy during reproduction as they may have both limited time and benefit from feeding while in the reproductive mode. Detailed reproductive energetic comparisons have been reported for a number of salmonid species (e.g. Gilhousen, 1980; Brett, 1995; Jonsson *et al.*, 1997; Hendry & Berg, 1999; Finstad *et al.*, 2002; Crossin *et al.*, 2004; Hendry & Beall, 2004; Kinnison & Hendry, 2004; Sloat *et al.*, 2014). For brown trout detailed comparisons can be found in Elliott (1994); Berg *et al.* (1998); Jonsson & Jonsson (1998); Berg *et al.* (2011) and Jonsson & Jonsson (2011).

Energetic Trade-Offs During Ontogeny

Brown trout have to cope with energetic trade-offs during ontogenetic development from egg to adult (Figure 8.1), as increased allocation of resources to one process necessarily diverts energy from others. Evolution will favour allocations that best combine somatic growth with energy stores to ensure survival in periods of energy limitation, and ultimately reproductive success.

Like other salmonids (Brannon, 1987; Heggberget, 1988), reproduction in brown trout is likely tuned in time and space to ensure favourable conditions for the emerging fry (Wootton & Smith, 2015). When salmonid fry emerge from the gravel, access to exogenous food resources is vital for survival and growth and thus the timing of the onset of exogenous feeding is important (e.g. Elliott, 1994; Skoglund *et al.*, 2012). An individual fish does not only need to grow in mass, but may also need to store energy for survival. An 'eco-genetic' model simulation of young temperate fish indicates that high risk of winter mortality and low predation select for high prioritization of energy storage (Ivan & Höök, 2015; Lori & Höök, 2015). The model was based on individual, density-dependent, energy acquisition and storage data with variable overwintering mortality and predation. Decreasing water temperatures is a typical signature of autumn and the forthcoming winter, which in northern or high elevation areas where brown trout occur, may last for more than six months. Seasonal patterns of storage by brown trout have been observed to change across latitudinal and altitudinal gradients (Berg *et al.*, 2011) and likely reflects contrasting thermal regimes, as observed in other salmonids (Bacon *et al.*, 2005; McMillan *et al.*, 2012). Seasonal adaptations are essential to understand patterns of growth and maturation in fish species living in temperate or polar zones. Allocation of resources involves diversions between different processes like growth and initiation of maturity. Such resource partitioning is dependent on a number of factors, such as sex and condition-dependent features like growth and body size (e.g. Jonsson & Jonsson, 2011).

Food and thus energy intake has to increase as a trout grows because of an increase in metabolic rate (M) with body mass (e.g. Wooton, 1998; Elliott & Hurley, 2001). The relationship between standard metabolism, R_S (which is an estimation of energy expenditure by a resting unfed fish) and fish mass (W) is typically described as $R_S = aW^b$, where both a and b are constants with the mean value of b typically around 0.86 (Wootton, 1998). Metabolism also varies in response to changing food levels and standard metabolic rate R_S of brown trout is flexible and can increase in response to elevated food levels. Those trout that have an elevated R_S also show the fastest growth, while growth at low food levels is highest among those individuals that depress their metabolic rate (Auer *et al.*, 2015).

Brown trout and Arctic char often co-occur in northern areas, and the two species appear to have quite different patterns of seasonal energy acquisition. Compared to Arctic char, brown trout have a higher energetic intake and are considered to be more aggressive with higher energy consumption. Brown trout are therefore unable to attain positive growth at as low a level of energy intake as Arctic char are capable of (Forseth *et al.*, 2003; Finstad *et al.*, 2011). The growth efficiency of brown trout is only about half that of Arctic char and Arctic char has nearly 50% efficiency over large parts of their thermal range (Finstad *et al.*, 2011). This difference in energy efficiency may explain why brown trout are not found in Polar and high altitude areas where Arctic char occur (Finstad *et al.*, 2011; Ulvan *et al.*, 2012). Ice cover provides shelter and may improve energetic status and broaden habitat use during winter (Watz *et al.*, 2016).

There is little evidence of local thermal adaptation in growth performance for brown trout, in spite of several investigations (Forseth *et al.*, 2009; Elliott & Elliott, 2010; Jonsson & Jonsson, 2011). Brown trout, however, will typically utilize different habitats and niches during their ontogeny and may thereby behaviourally adjust their thermal environment. Reproduction and early development are usually in running water, but on a seasonal basis, and as the trout grow, they may migrate into lakes and/or marine environments (e.g. Jonsson & Jonsson, 2011). There may also be a diet shift from e.g. benthic invertebrate feeding to piscivory (Jensen *et al.*, 2008; Vucic-Pestic *et al.*, 2010; Jensen, 2015). Morita *et al.* (2010) suggested a general pattern for fish, where optimal temperature for growth should decrease with increasing body size. The result was based on mass variation and growth maximization in the Beverton and Holt growth model. It was suggested that this pattern results in an ontogenetic change in thermal preference, where the larger individuals prefer cooler (usually deeper) lake water areas with increasing size, in order maximize growth performance. During juvenile growth, salmonid fish exposed to lowered temperatures tend to increase energy allocation to lipid stores, at a cost of somatic growth (Tocher, 2003). For fed juvenile brown trout (0+, 1+), their temperature preference is similar to their optimal growth-rate temperature, whereas for older fed juveniles their temperature preference is similar to their maximum food–growth conversion efficiency (Elliott & Derek, 2013).

The flexibility of physiological and ecological processes is a marked feature of brown trout biology and growth plasticity throughout life has been held as a major factor behind the invasive success of brown trout (Budy *et al.*, 2013). Brown trout 'appears to possess a genetic deck of cards from which any number of successful strategies for growth and life-history expression can be drawn given biota present and the environment' (Budy *et al.*, 2013). The conservation of genetic variability in e.g. seasonal energy store pattern is eased by central mechanisms in brown trout ecology like homing behaviour, habitat fragmentation and small population sizes which may maintain and increase brown trout variation and population persistence over time. Modelling of genetic variability persistence over time demonstrate that homing, fragmentation and small population size can be beneficial for maintenance of adaptive variability in the closely related brook trout (*Salvelinus fontinalis*) (Fraser *et al.*, 2014).

Food composition and availability varies markedly in temperate environments with marked consequences for brown trout energetics. Insects (larval and adult stages) are a major food source for trout (Budy *et al.*, 2013). Insect dispersal and their reproductive cycle often mean that adult aquatic insects live out of water during summer. Feeding patterns of brown trout therefore often display a shift from insect larvae and pupae in winter, spring and early summer to flying insects that land on the water surface, molluscs and permanent water living items in late summer (Milardi *et al.*, 2016). During autumn, as insect larvae grow in size, they often again play a larger role in the diet of brown trout (Elliott, 1994; Milardi *et al.*, 2016). Insect larvae and pupae have high energy content, with lipid content of around 20% of dry body-mass (Higgs *et al.*, 1995). With the seasonal change in temperature, light and composition of nutrition, one would expect strong seasonal cycles in brown trout energy storage. Lipid stores in trout increase markedly with decreasing water temperatures or winter length, and lipid stores become a major energetic pathway in low temperature environments (Figure 8.3; Berg & Bremset, 1998; Berg *et al.*, 1998; Berg *et al.*, 2001; Berg *et al.*, 2011). The pre-winter lipid stores of brown trout in Norway were 30% higher in northern rivers (71°N) experiencing longer winters compared with those further south (58°N) where winters were shorter (Berg *et al.*, 2011). A similar pattern was seen along altitudinal gradients, where high altitude trout experienced longer winters and had higher lipid stores in autumn (Berg *et al.*, 2011). Trout living in lakes during winter may have more abundant feeding opportunities and experience higher water temperatures and therefore have higher energy levels (Figure 8.3 upper part) in contrast to trout living in riverine conditions during winter (Figure 8.3 lower part). A marked feature of brown trout is its feeding flexibility with increasing body size and therefore its growth plasticity across the life span in different environments (Budy *et al.*, 2013).

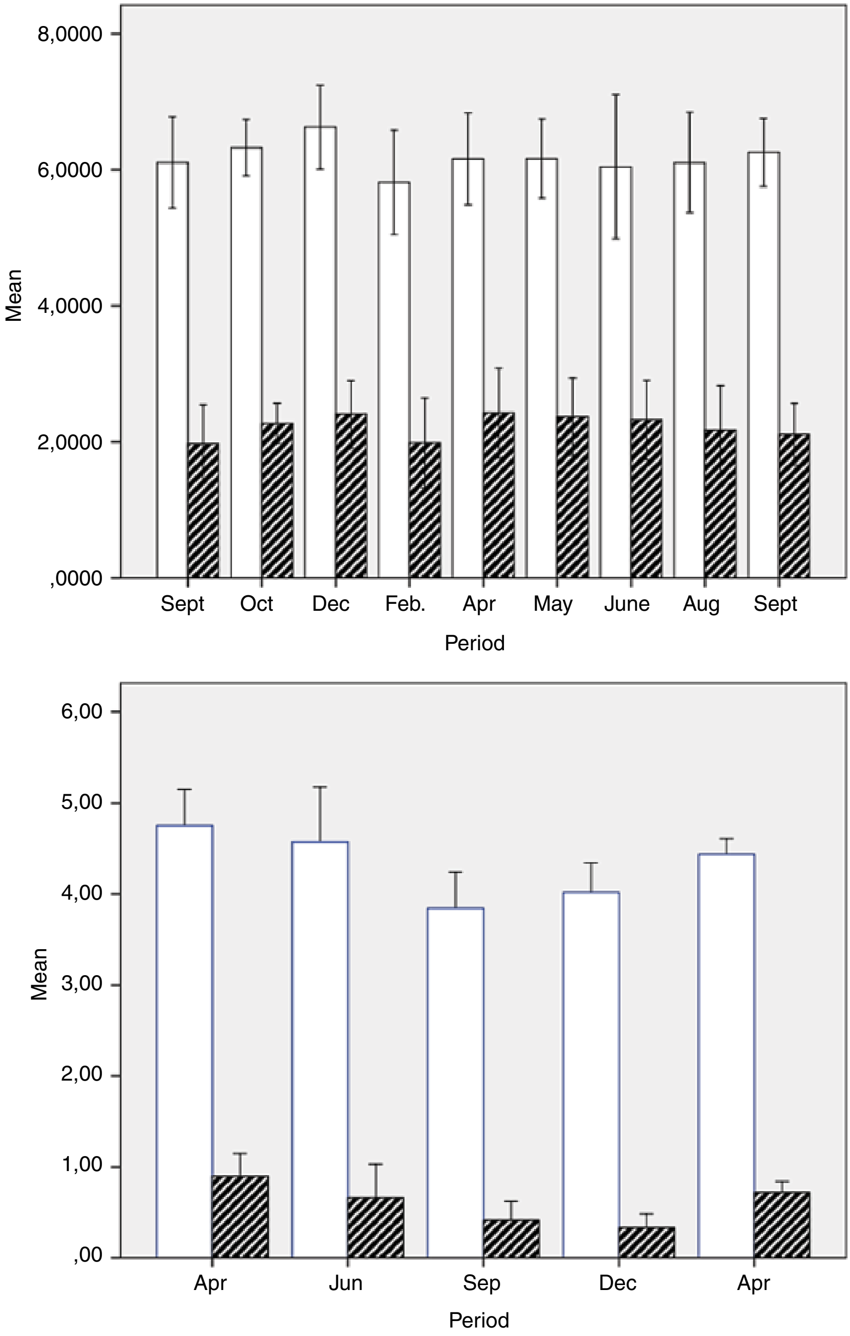

Figure 8.3 Annual cycle of specific energy (kJg^{-1} – open bars) and specific fat energy (kJg^{-1} – shaded bars) for immature trout in a temperate lake (upper graph) and a river (lower graph). Notice the that brown trout parr living in the river have lower mean energy content than those living in the lake and relatively greater seasonal changes in energy content. Data are from Berg & Bremset, 1998 and Berg *et al.*, 1998.

Allocation of Energy Resources in Reproduction

Size and Age at First Maturity – Reproductive Strategies and Tactics

The onset of maturation represents a major transition in life. From a situation where energy, time and matter have been allocated to growth and survival, resources are (re-) allocated to reproduction, usually in direct opposition to growth and survival.

Life-history theory provides a framework to predict life time allocation patterns, given defined environmental effects on age-specific mortality, growth and fecundity. It is assumed that selection processes favour genotypes that have age-specific energy allocation patterns that generate the highest per capita number of offspring, relative to other genotypes in the population (e.g. Charnov & Schaffer, 1973; Stearns, 1992; Schaffer, 2004; Jonsson & Jonsson, 2011). Age and size at maturity in brown trout varies between sexes, with males usually maturing at a younger age and more variable size than females (reviewed by Jonsson and Jonsson, 2011). A common phenotypic response to environmental change that increases growth of a fish, brown trout included, is a decrease in the age and or size at maturity (Alm, 1959; Klemetsen *et al.*, 2003; Sloat *et al.*, 2014). With higher growth rate the predicted current reproductive output in both energy terms and in number of gametes increases compared to slower growing individuals (Wootton & Smith, 2015). In the closely related Atlantic salmon, the reaction norm between growth rate and maturation was investigated by manipulation of water temperature and food composition. Increased temperature led to increased growth and earlier maturation. Extra energy intake reduced age at maturity in an additive effect, more than the effect caused by growth alone (Jonsson *et al.*, 2013). Trout exhibit a wide range of body-length at maturation with the reported minimum adult size at the onset of maturity for brown trout of 8–9 cm (7–8 g) (Klemetsen *et al.*, 2003; Jonsson & Jonsson, 2011), with maturing individuals exhibiting high lipid levels (Table 8.1), typical for maturing fish (e.g. Sloat *et al.*, 2014). Maturing salmonids, brown trout included, appear to have a similar combination of genetic factors and conditional states that interact to affect their decision/switch to mature or not (Sloat *et al.*, 2014).

In situations with lowered energy reserves, reproducing fish may respond by decreasing their allocation of energy into reproductive tissues (e.g. Berg *et al.*, 1998; Lambert & Dutil, 2000; Sloat *et al.*, 2014). An alternative strategy is to maintain reproductive investment at the expense of somatic condition or energy and thereby increase the risk of mortality due to exhaustion of energy resources.

Among the *Salmonidae* fishes, brown trout is one of the species that exhibits the most complex variation in sympatric migration strategies, expressed as a migratory 'continuum' (Boel *et al.*, 2014), but where those with lower lipid stores have shorter migratory distances compared with long-distance migrants (Boel *et al.*, 2014). This corresponds well with lipid density differences between the long-migrating Atlantic salmon (*Salmo salar*) smolts, which have a 2.4 times higher energy density than trout smolts (Jonsson & Jonsson, 2005). In anadromous brown trout, increasing parr growth is related to decreased sea age at maturity in contrast to Atlantic salmon (Jonsson & Jonsson, 2011). Moreover, high lipid stores may reduce the migratory tendency of brown trout. For instance, in rearing-facilities aiming to produce anadromous brown trout smolts, it is recommended that feeding be greatly reduced (by 50% or more) over several months prior to the migratory period to enhance migratory behaviour because rapidly growing individuals tend to become

Table 8.1 Trout male and female gonadal investment (mean ± SD) in GSI, mass specific energy or mass specific fat energy content for different maturation stages. For salmonids a scale 1–7 is often used to determine sexual maturation stage (e.g., Lagler, 1968), where 1 and 2 are immature with both testes and ovaries having a length less than half of the body cavity. Stage 3 indicates developing gonads where the gonads fill about half of the body cavity, whereas stage 4 have ovaries occupying about 2/3 of the body cavity. Stage 5 trout have gonads filling the length of body cavity, stage 6 are spawning with ripe running gonads and stage 7 are spent. GSI is based on the relationship, gonadal mass (energy)/net body mass (energy). Data are from an annual energy investigation of trout from a small mid Norway lake (Berg *et al.*, 1998).

Maturation stage							
	1	**2**	**3**	**4**	**5**	**6**	**7**
Male (N)	29	7	36	13	27	48	23
Specific energy (kJg^{-1})	5.7 ± 1.2	6.4 ± 0.5	6.1 ± 0.6	6.1 ± 0.6	5.9 ± 0.9	5.7 ± 0.7	5.6 ± 0.7
Specific fat (kJg^{-1})	1.8 ± 0.6	2.5 ± 0.3	2.3 ± 0.6	2.4 ± 0.6	1.6 ± 0.4	1.7 ± 0.4	1.6 ± 0.7
GSI	0.003 ± 0.005	0.001 ± 0.001	0.006 ± 0.006	0.006 ± 0.006	0.02 ± 0.01	0.03 ± 0.02	0.004 ± 0.003
GSI (energy)	0.007 ± 0.008	0.02 ± 0.05	0.007 ± 0.005	0.005 ± 0.005	0.03 ± 0.03	0.03 ± 0.01	0.007 ± 0.006
Length (mm)	170 ± 36	196 ± 27	201 ± 27	226 ± 17	208 ± 37	212 ± 30	206 ± 38
Female (N)	38	23	47	3	17	39	32
Specific energy (kJg^{-1})	6.2 ± 0.6	6.5 ± 0.5	6.2 ± 0.6	6.5 ± 0.6	6.7 ± 0.6	6.5 ± 0.9	5.3 ± 0.8
Specific fat (kJg^{-1})	2.2 ± 0.4	2.5 ± 0.5	2.4 ± 0.5	1.5 ± 0.6	1.2 ± 0.6	1.4 ± 0.7	1.6 ± 0.6
GSI	0.006 ± 0.03	0.009 ± 0.02	0.014 ± 0.016	0.105 ± 0.067	0.17 ± 0.06	0.14 ± 0.06	0.011 ± 0.005
GSI (energy)	0.01 ± 0.04	0.006 ± 0.003	0.11 ± 0.012	0.18 ± 0.13	0.30 ± 0.09	0.22 ± 0.11	0.010 ± 0.007
Length (mm)	157 ± 28	194 ± 19	214 ± 23	228 ± 43	229 ± 19	255 ± 19	235 ± 20

resident (Davidsen *et al.*, 2014). A review of the liability of anadromy versus residency in the closely related rainbow trout suggests that similar composite mechanisms related to partial migratory behaviour may be at work (Kendall *et al.*, 2015).

In the sister species, Atlantic salmon, a sex-dependent dominant locus controlling age at maturity has been described (Barson *et al.*, 2015). Age (and size) of maturity is often different between males and females, and the sex-dependent dominant locus can explain how selection on complex traits like age at maturity functions. The locus has a wide distribution in vertebrates and the same locus has also been found in humans, where it appears to have a major effect on the sexual differentiation between males and females. The locus VGLL3 may further serve to regulate the interaction between fat reserves (adiposity) and maturation in both salmon and humans (Barson *et al.*, 2015). It is therefore a strong candidate for improved understanding of the genetic control of condition-dependent initiation of maturation in brown trout.

Male and Female Allocation Patterns

Male and Female Sex Roles and Investment

Fishes as a taxonomic group (e.g. Hickman *et al.*, 2004) shows a wide array of different sex-dependent reproductive allocation patterns of energy and matter. Breeding systems reflect the degree of parental care and sexual selection, including the number of mates an individual acquires per breeding attempt, and the conflicting interests of the two sexes. In brown trout, males compete for access to ripe females (e.g. Sloat *et al.*, 2014). For both sexes, the operational sex-ratio (ratio of sexually active females to males) characterises the intensity of both inter- (e.g. mate choice) and intrasexual (e.g. male-male competition) selection (Fleming & Reynolds 2004). Associated with this, we expect energy dependent differences in mating behaviour to occur.

Investment in Gonads, Secondary Sexual Character and Breeding Behaviour

The production of tissues in an organism is typically classified in reversible somatic tissue (P_s) and released gonadal tissue (P_r). The universal energy budget illustrates the typical allocation conflict between these two sources:

$$P_s + P_r = C - (F + U + M)$$

Provided that the other components of the energy budget remain unchanged during the reproductive period, P_s and P_r can be considered as directly competitive processes for resources.

The egg production of females represents a large energetic investment compared to the male sperm production. Females typically produce energetically expensive eggs (e.g. Kamler, 1992), which are high energy packages for embryo development until the offspring are ready for initiation of exogenous feeding. The eggs of brown trout, like that of other salmonids, are typically large and lipid rich (Tocher, 2003), with reported values of neutral lipids that function as energy stores of about $1.4\,\mathrm{kJ\,g^{-1}}$ (Table 8.1). This contrasts with many other fish species that spawn small eggs in which polar lipids, essential for building of cell membranes and nervous tissues, dominate (Tocher, 2003).

Investment into egg production will have a direct influence on the number of offspring a female may produce and this typically increases with female body size. Furthermore, this number will be affected by egg size/quality, which affects offspring fitness, given that there is a limited amount of energy available for egg production (i.e. a trade-off between egg size and number). Trade-offs related to investment into individual progeny (Smith & Fretwell, 1974; Einum & Fleming, 2000; Einum *et al.*, 2004), including the conflict between egg size and number, will be treated in more detail later. During reproduction, females will also be expected to invest into an array of traits (e.g. behaviour such as nest construction) to ensure breeding success (e.g. Fleming & Reynolds, 2004).

Aside from the covering of eggs in the nest following oviposition, brown trout are not known to provide any other post-reproductive activity to protect offspring, such as nest guarding. Post reproductive activity in the form of parental care, however, is quite common in fishes and exists in 21% of families of bony fishes, with female only care being the rarest form (7% of the families with parental care) (Gross & Sargent, 1985; Wootton & Smith, 2015). This investment in the progeny after fertilization can further increase by the involvement by both sexes in the post-fertilization process of protecting and/or bearing the progeny. These post-fertilization processes may involve males or females or both and these processes may confound the typical male and female sex roles and reproductive budget associated with reproduction. Among the *Salmonidae* fishes, the only known examples of such post-reproductive activity is seen in the semelparous Pacific salmon (*Oncorhynchus*), which provide short-term, post-spawning guarding of their nests (Quinn, 2005).

For salmonid fishes, the male mass specific gonad energy is between 3.0 and 6 $\mathrm{kJg^{-1}}$ and that of the female is typically below 7.0 $\mathrm{kJg^{-1}}$ (e.g. Hendry & Berg, 1999; Berg *et al.*, 1998; 2001; Jonsson & Jonsson, 2011). Gonadal energy content values at various stages of maturation for brown trout from a stunted population (Berg *et al.*, 1998) are given in Table 8.1. While gonadal energy density may be similar for the two sexes, gonad size and therefore energy and matter stored in gonads is greater for females (see investment/GSI). The total gonadal energy of male brown trout is around 30 kJ or about 15% of that of females (about 180 kJ) of a similar body size (Berg *et al.*, 1998). The costs of constructing gonadal tissue (e.g. production costs of DNA), may be higher for many small gametes (sperm) than a few large gametes, but the degree to which this affects the difference in the gonadal energy budget of the two sexes is unknown as the energetic costs of spermatogenesis have not been quantified in fish (Wootton & Smith, 2015). There are suggestions that sperm production may be limiting to male reproduction and that males can become sperm-depleted. Females may therefore distribute their eggs among males (Wootton & Smith, 2015). Furthermore, energy allocation to gonads is likely to be traded off against other reproductive investments, such as secondary sexual traits, courtship, mate choice, nest preparation and intrasexual competition.

In order to increase the number of potential matings and thus reproductive success, males regularly invest in secondary sexual characters which include breeding colours, a hooked extension of the lower jaw (kype), thickening of the skin, and adipose fin enlargement (Fleming & Reynolds, 2004; Jonsson & Jonsson, 2011; Wootton & Smith, 2015). The secondary sexual characters may be used as weapons or in defence against other individuals (intrasexual competition) or as attractive ornaments (mate choice) (e.g. Dugatkin & FitzGerald, 1997; Fleming & Reynolds, 2004; Jonsson & Jonsson, 2011). Sexual selection for such traits that enhance mating success often acts more strongly on males

(Darwin, 1871; Anderson, 1994; Fleming & Reynolds, 2004; Jonsson & Jonsson, 2011) and results in pronounced sexual dimorphism. Moreover, as a result of such sexual selection, males appear to invest more of their energy budget into secondary sexual characters and mating behaviour than females, which invest more heavily in gonads. This sex dependent behavioural component of the reproductive effort of brown trout has still not been assessed.

Breeding Costs and Survival

What amount of energy should an individual invest in each reproductive event? The conflicts between current investment and future reproductive output are illustrated by the balance of bioenergetic equations, where increased allocation to one purpose will to a certain degree reduce residual energy available for other purposes. Numerous studies based primarily on birds and mammals, have generally shown a negative relationship between the investment of resources into current reproduction and parent survival until further reproduction or future fecundity (e.g. Stearns, 1992; Daan & Tinbergen, 1997; Berg *et al.*,1998; Ruusila *et al.*,2000; Lambert & Dutil, 2000). This principle has also been illustrated in a large number of empirical brown trout studies (Jonsson & Jonsson, 2011). For example, in an allopatric population of brown trout it was observed that first time spawners typically invested relatively little energy into current spawning, whereas repeat spawners invested more with a lower survival after spawning as a result (Berg *et al.*, 1998). Organisms may allocate such a high amount of resources and energy in current reproduction that further life is corrupted; this is called semelparous reproduction. Semelparous organisms reproduce by a single reproductive act, represented by e.g. many plants and insects, and a few vertebrates, notably fishes among the Anguillidae (eels) and Salmonidae of the genus *Oncorhynchus*. The majority of fish species, brown trout included, may reproduce repeatedly. Repeated reproduction is termed iteroparity (from the mathematical process of iteration – repetition of a process). The positive correlation between increased energy use in reproduction and mortality, yields an almost continuous scale for iteroparous spawners, where the semelparous situation represents an endpoint of the iteroparous spectrum in which the use of energy and matter in current reproduction is maximized.

Among the Salmonidae fishes, the different species fall into a reproductive allocation gradient of energy and matter. These species are often used as examples of life-history traits and phylogenetic constraints in the use of energy in reproduction. An extensive review of the topic is given by Kinnison & Hendry (2004). Semelparity is generally found in Pacific salmonids (genus *Oncorhynchus* spp. with iteroparous exceptions: e.g. rainbow trout (steelhead) (*Oncorhynchus mykiss*) and cutthroat trout (*Oncorhynchus clarkii*)). Semelparity appears to be connected to population parameters such as low prespawning adult survival and high juvenile survival (e.g. Groot & Margolis, 1991; Quinn, 2005). Iteroparity may have a benefit in unpredictable environments, where reproduction may be risky, increasing the value of future reproductive efforts. In such environments, the conflict between current reproductive effort versus survivorship of adults between successive breeding events, should be more evident than in less extreme environments (Sibly & Callow, 1986; Wootton, 1998; Schaffer, 2004). Semelparity may sometimes represent a discrete genetic innovation, but the difference between the Pacific semelparous salmon species and other iteroparous Salmonidae species appears to be a difference in degree of energy allocation and not a deeper fundamental difference (Kinnison & Hendry, 2004). In addition to the common phylogenetic relationship, parallel evolution seems to have contributed strongly to the suites of traits found within the different species, as both *Oncorhynchus* spp. and *Salmo* spp. have populations that are predominantly non-anadromous and iteroparous, whereas the anadromous populations of the Pacific salmonids are predominately semelparous. This indicates that parallel and convergent evolution have contributed to the current situation. Thus semelparity in salmonids is not necessarily a matter of shared ancestral history as it is a diversity of convergent life histories that arose in each genus (Kinnison & Hendry, 2004; Quinn, 2005). Trout in both the genus *Salmo* and the genus *Oncorhynchus* are iteroparous where brown trout is a typical iteroparous species.

Egg

Typical ovaries are either single or double structures, with or without symmetry. The anatomical features of different taxonomic groups have been reviewed by Bond (1996). The teleost egg normally consists of 20–40% dry matter (mostly protein and lipid) with corresponding energy content within the range 5–8 $\mathrm{kJ\,g^{-1}}$ (e.g. Jobling, 1994). There is little synthesis of yolk in the ovaries or oocytes, and the liver is the major site of the production of vitellogenin, which is transported in the bloodstream from the liver to the ovaries. In salmonids, for example, the diameter of the oocyte may increase a million fold in volume from 50 μm to approx 5 mm during the course of vitellogenesis (Jobling, 1994; Wootton & Smith, 2015). Kamler (1992) provides a review of inter- and intra-specific and intra-individual differences in egg sizes and egg composition among a wide array of fishes, where brown trout egg size represents an example of large eggs (Jonsson & Jonsson, 1999; Jonsson & Jonsson, 2011). Protein and lipid composition of brown trout eggs may vary according to migratory/resident life-history (Jonsson & Jonsson, 1999; 2011), repeat breeding (Jonsson & Jonsson, 2011), relationship between hatching time and water temperature (Jonsson & Jonsson, 2011) and environmental predictability/unpredictability (Einum & Fleming, 2004).

Testes

Like the ovaries, the typical testes are either single or double structures, with or without symmetry. The anatomical features of different taxonomic groups have been reviewed by Bond (1996). Testes size may vary widely both absolutely and relative to body size. In contrast to females, where usually an increase in number of eggs is directly correlated with an increase in fitness, there is usually no such direct correlation between gonad size and fitness in males. In brown trout, testes increase with male size (Jonsson & Jonsson, 2011). In addition to testis size, sperm may have different density and motility (Jonsson & Jonsson, 2011). Proximity to the female at spawning, intra- and inter-sexual selection including sperm competition and position of other males are other important factors determining fertilization success (Wootton & Smith, 2015).

Allocation of Resources to Individual Progeny

The amount of energy that the female invests into each single offspring may have pronounced effects on fitness (Bagenal, 1969, 1978; Crespi & Semeniuk, 2004). In oviparous fishes, a critical aspect of maternal provisioning (Bernardo, 1996) is the size and energy content of eggs. Juveniles originating from larger eggs are larger, and typically have higher growth, survival, and fitness (Hutchings, 1991; Roff, 1992; Ojanguren *et al.*, 1996; Einum *et al.*, 2004; Rollison & Hutchings, 2013 a, b; Florø-Larsen *et al.*, 2015). Thus, all else being equal, selection acting on offspring fitness should normally favour large, energy-rich eggs. However, from a maternal fitness perspective there will be a trade-off between egg size and number given limited resources available for egg production.

As a result, mothers and offspring are often in conflict as to the optimal amount of allocation into individual eggs (Crespi & Semeniuk, 2004; Wootton & Smith, 2015). From an evolutionary perspective, females should maximize their own fitness rather than that of their individual offspring. The distinction is important because maternal fitness is the product both of offspring fitness and the number of offspring produced (Einum & Fleming, 2000; Einum *et al.*, 2004). As such, the optimal egg size from the mother's perspective is that at which the increase in offspring fitness with a further increase in egg size, no longer exceeds the increase in maternal fitness that would attend the same proportional investment into egg number (Smith & Fretwell, 1974; Trivers, 1974; Mock & Parker, 1997; Einum & Fleming, 2000; Rollinson & Hutchings, 2013b).

Variation in egg size has been shown to have a genetic and environmental basis (Thorpe *et al.*, 1984; Jonsson & Jonsson 2011; Wootton & Smith, 2015). Among salmonid fishes, variation among populations can be large, and has been explained by reference to selection imposed by incubation temperature (Fleming & Gross, 1990; Jonsson & Jonsson, 1999), gravel size (Quinn *et al.*, 1995), and migration distance (Beacham & Murray, 1993). Variation within populations has been explained in some cases as a plastic response to growth conditions experienced by females during early life (Jonsson *et al.*, 1996; Lobon-Cervia *et al.*, 1997). In other cases, environmental quality parameters may vary between spawning habitats, and egg size may vary as a consequence of female phenotype (e.g. body size) due to the ability to access differing habitats (Einum & Fleming, 2002; Skoglund *et al.*, 2012; Rollinson & Hutchings, 2011 a,b; 2013 a; Reginier *et al.*, 2013). A promising further development, still in early stage, is the linking of watershed and habitat characteristics on genetics, production, energetics and reproductive characteristics of brown trout (e.g.Foldvik *et al.*, 2016; Östergren *et al.*, 2016).

Final Remarks

Reproduction can be regarded as the most important and interrelated process in living creatures, and most of the different processes an organism has evolved, have a direct or indirect involvement with reproduction. In this chapter, we have focused on factors governing energy transfer through different life stages in different environments. As illustrated by bioenergetic principles, each individual must make trade-offs between investing energy into the various tasks during ontogeny and subsequently associated with reproduction. A range of interacting abiotic (watershed characteristics etc.) and biotic factors, including competition, individual characteristics such as sex and phenotypic state, intrasexual competition, as well as environmental factors affecting growth and survival, will determine the optimal energy allocation pattern. Energy allocation patterns associated with reproduction vary accordingly. Bioenergetics yield a general currency where scientists with diverse backgrounds such as physiologists, behavioural ecologists and evolutionary biologists can find a common platform to develop understanding of the processes and interactions that determine the life of brown trout from egg to death.

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9

Impact of Embeddedness on *Salmo trutta* at Different Periods of their Early Ontogenesis

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Introduction

Over the past decades, anthropogenic activities as mining, forestry, intensification of agricultural practices or road construction have greatly favoured land erosion leading to an increase in fine sediments loading and deposition in salmonids streams (reviewed by Waters, 1995; see also Allan *et al.*, 1997; Sidorchuck & Golosov, 2003). River substratum granulometry may also be affected by climate change through the impact of pluviometry on hydraulics and watershed soils erosion (Scheurer *et al.*, 2009), while dams have a strong effect on sediment transport through sediment retention and change in water velocity (Wohl, 2012).

Fine sediment deposited on the riverbed can have deleterious effect on salmonid young stages. In trout streams, heterogeneous particle sizes cover the bottom surface with a majority being coarse gravel and pebbles, which provide suitable environment for females to reproduce. Eggs are buried under 10–15 cm of this substratum and the embryo-larval development occurs under gravels. Just before total yolk sac depletion, fry emerge from the gravels to settle on a territory. A number of studies have investigated the effect of embeddedness on the survival rate at emergence, showing an increase in mortality with the increase of fine sediments accumulation within the redd (reviewed by Chapman, 1988; Crisp, 1993a; Waters, 1995; Kondolf, 2000; Lapointe *et al.*, 2004; Suttle *et al.*, 2004; Meyer *et al.*, 2005). By filling the interstitial spaces between gravels, fine sediments reduce the rate of water renewal (which decreases oxygen water supply to embryo-larvae and the dispersal of toxic metabolic waste), and mechanically prevent the emergence of fry from the redd (Coble, 1961; McNeil, 1962; Silver *et al.*, 1963; Hausle & Coble, 1976; Chapman, 1988; Crisp, 1993b; Rubin, 1995; Rubin & Glimsäter, 1996; Massa, 2000; Guerrin & Dumas, 2001a,b; Ingendahl, 2001).

After their emergence from the gravels, juvenile trout growth and survival remain closely dependent on the substratum quality. Indeed, interstitial spaces offer small fish refuges against predation (Jenkins, 1969; Heggenes, 1988) or flood events (Good *et al.*,

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

2001), while stony coarse substrata increase visual isolation between individuals and contribute to reduce the size of fish territories (Kalleberg, 1958; Imre *et al.*, 2002). In addition, stones provide foraging sites and shelters for invertebrate populations, the main food supply for juvenile salmonids (reviewed by Cordone & Kelley, 1961; Chutter, 1969; Waters, 1995).

Despite this strong link between substratum and salmonids juvenile stages, little is known concerning the effect of embeddedness on their survival and behaviour in the wild, when compared to embryonic stages. One explanation is that mortality rates due to embeddedness at the embryonic stage are high and quite easy to measure. Indeed, embryonic stages are confined to the redd, which is limited and well defined in space, whilst distribution of juveniles is larger. The impact of habitat quality on their fitness (survival and growth) is then much more difficult to appraise owing to emigration processes.

A few studies provided evidence that embeddedness decreases growth and survival of juvenile salmonids and increases fish emigration (Bjornn *et al.*, 1977; Crouse *et al.*, 1981; Suttle *et al.*, 2004; Bolliet *et al.*, 2005; Harvey *et al.*, 2009; Ramezani *et al.*, 2014). This could result from a decrease in prey availability and an increase in juvenile aggressiveness in relation to a reduction in visual barriers and habitat carrying capacity (Kalleberg, 1958; Imre *et al.*, 2002; Suttle *et al.*, op. cit.; Bolliet *et al.*, op. cit.; Finstadt *et al.*, 2007). However, to our knowledge, these hypotheses have not been fully experimentally tested.

This chapter provides original data obtained in the wild, in a semi-natural stream and in a flume, that should contribute to a better understanding of the effects of embeddedness on young brown trout. Special attention was given to the mechanisms driving these effects. Through different experiments conducted over a 4-year period, (1) we investigated the effect of embeddedness on the larval survival in the wild; (2) on the embryo-larval survival and the emergence dynamics in a semi-natural stream; (3) we developed an accurate and repeatable method to measure the quantity of fine sediment at the surface of the stream bed; (4) we assessed density of juvenile trout and conspecifics in the wild relatively to embeddedness; and finally, (5) we investigated larval and juvenile behavioural mechanisms associated to embeddedness in a semi-natural stream, and in a flume.

Effect of Embeddedness on Larvae Survival in the Wild

The embryo-larval development of salmonids occurs in the undergravel compartment during winter and many factors such as hypoxia (e.g. Roussel, 2007), scouring/dewatering (Casas-Mulet *et al.*, 2015) or overdigging can deeply affect the number of survivors at the emergence time, which happens several months after egg laying. Nitrogen compounds, originating from surface water or from dead egg or larvae decomposition, might also affect survival (Massa, 2000; Dumas *et al.*, 2007). Hypoxia in the wild might result from high sedimentation, which reduces circulation of water in the spawning gravel and probably decreases oxygen availability (reviewed by Chapman, 1988; Waters, 1995; Kondolf, 2000; Soulsby *et al.*, 2001; Lapointe *et al.*, 2004; Suttle *et al.*, 2004; Meyer *et al.*, 2005). However, only few studies have investigated the effect of embeddedness on larvae survival, i.e. after embryos hatching. Massa (2000) attempted to evaluate mortalities during ontogenesis, but the very low survival rates at hatching led to zero survival at emergence, which make conclusions difficult to generalize. After hatching, oxygen consumption increases dramatically (Regnier *et al.*, 2010), and it is tempting to attribute the highest mortalities rates to the larval stage, although larvae should also be able to escape from lethal conditions by movement.

To investigate the link between embeddedness and larval survival, we conducted an experiment at the watershed scale in eight sites of the Nivelle River (South-west, France, Figure 9.1). The aim of the study was to investigate the variance in survival in relation to spatial heterogeneity, as well as the effect of substratum quality, oxygen, and nitrogen compounds levels, on brown trout post-hatching survival. Fertilized eggs were obtained from a large batch of brown trout eggs (60 genitors) originating from a fish farm (Lees Athas, Southwest France, 42°58’32”N; 0°37’14”W) on 1st December. Each redd

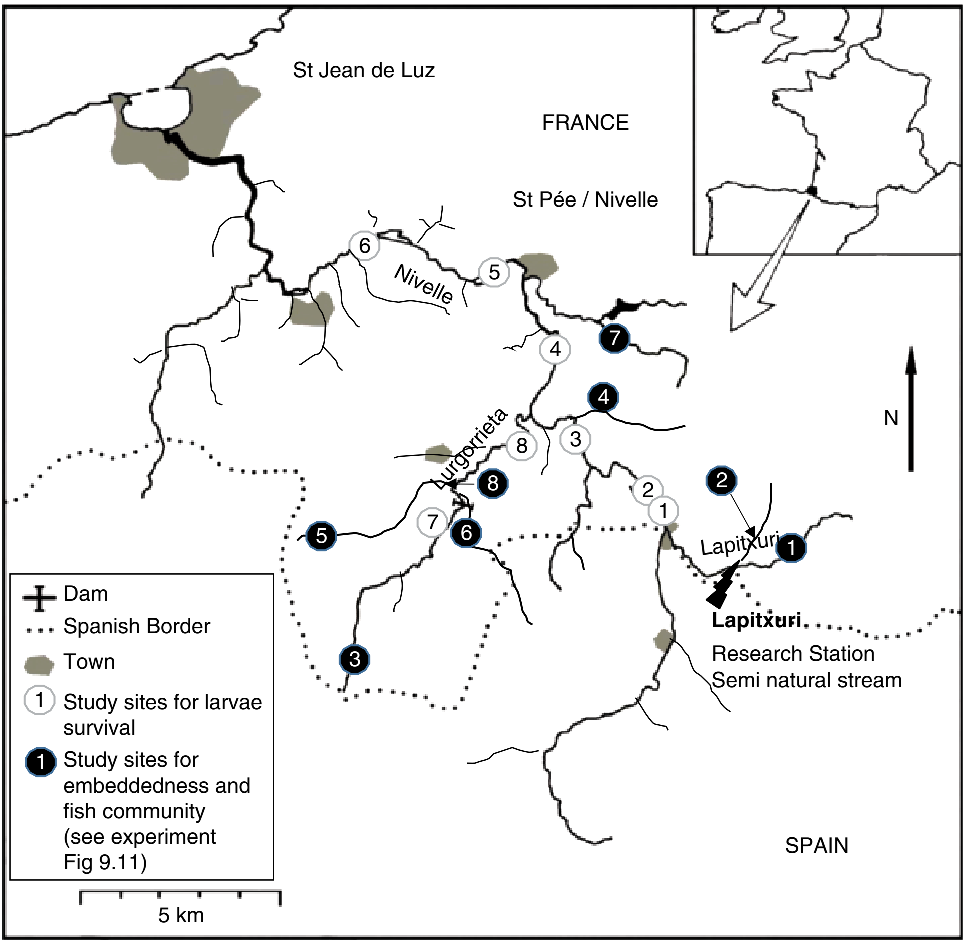

Figure 9.1 Map of the Nivelle watershed with the location of the eight sites chosen to study undergravel survival (○) and the eight chosen to compare fish community to streambed embeddedness (see experiment Fig. 9.11) (●).

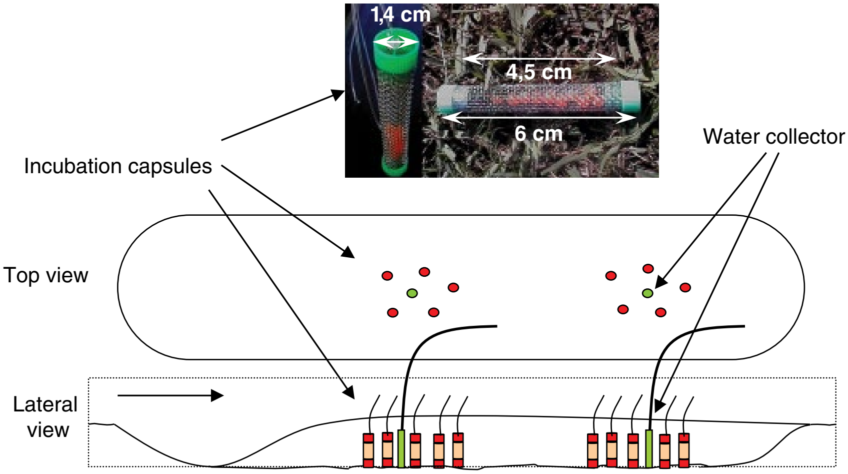

Figure 9.2 Lateral and top view of an artificial red built in the Nivelle watershed.

(Figure 9.2) consisted of 2x5 incubation capsules (1.4 cm in diameter, 6 cm long, mesh size 1.5 mm, Dumas & Marty, 2006), filled with 10 hatched larvae, that were buried on 1st February (at 484 degree-days). Control batch at the hatchery allowed estimating optimal survival. On the Nivelle River basin (39 km long), two artificial redds were built on eight sites. In order to investigate the role of capsule position within redd, five capsules were inserted at the upstream and five at the downstream part of the redd (Figure 9.2). The eight sites corresponded to natural spawning grounds and were distributed within the watershed, from the most downstream point (3.5 km above the endpoint of the dynamic tide, site 6, Figure 9.1) to the most upstream one (20 km upstream, sites 1 and 7, Figure 9.1). Substratum quality of the site was assessed using the Fredle index (geometric mean/sorting coefficient, according to Lotspeich & Everest, 1981), after a 2 liters sampling of the river substratum before capsules settling (at 10 cm depth) at the redds' location. Sites were spaced of 1 to 5 km to cover the whole watershed environmental conditions (De Maisonneuve, 1997). At each site two redds were built side by side at a flat/riffle transition, or one to few meters upstream the other when the width of the stream was reduced. Surface temperature was recorded every hour throughout the experiment using several reference loggers (VEMCO Minilog-8) distributed on the watershed. Temperature varied from 5 to 10°C during the experiment with a good correlation between sites (Correlation coeff >0.86 in all cases). Interstitial water was sampled twice (7th and 24th February), thanks to two intragravel water collectors inserted at the upstream and downstream part of the redd. Oxygen levels (WTW Oxi 330) and nitrogen compounds were measured at the same dates (see Dumas *et al.*, 2007 for the collection and treatment of water samples). Capsules were removed using their nylon thread between 24th and 26th February (larvae being at 658-667 degree-days of development, depending on sites), and the survival per capsule checked.

Oxygen levels in the surface water were always above saturation (100%). In interstitial water, oxygen fluctuated from 15% to 107% depending on the site (Figure 9.3A). Mean levels and standard deviations in ammonia nitrogen (N-NH$_4$: 1.8 ± 5.14 µg.l^{-1}, and 4 ± 5.36 µg.l^{-1} on 7th and 24th February, respectively) and nitrite nitrogen

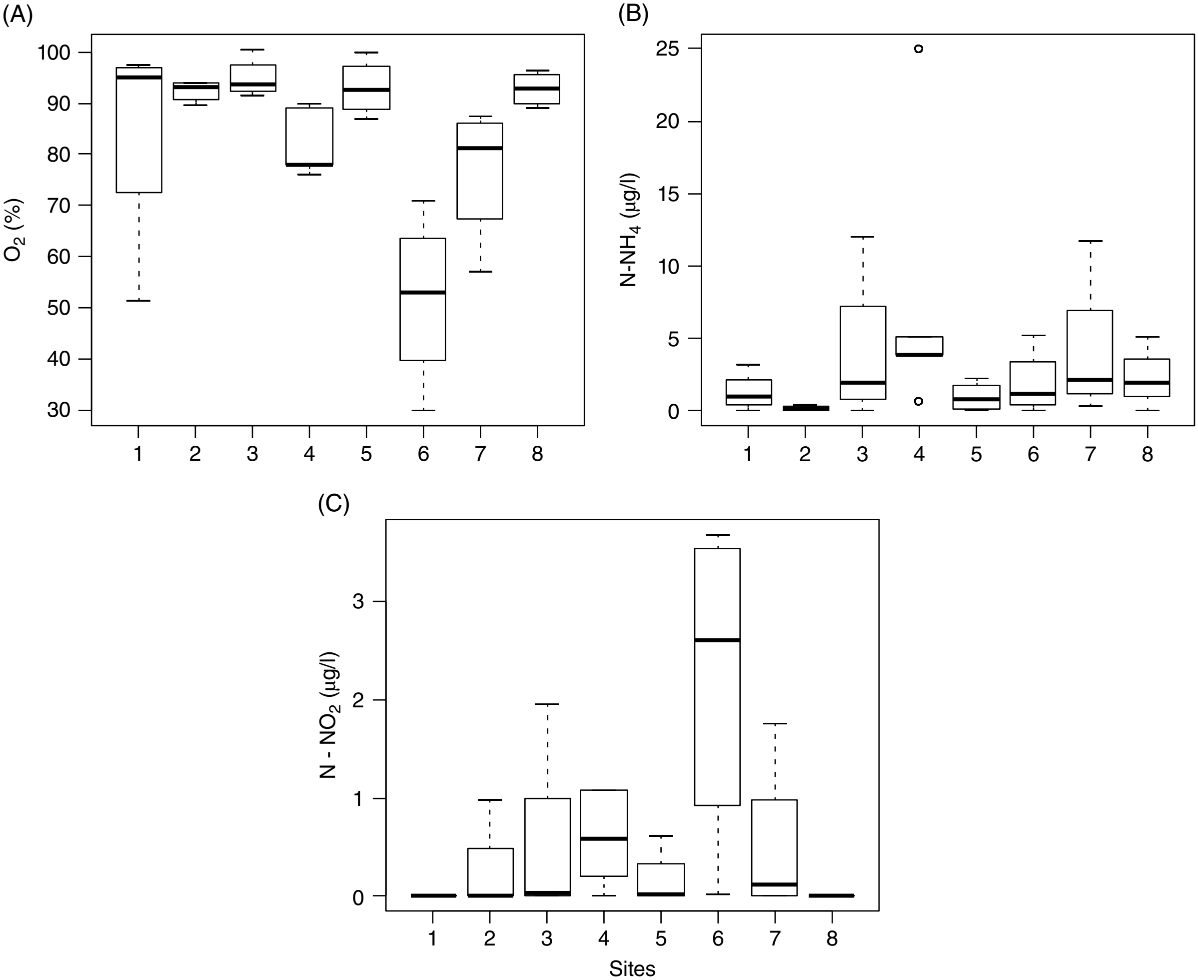

Figure 9.3 Mean levels of oxygen percentage saturation (A) and nitrogen compounds: N-NH$_4$ and N-NO$_2$ (B and C) in interstitial water of the eight sites of the Nivelle watershed; two measures (one per redd) from hatching to yolk resorption (two water sample dates).

($N\text{-}NO_2$: 0.21 ± 0.62 $\mu g.l^{-1}$ and 0.82 ± 1.8 $\mu g.l^{-1}$ at 7th and 24th February, respectively) in interstitial water fluctuated among sites (Figure 9.3B and 9.3C). Max level observed (25 $\mu g.l^{-1}$ for NH_4 and 7.4 $\mu g.l^{-1}$ for $N\text{-}NO_2$) remained far below critical values (100 $\mu g.l^{-1}$, Thurston *et al.*, 1978), fish embryos being especially tolerant to high environmental ammonia levels (Steele *et al.*, 2001). Survival was around 60% on average but it was highly variable among redds: up to 96% for 3 of the 16 groups of 10 capsules (and for the hatchery control), to less than 10% for 5 of them. At the watershed scale, the eight site's survival values ranged from 8 to 90%, with most of the sites (6/8) exhibiting a mean survival above 60%. In addition, upstream locations of the capsules in the redd resulted in slightly better survival than downstream ones. To study the relationships between environmental factors (oxygen level, nitrogen compounds, temperature, substrate quality) and larvae survival (1), and between spatial modalities (site, redd, position, capsule) and larvae survival (2), we used two General Linear Models (model: binomial – dead or alive, link: logit) with a nested procedure for the spatial model. Both were followed by ANOVAs.

The nested spatial model explained 66% of larvae survival. The 'Site' modality explained most of the deviance, even if others spatial scales (redd, position, and capsule modalities) contributed significantly (Figure 9.4). The most parsimonious environmental model explained 25% of larvae survival (Figure 9.5). The mean percentage of oxygen was the most important factor affecting survival (rather than minimum oxygen level), followed by the Fredle index (rather than geometric diameter) and the mean NO_2 (rather than max NO_2 or mean/max NH_4) (Figure 9.5).

As previously observed in studies on embryo-larval survival (Chapman, 1988; Crisp, 1993; Rubin, 1995, Massa *et al.*, 1998; Ingendahl, 2001; Dumas *et al.*, 2007), larvae survival in the present study depended mainly on oxygen levels. Massa *et al.*, (2000) reported that NO_2 might act in synergy with low oxygen concentrations to affect survival but it was not supported by our results (interaction mean O_2 level: mean NO_2 not significant, p = 0.77). In contrast, the mean O_2 level: initial Fredle index interaction was negative and significant (p = 0.007), although its contribution to explain the deviance

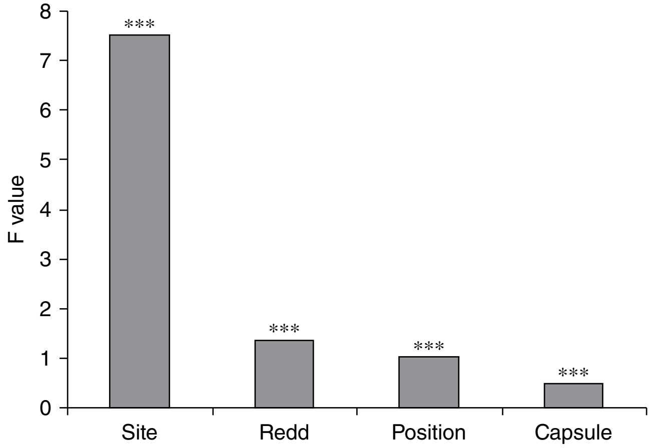

Figure 9.4 F statistic values as estimated on the deviance scores of Spatial nested Generalized Linear Model, testing the effect of site, redd, position in the redd (upstream/downstream) and capsule on survival at emergence.

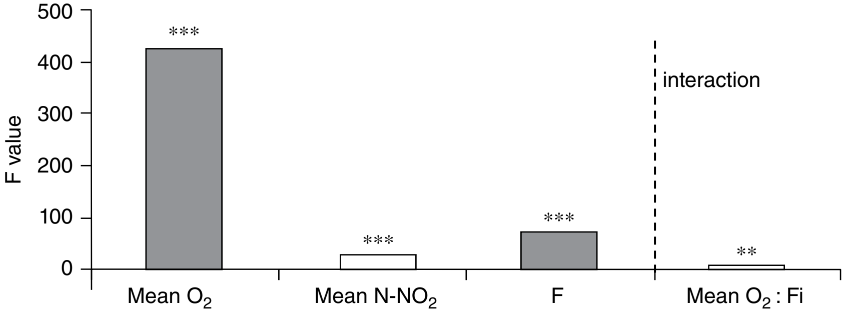

Figure 9.5 F statistic values as estimated on the deviance scores of Environmental Generalized Linear Model, testing the effect of O_2, nitrogen compounds and the Fredle index (Fi) on survival at emergence. Dark bars, positive effect on survival; white bars, negative effect on survival.

was very low (Figure 9.5). Examination of raw results indicated that this interaction may reflect that the Fredle index affected survival more strongly when oxygen levels were low. In an extensive field study, Heywood & Walling (2007) highlighted that the increased proportion of fine substrate (<1 or 2 mm) was negatively related to intragravel permeability and dissolved oxygen concentration. Atlantic salmon under gravel survival was also significantly related to these two parameters. However, in this last study, the Fredle index varied between 1.5 and 16, whilst in the present study, it ranged between 7 and 11, corresponding to values where variability in embryo survival was especially high in Heywood & Walling op. cited study.

Present GLM results also suggest that besides its effect on oxygen levels through water renewal rate, substratum has another effect on survival. This effect is much lower than oxygen level, but is significant, although difficult to identify. It may reflect interactions between fine sediment and pathogens occurrence such as fungus or bacteria, but such phenomena remain very poorly investigated in streams (Navel *et al.*, 2011). Pollution may be another candidate since finer fractions represent an important vector for the transfer and retention of numerous contaminants (Kemp *et al.*, 2011). Finally, our results evidence only a slight effect of nitrogen compounds on larvae survival. This could result from the low levels registered but one cannot exclude the fact that we have missed some marked and rapid increases in nitrogen levels because of our sampling schedule.

Effect of Embeddedness and Eggs Burial Depth on Survival and Emergence in a Semi-Natural Stream

In salmonids, female size variance can be very high, inducing a large variance in the depth of the redd (Kitano & Shimazaki, 1995; DeVries, 1997; Steen & Qinn, 1999). The processes driving the exchange of channel water with the hyporheic compartment include bed topography, bed permeability and surface roughness effects. The flux of oxygenated water through spawning gravels is influenced by a complex interaction between intragravels and extragravels factors (review by Greig *et al.*,

2007) and is controlled by gravel permeability and oxygen demands (biological oxygen demand + nitrogen oxygen demand). In addition, some studies have shown that clogging may create a physical barrier that prevent movement and emergence of fry from the redd (Chapman, 1988; Rubin & Glimsäter, 1996; Sternecker & Geist, 2010; Franssen *et al.*, 2012). However, to the best of our knowledge, impacts of incubation depth and substratum quality on embryo-larval survival and emergence dynamics have never been studied.

To investigate this question, we built redds in a semi-natural stream in which we manipulated the substratum quality from 0 to 30 cm depth. Capsule incubators were settled at two depths (D1 and D2) in two types of substratum quality (S1 and S2). The artificial stream used for the experiment is fed by the Lapitxuri brook, a tributary of the Nivelle river (South-west France). The channel consists of 13 sections each 10 m long by 2.8 m wide where it is possible to control abiotic variables such as flow rate, water height and gravel size. We used two sections of the channel and built 12 redds of 0.4 m^2 in each, in order to test four incubation conditions according to the substratum quality (S1: 7% of fines <2 mm; S2: 14% of fines <2 mm, Table 9.1) and the incubation depth (D1: 10 cm or D2: 20 cm). In-between and underneath redds, embeddedness was higher than in the redd itself, in order to mimick natural conditions (Table 9.1, S: 26% of fines <2 mm). Fertilized eggs were obtained by artificial crosses involving 30 females and 10 males of brown trout originating from the fish farm of Arrokia (Southwest France) on 27th December. Three replicates per incubation conditions (S1D1, S1D2, S2D1 and S2D2) were evenly distributed in each section. One month after fertilization (31th January), 10 incubation capsules (1.4 cm × 6 cm), filled with 10 eyed eggs, were planted in each redd (Figure 9.6). Five capsules were removed at hatching time (443 degree-days) and five at emergence time (675 degree-days). The hatching and emergence dates were estimated thanks to the control batch kept in the hatchery. An under-gravel box containing 100 eyed eggs was also inserted in each redd and connected to a free-water trap to study the dynamic of emergence (Bardonnet & Gaudin, 1990). The temperature and oxygen levels of the interstitial water were measured every week from the onset of the experiment (in early February) to the end of emergence (in early April, same method as in the previous heading, see Dumas *et al.*, 2007) (Figure 9.7). The temperature of the water surface was measured every hour by a temperature logger (VEMCO, Minilog-8).

Oxygen levels in the surface water were always above 100% saturation (data not shown). In the interstitial water, oxygen values decreased gently, but remained quite high during the first month of incubation and with a low variance. By the beginning of March, oxygen levels decreased, especially in the S2D2 condition. The decrease in oxygen levels may result

Table 9.1 Cumulative percentages (in mass) of the different gravel size in the surrounding substratum (S), S1 and S2 substratum. (Fi = value of the Fredle index).

Cumulative frequency (%)											
Gravel size	<0.063	<0.1	<0.2	<0.4	<1	<2	<5	<10	<20	<40	<80
S (Fi=2.79)	1.86	3.16	6.01	12.88	21.72	25.80	32.18	40.48	60.24	81.92	100
S1 (Fi=9.27)	0.96	1.69	2.59	3.81	5.74	7.92	13.18	33.45	68.17	100	
S2 (Fi=7.63)	1.30	2.04	3.11	5.77	10.00	14.39	22.2	40.21	70.79	99.57	100

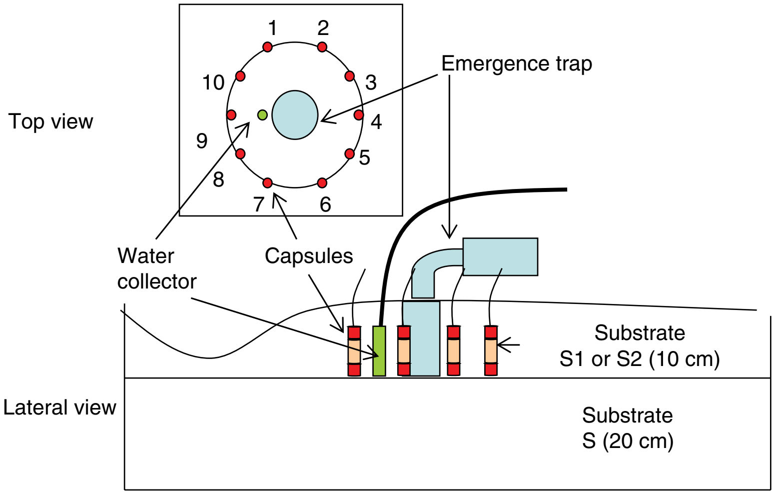

Figure 9.6 Schematic representation of the lateral and top view of an artificial redd in the semi-natural stream under the 10 cm depth configuration (redd size: 50 × 80 cm).

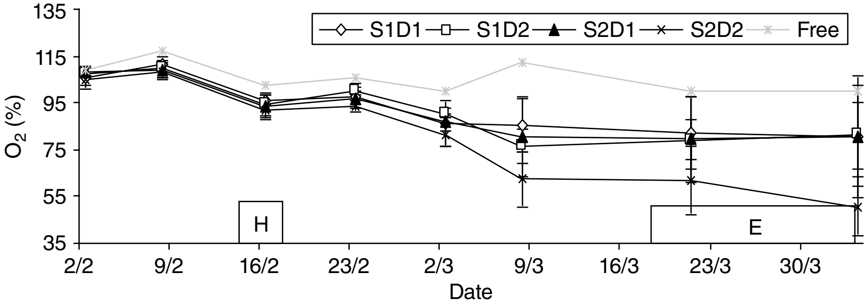

Figure 9.7 Oxygen levels (mean and SD per condition) measured each week in interstitial water (from eyed egg planting to emergence time) at 10 or 20 cm deep. S1: substratum containing 7% of fines <2 mm; S2: substratum containing 14% of fines; D1: eggs capsules buried at 10 cm depth; D2: eggs capsules buried at 20 cm depth. H: Hatching period, E: Emergence period.

from bio-geochemical activities, such as eggs, larvae and bacterial respiration and/or from in-coming fine elements from 'S' substratum, although such movement was probably limited owing to the semi-natural conditions (steady water flow). In the control batch, the survival rate reached 100% at hatching time (mid-February) and 96% at emergence. At both hatching and emergence times, and regardless to the depth of egg planting, survival rates were on average lower in redds built with 14% of fine sediments than in those built with 7% (Figure 9.8B).

Taking into account control batch survival, the difference in survival between hatching and emergence for all redd types was 8% only, and mainly due to the low survival under S2D2 conditions (Figure 9.8B). Embryo survival (eyed eggs to hatching) was better related to substratum quality than to oxygen values, which was not surprising since oxygen levels remained high during the first month of incubation. During the first developmental stages, fine sediment may have affected survival by surrounding eggs

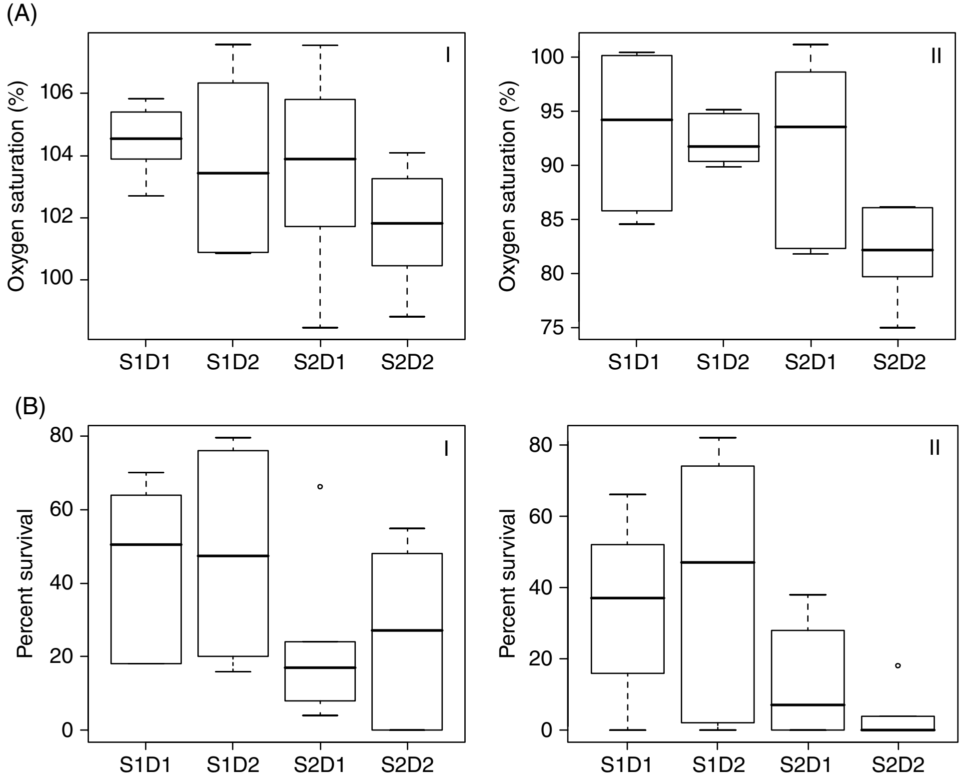

Figure 9.8 (A) Box plots representing the oxygen levels measured in interstitial water. I: from eyed stage to hatching and II: from eyed stage to yolk sac resorption. (B) Box plots representing survival from eyed stage to hatching (I) and from eyed stage to yolk sac resorption (II). S1: substratum containing 7% of fines <2 mm; S2: substratum containing 14% of fines; D1: eggs capsules buried at 10 cm depth; D2: eggs capsules buried at 20 cm depth.

and decreasing oxygen exchange across the chorion, whereas dissolved oxygen remained high in the interstitial water (Crisp, 1993b; Greig *et al.*, 2005). During larval development, oxygen levels decreased, especially under S2D2 conditions, which correlated well with the decrease in survival observed for that condition. However, survival remained quite high in this experiment and it contrasts with results obtained in the wild, where survival of the larval phase was low (see previous heading). This could be due to the huge variability exhibited by larval stage in their standard metabolism (Regnier *et al.*, 2010). Indeed, it is likely that in the semi-natural experiment, individuals with very high demand in oxygen already died as embryos. In the experiment in the wild, we put hatched larvae in the capsule, which developed from fertilization to hatching under optimal oxygen levels in the hatchery. The lack of selection at the egg stage could then explain the high larval mortality for the experiment conducted in the wild.

Emergence began on 6th March at 645 degree-days and ended 27 days later at 915 degree-days. Emergence date was delayed when eggs were incubated at 20 cm (D2) when compared to the shallower eggs burial depth, 10 cm (D1), and to our best knowledge this is a first evidence that burial depth largely impact emergence dynamics. Several studies have

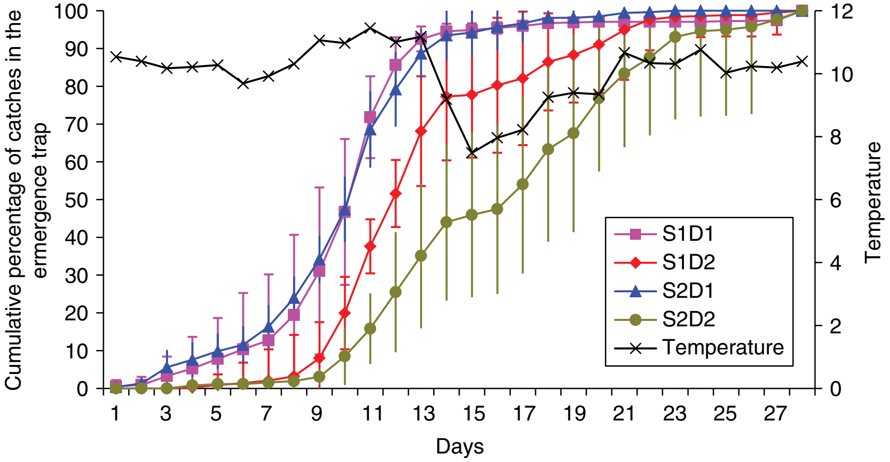

Figure 9.9 Dynamics of trout emergence (mean percentage and SD per condition) according to the daily checks of emergence traps. S1: 7% of fines, S2: 15% of fines, D1: eggs planted at 10 cm depth; D2: eggs planted at 20 cm depth.

reported that an increase in the percentage of fine sediments could delayed the date of emergence (Peterson & Metcalf, 1981; Chapman, 1988 and Crisp, 1993 a, b). In our study, such effect was observed in the D2 but not the D1 redds type (Figure 9.9). Dumas *et al.* (2007) related the delay in the development of larvae in capsules incubated in the wild to low oxygen levels. A relationship between low oxygen levels and embryo-larval development have also been reported in other salmonids (Ingendahl, 2001; Geist *et al.*, 2006), and Côte *et al.* (2012) observed a delay in hatching date under hypoxic conditions in *Salmo salar* eggs incubated under controlled conditions. These results, and the oxygen levels observed in our study during the larval stage (Figure 9.8, AII), suggest that the relationships observed between the percentage of fine sediments and the emergence date in the S2D2s redds type may involve oxygen level as driving force. However, the fact that emergence dynamics between S1D1 and S1D2 was different, whilst oxygen levels were similar, also suggests that the depth at which eggs were incubated may have directly affected the emergence dynamics, probably through the travel distance to reach the surface.

Finally, at high depth, S1D2 registered a 2 days delay for 50% emergence, while the delay reached 6 days under S2D2 conditions, when compared to S1D1/S2D1 emergence timing. A rapid drop in temperature on day 12 may have amplified the phenomenon but the lag was already clear before it (Figure 9.9).

A substantial depth for eggs incubation might protect embryos and larvae from stream-bed scours and digging by other female. However, late emergent fish will be exposed to a strong competition, because earlier emergent gain competitive superiority by being first to acquire a territory (Metcalfe & Thorpe, 1992; Cutts *et al.*, 1999a, b; Deverill *et al.*, 1999). In addition, it is generally accepted that late emergents have a lower caloric value than earlier ones (Lelong *et al.*, 2008, Regnier *et al.*, 2012), which suggests that they must feed rapidly. Their delayed arrival on the spawning ground, combined with this strong physiological constrain to feed, may induce a higher dispersal rate. As underlined in the introduction of this section, the egg burial depth is related to the size of the female and, in trout, the largest females are usually migratory fish (sea trout). This raises the question of a possible difference in early dispersal behaviour for alevins born from sea or resident trout. However, even if sea trout alevins emerge later than the ones laid by resident trout, they are also probably larger, as sea trout eggs are usually bigger than resident trout eggs. Then, the issue of a competition between late large emergents and early smaller ones is not that evident but it should deserve our attention. Indeed, the idea that a link may exist between early dispersal and further anadromous behaviour is quite an exciting hypothesis.

In our analysis, we considered temperature as a possible influencing survival factor, but its effect was not significant. It can however be emphasized that climate change, through the increase in the occurrence of extreme hydrological events (scouring) and the warming of water (which decreases oxygen solubility, Sternecker *et al.*, 2014) may add another threat on salmonids embryo-larval survival.

After emergence, fry settle on a territory and remain highly dependent on the substratum, which provides foraging sites, shelters against predators (or competitors) and visual barriers between conspecifics which limit competition. Substratum quality is also of prime importance as riverbed represents the habitat of invertebrates' larvae, the main trophic resources of young trout (especially, chironomids, Baetidae and Simulidae). In many fish species, especially benthic fishes, the importance of substratum in the choice of their micro-habitat has long been emphasized (e.g. Jowett & Boustead, 2001; Onoda *et al.*, 2009). However, surprisingly, there is no reliable and quick method to assess the level of embeddedness in the wild. In the next section, we developed and tested two methods to quantify fines.

Measure of Embeddedness on the Streambed

Bain *et al.* (1999) identified at least 29 different procedures ranging from visual estimation to more time-consuming measurement-based approaches, but there is a lack of accurate methods allowing quantification of fine sediment deposition on the stream-bed surface and within the superficial interstitial spaces. To estimate streambed gravel size, the visual methods can be sufficient for monitoring program intended to cover a large geographical area. There are rapid, inexpensive, require only one operator, but are not highly accurate (see Bain & Stevenson, 1999; Faustini & Kaufmann, 2007). Others methods, involving substrate samples and/or direct measurement, take a longer time than visual ones, are more expensive, and often require several operators. While visual evaluations may be considered as not enough reliable and repeatable to estimate embeddedness, substrate sampling as freezing core is unsuitable for upper layer sampling because of surface water warming of the ice core (Walkotten, 1976). Others techniques as the core substrate sampler of Mc Neil (Watschke & McMahon, 2005) often put fine sediments in suspension and can underestimate sediment deposition.

We developed two new, rapid and reliable methods to quantify fines at the surface of the streambed. The first one was inspired by that developed by Boulton (1985) to sample benthos from fine to coarse rocky substrate. The sampling device consists of a hand powered pump (Urchin ND 9210) fixed on a support enabling the operator in the field to keep the material above the water level when pumping. A grid (mesh size of 1 cm), was fixed at the end of the inlet pipe (3 cm in diameter, 150 cm long) to prevent large particles entering the hose. This method does not suspend sediment and one operator gently moves the hose extremity from place to place within an area delimited by a large

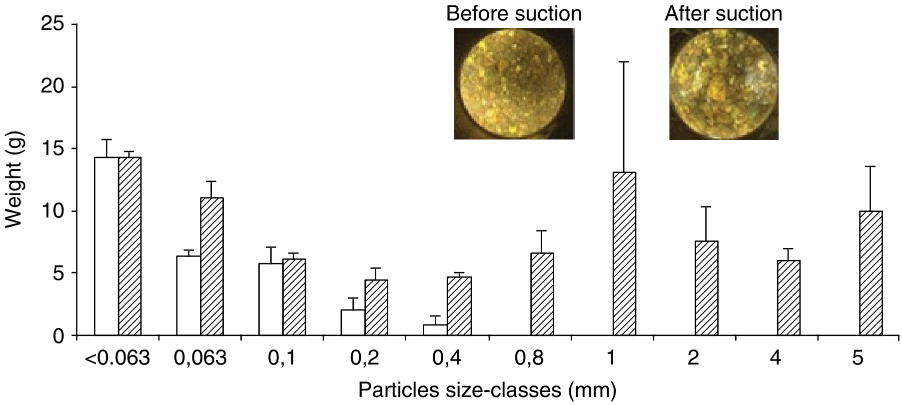

Figure 9.10 Weight and standard error of particle size-classes sampled on a substrate of known composition with the sediment suspension method (white bars) and the suction method (hashed bars). To facilitate comparison, the weight of all size-classes sampled with the suspension method was multiplied by a factor 10 to figure on the same scale than results from the suction method.

PVC pipe (80 cm height and 30 cm in diameter). This large pipe, positioned on the bottom of the streambed, allows a better vision of the substratum by preventing surface water current movement and standardizes the size of the sampling surface. The outlet pipe (3 cm in diameter, 150 cm long) allowed the collection of water and sediments in a bucket of 20 liters, a volume sufficient to allow a total sampling of the surface.

The second method used the same large PVC pipe placed on the streambed, but instead of pumping fine sediment, there were suspended. The surface of the streambed was gently brushed (brush = 10 cm^2, brush hair length = 2.5 cm) during 15 s. Then, while keeping the water in movement thanks to circular movements of the brush at the basis of the water column, 500 ml of water and suspended particles were quickly sampled in the water column with a plastic bottle with large opening. Both methods were tested in laboratory. Samples (20 l or 500 ml) were kept without movement for 48 h in order to allow the clearing of the water column. Then, the upper part of the water column was gently poured out and the bottom was collected dried, sieved and weighed.

Data showed a good repeatability of the results for both techniques. The suction method allowed sampling of particles up to 5 mm (Figure 9.10). It gives a good estimate of surface embeddedness and seems particularly adapted to assess fish juvenile habitat quality.

The suspension method was limited to particles under 0.4 mm, but appears very reliable to evaluate very small particles such as silt. If coarse sand is absent, this method presents great advantages in terms of feasibility and rapidity.

In the next section, we used the suction method to investigate embeddedness and corresponding fish assemblages within the Nivelle River watershed.

Effects of Embeddedness on Fish Populations in the Nivelle Watershed

Several field studies reported that an embedded substratum might reduce salmonids populations by increasing fish emigration and mortality (McCrimmon, 1954; Saunders & Smith, 1965; Elwood & Water, 1969; Barton, 1977; Bjornn *et al.*, 1977; Hillman *et al.*, 1987). However, such questioning has rarely been addressed at the fish community level and we investigated this question using eight sites of the Nivelle watershed (Figure 9.1). For each site, we characterized the streambed of glide geomorphological units thanks to the suction method described above, and the fish community by summer electrofishing of one glide/pool/riffle reach (De Lury method, three passages). We assumed that the level of fine sediment on glides characterized the relative levels of embeddedness between the eight sites. Results showed a high variability in embeddedness levels between sites (Figure 9.11A). Age-0+ trout was found mainly in riffles and was more abundant in sites 1, 2, characterized by the lowest embededdness (Figure 9.11C). 0+ trout was also abundant in site 5.

However, sampling was highly difficult to carry out in this site because it was a suite of little basins (very flat), separated by short steep riffles. We certainly overestimated embeddedness for this site because sedimentation was high in the basins where suction method was applied. These sites also showed the lowest biodiversity (Figure 9.11B). Most of the species other than trout (eel (*Anguilla Anguilla*), minnow (*Phoxinus phoxinus*), loach (*Nemacheilus barbatulus*), gudgeon (*Gobio gobio*), lamprey (*Lampreta planeri*)) found in the Nivelle watershed were localized in sites where trout were in low density. Several hypotheses may be proposed to explain the decrease in juvenile trout abundances in those areas. First, it could be hypothesized that trout are scarce because of low reproduction on these sites and/or of undergravel mortality of embryos. Another hypothesis may be linked to trout territoriality, as trout is known to be territorial against conspecific (Cutts *et al.*, 1999 a,b), and could exclude other species as suggested by Prenda *et al.* (1997). On the other hand, one cannot exclude the possibility that trout and others species might have different habitat preferences. While trout is usually found on coarse substratum, some others species might prefer more embedded ones (Pekarik *et al.*, 2012). For example, young stages of lamprey feed by filtration of silt and are only located in muddy bank (Ferreira *et al.*, 2013). Loach detect prey with their ‘barbillons’, particularly efficient in embedded substratum (Pekarik *et al.*, 2012) and gudgeon may exhibit a clear preference for sandy substratum (Copp *et al.*, 2010). In contrast, eels are very ubiquist, and as far as particle size is considered, minnows do not exhibit preferences neither (Lamouroux *et al.*, 2002).

In another tentative to better understand the effect of embeddedness on fish assemblages, a semi-natural stream (described in the before last heading) was used for an experiment involving minnows (*Phoxinus phoxinus*) and trout (*Salmo trutta*) (4–6 cm long). Four sections of the stream were separated longitudinally and sand was added on one side to produce eight half-sections with embedded and two with non-embedded substratum. In the two downstream end section, 70 trout (51.72 mm ± 6.92; 1.5 g ± 0.72) and 27 minnows (68.8 mm ±5.94; 2.95 g ± 0.75) were added in each embedded and control half-section. After one month, survival rate in embedded sections were 73 ± 0% in trout and 76 ± 2.8% in minnow, while in control sections, survival rates reached 87 ± 4.9% and 83 ± 12.7%, respectively. In trout, a significant and negative effect of embeddedness was observed on length and weight gain (ANOVA $p = 0.003$ and $p = 0.027$, respectively), while, in minnow, there was a slight but not significant decrease in length and weight gain in embedded sections (ANOVA, $p = 0.62$ and $p = 0.81$, respectively). In addition, the impact of embeddedness on survival was lower in minnow (7%) when compared to trout (14%), suggesting that the two species were not affected at the same level by embeddedness.

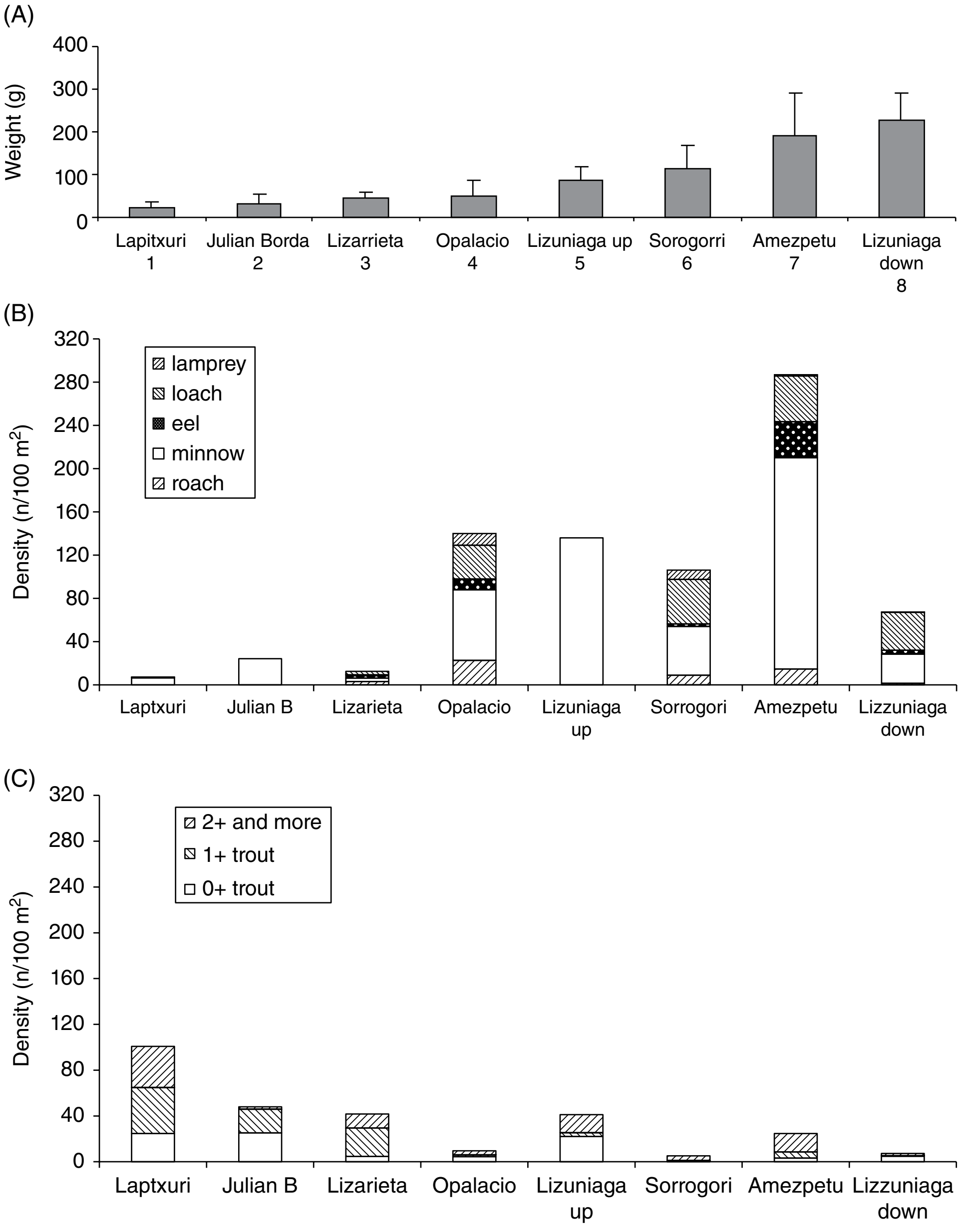

Figure 9.11 Substrate quality and fish densities in eight sites of the Nivelle watershed. (A) Mean weight of particles <2 mm at each sites (3 samples per site). The less embedded station was called station 1, and the most embedded one station 8. (B and C) Densities at each site (reach of riffle/pool/glide) for accompanying trout species (B) and trout (0+, 1+ and ≥2+) (C). Densities in riffle, pool and glide by age and species were first calculated using the De Lury method. Then, for each age of trout, and each species for accompanying trout species (densities per stage were summed in the last case), bars represent the average value of the geomorphological units densities for each site.

Possible mechanisms underlying these results could then be related to differences in territorial behaviour. Trout is territorial and mainly fed on drift, maintaining its position on its territory and chasing other fishes from it. However, they are very plastic and can also feed by picking on benthos (Crespin de Billy *et al.*, 2002 and see next heading). Minnows are organised in shoals and schooling has mainly been interpreted in regards to predator avoidance (Pitcher, 1986). However, in minnow, benefits of shoaling in embedded habitat could also be related to feeding. Indeed, we often observed that minnows located at the head of the shoal disturbed the substratum, inducing a cloud of drift. Then, shoaling minnows located downward crossed this cloud and some of them took items (maybe preys?).

In this experiment, results suggest that embeddedness affects growth in trout and in the last heading, we investigated some of the mechanisms involved in young trout growth and behaviour when submitted to different levels of embeddedness.

Effect of Embeddedness During the Ontogeny of Young Trout

The effect of embededdness on fish during the very first days after emergence was tested in a flow-through flume, which is an annular structure composed of two parallel sections 10 m long, 1 m wide and 0.8 m high (see Bardonnet & Héland, 1994 for details). Eggs of *Salmo trutta* were obtained from the fish farm of Lees Athas (Southwest France, 42°58’32”N; 0°37’14”W) and four batches of 35 larvae were planted in 4 redds (two per section) at 540 degree-days, so approximately one week before emergence. Each redd was built on an area of one m^2 delimited by nets. One section was embedded by adding sand while the other section was equipped with a mixture of heterogeneous pebbles, providing visual barriers and shelters (control). The behaviour of fish, once emerged from the gravel bed, was observed on five individuals, randomly chosen at 9:00, 13:00 and 16:00 during nine days. Each individual was observed during five minutes. Fish were fed with a daily distribution of live invertebrates sampled each day with a Surber sampler in the Nivelle river, close to the laboratory.

We observed no significant effect of embeddedness on the posture of emergent (‘resting on the substratum’ or ‘stationary swimming’), aggressiveness, movement within the section, food capture attempts or growth. According to Héland *et al.* (1995), fry settle on a territory approximately 12 days after emergence, the hierarchy being established between 5 to 10 days after emergence. These results suggest that embeddedness may not affect fish behaviour during territory establishment, at least when there is no difference in the invertebrates abundance. The fact that none of the followed behavioural parameters differs between the control and the embedded section suggest that prey capture efficiency was similar between the two sections. However, further experiments with lower food levels would be necessary to confirm that the catchability of invertebrates was not impacted by the difference in substratum quality.

In another experiment, we investigated the respective importance of fine sediment deposit on a decrease in benthic invertebrate availability and an increase in territoriality and competition due to reduced visual isolation (Suttle *et al.*, 2004). For that purpose, we studied the individual behaviour of 0+ brown trout in the semi-natural stream described in the third-last heading. We ran two experiments (in replicate) in two sections equipped with underwater observation chambers. An enclosure was stuck against underwater windows allowing behavioural observations (Figure 9.12). Enclosures were 2.0 m long and 0.5 m wide. In a first experiment (Figure 9.12, Exp. 1), we only tested the effect of a decrease in visual barriers on 0+ trout behaviour (density of 3 fish m^{-1}) The substratum of one of the enclosure was embedded by adding sand until pebbles were two-third embedded. In the second enclosure, substratum was composed of a mixture of pebbles providing shelters, foraging sites and visual barriers (control). Substratum of sections upstream both enclosures was as in control. Food supply, provided by invertebrate drift from the upstream production of the channel, was then similar in both enclosures, reflecting natural conditions of the channel. Water velocity in both enclosures reached 12–13 $cm.s^{-1}$. Two successive trials of 4 days were conducted in May (15–19°C) with three juveniles of similar size and weight (54 ± 0.61 mm, 1.63 g ± 0.06 g for trial 1 and 58.00 ± 0.84 mm, 1.93 ± 0.05 g for trial 2) in each enclosure.

In a second experiment (Figure 9.12, Exp. 2), the semi-natural stream was separated longitudinally by a plastic sheet. Enclosures were prepared as described above, but upstream the embedded enclosure, substratum was also embedded by sand addition (on 7 sections of 10 m long each). With this design, invertebrates drift in the embedded enclosure might be different from the control enclosure. After allowing 25 days for invertebrate community colonization, two successive trials of 4 days were

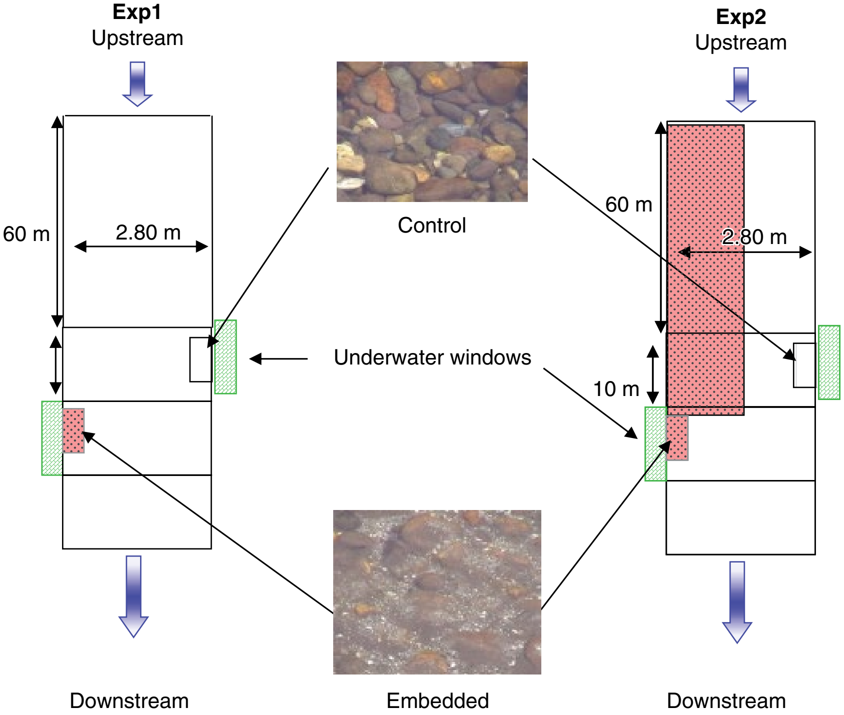

Figure 9.12 Schema of the experimental design of the semi-natural stream. Exp 1: the enclosure of one section was embedded by adding sand and Exp 2: the enclosure of one section and the upstream area was embedded by adding sand. Three fishes per trial were observed in each enclosure.

conducted in May as described for Exp. 1. Fish sizes and weights were 54 ± 0.00 mm, 1.73 ± 0.06 g for trial 1 and 51.8 ± 0.75mm, 1.39 ± 0.04 g for trial 2. Temperature fluctuated between 13.5° and 17°C.

After two days of acclimatization, fish behaviour was observed individually in all trials during 20 min, three times a day, at 8:00, 11:00 and 15:00. Fish observation rapidly allowed the individual recognition of the three fishes. Behaviours observed were: fish posture ('resting' or 'stationary swimming'), the number of food captures attempts, the distance of food capture attempts and the number of agonistic interactions (attack, intimidation). After each trial, and 24 h of fasting, fish were anesthetized for length and weight measurements. Hierarchy established rapidly and in each trial, the dominant fish was called 'fish 1', the intermediate, 'fish 2' and the more subordinate, 'fish 3'.

In the first experiment, (Exp. 1: embeddedness = physical habitat change only), attacks represented 70 to 80% of the agonistic interactions. The effect of embeddedness on the total number of agonistic interactions was not significant (ANOVA, p = 0.419). However, in embedded enclosure, the dominant fish was more aggressive than in the control one (on average 115 and 73 interactions, respectively). In embedded enclosures, fish were less often observed in stationary swimming than in control (ANOVA, p = 0.02), and they mainly rest on the bottom. Regardless of the substratum quality, fish 1 were more aggressive than the subordinates and were more often observed in stationary swimming than subordinates (ANOVA, p = 0.0001). Embeddedness reduced the total number of capture attempts (ANOVA, p = 0.044) as well as the occurrence of long distance ones (at more than 5 cm of distance, ANOVA, p = 0.025). This last effect was more pronounced for subordinates. Finally, after one week of experiment, fish 1 achieved a better growth than subordinates (ANOVA, p = 0.036), but there was no significant effect of embeddedness on growth. These results provide evidence that embeddedness affected inter-individual relationships. By suppressing visual isolation, fine deposit probably increased territory size and competition.

There was no consequence on growth, perhaps because of the short duration of the experiment, and/or because of feeding outside the behavioural observations.

In the second experiment, (Exp. 2: embeddedness = physical habitat and food supply changes), we observed, in both trials, the death of fish 3 (the subordinate) in the embedded enclosure after three days of observation. Then, control and embedded enclosure behavioural results can hardly be compared. However, considering only fish 1 (the dominant), results showed that food capture attempts were much more numerous in the embedded enclosure during Exp. 1 (388 attempts) than during Exp. 2 (85 attempts). In the meanwhile, there were quite similar in the control enclosures (575 in control Exp. 1 against 500 in control Exp. 2).

The effect of embeddedness on food supply has increased competition (when compared to change of physical habitat only), leading to the death of one individual. In accordance with the study of Suttle *et al.* (2004), embeddedness has also decreased the number of food capture attempts. This provides direct evidences that prey availability, and an increase in juvenile aggressiveness related to a reduction in visual barriers, may be the main mechanisms leading to the decrease in 0+ trout growth in embedded habitats. In their extensive study in the wild, Ramezani *et al.* (2014) brought out the effect of sedimentation at the reach scale. They confirm that siltation affects invertebrates' community and trout density and condition.

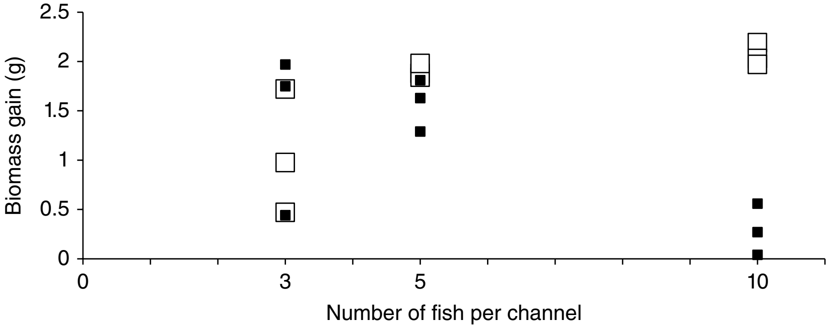

Figure 9.13 Total gain in biomass (g) in three control (open squares) and three embedded (black dots) artificial channels at three densities (3, 5 and 10 fish, corresponding to 0.75, 1.25 and 2.5 fish per square meter).

Finally, the effect of density on growth was tested in six artificial channels of 10 m long by 0.4 m wide. Four channels contained a mixture of heterogeneous pebbles while the four others were embedded by adding sand until pebbles were two-third embedded. Juveniles (5 to 6 cm in length) were obtained by electrofishing in the Lapitxuri Brook and kept 15 days in the channels at a density of 0.75 (3 fish; 8–24 July 2001), 1.25 (5 fish; 24 July–9 August 2001) and 2.5 (10 fish; 5–21 July 2003) individuals per square meter (3 replicates). At the end of the experiment, fish were sized and weighed after 24 h of fasting. Results showed that the negative effect of embeddedness was not noticeable at the lowest density 0.75 fish m^{-2}. At higher densities, competition was high enough for embeddedness to affect growth and this was particularly evident at 2.5 fish m^{-2} (Figure 9.13).

Conclusion

Adverse effects of embeddedness on salmonid fish has long been recognized, especially for the embryo-larval phase which develops in the intimate surroundings of the gravel bed. The present results will contribute to a better understanding of factors affecting mortality during the under-gravel development. Results from the experiment in the Nivelle catchment indicated that reach scale had a greater impact on survival than all other studied spatial scales: redd (all redds being built on a glide/riffle limit), position in the redd, or capsule. As widely reported in the literature, oxygen level was the most important factor affecting survival. Fine sediment, and to a lesser extent nitrogen compounds, also affected survival. The results from the semi-natural stream confirmed the role of oxygen levels and of sediment *per se* on survival. Emergence dynamics results showed that both incubation depth and oxygen levels (probably in relation with a delay in larval development as already reported by several authors), but not gravel size, affected the timing of fry emergence.

Increasing levels of deposited fine sediment can also be detrimental to young trout survival and growth. Our data suggested that the first feeding phase is not very sensitive to embeddedness (flume experiment), at least when prey abundance is not affected, while 0+ juvenile trout growth can be highly affected as shown by Bolliet *et al.* (2005).

Underlying mechanisms would involved an increase in territory size of dominant fish when streambed roughness is low, and an indirect effect of embeddedness on invertebrate availability. This high sensitivity of young trout to gravel bed quality might result in a discernible change in the fish community, as other fish species could be much less sensitive to embeddedness. We proved it to be true for minnows, since our results from a semi-natural stream demonstrated that they underscored a lower mortality and a more limited loss of growth than trout, when confronted with embeddedness.

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Section 3

Life-History

10

Habitat as Template for Life-Histories

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Introduction

Brown trout (*Salmo trutta*) life-histories vary among locations, presumably because site-specific environmental factors affect growth and influence population-specific life-history traits. Some important abiotic environmental features are water temperature, flow, depth, bottom substrate, ice cover, barriers to migration, nutrient richness, habitat coherence and consistency. Biotic factors and processes also contribute to the habitat template and function as population regulators. For instance, significant relationships exist between population density, growth, body size, and the presence of other species (Jonsson & Jonsson 2011). Nutrient richness influences primary and secondary production of aquatic systems, thereby contributing to the intensity of competition, growth rate, fish size and biomass production of populations. This is important for populations because individual growth and size are major determinants of reproductive success and recruitment, and hence, the size of subsequent cohorts. Thus, the habitat is a template for the ecology of brown trout, including mode of migration and reproductive behaviour, and there are associations between habitat and life-history variation (Jonsson & Jonsson 2011).

Here, we review relationships between life-history and habitat use, how young trout use running water at different times of the year, how populations are split in migratory and non-migratory individuals (partial migration), and how these aspects are influenced by environments. Migratory brown trout can perform long migrations in fresh water, but can also emigrate to estuaries and coastal sea for feeding. Environmental stimuli, such as photoperiod, water temperature and water flow function as cues influencing the time of migration. Migration can be dangerous and energetically costly. Alternations between distant environments influence the probability of surviving. Thus, in partly migratory populations, there will be trade-offs between early maturation and a non-migratory life-style and migration involving later maturation. Because of their opportunistic life-style, brown trout are excellent colonizers and one of the world's 100 most invasive alien species (Lowe *et al.* 2000). Jonsson & Jonsson (2011) give a more detailed account of these relationships.

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

Life-cycle and Habitat Use

Brown trout typically spawn on stone and gravel bottoms (particle diameter 0.5–15 cm) in rivers and streams with mean annual flow above 0.03 m^3s^{-1}, current velocity between 0.15 and 0.8 $m\,s^{-1}$ and at depths between 5 and 80 cm. However, spawning can also occur in upwelling areas and along exposed shores in lakes and estuaries (<4‰ salt) (Jonsson & Jonsson 2011 and references therein). Lake spawning is also known from other salmonids, such as Arctic charr (*Salvelinus alpinus*) and brook charr (*Salvelinus fontinalis*), but few if any other salmonid species exhibit a similarly large repertory of spawning conditions, simplifying colonization and establishment in new localities.

Spawning occurs in autumn and winter, earlier at higher altitudes and latitudes, presumably because of lower water temperatures and longer egg incubation period. For instance, in Norway, brown trout spawn typically in October and the spawning period lasts for 2–4 weeks. At southern latitudes in Europe, the spawning period is usually later in the autumn and prolonged relative to that at the same altitude in the north. For instance, Larios-López *et al.* (2015) reported a spawning period of up to 21–24 weeks in Spain. A prolonged spawning period may be an adaptation to spawning under unpredictable environmental conditions and/or when suitable conditions for early feeding lasts for a long time period. Also in other fish, such as anchovies, lengths of the spawning periods vary with latitude (Hopman & Gilbert 2014).

The eggs hatch in spring, and the larvae, called alevins, subsist for weeks on yolk that they carry in the yolk sac underneath their belly (Figure 10.1). The length of the egg incubation and endogenous feeding periods are temperature dependent, and longer the lower the temperature (Crisp 1988; Elliott & Hurley 1998). The alevins, ca. 20 mm in total length, emerge from the gravel when they have consumed most of the yolk, and they start to feed actively on small invertebrates that occur in or near the spawning area. This is typical for early life irrespective of later habitat use.

Habitat used during subsequent developmental stages varies among populations. Brown trout live in streams, rivers, lakes and coastal sea. The fish in these habitats are so different that Carolus Linnaeus in the 10th edition of his book *Systema Naturae*, the

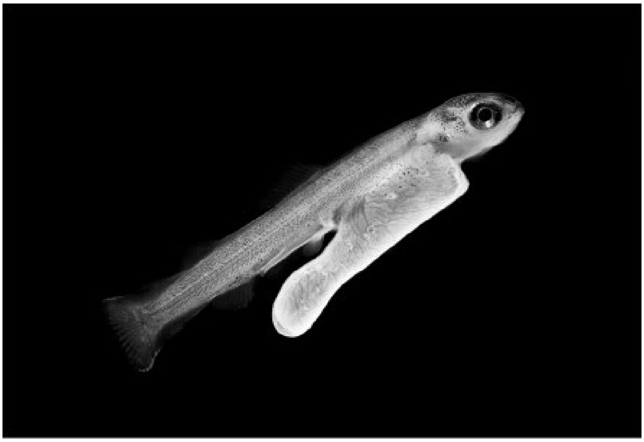

Figure 10.1 Alevin brown trout with yolk sac underneath the belly.

starting point of zoological nomenclature published in 1758, considered them different species. *Salmo trutta,* which was the first of the species described, was the river form. This phenotypic variation associated with habitat use has caused much taxonomic confusion (Jonsson & Jonsson 2011). However, today most ecologists working with salmonids consider *Salmo trutta* one species irrespective of the feeding habitat, although it is unknown whether hybrids between all the various forms will give fertile offspring.

Thus:

i) Brown trout can live in a brook during their entire life. These fish are typically small and short-lived (Ricón & Lobón-Cerviá, 2002; Sandlund & Jonsson 2016).
ii) With open connection between the stream and a larger river, the fish may migrate between the two for feeding and spawning, such as in the Søre Osa river system, eastern Norway (Jonsson & Sandlund 1979). There, brown trout used a small tributary, the Østre Æra, as spawning and nursery area and migrated to the larger River Søre Osa for feeding and growing large before returning for spawning. Similarly, Bagliniére *et al.* (1994) reported migratory 0+ trout from the nursery streams to the larger River Scorff in France. However, such migrations may terminate if feeding conditions in the habitats change. In the Søre Osa environmental conditions in the main-stem changed after a large part of the water was deviated away from the river and used for electric power production. Because of this, the trout migration terminated, and the fish in Østre Æra became small-sized residents in that tributary (Sandlund & Jonsson 2016). Thus, it appears that such migratory systems persist only as long as the migration is profitable.
iii) Lake feeding trout often spawn in inlet tributaries and/or the outlet river. They perform movements between the two habitats depending on their needs for food, shelter during adverse environmental conditions, such as winter, and reproduction (Figure 10.2; Arawomo 1981; Haraldstad & Jonsson 1983; Schei & Jonsson 1989; Jonsson *et al.* 1999; Forseth *et al.* 1999, Jonsson & Jonsson 2011). For instance, most of the young emigrate from tributaries to lakes in the Voss River during the first summer and autumn, but do not spread round the lake before the year thereafter. Brown trout living in afferent streams of Lake Femund, a mountain lake in eastern Norway, move from the natal streams into the lake when they are between one and eight years old, with most of them descending when 2 (40%) or 3 (27%) years old (Jonsson *et al.* 1999). In Windermere, the largest natural lake in England, brown trout emigrate from the tributaries into the lake at 1 (16%), 2 (70%) and 3 years of age (14%); Craig (1982).
iv) Anadromous brown trout (sea trout) spawn in many coastal rivers with free access from the sea. They feed largely in estuaries and coastal areas (Jonsson 1985; Jonsson & Jonsson 2002, 2009; Knutsen *et al.* 2004), chiefly in near-surface water (Lyse *et al.* 1998; Knutsen *et al.* 2001b; Rikardsen *et al.* 2007). These forms can stay in fjords and coastal waters for one summer only, or for one or more years before returning to their river of origin for spawning (Jonsson & Jonsson 2002, 2009, 2014; Davidsen *et al.* 2014a, Eldøy *et al.* 2015).

The length of the river stay is at least partly dependent on when they move to sea, because most return to fresh water in early autumn. In salt water, they spend most of their time in the area close to the river mouth, and they seldom occur offshore in the

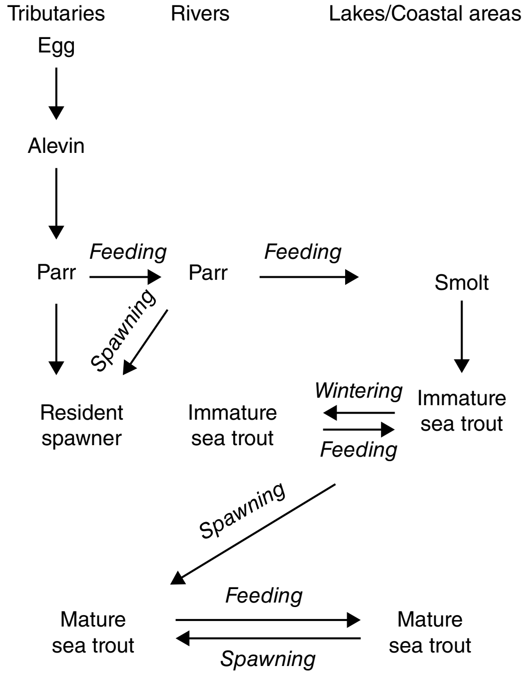

Figure 10.2 Life-cycle of brown trout.

ocean. However, a part of the population can be long distant migratory (Chernitsky *et al.* 1995; del Villar-Guerra 2014). Long distance migratory fish can for instance cross the North Sea from France to Scandinavia or move from southern to northern Norway (Anon. 1994; Jonsson *et al.* 1995), although most individuals appear to move less than 100 km from the mouth of the home river (Jonsson & Jonsson 2014). Long distance migratory trout spend more time in pelagic waters than short distance migratory ones, and they have slimmer body form at the start of the migration (Eldøy *et al.* 2015). At smolting, juvenile brown trout have low lipid density (Jonsson & Jonsson 1998), and the short-distance migratory trout have the very lowest triacylglycerid densities suggesting that they are more lipid depleted prior to migration than the long-distance migrants, and therefore inclined to terminate migration at the first given feeding opportunity (Boel *et al.* 2014). However, the slimmer body of the long distance migrants, despite higher triacylglycerid densities, may indicate that they represent a specialized ecotype, whether this is caused by adaptive plasticity or genetic specialization. There are differences in migratory distance among populations, due both to heredity and environment. Migratory patterns among populations differ when experimentally reared under similar conditions and released as smolts at the same sites (Svärdson & Fagerström 1982; Jonsson & Jonsson 2014).

In large river systems, all ecotypes of brown trout may occur sympatrically during parts of their life span (Figure 10.2). Environmental influences appear to determine whether an individual will stay in one habitat or migrate between habitats. Profitability in terms of surplus growth probably influences habitat choices (Werner & Gilliam 1984; Forseth *et al.* 1999; Sandlund & Jonsson 2016).

Stream and Lake Living Trout

Where do young trout prefer to stay in the nursery river? During their first year they dwell largely in shallow areas (<30 cm deep), often located along riverbanks with moderately fast-flowing water (0.2–0.5 ms^{-1}) (Roussel & Bardonnet 1999; Jonsson & Jonsson 2011). As they grow older and larger, the fish prefer deeper, slowly flowing parts of the stream (Heggenes 2002), but their habitat use in nature is flexibly dependent on habitat availability and time of the day and year (Elso & Greenberg 2001; Greenberg *et al.* 2001; Heggenes *et al.* 2002). They are more inclined to exploit pools in the river during night than during daytime. Trout prefer stony bottoms where they can hide under cover, but occur also on fine-grained substratum, such as gravel, sand, silt and mud (Heggenes *et al.* 1999). In lakes, brown trout exploit mainly littoral and near-surface waters, and few individuals feed deeper than 1–2 Secchi depths (a measure related to the turbidity of the water; Haraldstad & Jonsson 1983; Jonsson & Gravem 1985; Schei & Jonsson 1989; Langeland *et al.* 1991). The reason for feeding in epilimnic water is probably that they are visual hunters, and water clarity determines how deep they can find food.

In summer, trout are most active during twilight and night, but sometimes they feed continuously during day and night (Bunnell *et al.* 1998; Young 1999). During winter, when the water temperature is low, activity drops, and in open areas, they may seek shelter in interstitial spaces in the substratum during daylight, but may hold position on or close to the bottom in slow flowing water during dark hours. Brown trout can take food at temperatures down to 0 °C (Bremset 2000). Their ability to capture drifting prey decreases with temperature below 10 °C (Watz & Piccolo 2011; Watz *et al.* 2012), and they exploit more slow flowing and still water in winter than during summer. They switch from summer to winter activity when the water temperature drops below ca. 8 °C (Heggenes & Dokk 2001). Under ice cover in winter, brown trout are more day active than in open river stretches, possibly because of a lower perceived predation risk (Watz *et al.* 2013, 2015). Brown trout can leave small streams in the autumn to spend the winter in a lake (Jonsson & Jonsson 2011). In southern populations, where water temperatures in winter are higher, the seasonal difference in activity is smaller (Rincón & Lobón-Cerviá 1993).

In lakes, brown trout can segregate partly by age and sex (Haraldstad & Jonsson 1983; Jonsson & Gravem 1985; Langeland *et al.* 1991; Saksgård & Hesthagen 2004). Old and large individuals tend to extend their feeding habitat relative to younger and smaller conspecifics. They extend their habitat both horizontally into pelagic waters and vertically into deeper water along the bottom. Females more than males feed offshore (Schei & Jonsson 1989). As a consequence of the different habitat use between sexes, growth rate and parasite load can also differ (Jonsson 1989; Jonsson & Jonsson 2011). For instance, Shei & Jonsson (1989) reported that female brown trout in Lake Oppheimsvatnet, Norway were more heavily infested with plerocercoids of the cestode *Diphyllobotrium dendriticum* than males. They were probably infested by the tapeworm by eating copepods.

Partial Migration

In brown trout, there is a continuum from freshwater to completely anadromous populations. In other words, populations are often partly migratory, consisting of both resident and migratory individuals. Therefore, population abundance and production

Figure 10.3 Partially migratory brown trout are polyphenic, and non-migratory fish are mere dwarfs compared with the migratory individuals.

can increase above what one location can support alone (Jonsson & Jonsson 1993; Bohlin *et al.* 2001). This is partly because many of the fish assimilate most of their food outside the natal river (Jonsson & Jonsson 2003b), but also because the spawners bring resources back in form of gametes and fish that die after returning. Thereby, they bring nutrients useable for the biota, increasing the river production of invertebrates and fish (Elliott *et al.* 1997; Jonsson & Jonsson 2003a).

Partially migratory populations are typically polyphenic, with non-migratory fish being at times mere dwarfs compared with their migratory counterparts (Figure 10.3; Jonsson 1985). Adult freshwater resident brown trout are often less than 100 g in total wet mass, whereas anadromous individuals can weigh several kgs (Jonsson 1989; Jonsson *et al.* 2001). Non-migratory and migratory juveniles can grow up together and be morphologically indistinguishable during early ontogeny, but change from each other prior to the migration episode, *e.g.* during the smolting process of the migratory fish (Jones *et al.* 2015).

In partially migratory populations, males often predominate among residents, and females among migrants (Jonsson 1985; Dellefors & Faremo 1988). For brown trout in 17 coastal streams of Norway, on average 49% of the males, but only 3.7% of the females on the spawning grounds were resident trout, the rest were anadromous fish (Jonsson *et al.* 2001). Among the anadromous fish, the female/male ratio was approximately 1.5. From south Sweden, Petterson (2002) found ca. 10% stream resident and 90% anadromous female brown trout in one study stream. Thus, the ratio of non-migratory to migratory individuals differ, but typically males predominate among non-migrants and females among migratory fish (Jonsson & Jonsson 1993).

Why are males less migratory than females? This is probably because the selective premium of migration differs between the sexes. By migrating, the sexes increase their energy consumption and growth. Females exhibit one reproductive strategy and their fitness is strongly dependent on their size (Fleming *et al.* 1996). In males, this relationship is less strong because both small and large individuals can be reproductively fit, small males as sneakers and large males as fighters. Their fitness depends on their own competitive ability compared to that of other males, thus it is probably frequency-dependent (Gross 1985; Jonsson 1985).

Is partial migration environmentally or genetically determined? There is no simple answer: there are elements of both. Partial migration is partly influenced by inheritance. Rearing experiments have revealed that resident parents produce a lower proportion of migrants than anadromous parents (Skrochowska 1969). Elliott (1989) concluded, based on a series of studies with brown trout from the English Lake District, that there was strong evidence for genotypic differences between stocks controlling the migratory behaviour of brown trout. A field experiment by Jonsson (1982) supported this view. He demonstrated differences in migratory behaviour of young fish sampled above and below an impassable waterfall. Within partly migratory populations, however, differential food availability influences whether or not brown trout will migrate (Skrochowska 1969; Jonsson 1989). Improved juvenile feeding tends to increase the proportion of resident fish (Jonsson & Jonsson 1993; Olsson *et al.* 2006). This holds for freshwater populations as well as populations containing sea-run fish (Wysujack *et al.* 2009; Davidsen *et al.* 2014b; Jones *et al.* 2015).

Both resident and migratory parents from partially migratory populations can produce the two types of offspring, although not in equal proportions, and the probability of becoming migratory appears resource dependent, influenced by food assimilation and growth (Jonsson & Jonsson 2011). Thus, the tendency to migrate appears also density-dependent (cf. Olsson *et al.* 2006). The regulatory mechanism by which food assimilation is associated with tendency to migrate is unknown. There is no conflict between this view and the observation that there is genetic variation for the fish's tendency to migrate. The threshold for the environmental influence on the tendency to migrate varies among genotypes and appears associated with the growth-rate and size of the fish and expected fitness gains by migration (Jonsson 1985; Økland *et al.* 1993; Forseth *et al.* 1999).

Anadromous Trout

In anadromous brown trout, juveniles may smolt and migrate to sea for feeding when they have reached a certain length and age (L'Abée-Lund *et al.* 1989; Økland *et al.* 1993). Hence, not all individuals of a particular year-class smolt at the same age. In the British Isles, Fahy (1978) recorded six different age groups of smolts. In Norway, the corresponding number is eight (L'Abée-Lund *et al.* 1989). Field observations show that mean smolt age varies with latitude, probably because of differing water temperatures. Fahy (1978) found that mean smolt age was higher in Scotland (range 2.4–3.4 years) than in Irish and Welsh rivers (range 2.1–2.8 years). Furthermore, Jonsson & L'Abée-Lund (1993) reviewed the clinal variation in mean smolt age from 102 European rivers between 54 and 70°N, and found that it ranged from 2.1 years at 54°N to 5.6 years at 70°N. On the other hand, they found no correlation between smolt size and latitude. Rivers with small and large smolts occurred both in southern and northern parts of the distribution area. In small streams (annual mean flow $<0.2\ m^3s^{-1}$), however, mean smolt size and variation in size increase with mean water flow in streams with mean water flow $<1\ m^3s^{-1}$. Thus, the fish appear to abandon small streams early in life as an adaptive trait (Jonsson *et al.* 2001).

Within populations, fast-growers transform to smolts when younger and smaller than slow growers. The youngest smolts can be smaller than the oldest smolts were one year before they smolted (Økland *et al.* 1993). Thus, age at smolting is not only size, but also growth dependent. In addition, the feeding regime can influence the tendency to smolt. Reduced feeding prior to smolting can increase the proportion of sea-run migratory fish (Davidsen *et al.* 2014b). Similarly, Jones *et al.* (2015) showed that spring rationing reduced growth and growth-related variables and induced lakeward migratory behaviour in brown trout. Their result supports the idea that smolting and 'decisions' about migration are affected by spring food availability regardless of conditions in the previous autumn or winter, as is the case with Atlantic salmon *Salmo salar* (Vainikka *et al.* 2013).

Parr living in streams draining to brackish water may migrate to sea very young and small in size (Titus & Mosegaard 1989, 1992; Järvi *et al.* 1996; Jonsson *et al.* 2001). In the small stream Arån on the Swedish island Gotland; the parr migrate to the Baltic Sea at 3 months of age and ca. 30 mm in length (Landergren 2001). Water in the Baltic Sea is brackish (salinity 6–7‰) and smolting appears not essential for survival (Limburg *et al.* 2001). Landergren (2001) found no difference in survival and growth between parr raised in fresh and brackish waters. He concluded that the brackish water around the Gotland Island is not a physiological obstacle for the survival of early out-migrating parr, and imposes no cost in terms of growth reduction.

In the Atlantic Ocean, however, seaward migration typically imposes salinity-related regulatory problems and increased risk of predator encounters. The ability to survive in seawater increases with body size of the fish (Wagner *et al.* 1969; Finstad & Ugedal 1998). Experiments with hatchery-reared smolts show that large individuals (mean 199 mm, range 172–228 mm) established seawater tolerance about 2 weeks earlier than smolts from a smaller size group (mean 180 mm, range 143–210 mm). Better ionoregulatory capacity may be partly due to the decline in exposed surface area relative to mass as the fish grow in size (Handeland *et al.* 1998; Claireaux & Audet 2000). Moreover, large fish escape predators more easily than smaller conspecifics (Dill 1983). Therefore, the expected sea survival increases with the size of the fish. Estimates based on returns of tagged brown trout support this view (Jonsson *et al.* 1994).

Down- and Upstream Migration

The time of seaward migration varies among rivers and the developmental stage of the fish. The downstream migration takes place during two main periods, a feeding migration in spring and an overwintering migration in autumn and winter. In spring, smolts and larger fish spending the winter in fresh waters migrate to the estuary and coastal sea for feeding. The smolt migration takes place from March towards July, although downstream movement of pre-smolts can occur earlier, particularly at low latitudes where water temperatures during winter are relatively high (Le Cren 1985). At high latitudes, such as at 69°N in northern Norway, the fish migrate as late as June–July (Berg & Berg 1987, Berg & Jonsson 1989). The main spring migration may occur over a few weeks. In southern Sweden, Bohlin *et al.* (1993b) reported that 90% of the downstream smolt migration in Norumsån occurred during 29 days, with median times ranging from 26 April to 17 May. In addition, anadromous trout, which have overwintered in fresh water, migrate to sea for feeding in spring. As found in Norwegian streams, veteran migrants descend downstream to sea earlier in spring than the smolts (Jonsson 1985; Berg & Jonsson 1989; Jonsson & Jonsson 2002). It is assumed that brown trout prefer to spend the winter in fresh or brackish water because it is costly to stay in high salinity sea water (35‰) when the temperature is low.

Brown trout can descend to sea in autumn for wintering in brackish water. This is particularly the case in brooks and small streams as e.g. observed in the Baltic (Taal *et al.* 2014). Furthermore, in sea lochs on the west coast of Scotland, Pemberton (1976b) found that sea trout could move to sea in August and stay there to late spring. Furthermore, post-spawners can move to sea in the autumn. In the River Imsa, immature and mature migrants move to sea from October through January (Jonsson & Jonsson 2002). Annual growth was higher for sea trout spending the winter in seawater compared with those staying in fresh water (Jonsson *et al.* 2009).

After feeding in fjords and coastal waters, immature and mature trout can return to fresh water for spawning and/or wintering; most return to their river of origin (Jensen 1968; Jonsson 1985; Jonsson & Jonsson 2009). The fish move quickly against the current (Armstrong & Herbert 1997), and the oldest trout appear to move upstream earlier than younger ones (Jonsson & Gravem 1985; LeCren 1985; Jonsson & Jonsson 2002). The timing of the run varies considerably, from a peak in May in southwest England, to June and July in Cumbrian rivers and in the Burrishoole system in Ireland, although it is sometimes as late as October in the River Coquet, northern England.

In the Norwegian river Gudbrandsdalslågen, eastern Norway, lake feeding brown trout ascended the river from late June to mid-October (Jensen & Aass 1995), and in the River Istra, mid-Norway, most anadromous trout ascended during August and September, although the migration actually began in July and extended until October or November (Jensen 1968). In the River Imsa, southern Norway, the trout ascended in all months from April through December, but the main upstream migration (72%) occurred from August to October (Jonsson & Jonsson 2002).

For sea trout, the time of freshwater ascent appears to depend on river size. Fish spawning in large rivers ascend to fresh water some six months before actually arriving at the spawning areas (Campbell 1977), whereas trout spawning in small coastal streams often ascend in a short period of time just prior to spawning, in particular during periods of heavy rainfall. Trout spawning in small brooks typically leave the brook as soon as spawning is finished. Brown trout spawning in large rivers can stay in fresh water over winter and survivors migrate to sea in spring. In small systems without deep pools or lakes, the fish can spend the winter in brackish water or sea water.

Benefits and Costs of Migration

The benefits of migration are increased growth opportunities, larger body size and reproductive outputs (Jonsson 1985; Jonsson & Jonsson 1997, 1998, 1999), whereas the main cost is increased mortality and energy use (Jonsson & Jonsson 2006). Bohlin *et al.* (2001) provided a direct test on the meaning of the migratory energy cost for the distribution of anadromous fish in watercourses. They studied anadromous and non-anadromous populations on the southern coast of Sweden, and used elevation as proxy for migratory cost. At low elevations, juvenile density (as a measure of population productivity) was higher for migratory than for non-migratory populations, showing that migration was beneficial because it increased the production of juveniles. Juvenile density then decreased with increasing elevation in anadromous, but not in freshwater resident brown trout. At an elevation of about 150 m, juvenile density was similar for the two, suggesting that the cost of migration had reached the point where it offsets the benefits. As expected, the presence

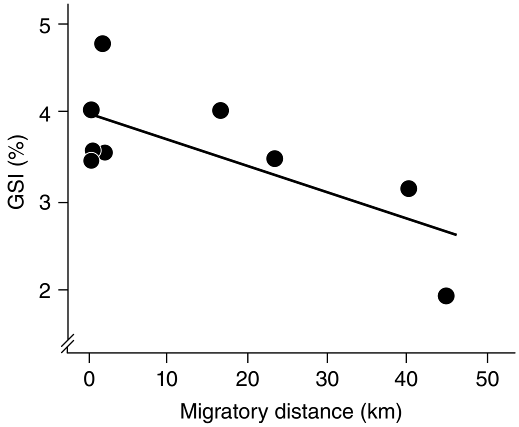

Figure 10.4 Relationship between mean gonado-somatic index (*GSI*) and migratory distance in the river of first-time spawning male anadromous brown trout.

of anadromous fish also disappeared at higher elevations. This evidence suggests that the energy costs of migration in addition to impassable barriers such as waterfalls, limit the distribution of anadromous brown trout inland.

That upstream migration is costly is also suggested by the fact that large trout migrate farther upstream for spawning than smaller conspecifics (L'Abée-Lund 1991; Jonsson & Jonsson 2006). Furthermore, Jonsson & Jonsson (2006) reported that condition factor decreased with migratory distance in fresh water, meaning that anadromous brown trout moving inland are slimmer than those spawning closer to the coast (Figure 10.4). In addition, they found that gonadal mass of first-time spawning anadromous males declined with migration distance as another indication of a migratory cost. This is probably because the fish had a reduced amount of reserve energy available for gonad development.

Smolting versus Maturation: Are they Competing Processes?

Migration and sexual maturation appear to be competing processes in brown trout (Jonsson 1985; Thorpe 1986, 1987). In anadromous populations, parr either mature or smolt before attaining maturity. Sexual maturation appears to inhibit smolting and vice versa (Jonsson 1985; Dellefors & Faremo 1988). In a few cases, however, mature trout smolt. If so, they do not spawn again the same year, but wait at least one year before spawning again. Other major niche shifts appear to have a similar delaying effect on maturation, as when brown trout switch from benthivory to piscivory (Jonsson 1977; Jonsson *et al.* 1999). Possibly, the delay is associated with increased energy assimilation and growth making it profitable to postpone maturation. In addition, female trout seldom attain maturity during the first summer at sea. Maturation appears delayed by the sudden increase in growth, which often is associated with ontogenetic niche shifts (Jonsson & Jonsson 1993).

Age and size at maturity vary among the sexes. Males usually mature younger and at a more variable size than females (Jonsson 1989). Males can mature as parr in the nursery stream, but they can also mature at a larger body size after a period of growth in a lake or at sea. Males may attain maturity from less than 10 cm in length and 1 year of age (Jonsson & Sandlund 1979; Dellefors & Faremo 1988; L'Abée-Lund *et al.* 1990), and mature parr males often constitute a large part of partly migratory populations. For instance, in the Norumsån and Arödsån, southwestern Sweden, the proportion of mature parr males varied between 17.9 and 57% (Dellefors & Faremo 1988), and in Norwegian rivers the proportion varied between 0.6 and 62% (L'Abée-Lund *et al.* 1990). However, in females maturation may be associated with the attainment of a certain body size (Jonsson 1977, 1985).

Food and Feeding

Brown trout are opportunistic feeders with a diet varying among habitats, seasons, fish sizes and ages (Bridcut & Giller 1995). However, individual fish may exhibit dietary specialization, rather than opportunism, meaning that they may for periods of time feed chiefly on one or a few food items (Grey 2001).

Young stream-living parr eat mainly insect larvae, chironomids in particular, but they can also take surface arthropods like flying insects. With increasing size, they gradually take larger food items such as Ephemeroptera, Plecoptera, Simulidae and Trichoptera (e.g. Haraldstad *et al.* 1987; Jonsson & Gravem 1985; Rincón & Lobón-Cerviá 1999; Steingrimsson & Gislason 2002).

In lakes, zoobenthos in shallow waters is the major food. The importance of pelagic food, such as chironomid pupae and zooplankton as well as surface arthropods, increases with increasing size and age of the fish. In some lakes, brown trout sometimes feed almost exclusively on zooplankton (Klemetsen 1967; Schei & Jonsson 1989), probably because this is the main food present, e.g. because of the steep gradient of the bottom contour. In populations were sub-adult and adult brown trout predominantly eat fish, brown trout may start fish feeding from a body length of ca. 15 cm (L'Abée-Lund *et al.* 1992), although even smaller fish can occasionally eat fish (Jonsson & Gravem 1985). Within brown trout populations, the fish gradually change to fish feeding with increasing size. Fast growing individuals change to piscivory at a younger age and smaller size than more slow-growing individuals do. Thus, fast growth early in life appears to predispose the fish to become a fish feeder. In Lake Femund, for instance, where all brown trout older than 10 years of age appear to be piscivorous, mean age and length of the youngest fish feeders were 4 years and 17.5 cm, whereas the oldest invertebrate feeders were 9 years and 36 cm (Jonsson *et al.* 1999).

The personality of individuals may influence their tendency to eat fish (Adriaenssens & Johnsson 2011). According to Keeley & Grant (2001), salmonids are predominantly fish feeding from a length of 31 cm, but as explained above, this varies among populations. The size of fish eaten increases gradually with the size of the predator (L'Abée-Lund *et al.* 1992; Næsje *et al.* 1998). In northern populations, the probability of fish feeding increases with temperature in spring and early summer. The period of maximum feeding in spring coincides with that of minimum fat content in the fish and high food availability (Jonsson & Jonsson 1997, 1998; Berg *et al.* 2000). This seasonal difference is smaller in southern Europe (Rincón & Lobón-Cerviá 1993).

Anadromous brown trout can feed heavily in the sea. The main food items are marine crustaceans, polychaetes, fish and surface insects (Pemberton 1976a; Fahy 1983; Grønvik & Klemetsen 1987; Lyse *et al.* 1998; Knutsen *et al.* 2001b). Polychaetes are most important in spring whereas fish, in particular Gobiidae and Clupeidae, dominate by mass in autumn and winter. Most of the prey taken are typical for shallow and brackish waters (Knutsen *et al.* 2001b). Trout appear to start fish feeding earlier at sea than in fresh water (Keeley & Grant 2001), but the importance of fish as food increases with trout size (Knutsen *et al.* 2001b, 2004). Anadromous trout can also feed after returning to fresh water in summer and autumn with small fish as the main food item. Females feed more in fresh water than males (Elliott 1997). In late autumn, however, feeding ceases, and most of them appear to metabolize stored lipid reserves during winter (Jonsson & Gravem 1985).

Brown trout are visual feeders, and water transparency appears to be an important determinant for their vertical distribution; i.e. they exploit deeper waters in clear than in turbid lakes (Langeland *et al.* 1991). Often, young and small fish feed closer to the surface and shoreline than older and larger individuals (Jonsson & Gravem 1985; Ovidio 1999). Allopatric populations may have a wider habitat use than those living together with other fish species such as Arctic charr or whitefish (*Coregonus lavaretus)*, both of which are better adapted to feeding along deep bottoms and in the pelagic zone than brown trout.

The quantity and quality of food eaten are very important for the growth rate of fish (Wootton 1998), and the ability to grow continuously during the entire life span depends heavily on whether the fish have opportunities to change to larger sized food items as they grow (Gorman & Nielson 1982).

Growth

Brown trout growth and size vary considerably among individuals and populations. Four-year-old fish may vary in wet mass from about 20 g in small sized brook-living trout to approximately 1 kg in fast growing ferox and anadromous trout (*e.g.* Jonsson & Sandlund 1979, 2016; Jonsson 1985; L'Abée-Lund *et al.* 1989; Landergren 2001). Variation in food consumption and temperature are probably main reasons for the large size variation (Alm 1959; Elliott *et al.* 1995), but also food particle size is important (Wootton 1998). With increasing size, fish need and can exploit gradually larger food items. One reason why anadromous brown trout grow faster than freshwater resident fish may be that they start fish feeding earlier (Keeley & Grant 2001). Therefore, the relationship between per capita resource available and body size is likely to depend on local conditions (Rincón & Lobón-Cervia 2002).

High population density also has a negative effect on growth. This occurs in both streams (Jenkins *et al.* 1999) and lakes (Jensen 1977). This is at least partly because high numbers of fish reduce food abundance, but there may be also a negative effect of intensified competition and aggressive encounters, as high fish abundance decreases food or habitat availability. Furthermore, individual variation in growth rate decreases with fish density in streams, probably because of intraspecific competition (Elliott 1994).

Temperature affects growth rate, other factors being equal. The lower critical temperature for growth is 3–6 °C and the upper critical temperature is 25–26 °C (Forseth *et al.* 2009). The optimal temperature for growth is between 13 and 18 °C, and it increases with increasing energy assimilation (Elliott & Hurley 2000; Ojanguren *et al.* 2001). The feeding rate parallels that of the growth rate, and the temperature at maximum feeding is only slightly higher than the optimal temperature for growth. The temperatures of commencement, termination and maximum growth decrease with decreasing feeding rate and stomach fullness. There is little evidence of genetic variability in the thermal performance of growth rates in populations from different geographical areas. Populations appear not to be genetically adapted to the temperatures of their natural habitats (Elliott 1994; Forseth *et al.* 2009) although the growth rate of fish in some very cold glacier fed rivers is surprisingly high (Jensen *et al.* 2000; Nicola & Almodovar 2004). Furthermore, Lobón-Cerviá & Rincón (1998) studying brown trout in the Spanish River Chaballos observed growth rates consistently higher than those predicted by the Elliott *et al.* (1995) growth model, and they suggested that this may be a local adaptation of the thermal regulation of growth. The same holds for anadromous trout (L'Abée-Lund *et al.* 1989). Alternative explanations are that the growth model underestimates the growth rate because the optimal temperature for growth is higher than estimated by Elliott *et al.* (1995), and that the energy assimilation is higher than the fish fed in Elliott & Hurley's (2000) experiment (Forseth & Jonsson 1994), e.g. because of compensatory growth after a period of low energy consumption.

Adult Size

Size at maturity varies among locations and depends largely on quality and quantity of available food and age at maturity. Adult wet mass can vary from approximately 10 g to 10 kg. However, for trout spawning in small streams water flow also influences adult body size (Jonsson *et al.* 2001). For instance, length at maturity of anadromous brown trout decreases with decreasing water flow in small streams. This holds for anadromous as well as sympatric resident male spawners sneaking at the nests of anadromous females. Resident females are few in most small streams. The increasing size of the non-anadromous males with water flow parallels that of the smolt size. Thus, there appears to be a selective advantage for trout to be small in the smallest brooks. Anadromous brown trout in the same area are larger (L'Abée-Lund *et al.* 1989). Hence, adult size differs because of differences in growth opportunities. In addition, genetic specialization of populations is possible because of their strong homing behaviour. Genetic analysis of brown trout from small streams shows that each supports a distinct population (Knutsen *et al.* 2001a), similar to what has been found elsewhere (Ponomareva *et al.* 2014), and tagging studies show that anadromous trout often stray very little among streams (Jonsson 1985; Jonsson & Jonsson 2009). Thus, sea trout appear to return to their stream of origin for spawning, and not enter streams depending on the size of the water flow (although exceptions may occur (*cf.* Berg & Berg 1987). However, as it is largely feeding in estuaries near mouths of rivers, they may enter other streams for short-time feeding, as charrs can do (*cf.* Armstrong 1974), but return to their home river when ready to spawn.

Brown trout often exhibit sexual size dimorphism (*SSD*), and anadromous males can be smaller or larger than corresponding females. Jonsson & Jonsson (2015) reported that in Norway, anadromous males were shorter than anadromous females at maturity in populations where the mean male body length was shorter than 49 cm (ln length = 3.89), and longer than females in streams where their mean length was longer. 49 cm is the mean length of males at spawning in rivers with mean flow of 41 m^3s^{-1} (Figure 10.5). However, this is flow measured at the outlet of the river and not on the spawning grounds. Thus, brown trout exhibited populations with female-biased *SSD*, no *SSD* or male-biased *SSD* depending on size of the home river. The slope of the regression of

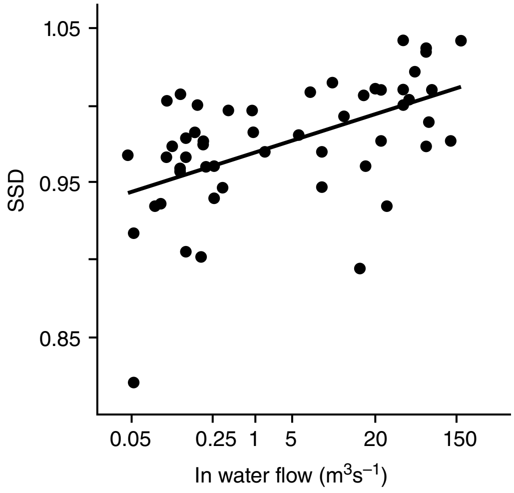

Figure 10.5 Regression of sexual size dimorphism in brown trout (*SSD*) and water flow (*Q*): $SSD = 0.008\ Q + 0.970$ ($r^2 = 0.28$, $F_{1,50} = 19.7$, $P < 0{\cdot}001$).

female on male length was 0.59 in agreement with Rensch's rule (Rensch, 1960). According to this rule, male body size varies more than female body size, and *SSD* typically increases with body size when males are largest, but decreases with increasing size when females are largest. Thus, among conspecific populations the slope usually is less than 1 when female sizes at maturity is regressed on the corresponding male sizes, as has also been found for Pacific salmon and trout *Oncorhynchus* spp. (Young 2005).

Natural selection should favour a large female body size because both fecundity and egg size increase with body size, given that the probability of dying is the same. Large males may be favoured by sexual selection because females may prefer to mate with large males. They display the most extreme secondary sexual characters (Petersson *et al.* 1999). Large males may be also favoured by natural selection because large males are stronger fighters. Thus, large males have access to more females and perform a higher number of spawnings than smaller conspecifics (Fleming *et al.* 1996). However, the success of large males may be low in narrow, shallow streams with low flow. Males fight intensively in the spawning area, and environmental conditions in small streams may limit the competitive success of large males more than that of smaller males. Females show little aggression during spawning (Fleming *et al.* 1996), and in small streams the reproductive success of large females may be less constrained than similarly large males.

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11

Life-history Plasticity in Anadromous Brown Trout: A Norwegian Perspective

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Introduction

Considerable effort has been invested into understanding the variation of various aspects of the life-history of the commercially and culturally important species of salmonid fishes especially in the genus *Salmo* and *Oncorhynchus* (e.g. Quinn 2005; Jonsson & Jonsson 2011). There is also a large literature on the brown trout *Salmo trutta*. However, less attention has been directed at the anadromous brown trout (sea trout). Accordingly, less is known about what drives the large within- and among-population variation in various life-history traits in these anadromous populations. There are, however, some long-term studies of anadromous populations and these have clearly documented considerable variation, either plastic or genetically based, in demography (Elliott 1994), life-history (Jonsson 1985) and migratory pattern (Jonsson & Jonsson 2009; Jensen *et al.* 2012, 2015). In this chapter we will summarize data on sea trout from Norway to try to understand what drives life history variation at different spatial scales (among and within population variation).

The brown trout is the most widely distributed freshwater fish in Norway (Huitfeldt-Kaas 1918). Rivers, streams and lakes from the sea level and up to an elevation of approximately 1300 m are inhabited by brown trout. As in most other areas of the world, trout have been translocated and stocked over long distances and throughout long times (see Budy *et al.* 2013). In Norway, such translocation started already more than 1000 years ago (Huitfeldt-Kaas 1918). This means that the trout can be found in all kinds of habitats, potentially leading to large variation in plastic responses and also large differences in how the species respond to different types and strength of selection.

Brown trout may support landlocked populations or, if the individuals have access to the sea, populations with individuals that either are anadromous or freshwater resident (Klemetsen *et al.* 2003). The presence of both migratory and stationary individuals within the same population is usually called partial migration (Jonsson & Jonsson 1993). The level of partial migration, and what trigger individual fish to be either migratory or

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

stationary is not well-known (Bohlin *et al.* 2001). Further, the timing of migration (at what age, when during the season), the length of the marine migration (how far out into the ocean, how long) and the timing of the return migration (at which age and size, when during the season) vary strongly. Understanding the proximate and ultimate factors leading to this large variation is a great challenge.

Here, we synthesize data on life-history variation in anadromous brown trout in Norway. Norway has a coastline extending over 12 degrees of latitude and also 17 degrees of longitude. This offers large variation in environmental conditions both in the freshwater and the marine habitat, potentially leading to large variation in phenotypically plastic responses as well as selection pressures. We focus especially on life-history traits that can be compared on a latitudinal scale.

Migratory Patterns

Smolt Migration

The transformation of the juvenile freshwater living parr with a territorial behaviour to a seawater-adapted fish with schooling behaviour is named smoltification (Folmar & Dickhoff 1980). This change in physiology and behaviour is preceding the migration of the smolt from the rivers to spend weeks, months or years in salt water.

The timing of the descent of brown trout smolt during spring has been recorded over several years ($n \geq 3$) in 11 Norwegian rivers covering around 12 degrees of latitude (58°50’ N–70°02’ N) (Figure 11.1). We have used the date when 50% of the total smolt run (median date) has been recorded as a metric for the timing of the downstream migration.

Downstream migration timing varied strongly among and within rivers. The earliest median date occurred in River Imsa, where 50% descent was recorded on April 10th, whereas the latest median date was recorded on July 18th in River Hals. We analysed the data on timing of downstream migration using a general linear mixed model, with river as a random factor, latitude and year as variables, and a normally distributed error term. This model, containing in total 123 year-river observations, explained 90.5 % of the variation in timing. The model revealed a significant spatial south-north gradient ($F = 13.20$, $P = 0.006$; slope 2.40 ± 0.66) (Figure 11.2). The slope indicates an average delay in downstream migration by approximately 2.4 days per degree of latitude northwards. The average median date of emigration (adjusted for the temporal trend) was at day 50 (May 20th) for the southernmost population (Imsa) and day 86 (June 25th) for the northernmost population (Hals). A similar geographical cline has recently been documented for the timing of smolt migration of Atlantic salmon *Salmo salar* (Otero *et al.* 2014). However, the descent of brown trout smolt appear about 10 days later than in Atlantic salmon at the same geographical scale (see Otero *et al.* 2014). The latitudinal trend in the timing of smolt migration that we observed in Norway seems to be similar over also larger geographical scales (Thorstad *et al.* 2016).

Some of the studies of the timing of smolt descent cover a long time span (13–30 years), whereas most time series are much shorter. Based on the mixed-effects model it was possible to use all data to test for a temporal change in timing. The effect of time was highly significant ($F = 15.46$, $P < 0.001$; slope $= -0.45 \pm 0.11$), indicating that downstream

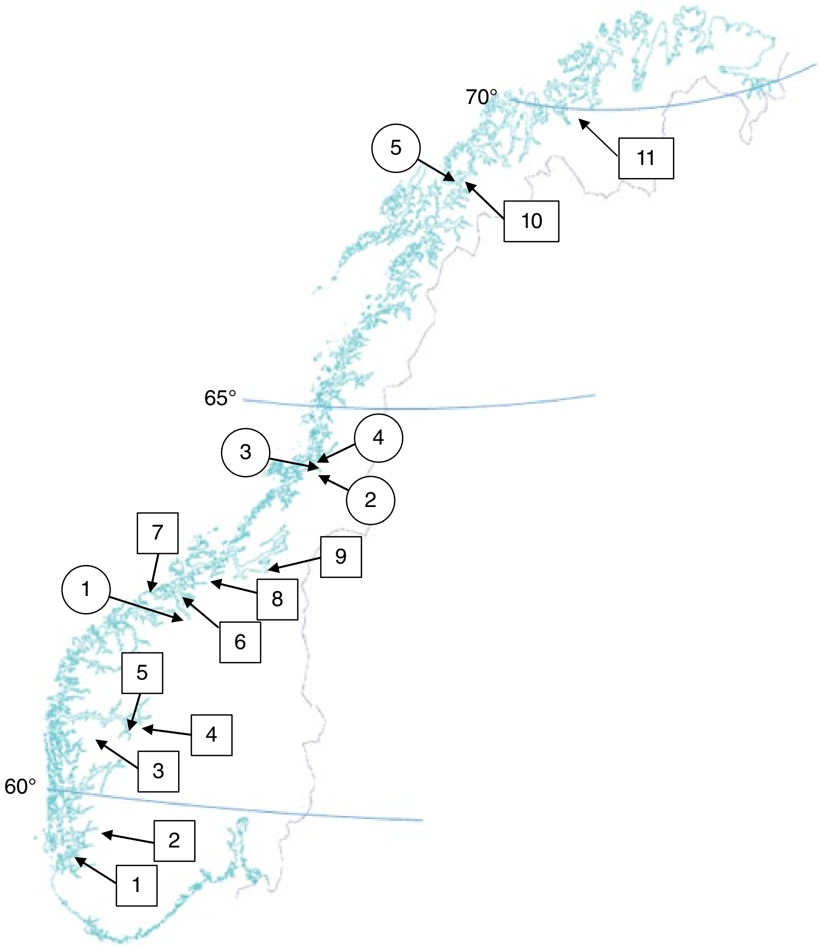

Figure 11.1 Location of the rivers used for modelling date of emigration of anadromous brown trout smolt (circles), and rivers where smolt were tagged and subsequently recaptured in salt water (squares). The names of rivers numbered in circles are given in Table 11.1, and names of rivers numbered in squares are given in Figure 11.3.

migration is happening early in the season in recent years. On average, the descent is becoming earlier by approximately 4.5 days every decade. This is a somewhat faster change than the 2.5 years per decade change that Otero *et al.* (2014) found for the downstream migration of Atlantic salmon smolt. We see at least two plausible reasons for this difference. First, Atlantic salmon smolt and brown trout smolt may respond differently to environmental cues. Secondly, the study of the variation in downstream migration of Atlantic salmon smolt covered a much larger temporal and geographical range (41°51’ N–70°02’ N) than that for brown trout (58°50’ N–70°02’ N). Otero *et al.* (2014) were also able to adjust for variation in a number of environmental factors. This is important if environmental change acts differently across latitudes.

The timing of the descent of brown trout smolt in different rivers seems to be triggered by the same environmental factors. Phenological traits, such as timing of migration, are

Table 11.1 Summary of the rivers used in the analyses on timing of smolt migration providing general information for each sampling site. Latitude and longitude indicate the location of the river mouth. Distance indicates the distance from the sampling site to the river mouth. [a] No recording 2006.

River	Latitude	Longitude	Years	Mean 50% date (range)	Distance (km)	Reference
1. Imsa	58°50’	5°58’	1976–2005	156 (130–173)	0.15	Jonsson & Jonsson (2009)
2. Suldal	59°29’	6°15’	1998–2004	155 (149–164)	2	Saltveit (2004a, b)
3. Vosso	60°38’	5°57’	2001–2007	180 (174–193)	0–0.4	Barlaup (2008)
4. Flåm	60°52’	7°07’	2002–2006	166 (157–174)	1	Sægrov *et al.* (2007)
5. Aurland	60°54’	7°11’	2001–2006	174 (159–183)	1	Sægrov *et al.* (2007)
6. Eira	62°41’	8°08’	2001–2013	170 (158–180)	1.2	Jensen *et al.* (2008, 2009, 2014a)
7. Hustad	62°58’	7°05’	2004–2010[a]	163 (155–180)	9.5	Lamberg & Strand (2011)
8. Surna	62°58’	8°39’	2011–2013	180 (175–185)	6.5	Ugedal *et al.* (2014)
9. Stjørdal	63°27’	10°54’	1991–2005	174 (164–183)	24	Arnekleiv *et al.* (2007)
10. Lakselv	69°14’	17°51’	2008–2013	205 (198–216)	0.6	Lamberg *et al.* (2015)
11. Hals	70°02’	22°58’	1988–2012	216 (200–230)	0.1	Jensen *et al.* (2012)

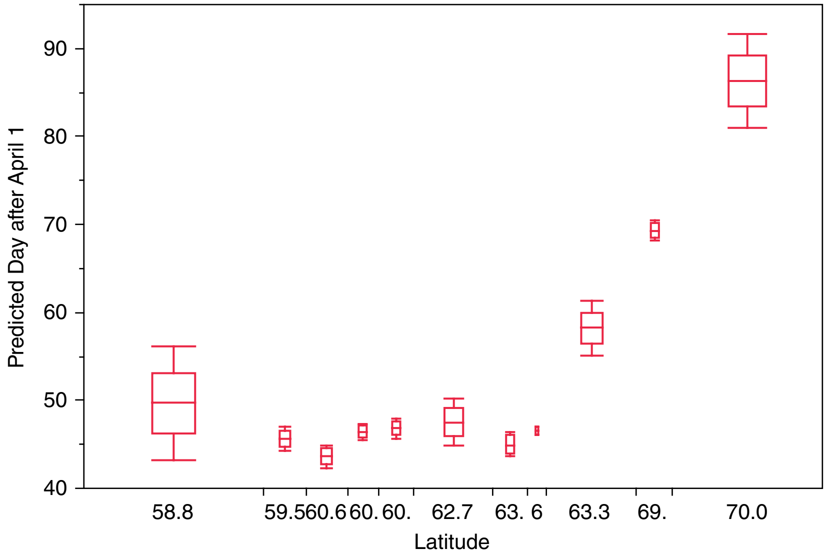

Figure 11.2 Distribution of the estimated time of downstream migration of anadromous brown trout (day after April 1 when 50% of the smolt have descended) in several Norwegian rivers along a latitudinal gradient. Information of the rivers are given in Table 11.1.

usually cued by stable environmental factors such as photoperiod, and Zydlewski *et al.* (2014) demonstrated experimentally that photoperiod controls the initiation of downstream movement in Atlantic salmon smolts. However, much of the within-location variation in timing of downstream migration has to be driven by variation in other environmental cues than photoperiod. The long-term study of smolt migration in the River Hals (Jensen *et al.* 2015) revealed that water flow explained most of the day-to-day variation in the intensity of the smolt runs, although also water temperature significantly contributed to the model. The model explained, however, only 13% of the variation in the median date of the smolt run. A much shorter study of anadromous brown trout smolt in the River Stjørdal also concluded that the smolt run was significantly correlated with water discharge and water temperature (Hembre *et al.* 2001). In that study, it was found that those two parameters explained 28% of the variation in smolt migration. The intensity of the descent increased with both increasing water discharge and temperature. In the southern part of Norway, the descent of anadromous brown trout has been documented from the River Imsa (Jonsson & Jonsson 2002). They divided the descending fish into two size classes (≤30 cm and >30 cm). The smaller size class was made up of both smolt and fish making their second marine sojourn. During spring, water temperature, but not water discharge, significantly influenced the number of descending individuals. The model explained 14% of the variation in the descent. The descent increased with increasing water temperature. All studies presented models that explained less than 30% of the variation in the timing of the smolt descent.

However, river discharge and water temperature were important factors, and analysing the years separately a model explaining much higher variation (61%; Hembre *et al.* 2001) could be achieved. Whereas river discharge was important in the rivers Stjørdal and Hals, this factor did not have any significant effect in the southern most River Imsa. One reason for this is probably the lack of a typical Norwegian spring flood in River Imsa connected to the melting of snow in spring. Anadromous brown trout smolt in the rivers Hals and Stjørdal indicated a threshold water temperature at 4 °C, although migration could take place also at lower temperature but at considerable lower intensity (Carlsen *et al.* 2004, Hembre *et al.* 2001). In River Imsa, a temperature threshold was not clear, but a marked increase in the number of migrants were observed at 9 °C (Jonsson & Jonsson 2002).

The large variation in the timing of the downstream smolt migration, and the suggestions that most populations respond differently to the same environmental factors indicates that there is a genetic basis for this. Local adaption in the timing of downstream smolt migration has been documented for Atlantic salmon (Stewart *et al.* 2002). Otero *et al.* (2014) suggested that sea temperature experienced by the smolt when they enter seawater is the main selective driver for variation in timing of smolt migration. High sea temperature during the spring smolt migration is suggested to increase the smolt survival (Jutila *et al.* 2005). Sea surface temperature along the Norwegian coast is very variable, and spring heating depends strongly on both insulation and large-scale current patterns and current speed. Hvidsten *et al.* (1998) showed that Atlantic salmon smolts from five Norwegian rivers leave their natal river when the sea surface temperature close to the river mouth is above 8 °C. Most probably a similar phenomenon may explain why anadromous brown trout smolt leave the rivers earlier at southern than northern latitudes. This indicates that trout at different latitudes respond to the same environmental cue (photoperiod) differently.

The overall descent advancement along the Norwegian coast of >4 days per decade is faster than recently shown for the phenological responses of 2.8 days per decade in spring across the northern hemisphere for multiple taxonomic groups (Parmesan 2007) and of 1.5–2.5 days per decade for several salmon species (Kovach *et al.* 2013; Otero *et al.* 2014). This phenological shift might be associated with the impacts of current climatic changes, and especially related to warming. Recent global analyses show that oceanic and terrestrial ecosystems (Burrows *et al.* 2011) and coastal regions (Lima & Wethey 2012) have experienced significant increases in temperature since the middle of the last century. Despite evidence that adaptive microevolution can occur rapidly in many populations, separating the contribution of genetic adaptation and phenotypic plasticity is difficult (Hoffmann & Sgrò 2011).

Migration at Sea

In contrast to Atlantic salmon that migrate over vast oceanic distances, anadromous brown trout conduct their marine migration in more coastal areas (Klemetsen *et al.* 2003). Studies of the movement of individually tagged anadromous brown trout have been performed in different parts of Norway. In general, most recaptures of tagged individuals were from the fjord within which their natal river belonged. However, the average distance from the river to the recapture site differs somewhat among these populations. Although the data set is small for some rivers, approximately 50% of the trout recaptured in the marine environment were recaptured within <40 km of their home river (Figure 11.3). Marine migrations of sea trout has also been studied in other countries, and overall sea-trout usually remain in near-coastal areas close to their river of origin (<80 km), although some individuals show remarkable migration distances > 500 km (Thorstad *et al.* 2016). There were some differences between the Norwegian populations, and these differences may reflect the size of the fjord system. However, these data

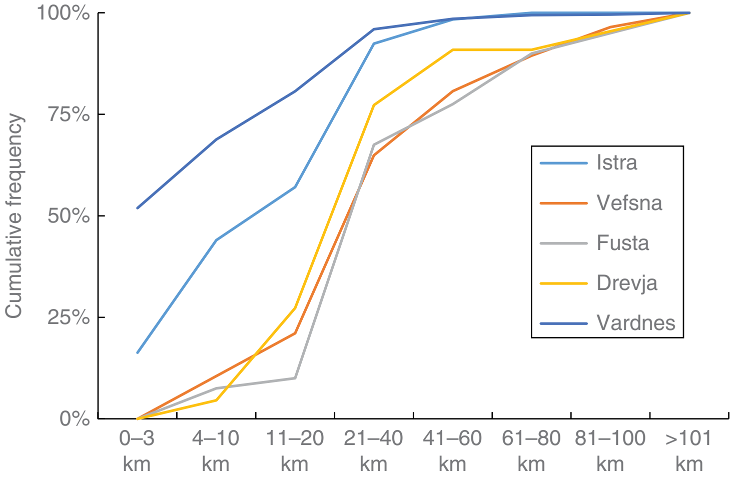

Figure 11.3 Distribution of cumulative recaptures in the fjord system of anadromous brown trout tagged in their natal river. The rivers are: 1 – Istra (Jensen 1968), 2 – Fusta (Johnsen & Jensen 1999), 3 – Drevja (Johnsen & Jensen 1999), 4 – Vefsna (Johnsen & Jensen 1999), 5 – Vardnes (Berg & Jonsson 1989).

may be biased since recreational fishers made most of the recaptures. Thus, the site of recapture may indicate where the good fishing localities are situated rather than trout behaviour.

Brown trout from local rivers may have evolved particular migratory behaviours over time. This can be inferred from the comparison of recaptures of tagged native and non-native trout released in the same fjord system. Recaptures of hatchery-reared brown trout of two different populations (River Lærdal and River Imsa) do indeed show different pattern of fjord migrations when released in a non-native fjord system (Jonsson *et al.* 1995). Jonsson & Jonsson (2011) further cites an unpublished study showing that the dispersal of the trout at sea increases linearly with the length of fjord draining their nursery river. However, recent studies have also revealed that some anadromous brown trout at sea choose the inner and warmer parts of the fjord (Rikardsen *et al.* 2007; Jensen *et al.* 2014b). Thus, more knowledge is needed about what parts of the coastal ecosystem that the trout use.

Few detailed and long-term studies have been conducted to elucidate the temporal extent of the marine migration of anadromous brown trout. In general, the sojourn lasts longer in southern than in northern Norway. In addition, most anadromous brown trout populations exhibit one major descent in spring–early summer, followed by a major ascent in late summer and autumn (but see Jonsson & Jonsson 2009; Eldøy *et al.* 2015). The duration of this sojourn for trout in River Hals (70°N) is about 55 days (A.J. Jensen, personal communication). Trout in the rivers Vardnes and Lakselv (69°N) stay approximately 70 and 40 days at sea, respectively (Berg & Berg 1989; Lamberg *et al.* 2015). In central Norway, Jensen (1968) showed that the sojourn for trout from River Istra (62°N) lasted approximately 108 days before most individuals ascended in August and September, and Eldøy *et al.* (2015) showed that brown trout from the rivers Søa and Snilldal (63°N) stayed on average 100 days in the fjord system. In River Imsa (59°N), however, the pattern was more diverse. The individuals descending in January–June stayed 6–9 months at sea, whereas those descending in July-December stayed for 8–18 months at sea.

These patterns suggest that anadromous brown trout in the southern Norway may overwinter in salt or brackish water, whereas northern populations of trout generally overwinter in fresh water. However, by the use of acoustic telemetry, Jensen & Rikardsen (2008) showed that riverine anadromous brown trout in a north Norwegian river spent long parts of the winter in brackish and possibly partly in salt water. Capture of feeding anadromous brown trout in salt water during winter in the same region support the telemetry study (Rikardsen *et al.* 2006). In more southern populations trout are commonly encountered and fished in the sea during winter, and they are actively feeding (Knutsen *et al.* 2001, 2004). The tendency of leaving the river or continue staying at sea during winter may depend on the river characteristics and food availability at sea. Lack of lakes within the anadromous reach may induce the anadromous brown trout to descend after spawning rather that overwintering in freshwater (Jensen & Rikardsen 2012). Thus, there seems to be evidence for active use of brackish and salt water during winter among populations from many regions along the Norwegian coast. Still, there is very limited knowledge about this part of the lifecycle of the trout (Thorstad *et al.* 2016).

The trout is usually returning to the river for spawning during autumn. However, there is large variation in the timing of the return migration. In a recent study, Quinn *et al.* (2016) focused particularly on the pattern of when various salmonids return to their river for spawning. Of special interest here is the observation that the ascent into the rivers may take place several months prior to the spawning; this phenomenon is called premature migration. The anadromous brown trout in Norway are interesting in this case. According to Quinn *et al.* (2016), premature migration may be favoured where temperatures and flows are moderate or where lakes provide safety from predators and reduce energetic expenditure. Premature migration has been demonstrated for trout inhabiting the River Imsa (Jonsson & Jonnson 2009). This river is characterized by moderate flows, and a lake was accessible for ascending salmonids until 1993. As far as we know, there is no other documentation of premature migration for sea trout in Norway.

The presence of accessible lakes varies among the other Norwegian rivers where the return migration of anadromous brown trout have been studied, whereas they are rather similar in precipitation and flow regime. During autumn and prior to spawning there commonly is increased precipitation that improves migration conditions in rivers and stream. Thus, the timing of the ascent of anadromous brown trout in Norwegian rivers may be described as ‘making the best of a bad situation’ (Quinn *et al.* 2016).

Another interesting behaviour exhibited by anadromous brown trout is the use of several different rivers during their life span. In a recent study of tagged anadromous trout originating from the River Hals in Northern Norway, Jensen *et al.* (2015) showed that many immature trout overwintered one to four times in other watersheds before most of them returned to the natal river upon maturation. If this behaviour is common in anadromous brown trout, previous studies on the homing precision of trout and probably also other anadromous salmonid fishes should be revisited or at least treated carefully. Traditionally the recapture of a tagged fish in a non-natal river has been categorized as a straying individual, potentially leading to an overestimation of straying rate. The published straying rate of trout to other rivers varies considerably. Berg & Berg (1987) found a minimum straying rate of 15.5% in the anadromous brown trout population in River Vardnes, whereas straying rate of <2% has been reported in other Norwegian populations (Nordeng 1971; Jonsson & Jonsson 2014). Clearly, more studies on homing and straying in anadromous brown trout are necessary in order to fully understand the level of gene flow among local populations.

Juvenile Growth

In all ectotherm animals, growth is directly impacted by temperature. We should therefore expect large among-population variation in juvenile growth in Norwegian anadromous brown trout, given the large latitudinal gradient that it covers. In the first comparative study of life-history of 34 populations of anadromous brown trout, L’Abée-Lund *et al.* (1989) showed considerable latitudinal differences in juvenile growth. The annual length increment during the second year in freshwater and during the first summer at sea both declined significantly with latitude (58 to 70° N). The length increment of the juveniles in freshwater was correlated to river temperature, whereas length increment at sea was more correlated with latitude. River temperature alone explained 70% of the variation in length increment during the second year of life. The effect of temperature on metabolic processes and growth in fish is well-known. What is more impressive in this study is the importance of water temperature despite considerable variation among rivers in other characteristics.

In twelve Norwegian anadromous brown trout populations situated between 61 and 69° N, Jensen (1990) showed that mean growth performance varied between 76 and 136% of the predicted maximum growth rate for that temperature. He attributed this to genotypic differences between populations in growth performance, although an alternative explanation could be differences in food intake. In a follow-up study, Jensen *et al.* (2000) increased the sample of populations and analysed the growth pattern in juvenile anadromous brown trout in 22 Norwegian populations. Annual growth rates were significantly negatively related to latitude and positively related to annual mean temperature. But, the ratio between observed and predicted annual growth rate were significantly and negatively correlated with annual mean temperature. Observed annual growth was higher than predicted growth in cold rivers, i.e. rivers with an annual mean temperature <5.1 °C. This indicates some kind of thermal adaptation in brown trout populations in cold rivers.

Thermal adaptation in ectotherms may be explained by two hypotheses. Levinton (1983) postulated the hypotheses related to adaptation to local optima. This implies that variation in brown trout growth reflects thermal adaptation to their natal stream environment. The counter-gradient hypothesis was raised by Levins (1969) saying that populations from hostile environments perform better at all temperatures than conspecifics from benign environments. There is some evidence for this in fish (Conover and Present 1990). However, in an experimental study using eight Scandinavian populations of brown trout Forseth *et al.* (2009) did not find any support for any of the two hypotheses. Thus, the evidence here is conflicting and the importance of local adaptation is not clear.

Maturation Pattern

Brown trout show considerable variation in maturation pattern. Both females and males may become sexually mature at a young age and small size (freshwater resident), or at older age and larger size (anadromous). This variation may be due to a mixture of genetic or plastic effects (Jonsson & Jonsson 1993, 2011). Age at maturity is clearly influenced by growth opportunity and local environmental conditions. In large and complex river systems, the potentially heterogeneous habitat may provide large variation in food quantity and quality. Thus, habitat heterogeneity may lead to increased variation in expressed life-history tactics within the population. Particularly the presence of lakes in the river system may have a strong effect on growth (Haraldstad *et al.* 1987). Thus, to avoid any lake effect, L'Abée-Lund *et al.* (1990) studied the proportion of male parr maturation in eight Norwegian rivers (58–67° N) without lakes. The percentage of mature males (varying between 0.6 to 62.3%) increased significantly with the mean length of 0- and 1+ old immature individuals, and decreased significantly with increasing smolt age. Moreover, mean age at maturity decreased significantly with increasing mean length of the two age groups. No effect of latitude was found. Thus, in populations with low smolt age, there was a higher percentage of male parr maturing prior to smoltification than in populations with a higher smolt age.

The effect of stream size was the focus when 17 coastal streams (58–63° N) with anadromous and freshwater resident brown trout were investigated (Jonsson *et al.* 2001). Overall, the average frequency of resident females on the spawning grounds was low (3.5%) compared to the much higher frequency (48.9%) of resident males.

Mean annual discharge was positively correlated with mean body length at maturity of resident males and anadromous individuals. Similar trends were documented by L'Abée-Lund *et al.* (1989) when they studied 34 anadromous populations in Norway (58–70° N) in a larger variety of river systems. Mean sea age at maturity varied between 1.5 and 3.6 years and increased significantly with latitude. Sea age at maturity was significantly affected by the relative growth first and second year at sea. When growth during the first summer at sea was much higher than during the second summer, the trout became sexually mature at a younger age than when the ratio was low.

Most studies have focused on variation among populations from different watersheds. The results from such studies may be biased as a watershed may consist of several reproductively isolated populations with different characteristics. Thus, L'Abée-Lund (1991) investigated adult size and sea age at maturity in nine populations from two large watersheds in central Norway (approx. 64° N). Mean sea age at maturity and length of adult fish increased with altitude of the natal tributary, distance from river mouth to the natal tributary, and annual river discharge of both males and females. The increase in age and length may be an adaptation to the greater energy expenditure needed to reach the uppermost natal spawning areas. The effect of migratory costs on life-history traits was also studied by Jonsson & Jonsson (2006) in nine streams in southern Norway (59° N). Mean size of mature anadromous brown trout increased with migration distance, as did age at sexual maturity. The gonadal mass of first-time spawning males declined with increasing migration distance, whereas fecundity increased with migration distance. The migration effect on fecundity was opposite that found in two rivers in central Norway (approx. 64° N) where L'Abée-Lund & Hindar (1990) showed lower fecundity and larger eggs in individuals migrating upstream than individuals spawning in the lower reaches. Moreover, L'Abée-Lund & Hindar (1990) showed that fecundity and egg size differed significantly among seven watersheds (59–64° N) but was not associated with latitude.

In a recent study, Jonsson & Jonsson (2015) merged data from different studies and analysed how sexual size dimorphism varied across 52 anadromous brown trout populations in Norway (58–70° N). They found that females were larger than males in populations where male mean total length at maturity was below 49 cm. In populations were males was larger than 49 cm, females were smaller than males. The sexual size dimorphism (ratio between mean length of males and females) increased significantly with discharge and latitude. Thus, anadromous brown trout exhibit large variation in adult length being female-biased, male-biased or without any sex bias. All this variability cannot adequately be explained by variation in the strength of sexual selection.

Anadromous brown trout demonstrate a latitudinal cline (58–69° N) in longevity (Jonsson *et al.* 1991). Brown trout in southern Norway had a shorter (approximately 2 years) life span than trout from northern rivers. Moreover, longevity was negatively correlated with temperature and growth rate in freshwater and at sea. Jonsson *et al.* (2001) focused on longevity at a smaller geographical scale and found that anadromous trout inhabiting small watercourses was smaller and lived shorter than conspecifics from larger watersheds.

Anadromous brown trout demonstrate great variation in the maturation pattern. So far, we are not aware of any study that have been able to disentangle the genetic component from the variability caused by plastic responses to the environmental conditions.

Age and Size of Smolts

Variation in the age- and length distribution of smolt can be analysed by sampling descending individuals, and by analysing scales of individuals caught after being one or several summer at sea. The effect of stream size was the focus when the populations in 17 coastal streams (58–63° N, mean annual discharge <1 m^3/s) inhabiting anadromous and freshwater resident brown trout were investigated (Jonsson *et al.* 2001). Mean smolt age and length were positively correlated with latitude and discharge, but with little effect when discharge exceeded 0.2 m^3/s. By studying 34 anadromous populations in Norway covering a larger geographical area (58–70° N) and variety of river systems (mean annual discharge 0.1–300 m^3/s), L'Abée-Lund *et al.* (1989) showed that smolt age increased with passable river length and latitude, and decreased with river temperature. There was no significant correlation with discharge. Mean smolt length increased with latitude, river length and discharge, and decreased with river temperature. Overall, mean smolt age and length varied from 1.5 years and 10.7 cm in a river in the south to 5.6 years and 22.6 cm in the River Tana in northern Norway.

Based on the large variation in age and size at smolting, Økland *et al.* (1993) tested the hypothesis that within populations there is a threshold size regulating the age and size at smolt transformation. The test used anadromous brown trout from four Norwegian rivers (59–67° N). They rejected the hypothesis. Their results indicated that it is more advantageous for slow growing individual to smolt at an older age and a larger body size than fast growing individuals. Thus, clearly there is large phenotypic plasticity in age and size at smolt transformation.

Concluding Remarks

Anadromous brown trout inhabiting different Norwegian watersheds demonstrate considerable variation in several life-history traits. This variation is a consequence of large-scale variation in habitat characteristics, especially water temperature and discharge in the spawning and nursery area. Moreover, similar variation has also been shown among populations within one watershed. The stability of the traits has not been tested by transplanting individuals from one population in one river to another river with another set of environmental conditions. However, based on various migratory patterns and growth and maturation schedules among Norwegian anadromous brown trout it seems reasonable to assume significant among-population genotypic differences as well of large-scale phenotypic plasticity.

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12

Life-History of the Adfluvial Brown Trout (*Salmo trutta* L.) in Eastern Fennoscandia

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Introduction

Changing environmental conditions and habitat characteristics both over geological time and more contemporary time scales have resulted in diverse life-history strategies of brown trout (*Salmo trutta* L.) through adaptation and favouring extensive phenotypic plasticity both within and among populations (Elliott, 1994; Klemetsen *et al.*, 2003). There is a high level of genetic differentiation among brown trout populations occupying adjacent watersheds, within a watershed among adjacent rivers, and even within a river among its tributaries and main stem (Huusko *et al.*, 1990; Hindar *et al.*, 1991; Carlsson & Nilsson, 2000; Giger *et al.*, 2006; Swatdipong *et al.*, 2010; Kohout, 2013). The highest level of differentiation has been observed in resident brown trout that spend their whole life-cycle in their natal river or stream. In comparison, isolation-by-distance is lower among migratory types (adfluvial and anadromous), but still clearly higher than, for example, that of Atlantic salmon (*Salmo salar* L.) (Swatdipong *et al.*, 2010). Thus, the brown trout seems to be a highly structured species where the basin-wide stock complex is constructed from separate building blocks which may interact with each other to variable extents (Schindler *et al.*, 2010).

Elliott (1994) differentiated four basic types among brown trout populations on the basis of their life-cycle patterns: resident, potamodromous, adfluvial, and anadromous. Broadly, brown trout spawn in running water, where their offspring called parr usually spend the first year of life. In following years, however, habitats may vary considerably between populations. In the simplest case, brown trout remain in their natal stream throughout their life, so these fish are resident. In a fluvial potamodromous life-cycle

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brown trout hatch in upstream freshwater habitats and as juveniles they migrate downstream, often into the main stem of the river. After maturing, the adult fish migrate back to their natal stream just before spawning. Thus, both resident and fluvial potamodromous types spend their whole life in running water, distinguishing them from the other two types. Adfluvial and anadromous brown trout migrate either to large lakes (adfluvial, lake-run) or the sea (anadromy, sea-run) for one to several years before returning to their natal river or stream to spawn. In addition, single populations may have both migratory and resident individuals, which are thus known as partially migrating populations (Jonsson & Jonsson, 1993; Olsson & Greenberg, 2004).

Brown trout have been shown to occur at least temporarily in sympatry with all possible migration strategies in stream habitats (Jonsson, 1985; Jonsson & Jonsson, 2011). Phenotypic variation is traditionally parsed into components of genetic and environmental variation, and their interaction. However, the relative importance of genes vs. environment in the phenotypic variation in migration behavior in brown trout is not yet completely understood (Olsson & Greenberg, 2004). It is assumed that different migration strategies can originate from the same gene pool (Hindar *et al.*, 1991; Jonsson & Jonsson, 1993; McKinney *et al.*, 2015; Baerwald *et al.*, 2016). To this end, it has recently been hypothesized that the observed life-history plasticity in the migration behavior of brown trout and other salmonids may be controlled by an epigenetic response threshold, which integrates parentally inherited factors, environmental factors and developmental history (Bossdorf *et al.*, 2008; McKinney *et al.*, 2015; Baerwald *et al.*, 2016). Nevertheless, certain migration patterns appear to be controlled by very few genes in rainbow trout (*Oncorrhynchus mykiss* Wallbaum) (Hess *et al.*, 2016) and in Atlantic salmon (Barson *et al.*, 2015; Ayllon *et al.*, 2015).

It has also been suggested that propensity to migration in brown trout is related to growth or growth-related variables such as food availability, especially in spring immediately before the out-migration period (Olsson *et al.*, 2006; Jones *et al.*, 2015). Giger *et al.* (2006) were not able to show existing inherited genetic differences between the resident and migratory types among their study populations, but a very distinct difference in their gene expressions, i.e. phenotypic variation in gene expression determined whether or not brown trout acquired a migratory life-style. Indeed, Giger *et al.* (2006) concluded that it is possible to classify individuals almost unambiguously into resident vs. migratory types based on the expression levels of a subset of genes, well before the obvious physiological transformation from stream-living parr to smolts begins in migrant individuals (see also Meier *et al.,* 2014; McKinney *et al.*, 2015; Baerwald *et al.*, 2016). Notably, it is not known exactly at which age and why certain individuals make the physiological decision to smoltify and migrate, creating an opportunity for genetic differences in a gene control region among migration types.

Eastern Fennoscandia, with thousands of lakes and rivers, is home to all of Elliott's life-cycle types: anadromous (sea-run) brown trout along the coasts of the Baltic, White, and Barents Sea; resident slow growing, early maturing populations with no major migration in the headwater streams; fluvial potamodromous populations in river systems; and adfluvial (lake-run) populations in the inland watercourses. In this chapter, we focus on the adfluvial brown trout by reviewing its basic life-history and ecology based on retrospective and present data from several eastern Fennoscandian lake basins. Historically and today, the adfluvial brown trout has been and is considered iconic and charismatic, and also a commercially and recreationally valuable species, having a status comparable to that of Atlantic salmon in marine environments and sea-flowing rivers. Unfortunately, today many adfluvial brown trout populations are endangered and currently only a few naturally reproducing, self-sustaining adfluvial brown trout stocks exist in eastern Fennoscandia. The main threats to adfluvial brown trout populations in this native area include overfishing, river damming, loss of spawning habitats and changes in land use. A detailed description of such threats and their impacts can be found in Syrjänen *et al.* (Chapter 28, this volume). Therefore, in this chapter, we will only mention these issues in terms of understanding the present life-history dynamics of adfluvial brown trout among the reviewed populations.

Study Areas and Populations

Lake Basins

We reviewed published retrospective and present data, as well as unpublished data bases of recognized scientists, on adfluvial brown trout from six eastern Fennoscandian drainage basins located between the latitudes of 61–69°N (Figure 12.1, Table 12.1).

The Lake Inarijärvi Basin is a large lake system in the north of Finland, flowing via River Paatsjoki into the Barents Sea. The central lake of this system is Lake Inarijärvi, and the main rivers ascended for spawning by adfluvial brown trout are the River Ivalojoki and the River Juutuajoki (Swatdipong *et al.*, 2010).

The Lake Notozero Basin is mostly located in northwest Russia, with Lake Notozero being the largest central lake in the system, draining via the River Tuloma into the Barents Sea. In its natural state, the area of Lake Notozero would be about 80 km^2, but after the construction of a hydroelectric plant in the 1960s on the River Tuloma, the water level increased, and at present, the lake is, for all intents and purposes, a reservoir. The River Luttojoki and the River Nuorttijoki are the main spawning rivers for adfluvial brown trout, flowing from west into Lake Notozero (Aalto *et al.*, 1998).

The main stem of *the Lake Pyaozero Basin* flows down to the White Sea through River Kovda, northwest Russia. The main lake is Lake Pyaozero and the main adfluvial brown trout spawning river system, the Olanga, flows from the west. In the most western part of the basin there is a sub-basin, Lake Kitkajärvi, draining through the River Kitkajoki into the River Oulankajoki (Figure 12.1). The Jyrävä Falls, located approximately mid-course of the River Kitkajoki, prevent the upstream migration of fish and thus isolate *the Lake Kitkajärvi Basin* from fish populations downstream of Jyrävä Falls. In the Lake Kitkajärvi Basin, adfluvial brown trout descend trait-specifically from Lake Kitkajärvi into the upper reaches of the River Kitkajoki to spawn, and the smolts then migrate back upstream to the lake (Keränen, 1978; Huusko *et al.*, 1990).

In southern Finland, two major drainage areas form the present Finnish Lake District which flow via major rivers, the River Vuoksi and the River Kymijoki, into the Baltic Sea. Several watercourses characterized by relatively large lakes connected by straits and relatively short rivers, flow into both of the main lakes: *Lake Päijänne* (the main inflowing watercourses of Saarijärvi, Viitasaari and Rautalampi; Figure 12.1) and *Lake Saimaa* (the main inflowing watercourses of Pielinen and Heinävesi; Figure 12.1). Adfluvial brown trout use such straits and short rivers as their spawning and nursery areas (Seppovaara, 1962; Syrjänen, 2010). As regards such purposes, the environmental

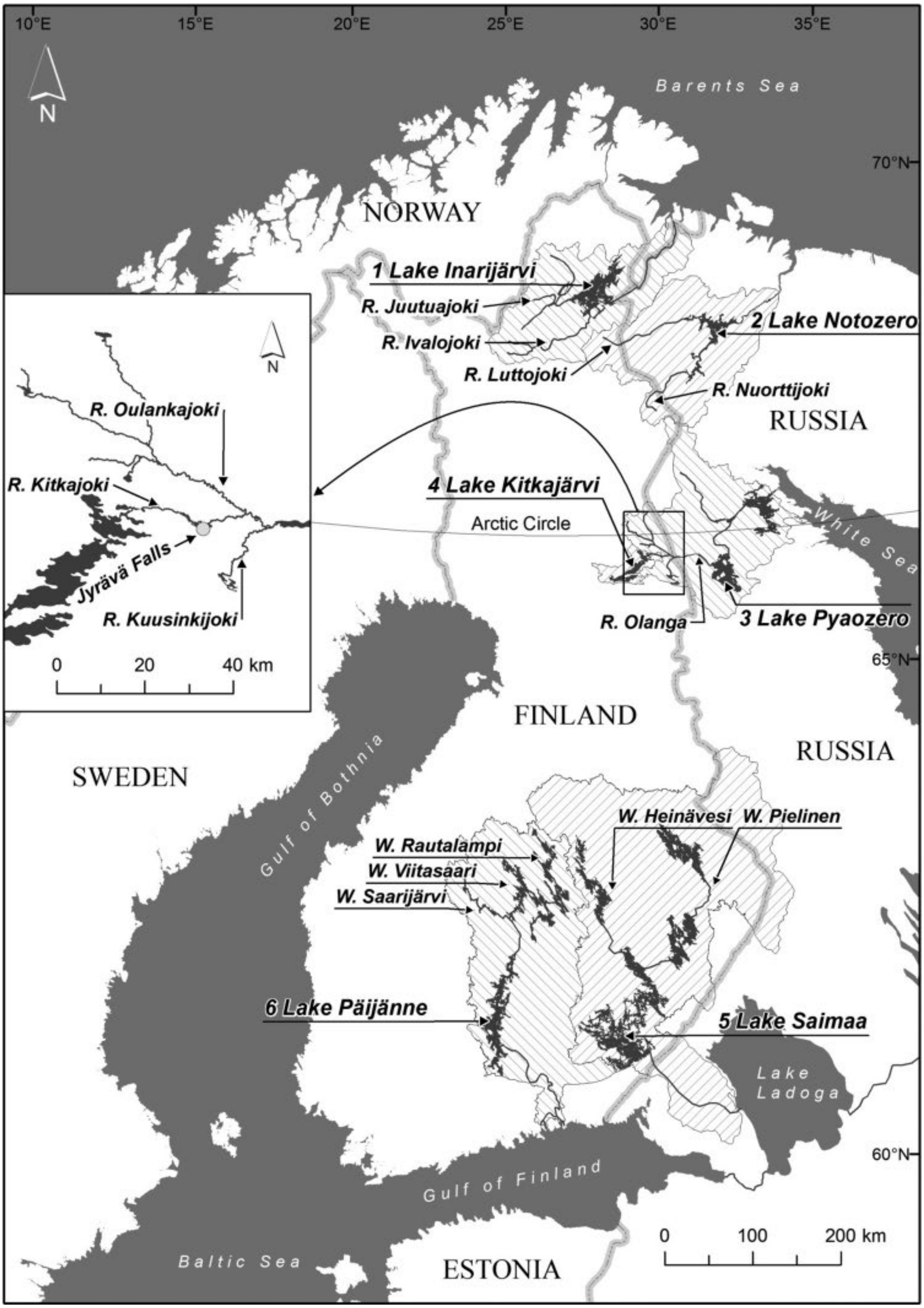

Figure 12.1 Location of the lake basins and the main spawning rivers (e.g. R. Juutuajoki) and watercourses (e.g. W. Pielinen) of the adfluvial brown trout populations reviewed in the text. A detailed presentation of the borderline (Jyrävä Falls) between the Lake Pyaozero and the Lake Kitkajärvi Basins is given in the separate box.

Table 12.1 Basic characteristics of the lake basins of the adfluvial brown trout populations reviewed in the text.

Code (see Figure 12.1)	Lake Basin	Location	Outflow river	Lake surface level, m a.s.l.[1]	Lake surface area, km[2]	Mean depth (max. depth), m	Main pelagial prey fish species	Main spawning rivers* or watercourses**
1	Inarijärvi	69.0 N, 27.6 E	Paatsjoki	118	1040	15.0 (92.0)	Dwarfed Whitefish[2], Vendace[3]	Ivalojoki* Juutuajoki*
2	Notozero	68.5 N, 31.2 E	Tuloma	80	745	15.5 (70.0)	Vendace	Luttojoki* Nuorttijoki*
3	Pyaozero	66.3 N, 31.1 E	Kovda	109	900	17.7 (49.0)	Vendace, Smelt[4]	Oulankajoki* Kitkajoki* Kuusinkijoki*
4	Kitkajärvi	66.1 N, 28.7 E	Kitkajoki	240	295	6.6 (41.2)	Vendace	Kitkajoki*
5	Saimaa	61.2 N, 28.1 E	Vuoksi	76	4400	17.0 (84.0)	Vendace, Smelt	Heinävesi** Pielinen**
6	Päijänne	61.5 N, 25.4 E	Kymijoki	78	1080	16.2 (95.3)	Vendace, Smelt	Saarijärvi** Viitasaari** Rautalampi**

[1] Meters above sea level; [2] *Coregonus lavaretus* L.; [3] *Coregonus albula* L.; [4] *Osmerus eperlanus* L.

conditions of the Finnish Lake District basins differ from those of northeastern Fennoscandia, which are characterized by long rivers flowing into a single large lake. However, both types of water systems provide diverse freshwater habitats for brown trout residency, migrations, foraging and spawning. The water quality is good to excellent in all of the above mentioned lake basins and as such, there is nothing to restrict brown trout stocks except for increasingly high summer temperatures in some southern headwaters and between-lake rivers (Toivonen, 1972; Niemi *et al.*, 2004).

Phylogeographic History

The paleogeographical history of the lake basins of Fennoscandia (details in Saarnisto, 1970; Koutaniemi, 1999) and the phylogeography of salmonids of eastern Fennoscandia (Asplund *et al.*, 2004; Tonteri *et al.*, 2005; Lumme *et al.*, 2015) have revealed that salmonid populations originated from freshwater lakes on the eastern margin of the retreating continental ice sheet. The genetic analyses of landlocked Atlantic salmon and brown trout have shown significant differences in mitochondrial haplotypes in accordance with the paleogeographical isolation history of Fennoscandian water basins, providing evidence that the populations of both species in the northeastern lake basins originate from the Karelian (White Sea) Ice Lake and the southern populations from the Baltic phase Ancylus Lake (Heikkinen & Kurimo, 1977; Lumme *et al.*, 2015). The divergence of brown trout populations between different lake basins is postglacial as is the divergence between separate rivers and watercourses draining into the central lakes, which occurred 8000–5000 years ago (Saarnisto, 1970). For example, after the last glaciation period, as a result of deglaciation and later isostatic land uplift, there have been several phases of divergence in today's Finnish Lake District, including the Great Lake of Central Finland which almost totally covered both the present Lake Päijänne and Lake Saimaa Basins (Saarnisto, 1970). The present areal extent and seaward drainage routes of the two separated lake basins has remained the same for approximately 6000 years. Correspondingly, the isolation of the lake basins in northeastern Fennoscandia, as well as transgression and water withdrawal, proceeded approximately within the same timeframe (Saarnisto, 1970; Koutaniemi, 1999; Lumme *et al.*, 2015).

The Current Status of Wild Adfluvial Brown Trout Stocks in Eastern Fennoscandia

Naturally reproducing, self-sustaining adfluvial brown trout stocks in the lake basins of eastern Fennoscandia have suffered from human actions, such as poorly regulated fishing, hydropower developments, and environmental degradation (Syrjänen *et al.*, Chapter 28, this volume). As a consequence, wild adfluvial brown trout populations in Finland are considered endangered in the area south of the Arctic Circle, and near threatened in the north (Rassi *et al.*, 2010). In northwest Russia (Karelia), the adfluvial brown trout is on the red list of endangered species (Kaukoranta *et al.*, 1998). The most viable wild adfluvial brown trout populations are found in the northeastern lake basins. Stocks in the Lake Pyaozero and Lake Notozero Basins are self-sustaining although the spawning rivers of the Lake Pyaozero Basin are stocked annually with a small number of one-year-old parr (Aalto *et al.*, 1998; Saraniemi, 2005). These lake basins are located in the Green Belt of Fennoscandia (Ministry of Environment, 2014). The remote location and difficulty of access have partly protected these stocks from adverse human activities in history and more important, during the past 50 years of developmental growth.

Also, the northern Lake Inarijärvi Basin sustains naturally reproducing, harvestable adfluvial brown trout populations (Swadtipong *et al.*, 2013). The water level in the lake has been regulated since a series of hydroelectric dams and stations were constructed during 1950–1978 on the River Paatsjoki, which connects the Basin with the Barents Sea. Supportive stocking, based on regularly renewed brood stock (wild-caught spawners), has been carried out to compensate the impacts of water level regulation, with the annual release of approximately 100,000 three-year-old hatchery-reared smolts during the last decades. Based on tagging studies, the proportion of supplemented adfluvial brown trout has been estimated to represent over half of the total catch (Niva *et al.*, 2013).

In the southern lake basins and also in the Lake Kitkajärvi Basin, the status of original adfluvial brown trout populations differ considerably from those in the northeast. Until the mid-twentieth century, these populations were healthy (Järvi, 1936; Seppovaara, 1962; Syrjänen *et al.*, Chapter 28, this volume). Since then, there has been extensive development in poorly regulated gill-net fishing in the lakes and rivers, resulting in the collapse of adfluvial brown trout stocks by the 1980s (Keränen, 1978; Syrjänen & Valkeajärvi, 2010). Efforts to rebuild the populations with supplementary stocking since the 1970s have not stimulated recovery and at the present time, the annual spawning populations of adfluvial brown trout are extremely sparse, if not virtually non-existent in these lake basins (Syrjänen *et al.*, Chapter 28, this volume). As a consequence, adfluvial brown trout populations have been maintained in hatcheries through artificial propagation and hatchery-reared brood stocks. Moreover, in the lake basins of southern Finland, the catch of this species is almost completely based on stocked hatchery-reared fish (Syrjänen *et al.*, Chapter 28, this volume). Hatchery brood stocks have only rarely been renewed with fish, mainly parr, caught in the wild creating the risk of genetic domestication and the increased frequency of potential resident life-cycle genes, as most parr in the wild originate from resident parents (Syrjänen *et al.*, Chapter 28, this volume).

The Life-Cycle of Adfluvial Brown Trout

The basic life-cycle of adfluvial brown trout in naturally reproducing populations includes nursery (egg, alevin and parr) stages of two to six years in the streams or short rivers connecting lakes. After this the parr smoltify and the smolts migrate to forage in lakes. After reaching maturation size and age, typically after two to five years in a lake, the adult fish migrate back to their natal riverine habitat for spawning. Having spawned, the fish migrate back to the lake and perform new spawning runs in forthcoming years. Thus, adfluvial brown trout show high variation in life-history traits, including large variation in the duration of riverine and lake phases, age at maturity and number of repeat spawning runs (Table 12.2). Depending on the population, there are 20–30 smolt age and lake age combinations for virgin trout, and the number of combinations increases even further, when repeat spawners are included (Aalto *et al.*, 1998; Saraniemi, 2005). The staggered age structure, combined with variable combinations of river and lake years and repeat spawning runs, upholds population and life-history diversity that acts as a bet hedging strategy, and reduces the probability that all individuals in a cohort of siblings will encounter an occasional reproductive failure or other environmental challenges over the course of a life-cycle.

Table 12.2 A dense summary of main life-history characteristics of the adfluvial brown trout populations reviewed in the text. NA = no exact data available.

	River-phase			Lake-phase					
Lake Basin (see Figure 12.1 and Table 12.1)	Timing of spawning on an average	Mean number of years parr spend in a river (range)	Mean length (mm) of smolts	Mean number of years spent in a lake before the first spawning run (range)	Mean length (mm) and mass (g) of the first time spawners	Mean length (mm) and mass (g) of the fish in spawning population	Percent of females in the spawning population	Timing of the main spawning run	Rhythm of the spawning runs
Inarijärvi	Late September–early October	4.0 (3–6)	NA	NA (2–6)	NA*	630 3200	64.0	August	Biennial
Notozero	Late September–early October	4.9 (3–7)	247	2.4 (1–6)	NA	510 1600	65.9	July	Biennial
Pyaozero	Late September–early October	3.5 (2–5)	223	3.2 (2–6)	632* 3200	690 4100	64.2	July	Biennial
Kitkajärvi	Late September–early October	3.3 (2–5)	235	NA (2–6)	NA	640 3700	73.3	NA	NA
Saimaa	October	2.9 (1–4)	267	NA (1–4)	NA	720 4500	NA	August–September	Both annual and biennial
Päijänne	October	2.9 (2–4)	268	NA (1–4)	NA	730 4800	71.3	August–September	Both annual and biennial

*Based on PMRN-analysis (see text): $L_{50} = 549$ mm for the Lake Inarijärvi Basin and $L_{50} = 552$ mm for the Lake Pyaozero Basin.

Spawning and Emergence of Larvae

The timing of adfluvial brown trout spawning shows latitudinal phenology, occurring in the second half of September in the northern lake basins of eastern Fennoscandia, while in the Finnish Lake District mainly in October (Seppovara, 1962; Saraniemi, 2005; Niva *et al.*, 2013). The exact timing is largely determined by the photoperiod, temperature, and physiological ability (readiness) of the fish to spawn (see Crisp, 2000). Saraniemi *et al.* (2008) suggested that day length may have a major impact on timing, as adfluvial brown trout spawn approximately at the same time every year despite annually variable water temperatures, ranging from two to thirteen degrees Celsius. Before spawning, male adfluvial brown trout develop secondary sexual characteristics similar to anadromous brown trout and salmon, typically a kype at the terminal end of the lower jaw. Also, the silvery colour of migration-stage fish becomes tinged with a darker appearance and more colour by spawning time (Figure 12.2). Fish that have spawned remain dark in colour until the following spring when the lake migrants become a silvery colour again and the river residents resort to their typical yellow-brown spotted coloration. Fish that have spawned can be identified by their thin form typically until June.

The eggs, buried among the runs and rapids of the spawning rivers in well aerated gravel fields (Louhi *et al.*, 2008), incubate during the winter, after which the alevins hatch in March-April in the rivers of the southern lake basins and in April–May in the northern rivers (Syrjänen *et al.*, 2008; Louhi *et al.*, 2010). The alevins stay in the gravel until they have depleted their yolk-sac and thereafter start emerging from the gravel, begin active swimming, external feeding, and intensive growth. Their emergence, a critical stage in the life-cycle of brown trout, generally occurs within a relatively short period of time in late May-early June in the southern lake basins (Syrjänen *et al.*, 2008), and one to three weeks later in the northern basins (Louhi *et al.*, 2011), usually well after the highest flood flows induced by snowmelt. Thus, the total length of time spent by the

Figure 12.2 A male adfluvial brown trout (mass 7.9 kg, length 83 cm, age 10 years, the fish being on its second spawning run) caught in August in the spawning river of the Lake Pyaozero Basin, showing typical signs of developing secondary sexual characters. Photo by Tero Törmikoski.

eggs, embryos and alevins in the gravel is as long as 7–9 months in eastern Fennoscandia. Further, the emergence phenology is opposite to spawning time phenology due to climatological differences along the Fennoscandian latitudes (61–69 N), i.e., the duration of winter with near zero water temperature, and the pace of autumnal cooling and vernal warming accumulating the sum of day degrees Celcius for embryonic development (Elliott & Hurley, 1998; Crisp, 2000; Syrjänen *et al.*, 2008).

Parr River-Phase and Smolting

Depending on latitude, environmental conditions, and genetics, the juveniles of adfluvial brown trout (parr) remain in riverine habitats for 2–6 years (Table 12.2; Figure 12.3) before they smoltify and migrate to a lake. Adfluvial brown trout smolts are silvery, resembling smolts of the anadromous type, and they differ from their stream-resident congeners that exhibit parr-like coloration. The average body length of smolts is usually 200–350 mm, depending on age, but there is considerable variation between the lake basins in parr growth rate and the age structure of migrating smolts (Table 12.2; Figure 12.3). Annual length increments during the river phase are clearly larger in the southern lake basins, with parr reaching smolt size on average within 3 years, while in the northern basins typically within 3 to 5 years. Interestingly, the youngest smolts observed in the Lake Saimaa and Päijänne Basins located in southern Finland have been 1-year old and about 80–100 mm long (Seppovaara, 1962) while in the northern Lake Inarijärvi and Notozero Basins even 2-year-old smolts are rare (Aalto *et al.*, 1998; Niva *et al.*, 2013).

However, the number of reported historical samples of smolt age structure is small for the lake basins of the Finnish Lake District, i.e. the Lake Päijänne and Lake Saimaa Basins (Figure 12.4; 18 and 35 individuals, respectively; Järvi, 1936; Seppovaara, 1962), and consequently, the corresponding smolt age frequency distributions contain large uncertainty. Based on scale readings and back-calculated lengths of fully adfluvial brown trout individuals, the average length of 3- and 4-year-old wild smolts in these lake basins has been estimated to be 272 ± 40 mm (mean ± SD) and 322 ± 55 mm, respectively, with 3-year-old smolts in the majority (Figure 12.4; Järvi, 1936; Seppovaara, 1962). Old recreational fishing statistics (with a 300 mm minimum length for legal catch) from the rapids and run stretches of the rivers in these lake basins have shown that about half of the summer-time brown trout catch during the last century consisted of individuals between 300 to 350 mm in length (Seppovaara, 1962; Eloranta, 1993).

More recently, wild brown trout catch samples from some of the rapids sections in the Lake Päijänne Basin have shown similar frequency distributions where about 60% of the brown trout typically belong to the 300–350 mm length-class among fish over 300 mm in length (P. Valkeajärvi, Konnevesi Fisheries Society, unpublished). Thus, the catch statistics reveal that a remarkable proportion of brown trout may have resided in the short rivers between the lakes longer than required to reach typical smolt size: most likely because these fish have adopted a partial or completely resident life-history, potentially due to good feeding conditions in the river sections. Relatively stable hydrodynamic conditions and ample food resources in lake outlet rivers apparently favour a non-migratory life-history (Jonsson & Jonsson, 2011; Jones *et al.*, 2015). However, there are no data for even roughly estimating the proportions of resident and adfluvial types

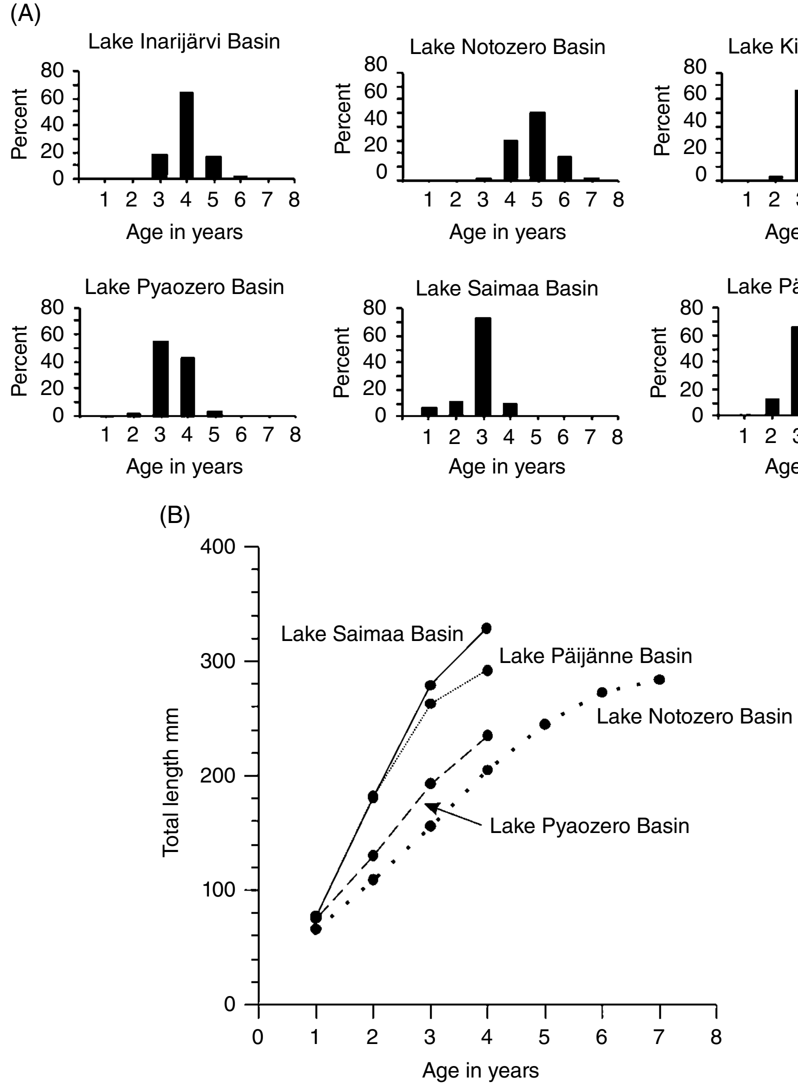

Figure 12.3 A: Age-class frequencies of adfluvial brown trout smolts in the lake basins (see Table 12.2). B: Adfluvial brown trout total length by age during the riverine phase in the main spawning rivers of the four lake basins. The lengths are derived from the scale readings and the relationship between fish total length and scale total radius. Data from Järvi (1936), Seppovaara (1962), Hurme (1965), Keränen (1978), Aalto *et al.* (1998), Saraniemi (2005), Niva *et al.* (2013) and A. Huusko (unpublished).

during the two contrasting periods before the mid-twentieth century when fishing pressure was low and thereafter when harvesting pressure in the lakes increased. Syrjänen & Valkeajärvi (2010) and Syrjänen *et al.* (Chapter 28, this volume) suggested that a probable change from populations dominated by an adfluvial life-history to those dominated by a resident life-history has occurred in the Lake Päijänne Basin during the few last decades, due to the overexploitation of adfluvial brown trout individuals during their feeding migration, a possibility indicated to be realistic by several recent studies on fishing-induced evolutionary changes (Thériault *et al.* 2008; Uusi-Heikkilä *et al.*, 2015, see also Hard *et al.*, 2008).

Smolt-Run

The smolts of anadromous brown trout typically migrate from river to sea slightly earlier than the smolts of Atlantic salmon, taking place in spring–early summer at water temperatures of 5–10 °C (Bohlin *et al.*, 1996; Jonsson & Jonsson, 2011). However, there are no exhaustive field studies on when adfluvial brown trout smolts actually migrate from the rivers. The few published studies suggest that the timing of smolt-run may be similar to that of anadromous brown trout. Based on the monitoring of tagged smolts in the River Kitkajoki, the Lake Kitkajärvi Basin, Keränen (1978) judged that the exceptional upstream smolt migration in this population peaked during a week in mid-June at a water temperature of 10–12 °C, while the total migration period lasted about three weeks. The upstream migration speed of these smolts was estimated to be 2.2 km day^{-1} on average. In experimental stream-like set-ups Pirhonen *et al.* (1998) monitored the swimming behavior of both adfluvial and anadromous brown trout during the smolting period. The results suggested that the smolt migration period occurred simultaneously, regardless of whether they belonged to an anadromous or adfluvial population and peaked at a water temperature of 6–10 °C for about three weeks. During their most intensive period of movement, the smolts swam downstream at a speed 20% faster than the water velocity (1.2 body length s^{-1}, corresponding to about 20 km day^{-1}), but at all other times they orientated head upstream and drifted downstream slower than the water velocity (about 7 cm s^{-1} vs 20 cm s^{-1}, respectively, corresponding to about 6 km day^{-1}).

Based on genetic mixed-stock analysis of catches derived from Lake Inarijärvi, Swatdipong *et al.* (2013) and Mäkinen *et al.* (2015) showed that the majority of adfluvial individuals originated either from the main stems or major side channels of the main spawning rivers of the Lake Inarijärvi Basin, with populations in upstream tributaries contributing insignificantly to lake stock. Likewise, in the Lake Pyaozero and Lake Kitkajärvi Basin, brown trout with an adfluvial life-history seem to originate from the main stems of the spawning rivers (Keränen, 1978; Huusko *et al.*, 1990; A. Huusko, unpublished). These observations reveal that the propensity for an adfluvial life-history can be high in the main stems of such rivers and low in the headwaters of basins in the northeastern stream-lake systems of Fennoscandia. However, in the Lake Notozero Basin, the smolts of adfluvial brown trout seem to mainly originate from headwater tributaries, indicating that river specific characteristics and fish species assemblage have a role in the basin-wide origin of an adfluvial life-cycle, for example whether suitable spawning habitats in the main stem of the river are used by Atlantic salmon forcing brown trout to use tributaries for spawning and nursery activity (Orell *et al.*, 2011).

In the Finnish Lake District stream-lake systems draining into the main lakes are characterized by watercourses with relatively large lakes connected by straits and relatively short rivers and rapids. Historical reports and present day observations (Järvi, 1936; Seppovaara, 1962; Syrjänen *et al.*, 2014; P. Valkeajärvi, Konnevesi Fisheries Society, unpublished) have indicated that some smolts have migrated long distances to the main lake of the basin, whereas others have swum up- or downstream from their natal river stretch to the nearest lake within the watercourse, to dwell there until maturity. Thus, in the southern lake basins there seems to be a continuum of migration distances, however, the reasons for the propensity to migrate long distances or to stay relatively close to the natal river, are unknown. Interestingly, small inland tributaries with direct outlets to large rivers and small brooks with direct access to lakes are not known to support adfluvial brown trout in the Finnish Lake District area, although small streams are utilized by anadromous brown trout, for example, in the Baltic Sea area. However, the current absence of spawning adfluvial brown trout in many inland brooks does not reveal whether this situation has always been so or whether adfluvial populations have disappeared due to heavy fishing or past environmental events (Syrjänen *et al.*, Chapter 28, this volume). Currently, many such brooks still support resident brown trout.

Lake-Phase

Growth in Lakes

Once the smolts have successfully entered the lake, they start feeding in the littoral zone. However, they soon change to the pelagial zone becoming almost totally piscivorous. Hyvärinen & Huusko (2006) reported that all adfluvial brown trout larger than 300 mm in total length were piscivorous, and also the majority (75%) of those in the 170–300 mm length classes preyed on fish in Lake Oulujärvi, northern Finland (64° N, 27° E). Vendace (*Coregonus albula* L.) and smelt (*Osmerus eperlanus* L.) are typically the most abundant pelagic planktivores in the large lakes of Fennoscandia, and are highly exploited by adfluvial brown trout as well as many other fish predators (Heikinheimo, 2001; Nyberg *et al.*, 2001; Hyvärinen & Huusko, 2006). A temporal match between the arrival of adfluvial brown trout smolts and the appearance of a new vendace year class, the latter providing abundant prey, in the pelagial zone of the lake seems to be important for the performance of brown trout smolts: a perfect match typically occurs in the second half of June in southern lake basins and at the turn of June to July in northern lake basins (Huusko *et al.*, 1995; Hyvärinen & Huusko, 2006). However, there are no studies on how fluctuations, typical among vendace for instance, in main prey species populations (Salojärvi, 1987; Heikinheimo, 2001) affect adfluvial brown trout survival and growth in lakes. Hyvärinen & Huusko (2006) showed that if main prey abundance, typically vendace, decreased to a low level, brown trout switched to exploit other pelagial prey, such as smelt. In all the reviewed lake basins located in Finland, vendace stocks are harvested by commercial and recreational fishing which could potentially reduce the availability of prey.

However, the estimated potential ecologically sustainable yield of vendace from Finnish lakes is much larger than the average realized total inland vendace yield (Marjomäki *et al.*, 2016). In view of the good observed growth and condition of lake-caught brown trout, this suggests that currently harvesting the main prey of adfluvial brown trout most probably does not, in general, seriously affect the foraging of trout in lakes.

The growth rate of lake-phase adfluvial brown trout is rapid although there is some variation between the lake basins (Figure 12.4, Table 12.3). Brown trout can grow

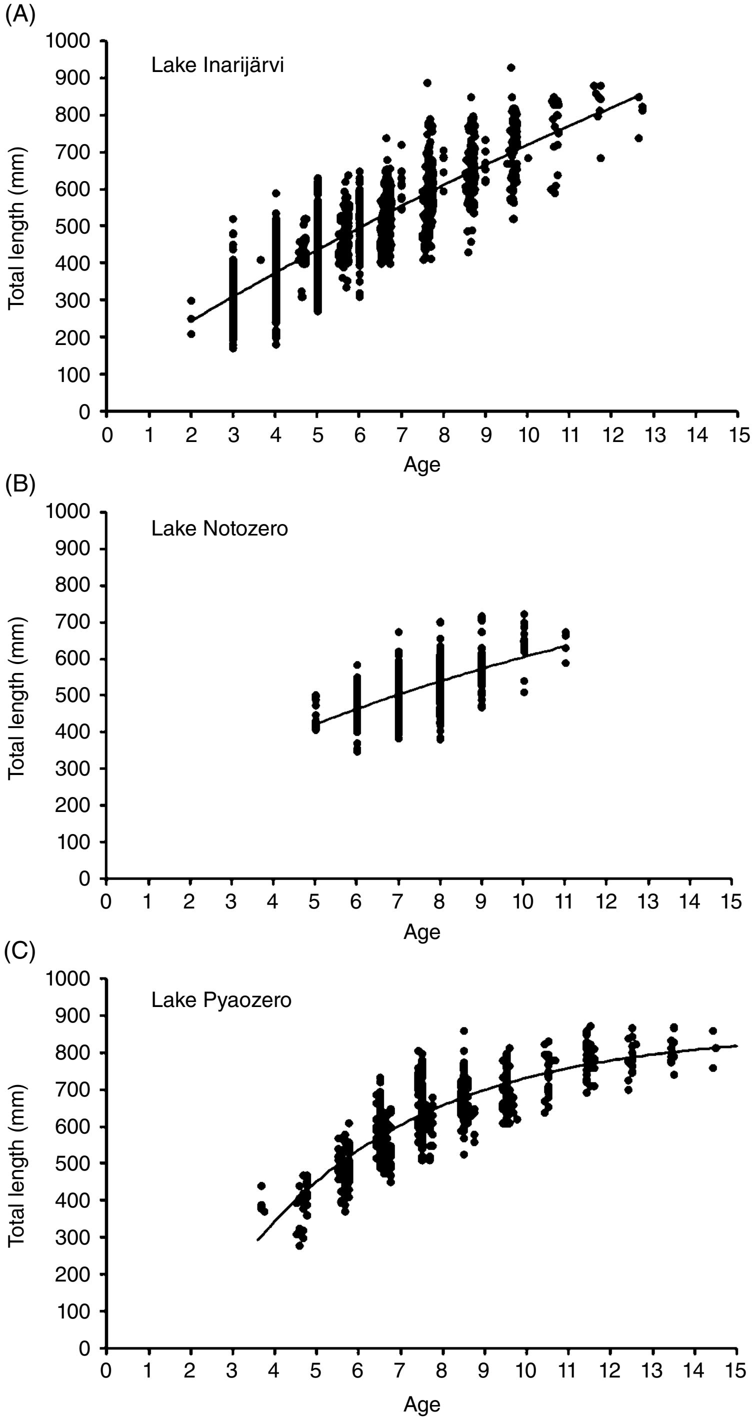

Figure 12.4 Distributions of length by age of adfluvial brown trout (fish individual marked by a dot) in the lake basins of eastern Fennoscandia. The lines represent estimated von Bertalanffy growth functions (von Bertalanffy, 1957) fitted to age data range available for each of the lake basins. Data for D–F are mainly based on the individuals stocked at the age of 2–3 years into the lakes. Data from Järvi (1936); Seppovaara (1962); Hurme (1965); Keränen (1978); Aalto *et al.* (1998); Saraniemi (2005); Niva *et al.* (2013); unpublished datasets of the authors of this chapter; and unpublished archives of the release and recapture data of tagged adfluvial brown trout; databases compiled and provided by the tagging office of the Natural Resources Institute Finland, Helsinki.

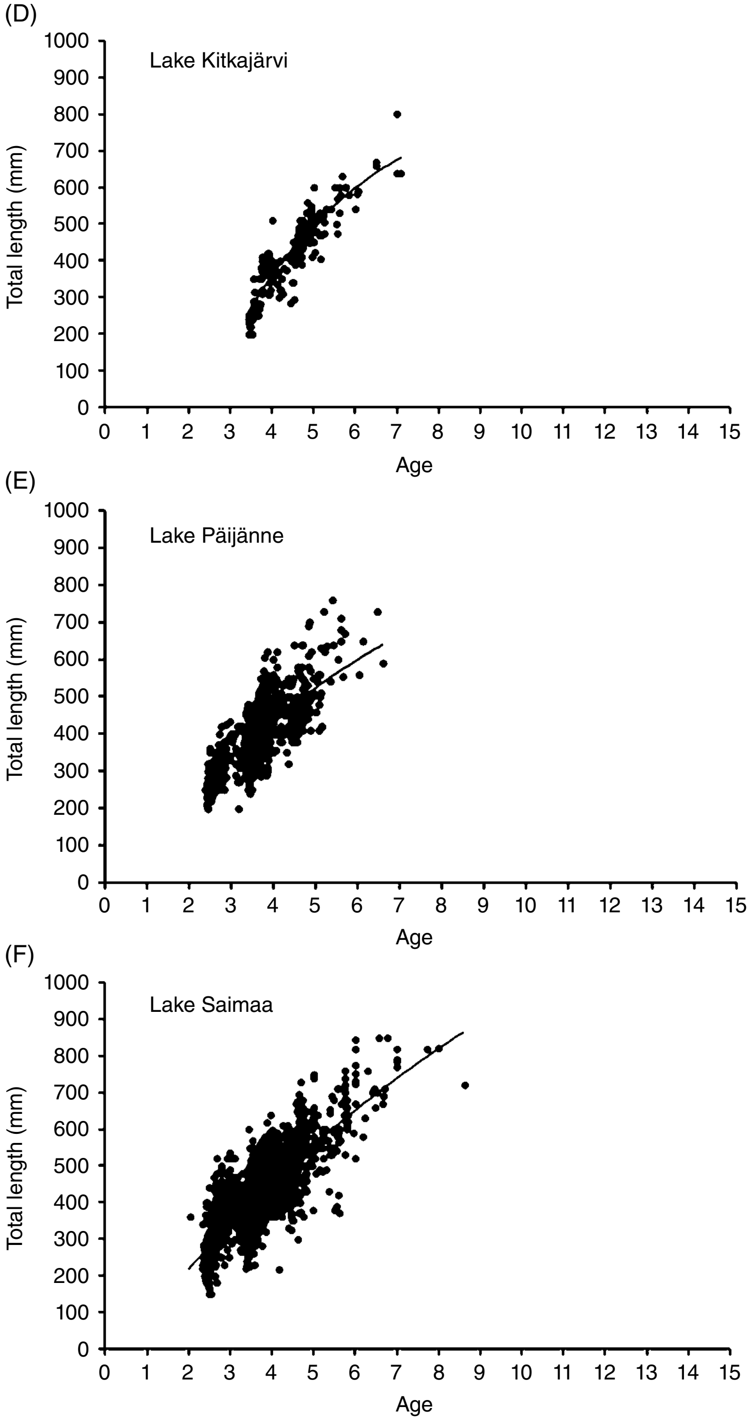

Figure 12.4 (Continued)

Table 12.3 von Bertalanffy's growth function (von Bertalanffy, 1957), $L(t) = L_\infty(1-e^{-K(t-t_0)})$ parameters, and parameters for length mass conversion using equation $M = aL^b$ (M is mass in g, and L is length in mm) for different adfluvial brown trout stocks. Age range indicates the fish ages within which the parameters of the growth functions are considered valid. The estimated mean asymptotic total lengths (L_∞ (mm)) for the majority of the population are clearly too long due to limited age-specific data available in the samples (see Figure 12.4). The data for the Lake Inarijärvi, Kitkajärvi, Päijänne and Saimaa Basins include individuals that have been hatchery-reared and stocked at the age of 2 or 3 years in the lakes. Data sources are given in the legend of Figure 12.4.

Population	t_0	K	L_∞ (mm)	a	b	Age range	N
Lake Inarijärvi Basin	−0.403	0.062	1586	5.404×10^{-6}	3.122	2–12	1938
Lake Notozero Basin	−2.441	0.0690	1050	2.573×10^{-6}	3.232	5–11	595
Lake Pyaozero Basin	1.843	0.238	855	1.510×10^{-6}	3.316	3–15	618
Lake Kitkajärvi Basin	2.262	0.292	901	1.071×10^{-5}	3.019	3–7	211
Lake Päijänne Basin	0.413	0.138	1116	0.696×10^{-5}	3.077	2–6	1006
Lake Saimaa Basin	0.410	0.084	1739	1.659×10^{-5}	2.930	2–8	4207

t_0 = a hypothetical age at which the fish would have been zero length; K = Brody's growth coefficient (Brody, 1945).
L_∞ (mm) = mean asymptotic total length.

over 100 mm in length during the first year in the lake. In subsequent years, especially after reaching maturity, annual length increments, but not always mass increments, decrease steadily. After maturity, at the age of six to eight years on average, total annual length increments decrease to 10–50 mm depending on the age of the fish: the older the fish, the less they grow in length (Seppovaara, 1962; Keränen *et al.*, 1974; Saraniemi, 2005). This is particularly noticeable in the Lake Pyaozero Basin where the wild population still includes old individuals, which would have already been harvested from the other lakes (Figure 12.4). Keränen *et al.* (1974) speculated that in the Lake Pyaozero Basin adfluvial brown trout stop growing in length when aged over 11 years, after the third spawning run. They also start to lose mass and their condition decreases as a consequence of senescence (Figure 12.4). Although the maximum longevity of brown trout is often observed to lie between 11–12 years elsewhere (Jonsson *et al.*, 1999), the datasets reviewed here reveal that the maximum longevity of eastern Fennoscandian adfluvial populations is likely to be approximately 15 years, potentially longer in the north than in the south (Figure 12.4). In the Lake Inarijärvi Basin, where the adfluvial brown trout population consists of wild and hatchery individuals (Niva *et al.*, 2013; Swatdipong *et al.*, 2013), fish of both origins grow similarly and at approximately the same rate as in the Lake Pyaozero Basin (Figure 12.5). In the Lake Notozero Basin, the growth of adfluvial brown trout, all of wild origin, is slower than in the other lakes examined, with the fish reaching, for instance, a length of 600 mm at the age of ten, on average (Aalto *et al.*, 1998). As regards the other lake basins in this study, the available material was based on the recapture of hatchery-reared, tagged adfluvial brown trout stocked in the lakes at the age of two or three years (when approximately 200–300 mm in length), and on historical samples of some large fish from the first half of the twentieth century (Järvi, 1936; Seppovaara 1962). Due to heavy fishing pressure, most of the fish were removed legally within two years of stocking until 2014, and even currently as

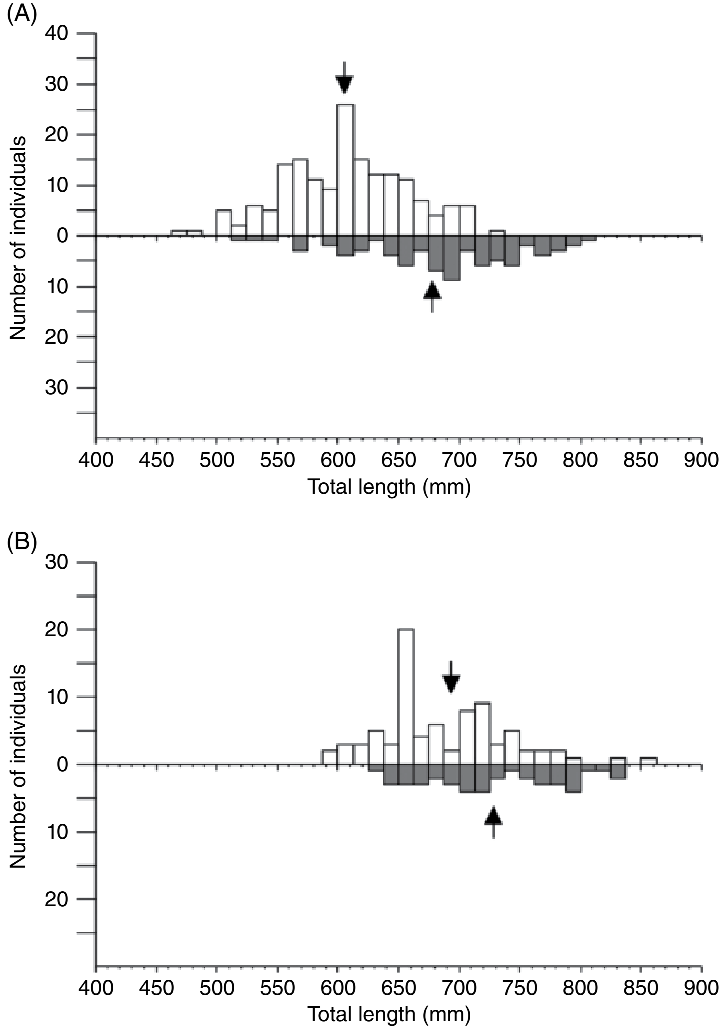

Figure 12.5 Length distributions by female (white bars) and male (gray bars) adfluvial brown trout on their first (A), second (B), third (C) and fourth (D) spawning run in the main spawning river system in the Lake Pyaozero Basin in 2014. Arrows indicate the mean total length of fish in each of the groups. Data provided by A. Huusko (unpublished).

gillnet by-catch despite the 500 mm (stocked fish) or 600 mm (wild fish) minimum size limit. The growth of the stocked fish seems to be rapid in the lakes during immaturity but the growth rate development of mature fish remains unsolved due to the absence of old, mature individuals. However, in conclusion, the fastest growth appeared to occur in the southern lakes (Lake Saimaa and Päijänne Basins) and the slowest in the northeastern lakes (Lake Notozero Basin). The maximum size of adults is more than 10 kg according to historical reports on all the reviewed lake basins (Syrjänen *et al.*, Chapter 28, this volume).

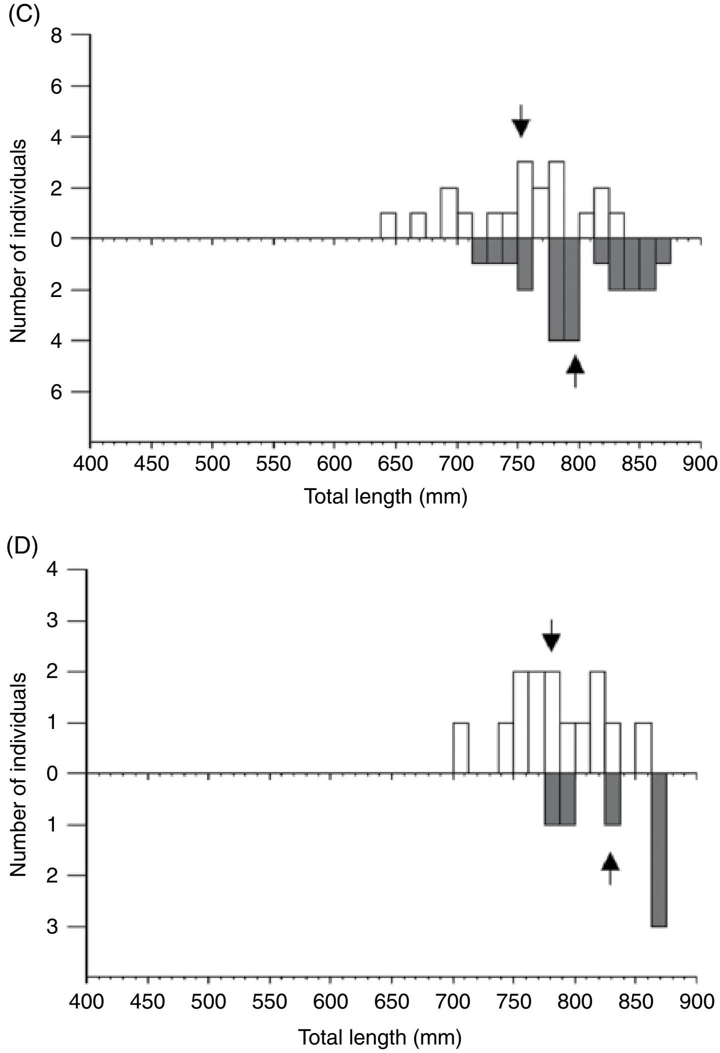

Figure 12.5 (Continued)

The length–weight relationship indicated that fish were leaner (exponent b 2.9–3.0) in the lake basins where no or only sparse datasets on mature adfluvial brown trout were available (Lake Kitkajärvi, Lake Päijänne, and Lake Saimaa Basins), compared to the other lake basins (b 3.1–3.3) (Table 12.3). Thus, it is apparent that adfluvial brown trout growth in length in relation to growth in mass slows down after reaching maturity when the fish are investing in gonadal production in addition to somatic growth. However, due to a lack of data on the individual timing of maturation, it was not possible to fit more mechanistic growth models. For any population modelling purposes, it would be desirable to have separate data on the size-at-age of parr, and on fish spending a year in a river or a lake between two spawning years. It should also be noted that population level data confuses potentially size-selective mortality patterns with the actual rates of individual growth, which can most typically lead to underestimating growth in older and larger individuals, which also face the highest mortality due to size-selective fishing.

Sexual Maturation and Spawning Populations

Adfluvial brown trout mature after one to six lake years (lake-winters), but the typical number of years spent in a lake is from two to five years, including the tendency to mature when older in northern lakes than in southern lakes (Table 12.2; Järvi, 1936; Seppovaara, 1962; Aalto *et al.*, 1998; Saraniemi, 2005; Niva *et al.*, 2013). There is a negative correlation between the number of years spent in a river and the years spent in a lake before maturity, i.e. the older the smolts are when they migrate to the lake the sooner they mature in the lake (Aalto *et al.*, 1998; Saraniemi, 2006; A. Huusko, unpublished). A similar life-history strategy has also been reported to be common in anadromous brown trout (Jonsson *et al.*, 2001) and Atlantic salmon populations (Erkinaro *et al.*, 1997). Age and size at maturity is often described when 50% of the individuals of a population are mature or by the probabilistic maturation reaction norm (PMRN) that can account for the effect of both size and age on the individual probability to mature (Heino *et al.*, 2012). It was only possible to fit a logistic regression model to explain maturity by fish length for adfluvial brown trout of the Lake Inarijärvi Basin (L_{50} 549 mm) and the Lake Pyaozero Basin (L_{50} 552 mm) (Table 12.3). However, it should be noted that the used datasets may not have been representatively balanced between immature and mature fish, and the L_{50} values should be used with caution to represent individual maturation probability by size. No representative maturity data were available for the other lake basins. Depending on the lake basin, the average total length of fish after two to four lake years, indicating approximate size at maturity, has been between 550 mm and 700 mm (except for the Lake Notozero Basin, 490 mm).

Obtaining representative samples of maturing and immature adfluvial brown trout individuals remains a challenge for future research. Moreover, only age and size based PMRNs could reveal whether maturation in adfluvial brown trout is size dependent or if late-maturing individuals compensate for the potential risk of dying without offspring by spawning at a very large size, as in Atlantic salmon (Vainikka *et al.*, 2010). Such compensation would occur through a genetic correlation between growth rate and maturation (Gjerde, 1984; Gjedrem, 2000).

The total spawning population of adfluvial brown trout consists of individuals on their first spawning run and typically of fish on their second or third spawning run. The average fish size in the spawning populations of lake-run brown trout in different lake basins has been approximately 600 to 750 mm in length and three to five kilograms in mass (Table 12.2) with the exception of the Lake Notozero Basin spawners, which have been smaller (mean length 510 mm, mean mass 1.6 kg (Aalto *et al.*, 1998)). However, these figures for the Lake Saimaa, Lake Päijänne and Lake Kitkajärvi Basin are from the time before excessive harvesting led to the collapse of brown trout stocks. Today, spawning populations of adfluvial brown trout are almost non-existent (Figure 12.4; Syrjänen *et al.*, Chapter 28, this volume), with the probable dominance of residency within the populations (Syrjänen & Valkeajärvi, 2010).

More comprehensive data from the Lake Pyaozero Basin revealed that the proportion of first time spawners varied between 47–82% annually, and even included fish on their fifth spawning run (Khalturin, 1971; Keränen *et al.*, 1974; Huusko *et al.*, 1990; Saraniemi, 2005). In this lake basin, adfluvial males were larger than females (males: mean length 720 mm, mass 4.7 kg; females: 650 mm, 3.6 kg, respectively) and the size difference seemed to prevail among mature individuals on different spawning-run times (Figure 12.5). A partial reason for this is that the adfluvial males matured later than the females (55% of males spent four years, and 56% of females three years in the lake before maturity (Saraniemi, 2005)) thus reaching larger body size by the first spawning run. Both sexes had, however, similar longevity. Interestingly, data sets from spawning time tagging studies conducted between 1922–1945 in seven lake outlet rivers in the Lake Päijänne Basin (P. Valkeajärvi, Konnevesi Fisheries Society, unpublished) showed that the maximum mass of males was significantly larger than that of females, lending support to the similar size pattern of males and females observed in the Lake Pyaozero Basin. Limited data sets from the Lake Inarijärvi Basin and Lake Notozero Basin indicated no such difference between the size of adfluvial male and female spawners (Aalto *et al.*, 1998; Niva *et al.*, 2013). In general, in anadromous brown trout populations, adult females have been shown to be, on average, larger, older and less heterogeneous in size while attaining maturity at an older age than males (Jonsson & Jonsson, 2011), due to their higher propensity to adopt a migratory life-history compared to males. But there is no evidence that males and females occupying the same feeding habitat would grow at different rates (L'Abee-Lund *et al.*, 1989; Jonsson *et al.*, 2001). Therefore, the observations on mature adfluvial brown trout in the Lake Pyaozero and Lake Päijänne Basins seemed unique. However, due to limited datasets from the other lake basins, it was not possible to prove the generality of the sex related difference in growth, warranting further detailed monitoring of wild adfluvial brown trout populations.

Similar to anadromous brown trout populations (Jonsson & Jonsson, 2011), females clearly seem to dominate in the sex-ratio among individuals in wild adfluvial brown trout populations with the proportion of males being one third of the individuals on average in the spawning populations (Table 12.2; Järvi, 1936; Seppovaara, 1962; Keränen, 1978; Saraniemi, 2005; Niva *et al.*, 2013). However, there are no reported data on the sex-ratio of adfluvial brown trout smolts: whether in the case of a balanced smolt sex-ratio, male survival would be lower than female during the lake-phase, for example due to later maturation than in females (with higher mortality in the lake phase), or whether the sex-ratio is already dominated by females during the smolt stage. The latter would indicate that females are generally more migratory than males, most obviously due to the larger benefits of migration for females than for males. Ultimately, the level of fitness of individual fish depends on their growth rate and size, more among females than males, and higher fitness can be achieved by migrating to a more benign environment (Klemetsen *et al.*, 2003).

Spawning-Run

The spawning migration of the adfluvial brown trout usually occurs between spring and autumn, and may extend over hundreds of kilometers in the river systems (Table 12.2). The timing and duration of the spawning migration seem to be variable and system-specific. For example, in large river systems the brown trout may start ascending several months before settling in their spawning areas (Klemetsen *et al.*, 2003). Saraniemi (2005) and Saraniemi *et al.* (2008) reported that after entering a river, the spawning migration patterns of adfluvial brown trout in the Lake Pyaozero Basin resembled those of anadromous salmonids, including steady progress with periods of active upward swimming alternating with stationary periods, followed by a residence period before spawning, and finally a short migration upstream, just before spawning (Thorstad *et al.*, 1998; Økland *et al.*, 2001).

In the Lake Pyaozero and Notozero Basins, adfluvial brown trout start their spawning migration in June soon after the spring flood peak, at a water temperature of 5–10 °C (Aalto *et al.*, 1998; Saraniemi, 2005; Orell *et al.*, 2011; A. Huusko, unpublished). The migration typically peaks between the last ten days of June and the end of July, but the ascent continues until August turns to September. The monitoring of radio-tagged individuals in the River Olanga system (Lake Pyaozero Basin) has indicated that there is high individual variation in migration speed, with some individuals making a riverine journey of approximately 50 km in 4–7 days while others spent 50–70 days travelling the same distance, the latter individuals obviously residing temporarily in the lacustrine sections of the migration route during the warm mid-summer period (Saraniemi *et al.*, 2008; A. Huusko, unpublished). In the Lake Inarijärvi Basin, adfluvial brown trout start their migration into the River Juutuajoki at the end of July, with a migration peak at the end of August, which is about 50 days later than in the River Olanga system (Niva *et al.*, 2013). In the River Ivalojoki, however, the spawning-run starts earlier than in the River Juutuajoki (Niva *et al.*, 2013), and resembles the run-timing observed in the rivers of the Lake Pyaozero and Notozero Basins.

In the lake basins of the Finnish Lake District, the movement of adfluvial brown trout towards their spawning areas seems to follow a similar pattern to the River Juutuajoki, Lake Inarijärvi Basin, with the migration starting in mid-summer and peaking in September close to spawning time (Järvi, 1936; Seppovaara, 1962; Hurme, 1965; Eloranta, 1993; P. Valkeajärvi, Konnevesi Fisheries Society, unpublished). Having spent their lake phase in the main lake of the basin, adfluvial brown trout typically head to their natal river stretches in the second half of summer (Hurme, 1965). Prior to spawning, this is followed by a residence period in a lake adjacent to the target spawning environments to where the brown trout then move immediately before spawning, together with other brown trout that have spent their lake-phase in the adjacent lake. This late entry to spawning environments is also supported by fishing statistics.

The catch data from several rapids of the watercourses of the Lake Päijänne Basin covering the whole of the twentieth century (Eloranta, 1993), showed that large (over 2.5 kg in mass) brown trout comprised on average only 3.8% of the total annual catch for the angling season that lasted from May to 10th of September. However, post-season (September–October) brown trout catches for artificial breeding purposes from the years 1922–1945 in the five rapids sections (Eloranta, 1993) indicated an annual yield of tens of large-sized (over 4 kg in mass) adfluvial brown trout from each of the rapids (P. Valkeajärvi, Konnevesi Fisheries Society, unpublished).

After spawning, adfluvial brown trout kelts either overwinter in the stream or descend back to the lake. Thus, there are two different behavioral patterns: the autumn and the spring descent-migrations after spawning (Saraniemi *et al.*, 2008; Niva *et al.*, 2013). Factors such as hydrodynamic conditions, particularly the availability of suitable overwintering habitats, migration distance and size of the spawners, are likely to play a role in the process. The propensity to migrate immediately after spawning may be more common in relatively small rivers (Rudstadbakken *et al.*, 2004), where ice conditions can be very severe in winter (Huusko *et al.*, 2007). Habitats with slow water flow, such as deep pools that are often absent from small streams, are typically used as overwintering sites by adult salmonids (Huusko *et al.*, 2007; Saraniemi *et al.*, 2008). The main stem of the River Oulankajoki, Lake Pyaozero Basin, has long river stretches with deep pools in which, having spawned, over 80% of adfluvial brown trout overwinter. However, 80 to 90% of adfluvial brown trout leave the two large tributaries of the River Oulankajoki: the River Kitkajoki and the River Kuusinkijoki, after spawning and head for the main lake, due to the limited number of slow flowing deep stretches (Saraniemi *et al.*, 2008; A. Huusko, unpublished).

The philopatric homing of salmonid fish, where they accurately return to natal spawning grounds from lacustrine or marine areas for reproduction, is very well-known (Youngson *et al.*, 2003). The recognition of the natal stream by the fish has primarily been attributed to olfactory cues, with the first speculations on this dating back to the 19th century and being resurrected several times since then, by various scientists (Scholz *et al.*, 1976; Stabell, 1992). Huusko *et al.* (1990) observed no adfluvial brown trout strays among repeat spawners in tagging experiments conducted in the spawning rivers of the River Olanga system, Lake Pyaozero Basin. In addition, genetic analyses have revealed that in this lake basin, there is relatively insignificant gene flow between the adfluvial brown trout populations in different spawning rivers (Huusko *et al.*, 1990; Aspi *et al.*, 1999), lending support to breeding-stream fidelity.

However, many aspects of wild adfluvial brown trout homing behaviour in natural conditions are still unclear as well as the homing behavior of hatchery-reared fish, stocked to restore threatened populations. For example, Huusko & Korhonen (2004) reported on a simple transplantation experiment in the River Olanga system, Lake Pyaozero Basin, examining the homing behavior of hatchery-reared adfluvial brown trout to discover whether their homing instinct was inherited (driven by genetics) or guided by imprinting to the stream where the fish had spent their riverine phase (driven by the environment). The researchers brought fertilized eggs of wild native adfluvial brown trout from the River Kuusinkijoki, a large tributary of the River Oulankajoki, into a hatchery located by the River Kitkajoki, another large tributary of the River Oulankajoki (Figure 12.1), and reared the fish until they became three-year-old smolts, and then released 2500 tagged individuals into the lower reach of the River Oulankajoki. Based on the riverine recaptures of tagged fish, and contrary to expectations based on genetic differences reported between the stocks in these rivers (Huusko *et al.*, 1990; Aspi *et al.*, 1999), the majority of the adfluvial brown trout ascended to the River Kitkajoki on their spawning run, where they were reared in the hatchery, and not to the River Kuusinkijoki from where they originated. The transplantation study showed that the characteristics of the river, most obviously specific olfactory cues in the river water, were important factors in guiding the homing of adfluvial brown trout. In conclusion, to successfully restore degraded adfluvial brown trout stocks, it is important to imprint the stock to the target river. This in turn requires that the fish should be stocked as young as possible instead of using smolt-sized fish, to ensure homing to the stream of release (Syrjänen *et al.*, Chapter 28, this volume).

In the northeastern lake basins of Fennoscandia, where distances from lake to spawning areas are often long (up to 150 km, Saraniemi, 2005), adfluvial brown trout follow a biennial spawning-run rhythm, spending a gap-year in the lake between successive runs (Table 12.2; Keränen, 1978; Aalto *et al.*, 1998; Saraniemi, 2005; Niva *et al.*, 2013). Based on annual tagging studies in the years 1965–2003 in the River Oulankajoki, Saraniemi (2005) reported that 95% of recaptured tagged fish followed a biennial spawning rhythm, with 5% of the fish spending two years in the lake between successive spawning runs, and none spawned every year. In the lake basins of the Finnish Lake District the exact spawning rhythm of adfluvial brown trout is not known. The majority of recaptures (42%) from spawning time (autumn) tagging operations during 1922–1945, in the seven outlet rivers in the Lake Päijänne Basin (Hurme, 1965; P. Valkeajärvi, Konnevesi Fisheries Society, unpublished) were dated the following spring, 5–7 months after tagging. At the time, the fish were probably moving from their spawning areas to the lakes after overwintering near areas of rapids and/or due to the increased activity of fishermen after winter, with only few recaptures (about 4%) in sampling the following autumn (August–October, for artificial breeding), indicating that only some fish spawned annually. Interestingly, about 18% of the recaptures were caught during autumnal fishing two years after tagging, revealing a biennial spawning rhythm. Thus, it seems that in the southern lake basins wild adfluvial brown trout spawn either annually or biennially but the exact proportions among the current extremely scarce populations remains unsolved (Järvi, 1936; Seppovaara, 1962; P. Valkeajärvi, Konnevesi Fisheries Society, unpublished).

Concluding Remarks and Research Needs

Eastern Fennoscandian adfluvial brown trout show diverse life-history patterns indicated by variations in characteristics such as mean smolt age, growth rate, age and size at maturation, and longevity. Depending on the population, there are tens of smolt age and lake age combinations for virgin trout, and the number of combinations increases even further when repeat spawners are included. Smolt-ages differ from lake-ages so that mean smolt-age declines with increasing lake-age. These population characteristics can still prevail in the northeastern populations of Fennoscandian adfluvial brown trout. Unfortunately, a repertoire of human action has overshadowed the interpretation of the characteristics of wild adfluvial brown trout populations in the lake basins of southeastern Fennoscandia (Syrjänen & Valkeajärvi, 2010; Syrjänen *et al.*, Chapter 28, this volume), and traits such as longevity are very difficult to assess in nature. On the other hand, the co-occurrence of multiple life-history strategies such as resident or migratory, within a river system has the potential to instil notable resilience to brown trout populations, and perhaps explains why the brown trout still exists in systems with, for example, intensive lake fishing.

Further research is clearly necessary to better understand the level of ecological and evolutionary uniqueness of different adfluvial brown trout populations and to profile in more detail the life-history of this less intensively studied type of brown trout. In a shorthand bulleted list below, we suggest important research topics that arise from our review of published retrospective and present data:

- Determinants of adfluvial vs. resident life-history types, including parentally inherited factors, environmental factors and developmental history (role of epigenetics).
- Density dependence in survival and growth in riverine and lacustrine phases.
- Timing and characteristics of relatively unknown life-history events, such as emergence and smolt migration.

- Carry-on effects on later life stages of conditions experienced in early life.
- Standing variation in the size and age at sexual maturation (PMRNs).
- Propensity to adfluvial life-history between the sexes, the reasoning for having female dominance among returning spawners.
- Mechanisms of philopatric homing, and the extent of straying.
- The potential existence of a link between water temperature during early development and later performance such as lake growth and sexual maturation.
- Impact of climate change on different life-history types of brown trout: is there enough genetic variability left in the endangered stocks to adapt to climate change?

Existing historical databases combined with present day studies and monitoring of the performance of adfluvial brown trout populations in different lake basins, thoroughly analyzed by modern methods in ecology, genetics, and fisheries sciences (fisheries induced evolution and management), would most probably help in the efforts to conserve the so far viable stocks and to rebuild degraded stocks. Moreover, these attempts would also add to understanding the mechanisms of plasticity that exist among brown trout populations.

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Section 4

Population Dynamics

13

Discharge-Dependent Recruitment in Stream-Spawning Brown Trout

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> *At its simplest, recruitment is the survival from the eggs that were laid*
> D.H. Cushing (1996) *Towards a science of recruitment in fish populations.* Excellence in Ecology, No. 7. Ecology Institute, Oldendorf, Germany

Introduction

Identifying the causes of temporal fluctuations of population size is a central goal of ecology and of paramount importance for the design of fishery management. More specifically, elucidating the relative roles of density-dependence (Nicholson 1933) *versus* density-independence or environmental drivers (Andrewartha & Birch 1954) has been a major focus of research in animal ecology and given the importance of fishery economy, substantial efforts have been devoted to fish populations. The operation of endogenous, density-dependent feedback loops implies a numerical equilibrium of populations as a long-term stationary probability distribution of densities (Dennis & Trapper 1994) where the populations fluctuate over time around mean densities with bounded variances (Royama 1977, Turchin 2003). Under density-independent determinants, there is no equilibrium, but the populations fluctuate over time as 'statistically random walks' with variances increasing over time (Murdoch 1994). Thus, density-dependence is necessary for generating stability and resilience and as a consequence, finding empirical support for the 'paradigm of density-dependence' or that the populations are regulated by density-dependent feedback mechanisms has been a major focus of ecological and fishery research for decades (Coulson, Rohan & Pascual 2004).

In fish populations, the youngest juveniles are called 'recruits and are defined as 'the number of the surviving juveniles that, resulting from an annual reproductive event, incorporate to the population to commence a new cohort'. The magnitude of recruitment is deemed to be

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† Deceased

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

set at, during, or soon after hatching and emergence (Cushing 1996). The notion that recruitment is a major determinant of adult abundance (i.e., the recruit-adult abundance hypothesis, Menge 2000) has been documented in marine and freshwater fishes including salmonids (Knapp, Vredenburg & Matthews 1998, Lobón-Cerviá, Gonzalez & Budy 2011). Recruitment strength may be reflected in the age structure of the population and may be capable 'per se' to establish patterns of population size. As a consequence, understanding the regulatory processes of recruitment is essential to understand the dynamics of fish populations. However, unequivocal identifications on the relative roles of density-dependent *versus* density-independent factors determining recruitment remain sufficiently elusive to be considered an '*Enigma*' (Frank & Leggett 1994) to the extent that several authors have claimed for a '*Science of Recruitment in Fish Populations*' (Cushing 1996).

A core hypothesis assumes that the number of recruits is mechanistically but not linearly linked to the reproductive component of the population. Such a link assumes that, independently of the factors causing mortality during the egg-to-recruit stage (Cowen & Sponaugle 1997), the reproductive component of the population is a major predictor of recruitment (Trippel, Kesbu & Solemdal 1997). Therefore, the exploration of relationships between the abundance of the parental component and the subsequent recruitment is an essential tool to test hypotheses related to the population regulation (*sensu* Nicholson 1933). Assumedly, in populations where the number of recruits is determined by density-independent or environmental factors, recruitment might show no relationship with the parental density and can be only predicted from the corresponding environmental determinants. In populations where recruitment is determined by the parental density, recruitment may increase linearly or potentially with no upper limit with increased parental density or may become asymptotic or domed shaped under compensatory or over-compensatory effects at high parental densities. Therefore, the operation of parental-dependence is not sufficient evidence for the occurrence of recruitment 'regulation'. The latter requires compensatory adjustments in the form of constant or declined recruitment at high levels of parental density.

Despite the proliferation of studies on stream-living salmonids across habitats and geographical regions (Northcote & Lobón-Cerviá 2008), it is surprising, not to say frustrating, that unequivocal responses to key questions of paramount importance for their correct management, including the protection and recovery of declining populations, remain controversial. Consensus on foundational principles as those related to recruitment determinants are lacking. Results from recent studies differ substantially from each other and subsequent debates confuse more than clarify. Therefore, the objective of this study was to explore whether a consensus on the factors determining recruitment in stream-spawning brown trout is at all possible. To this aim, this study reviews, re-visits and compares long-term recruitment studies and the underlying factors in populations of stream-spawning brown trout within its natural European distributional area.

Setting of the Study: The Populations of Stream-Spawning Brown Trout

Across its European distributional range, brown trout spawn at the very end of the autumn or at the beginning of the winter during a more or less variable period related to latitudinal clines (Larios-Lopez *et al.* 2015). Brown trout spawn rather large amounts of eggs in redds of variable size and depth (Crisp & Carling 1989, De Vries 1997) that, individually, may range from 50 eggs spawned by a 11 cm long resident female (Lobón-Cerviá *et al.* 1997) to hundreds or thousands spawn by large-sized sea-migratory or lake-migratory females (Elliott 1994, Jonsson & Jonsson 1999), and depending on the stream temperature regime, the eggs hatch and the fry emerge 2 to 4 months later. As in all fish populations, severe mortalities may occur during the egg-to-recruit stages and/or when the youngest juveniles have completed their endogenous feeding and leave their redds as free-swimmers in search for feeding positions across the water column in the nearby shallow reaches. Recruitment magnitudes are deemed to be set at, during or soon after that time period. Consequently, in stream-spawning brown trout recruitment refers to the number of the youngest juveniles surviving from a winter spawning event and commences a new cohort during the next spring around March to May.

Several studies have reported juvenile densities of stream-living brown trout populations but their quantifications in different dates hinder broad comparisons. Nevertheless, several published and unpublished long-term data sets collected in natural, unexploited populations monitored over prolonged time periods (>15 years) may be used to illustrate recruitment features and permit explorations on the underlying factors. These populations, located at long distances from each other within the European continent, belong to the three life history modes that typify brown trout. Specifically, this study encompasses the resident populations inhabiting four Rio Esva tributaries in northwestern Spain reported by Lobón-Cerviá & Rincón (2004) and Lobón-Cerviá (2007, 2014); the sea- migratory population of Black Brows Beck (BBB, northern England) reported by Elliott (1984, 1985, 1987, 1993, 1994), Elliott *et al.* (1997) and Elliott & Elliott (2006); a lake-migratory population inhabiting Bisballe Baeck (BB, Denmark) reported by Mortensen (1977, 1985) and Lobón-Cerviá & Mortensen (2005, 2006) and two previously unreported, sea-migratory populations inhabiting Tjaerbaeck (TJB) and Brandstrup (BRB) Baecks (Rasmussen 2016). These three Danish streams inhabited by a lake-migratory and two sea-migratory populations are tributaries of the Gudenaa River in central Jutland.

The three sets of streams differed to some extent. The northwestern Spain streams are typical V-shaped mountainous, fast-running waters flowing over stony substratum and quartzite bedrock. The northern streams from UK and Denmark are U-shaped of glacial origin whose running waters flow over gravel, pebble and sand substratum.

Sampling schemes and the number of sampling sites differed among streams. In the British BBB and the Danish BB, recruitment was monitored in a single stream site (area = 60 m^{-2} in BBB and 146 m^{-2} in BB, respectively). Substantially larger geographical scales were used in the four Spanish streams and in two Danish streams. In Rio Esva, recruitment was monitored at 12 fixed sites (mean length ≤ 100 m and mean area of each site = 250 m^{-2}; range 100–300 m^{-2}) selected along four different tributaries. Eight fixed sites (total area = 510 m^{-2}) were selected along a 3.6 km stretch of the Danish BRB and eleven fixed sites (total area = 1994 m^{-2}) were monitored along a 4.4 km stretch of TJB.

According to Elliott (1984), emergence in the British BBB occurs from early April to mid-May, a date more or less similar to the Danish populations and about a month later than in Rio Esva where emergence occurs early to mid-March. Recruitment in BBB was quantified by end of May or early June; in the Danish BB, BRB and TJB by mid-April to mid-May and in the Spanish streams by mid-May.

In all populations, the number of recruits was quantified with electrofishing techniques by applying the successive removals methods. In the British BBB successive removals until no more individuals were collected was applied. In the three Danish BB, BRB, TJB and the four Rio Esva tributaries, three-removals were applied and the Zippin's method (Zippin 1958) was run to estimate the total number of individuals in each site and date (Lobón-Cerviá 1991). Quantifications of the sites area based on bathymetric maps of each site and date drawn just after sampling enabled description of densities in individuals per square meter (ind. m^{-2}), otherwise stated.

The abundance of fertilized eggs in the gravel was used as subrogate of parental density in the British BBB. This is described as No. eggs m^{-2}. In Rio Esva, the parental stock was quantified as the number of female spawners at each site and year prior to spawning and is described as No. female spawners m^{-2}. Unfortunately, no data on the parental density was available for the three Danish populations.

Among the numerous environmental variables that were 'a priori' deemed relevant as recruitment determinants, previous studies in the Spanish Rio Esva tributaries and in the Danish BB emphasized the importance of the stream discharge conditions during the recruitment process. As a consequence, this study focuses essentially on discharge data collected from the nearest gauging stations from the study streams. In the British BBB, discharge was reported by a local station identified as: 'National River Flow Archive'; Database, nrfa-public name; Station: 73010; name: 'Leven at Newby Bridge, FMS'; Grid reference SD367863 that records gauged daily flows in m^3/s. The gauging station in Rio Eva located at a mid-distance from the four tributaries and reports discharge data in Hm^3/day. Assumedly in Rio Esva, rainfall-induced discharge operates simultaneously over the whole river basin and all tributaries fluctuate simultaneously over time.

In previous studies on the Danish Bisballe Baeck, no discharge data was available and rainfall was used as a surrogate (Lobón-Cerviá & Mortensen 2005). However, more recent studies have shown that the three Danish streams of this study, located about 30 km apart (BB about 20 km from BRB and TJB whereas the latter two streams only 3 km apart) flowing over the flatlands of central Jutland, are subject to the same rainfall conditions and stream discharge are highly correlated and fluctuate simultaneously. During the study years, discharge *vs.* water level, Q/h, was established for Brandstrup Baeck and Tjaerbaeck. The daily mean discharge of the two streams was inferred from the nearby Moelballe gauging station (Station 211663 in the Gudenaa river system) that provides data in m^3/sec. Moreover, rainfall data over Bisballe Baeck was highly correlated with the discharge of Brandstrup Baeck ($R^2 = 0.75$, $p < 0.001$). Therefore, the more detailed discharge data set from Brandstrup Baeck was used as proxy of the discharge of the three streams.

Data Analysis

To elucidate whether parental density (ST, ind m^{-2}) is a major determinant of recruitment (RC, ind m^{-2}), we explored the validity of a Ricker's stock-recruitment model (Ricker 1954) previously used in studies of stream-living Brown Trout by Elliott (1984, 1985, 1987, 1993, 1994), Elliott *et al.* (1997) and Lobón-Cerviá (2005, 2007), in the form:

$$RC = A * ST^{(-B*ST)} \qquad \text{Model 1}$$

Where RC is recruitment, ST the parental density, DIS discharge and A and B constants to be determined. Moreover, to explore whether the interaction density-dependence*stream discharge determine recruitment, Model 1 can be extended to include the two factors, in the form:

$$RC = A * ST^{(-B*ST+C*DIS)} \qquad \text{Model 2}$$

a model with three parameters A, B and C to be determined.

Tests of two basic hypotheses *RC = Mean RC* (i.e., recruitment fluctuates around a mean value with no tendency) and *RC = A * ST* (i.e., recruitment depends linearly of the parental density) are required before fitting and assuming the validity of either of the two models (Belows 1981, Lobón-Cerviá 2014).

Visual inspections of the relationships between recruitment and stream discharge highlighted continuous ascent/descent trajectories. To smooth those trajectories we explored the plausibility of two alternative models, a parabolic function in the form:

$$RC = A + B * DIS + C * DIS^2 \qquad \text{Model 3}$$

where RC and DIS are recruitment and discharge, respectively and A, B and C are constants to be determined and a split-lined regression in the form:

$$RC = A_1 + B_1 * DIS(DIS < K) + A_2 + B_2 * DIS(DIS > K) \qquad \text{Model 4}$$

That is a two-phase linear regression with the restriction for continuity $A_1 + B_1 * K = A_2 + B_2 * K$ at the threshold point (*K*), where the slope changes direction. This two-phase regression can be re-written as:

$$\begin{aligned} RC = {} & (A + B_1 * DIS) * (DIS < K) \\ & + (A + (B_1 * K + B_2 * DIS - B_2 * K)) * (DIS > K) \end{aligned} \qquad \text{Model 5}$$

where only A, the intersect; B1 and B2, the positive and negative slopes and K, the threshold upon which the trajectory changes from positive to negative, are to be estimated.

The Akaike Information Criterion (AICc) was used to select the most plausible Model among two or more competing models for any single data set. Overall, the model with lower AICc values is the correct. However, the difference between AICc values (ΔAIC) obtained for each model provides an estimate of how many times more likely the model is. A difference $AIC_2 – AIC_1 = 0$ implies that the two models have exactly the same 50% probability of being correct. A difference $AIC_2 – AIC_1 = 2$ indicates a 73% probability and differences from 5 to 10 indicate 90 to 100% probability that AIC_2 model is the correct. Further details can be seen in Burham & Anderson (2002) and Motulsky & Christopoulos (2004).

Results

Recruitment Variability in the Study Populations

Visual inspections of the recruitment values across populations highlighted overwhelming variations (maximum range 0.01 to 15.8 ind m^{-2}) under irregular temporal patterns with differences by orders of magnitude among successive years in either population.

An ANOVA for the eight populations ($F_7 = 119.2$, $p < 0.001$) highlighted population-specific recruitment and substantial differences among both nearby populations and those located at long distances. In the U-shaped Danish BRB, recruitment varied between 0.37 and 8.20 ind m^{-2} (mean = 2.6 ind m^{-2}) compare with the nearby U-shaped lake-migratory population where recruitment attained a maximum at 15.8 ind m^{-2} and a mean of 5.4 ind m^{-2}. These figures recall the British BBB that varied within 2.2 and 7.7 ind m^{-2} with a mean of 5.1 ind m^{-2}. However, all these populations show recruitment magnitudes markedly higher than the nearby U-shaped Danish TJB where recruitment only varied between 0.09 and 0.8 ind m^{-2} with a mean at 0.35 ind m^{-2} and the four V-shaped streams of northern Spain with a maximum at 2.1 ind m^{-2} and means at: Chaballos = 0.31 ind m^{-2} (range 0.01–1.62); Viella = 0.43 ind m^{-2} (range 0.01–2.1); Castañedo = 0.16 ind m^{-2} (range 0.02–0.47) and Choudral = 0.14 ind m^{-2} (range 0.01–0.34), respectively.

Apparently, the V-shaped Spanish streams inhabited by resident populations sustain the lowest recruitment magnitudes whereas the U-shaped northern streams inhabited by migratory populations sustain much more variable levels ranging from very low and similar to the V-shaped streams to exceptionally high as in the Danish BB.

Recruitment Variability Across Rio Esva Tributaries

The resident populations of Rio Esva tributaries permit a detailed exploration into the underlying factors across the environmental heterogeneity that typifies the mountainous Cantabrian river drainages (northwestern Spain) and further explore whether density-dependence or independence predominate across streams and sites and/or whether their operational levels are context-dependent.

The study streams, two right-sides (Chaballos and Castañedo) and two left-side (Viella and Choudral) tributaries of Rio Esva differed in channel structure, physiography, substratum composition, canopy, water current, width and depth. Recruitment was quantified over the years 1986–2012 at four sites of Rio Chaballos (Ch1, Ch2, Ch3 and Ch4; 106 cohorts in total), three sites in Viella (V5, V6 and V7; 69 cohorts in total), Castañedo (C8, C9 and C10; 42 cohorts in total) and two sites in Choudral (CHo11 and Cho12; 46 cohorts in total). Detailed geographical location of the streams, sites, sampling scheme and data collection have been reported elsewhere (Lobón-Cerviá 2007, 2014).

A meta-comparison at three increasingly larger geographical scales, sites, streams (sites pooled) and river drainage (streams and sites pooled) were implemented (Figure 13.1). As an early exploration, a hierarchically nested ANOVA was run to detect the effects of stream, site and year. This ANOVA revealed highly significant effects of the river ($F_{3,8} = 17.9$, $p < 0.001$), site ($F_{8,229} = 17.4$, $p < 0.001$) and year ($F_{26,225} = 11.1$, $p < 0.001$). Overall, recruitment was twice higher at a right side (Chaballos, RC = 0.31 ind m^{-2}) and a left side (Viella, RC = 0.42 ind m^{-2}) tributaries than in other two, right side (Castañedo, RC = 0.14 ind m^{-2}) and left side tributaries (Choudral, RC = 0.14 ind m^{-2}). Moreover, visual inspections of Figure 13.1 highlighted, consistent with the effects of site in the ANOVA, the occurrence of sites interspersed along the streams with markedly different recruitment levels either located in the same stream or at long distances in another stream. For example, weakly recruited sites such as RC = 0.10 and 0.11 ind m^{-2} in sites C10 in Castañedo and Ch4 in Chaballos, respectively. At the opposite extreme, several sites located in the same stream or at long distances in other

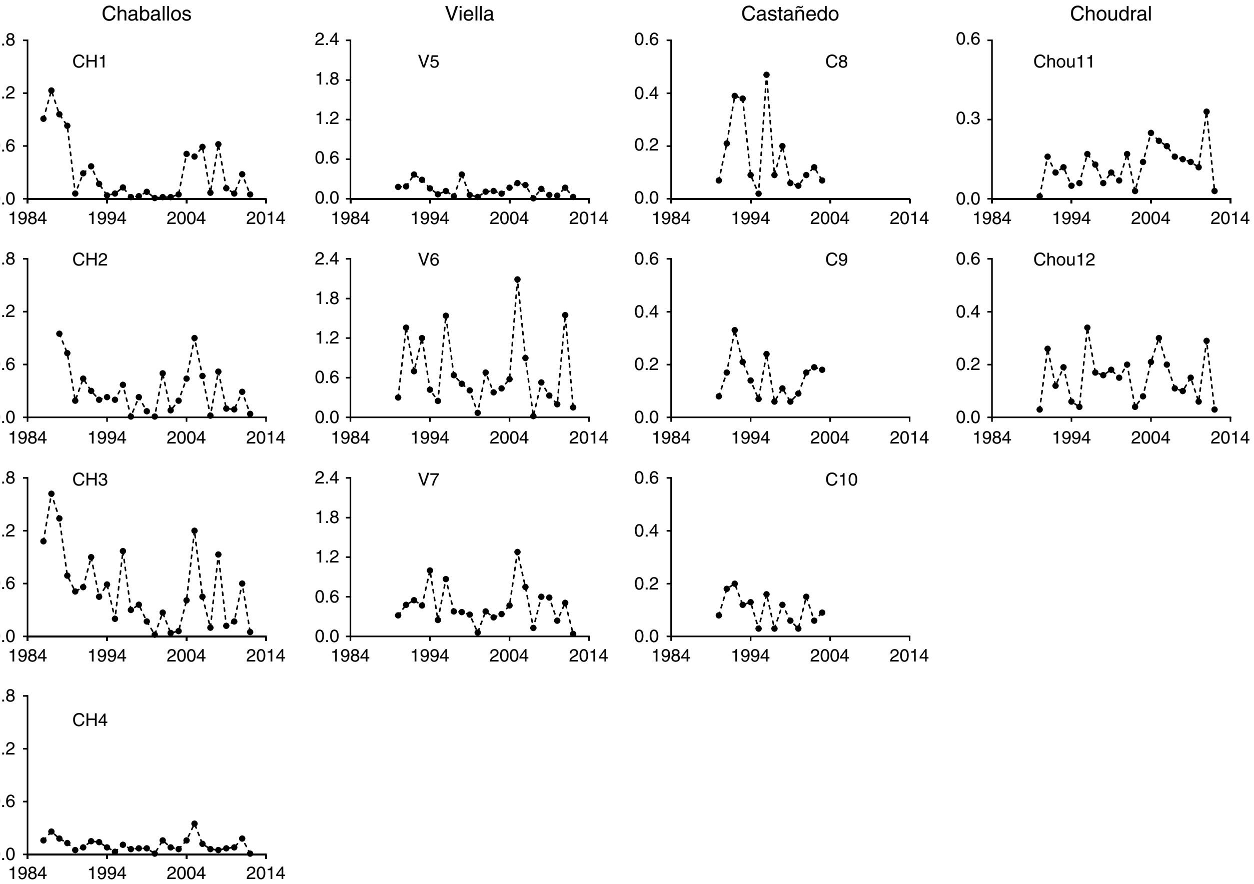

Figure 13.1 Recruitment (RC, ind m^{-2}) quantified at 12 sites spread along two right-side and two left-side Rio Esva tributaries (northwestern Spain). Each dot represents the recruitment of a cohort out of 263 cohorts in total in the following streams, sites and years: Chaballos, 27 years (1986–2012) at sites Ch1, Ch2 and Ch4 and Chaballos, 25 years (1988–2012) at site Ch2. Viella, 23 years (1990–2012) at sites V5, V6 and V7. Castañedo, 14 years (1990–2003) at sites C8, C9 and C10 and Choudral, 23 years (1990–2012) at site Cho11 and Cho12.

stream showed persistently higher recruitment such as in Ch3 in Chaballos with RC = 0.53 ind m^{-2} and V6 located at a long distance in Viella with RC = 0.66 ind m^{-2} or its nearest site V7 with RC = 0.47 ind m^{-2}. Highly relevant was also the effect of the year with sets of years in which recruitment was remarkably low at the 12 study sites of the four streams as 2000 and 2012, with a mean recruitment across sites of only RC = 0.05 ind m^{-2} or in 2007 with RC = 0.08 ind m^{-2} compared with highly recruited years as 1987 with a mean of RC = 1.04 ind m^{-2} or 2005 with RC = 0.8 ind m^{-2}. Clearly, these results strongly suggest the operation of concurrent factor(s) operating all over the river drainage and other factor(s) operating at a site scale.

Discharge Conditions vs. Parental Densities as Determinants of Recruitment

To what extent are the parental densities responsible for the extremely high variability in the recruitment observed across scales of space (among sites and streams) and time (among years)? Given the strong effects of the site and of the stream on recruitment highlighted by the ANOVA above, firstly we examined whether sites with persistently high, intermediate or low recruitment levels were related to persistently high, intermediate or low parental densities. Such comparison highlighted no obvious relationship between parental density and recruitment among sites or streams. Either sites or streams with persistently high parental densities did not concur with persistently high recruitment and those with persistently low parental densities did not concur with persistently low recruitment. Actually, high recruitment levels were observed at sites with either high or low parental densities. For example, the highly recruited site V7 in Viella concurred with the lowest parental density whereas the highly recruited CH3 in Chaballos concurred with the highest parental density. And, sites with persistently low recruitment concurred with the lowest parental density in C10 and with the highest parental density in CH4. Lack of consistent patterns was also evident when comparing streams (sites pooled).

Recruitment (RC, ind m^{-2}) *versus* parental density (ST, ind m^{-2}) for each single site, for streams and for the river drainage are showed in Figure 13.2. The application of the Akaike criterion to the stock-recruitment Model 1 *versus* the two basic hypotheses *RC = Mean RC* and *RC = A * ST* highlighted a markedly higher probability that the *RC = mean RC* is the most plausible model in practically all instances and their probability to be the most plausible model for sites, streams and river drainage was > 75%. The only exception was site CH1 where *RC = A * ST* showed to be better; that is the probability for this model to be the most plausible model was >90%. Strongly consistent with these results, the fits of Model 1 (i.e., the Ricker model) to all data sets proved to be definitively inconsistent in all instances. Importantly, the application of the Akaike Criterion to Model 2 that includes the interaction parental density * discharge *versus* the two basic hypothesis highlighted quite similar results where *RC = mean RC* proved to be the most plausible model for all 17 instances, sites, streams and river drainage.

Consequently, we explored the role of discharge as a single factor operating on recruitment. Visual inspections of the plots recruitment *versus* discharge, log-transformed recruitment *versus* discharge and log-transformed recruitment *versus* log-transformed discharge for each site, stream and river drainage highlighted, in all instances, strongly consistent ascend/descent trajectories where the lowest recruitment occurred in years with lowest discharge; increased in years with increased discharge to

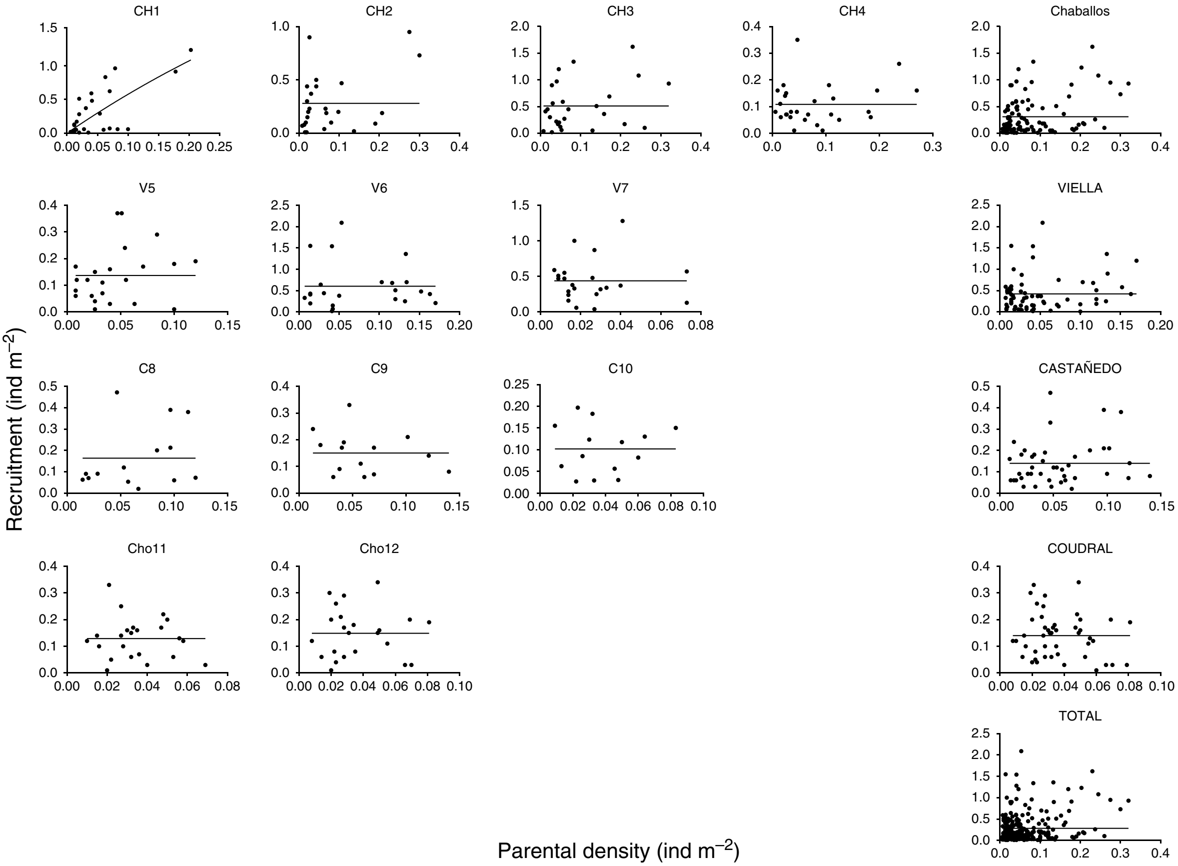

Figure 13.2 Recruitment (RC, ind m^{-2}) *versus* parental density (ST, ind m^{-2}) at the 12 study sites spread along two right side and two left side tributaries of Rio Esva (northwestern Spain) for the same cohorts and sites of Figure 13.1 and for streams (sites pooled) and river drainage (all sites pooled). Horizontal lines by the figures indicate the most plausible model *RC* = *Mean RC*, implying that recruitment fluctuates around the mean parental densities with no consistent trend.

reach a maximum at intermediate conditions upon which recruitment declined in years of increased discharge to attain again low values in years of highest discharge of magnitudes similar to those at the opposite, lowest discharge.

A comparison with the Akaike's criterion indicated that log-transformed recruitment *versus* discharge was the most plausible model for all data sets including sites, streams and river drainage (probability of being the correct model >78% in all instances). Moreover, a new application of the Akaike criterion to the log-transformed recruitment *versus* discharge supported the selection of parabolic functions (Model 3, probability of being the correct model >75%) relative to two-phase regressions or Model 5 for sites and streams with only two exceptions, Chaballos and total drainage where two-phase regressions proved to be better (probability of being better >75%). However, for consistency, parabolic functions were fit to all data sets that showed to be highly significant ($p < 0.01$) and explained between 41.6% and 71.0% of the recruitment variations due to the year-to-year variation in stream discharge during the month of March. Log-transformed recruitment *versus* discharge relationships with parabolic functions fitted to data for sites, streams and river drainage are summarized in Figure 13.3.

The analyses of these long-term, large scale recruitment data in relation to parental density and hydrological factors permit rejection of two core hypotheses: the role of parental density as a single factor and the interaction parental density* discharge as determinants of recruitment. Remarkably, these results emphasize the importance of the stream discharge conditions during the recruitment process as a major determinant of recruitment determining the strength of annual recruitment across sites and streams within the Rio Esva drainage.

Recruitment Determinants in the Sea-Migratory Black Brows Beck Population (UK)

Elliott (1984, 1985, 1987, 1989, 1993, 1994), Elliott *et al.* (1997) and Elliott & Elliott (2006) analyzed a long-term data set collected in a stream section of Black Brows Beck (northern England). Elliott (1984, p. 340 and 1985, p. 620) reported numerical data on the number of eggs as a surrogate of the parental density and the subsequent recruitment of the 1966-1983 cohorts. A new data set including 13 additional cohorts (1984–1996) was reported in the form of figures by Elliott *et al.* (1997). For the purpose of this study, Figures 1 and 2 in Elliott *et al.* (1997, pp. 1232–1233) were scanned with an image analyzer to complete a 30-year data set including 1966 to 1996.

The analyses of Elliott and co-workers offered evidence of direct relationships between parental density and recruitment and importantly, a parental-dependent regulation of recruitment in the form of a domed shaped, stock-recruitment relationship. This relationship with a Ricker model fitted to data is shown in Figure 13.4A. Such highly significant and smooth relationship with so little variance over the whole range of parental densities appears conclusive enough to assume that the operation of parental-dependence as driver of recruitment is omnipresent and precludes further explorations on the potential effects of other ancillary factor on recruitment.

Nevertheless, based on previous highlights on the relative importance of stream discharge during the recruitment process elucidated for the resident populations of Rio Esva, a similar relationship was explored for this British sea-migratory population. A plot of recruitment (RC, ind m^{-2}) *versus* discharge in April (m^3/s) highlighted

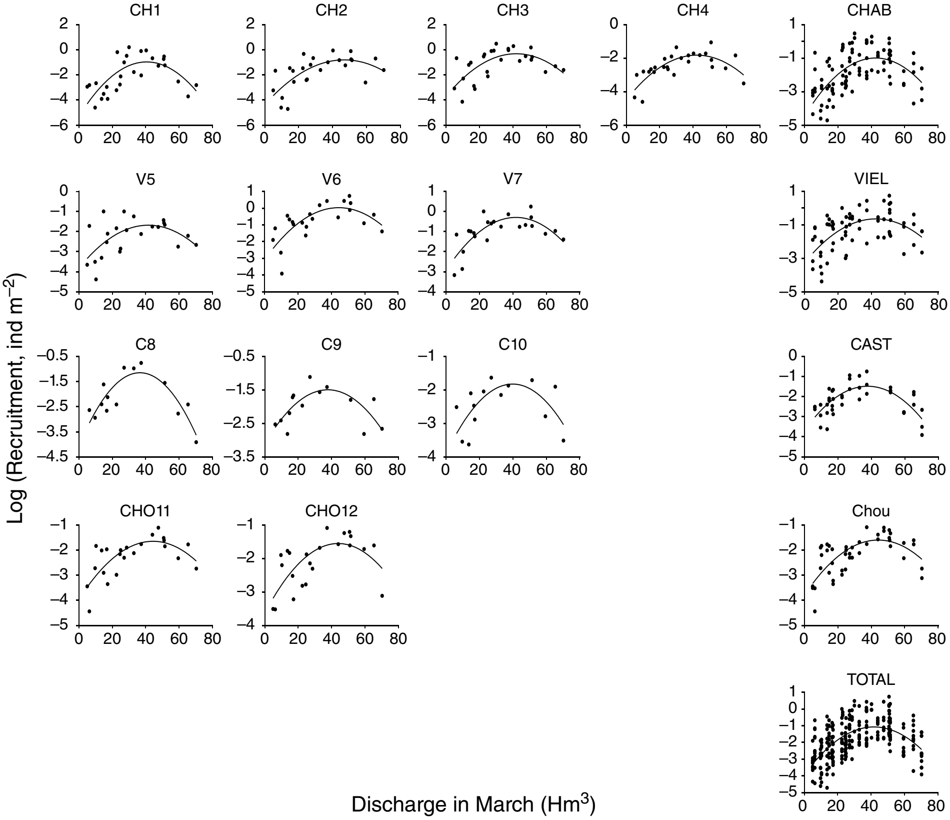

Figure 13.3 Log-transformed recruitment (RC, ind m^{-2}) *vs.* stream discharge in March (Hm^3/month) for the very same study sites and years of Figure 13.1 with parabolic functions fitted to data. The amount of recruitment variance explained by discharge variation for single sites are: For Chaballos. Ch1 = 58.6%, Ch2 = 50.0%, Ch3 = 41.0% and Ch4 = 48.7%. For Viella: V5 = 37.8%, V6 = 53.6% and V7 = 46.1%. For Castañedo: C8 = 61.0%, C9 = 41.6% and C10 = 40.4% and For Choudral: Cho11 = 48.7% and Cho12 = 54.5%. All significant at least at $p < 0.01$ for all parameters.

a strongly consistent ascend/descent pattern over the whole range of discharge values. Strongly consistent with patterns elucidated for the Rio Esva populations, the lowest recruitment occurred in the years with lowest discharge; increased in years with increased discharge to reach a maximum or a threshold in years of average discharge upon which recruitment declined with increased discharge to attain again markedly lower magnitudes in years of maximum discharge (Figure 13.4B).

We further explored the hypothesis that recruitment may result from interactions between the two factors, parental density*discharge. To this end, a fit of Model 2 that includes that interaction to data explained an 85.1%. However, the effect of parental density was significant ($p < 0.001$) but the effect of discharge was not significant ($p = 0.55$). We compared the three models *via* the Akaike's information criterion, calculating the ΔAICc and their subsequent probabilities or the Akaike's weights (W), W_{PD} for parental density, W_{DIS} for discharge dependence and W_{PDDIS} for the interaction. A pair wise comparison highlighted that the AICc score for the discharge dependent

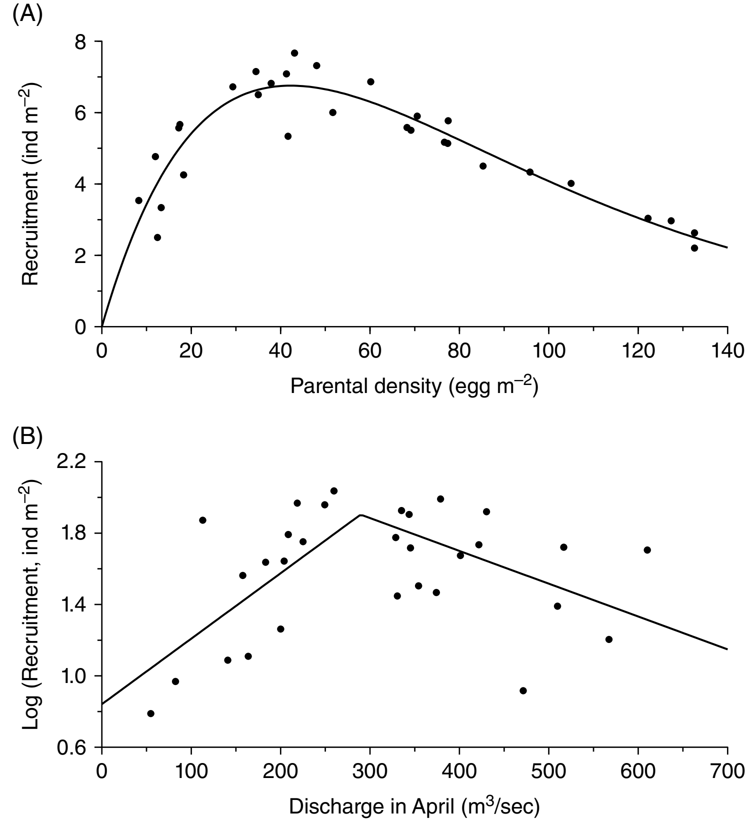

Figure 13.4 (A) Re-calculated and re-drawn from Elliott *et al.* (1997). Recruitment (ind m^{-2}) *vs.* parental density (egg m^{-2}) of the sea-migratory population of Black Brows Beck (UK) over the years 1966-1996 with a Ricker's stock-recruitment relationship fitted to data. Constants, variance explained and significant level are: $A = 0.43$, $B = 0.02$, $R^2 = 84.4$, $p < 0.001$. AICc score = −22.6. (B) Log-transformed recruitment (RC,%) *versus* discharge in April (m^3/sec) with a two-phase regression fitted to data. Constants, variance explained and significant level: $A = 0.84$, $B = 0.004$, $X = 289.5$ and $K = -0.018$; $R^2 = 42.6\%$, at least $p < 0.05$ for the parameters estimated. AICc = −65.89.

model was the lowest far apart. The differences between the AICc and subsequent probabilities of being the correct model attained $W_{PD}-W_{PDDIS} = 46.7$ and $_{WDIS}\text{\_}W_{PDDIS} = 45.0$ offering overwhelming evidence or a 100% probability that the discharge dependent model is the most plausible or the correct model.

Clearly, the remarkably high R^2 values obtained for both the Ricker and the interaction models (i.e., 84.4% and 85.1%, respectively) may prompt anyone to conclude that the two models are excellent fits to data. However, the examination of AICc and W_I scores emphasizes that the two models show a remarkably weak explanatory power relative to the most plausible and better log-recruitment-discharge model whose fit explained 42.3% of the variance. The latter model and the original stock-recruitment model fitted to data (re-drawn and re-calculated from Elliott *et al.* 1997) are compared in Figures 13.4A and 13.4B.

Recruitment Determinants in a Lake – Migratory and Two Sea-Migratory Danish Populations

The analysis of the three Danish populations encompasses 21 cohorts (1979–1999) and 16 cohorts (1981–1996) of two sea-migratory populations, respectively and 17 cohorts of a lake-migratory populations; 54 cohorts in total. Overwhelming differences in the recruitment magnitudes among populations (ANOVA, $F_{2,51} = 16.8$, $p < 0.001$) characterized these sea- and lake-migratory populations. The recruitment of the Bisballe Baeck lake-migratory population, averaged over the years, attained RC = 6.0 ind m^{-2}; in Brandstrup Baeck attained RC = 2.6 ind m^{-2} whereas in the nearby Tjaerbaeck attained only RC = 0.35 ind m^{-2}. Given such differences and to facilitate comparisons the recruitment values we re-scaled as the % of the highest recruitment considered to be 100 for every single population and described the new values after log-transformation.

No parental density data was available for these populations therefore we focused directly on the potential effects of stream discharge during the recruitment period. Visual inspection of the plots log-transformed recruitment (%) *vs.* discharge for each single population highlighted strongly consistent ascent/descent trajectories in which the lowest recruitment concurred with lowest discharge, increased with increasing discharge up to a threshold upon which recruitment declined with increased discharge. For each single population, two-phase regressions proved to be more plausible than parabolic functions (the probability to be better >70% for the three populations). Fits of two-phase model for the 21 cohorts of Brandstrup Baeck, 16 cohorts of Tjaerbaeck and 17 cohorts of Bisballe Baeck significantly explained 37.5%, 31.2% and 50.4% of the recruitment variations in due to variation in discharge.

A plot of the 54 cohorts of the three populations pooled also highlighted a smooth and continuous ascend/descent relationship (Figure 13.5) consistent with the patterns highlighted for every single population. Expectedly, this ascent/descent pattern common to the three populations highlighted that the lowest recruitment of the three populations concurred with each other and occurred in years of lowest discharge, increased in years of increased discharge to maximize in years of average conditions upon which recruitment decreased to attain lowest levels in years of highest discharge. For the three populations pooled (54 cohorts) the differences between the scores indicated that a two-phase regression was only slightly better than a parabolic function (ΔAICs = 1.1, probability of being the correct model = 60% relative to 40% for the parabolic function). For consistency with the results for previous populations above, we smoothed this relationship fitting a two-phase regression that showed to be highly significant and explained a $R^2 = 42.0\%$ of the total variation in recruitment due to variation in discharge (Figure 13.5).

Consequently, the discharge-dependent recruitment as the best model for this relationship including a lake-migratory and two sea-migratory populations in tributaries of Gudenaa River matches the ascent/descent threshold-like as the best models for the Rio Esva resident populations and a sea-migratory population in northern England and all together emphasizes that the stream discharge conditions over the recruitment period is a major determinant of the annual recruitment strength and describe the very same ascent/descent, threshold-like patterns across populations.

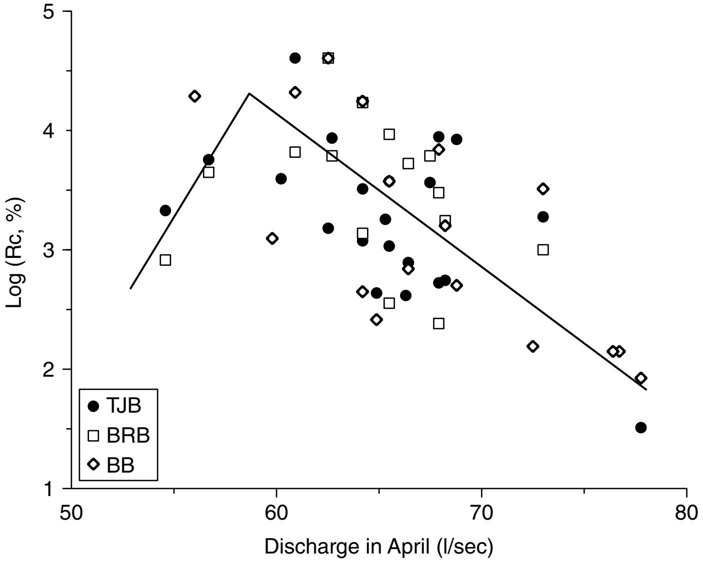

Figure 13.5 Ascent/descent, threshold-like patterns described by recruitment values after log-transformation of the original values as % of the maximum recruitment observed in each single population of two sea-migratory and one lake-migratory populations in tributaries of Gudenaa River (central Jutland) over the years 1979–1999. A two-phase regression fitted to the three populations pooled. Constants, variance explained and significant level are: $A = -2.06$, $B = 0.098$, $X = 60.9$, $K = -0.11$. $R^2 = 42.0\%$, $p < 0.01$ for the parameters estimated. The recruitment variances explained by discharge for each single population are: For TJB, $R^2 = 38.5\%$; for BRB, $R^2 = 30.1\%$ and for BB, $R^2 = 50.4\%$. All significant in at least $p < 0.01$ for all the parameters estimated.

Discussion

The objective of this study was to review long-term studies on the recruitment of stream-spawning brown trout populations and re-analyze original and new data sets in an attempt to elucidate whether recruitment features were comparable among populations and whether the underlying driving factors, either density-dependent or density-independent, are common to all populations and if yes, whether the patterns elucidated are similar or comparable among populations. Several long-term, published and unpublished data sets of populations belonging to the three life history modes that typify brown trout within its natural European distributional range permitted this comparison.

Recruitment variations are overwhelming. Their magnitudes and ranges of variation appeared to be population-specific. The recruitment variations observed in the study populations actually include all the variation reported in the literature for populations across geological/climatic regions and life history modes within its natural European distributional area that include, at least, UK (Milner, Gee & Hemsworth 1978, 1979, Mann *et al.* 1986, Crisp 1993, Elliott 1993A), France (Cattanèo *et al.* 2002); Norway (Jensen & Johnsen 1999, Lund, Olsen & Vollestad 2003); Denmark (Mortensen 1977, 1985); Austria (Unfer, Hauer & Lautsch 2011), Switzerland (Richard, Cattaneo & Rubin 2015) and Spain (Nicola *et al.* 2008; Nicola, Almodovar & Elvira 2009).

And also across exotic regions including different geological/climatic regions of North America as Michigan (Nuhfer, Clark & Alexander 1994, Zorn & Nuhfer 2007), Colorado (Latterer *et al.* 1998) and Virginia (Carline 2006) and as far as New Zealand (Jowett, Richardson & Bonnett, 2005; Hayes, Olsen & Hay 2010). Actually those studies have reported recruitment magnitudes that only rarely exceed 1.5–2.0 ind m^{-2}. Magnitudes as high as those recorded for the lake-migratory Danish BB and the sea-migratory British BBB appear uncommon. Moreover, recruitment differs by orders of magnitudes between nearby streams and nearby sites and also by orders of magnitude from year to year and those variations also appear population-specific and/or stream or stream site-specific.

Across study sites within the Rio Esva drainage both parental density and recruitment were site-specific. A comparison among sites and streams showed no consistent relationship between parental density and recruitment. At sites where the parental density was persistently high, low or intermediate were unrelated to persistently high, low or intermediate recruitment. Importantly, explorations into the occurrence of stock-recruitment relationships at the scale of site, stream and river drainage permitted to reject any hypothesis related to a parental regulation of recruitment. Moreover, further explorations into the relative importance of interactions parental density*discharge on recruitment also rejected any hypotheses related to their combined role as recruitment determinants. These results for resident populations contrast markedly with those highlighted by Elliott and co-workers who offered evidence for the occurrence of stock-recruitment relationships in the sea-migratory population of the British BBB.

Despite these markedly different results, stream discharge during the recruitment process appears to be a major underlying recruitment in all the study populations independently on whether density-dependence may or may not operate on recruitment including Danish populations where no parental density data was documented. Current results emphasize the '*modus operandi*' of just one single environmental factor, namely, the rainfall/discharge conditions at, during or soon after emergence as a major determinant of recruitment.

It is doubtful that two opposing factors as stream discharge and parental density operate simultaneously on recruitment to generate patterns difficult to reconcile. Consistency among discharge-dependent patterns across populations strongly support that a unique density-dependent regulation of recruitment as emphasized by Elliott (1984, 1985, 1987, 1993, 1994), Elliott *et al.* (1994) and Elliott & Elliott (2006) for the British BBB population is most unlikely, particularly in extremely variable and unpredictable habitats as streams subject to extremely variable rainfall-dependent discharge. Instead, year-to-year differences in the rainfall/discharge conditions impose an annual specific stream water volume. The concurrent availability of space underlying the abundance of micro-habitats suitable for the youngest juveniles appears to be critical for the survival of the youngest juveniles (Lobón-Cerviá & Rincón 2004). Annual-specific discharge conditions during the recruitment process impose an annual-specific carrying capacity to sustain recruits that maximize at intermediate conditions; decline above and below those threshold-like patterns and minimize in years at the two extremes of lowest and highest discharge.

This conclusion finds confirmation in several studies on native and introduced populations including Solomon & Paterson (1980); Mann *et al.* (1989), Jensen & Johnsen (1999); Spina (2001), Cattaneo *et al.* (2002), Unfer, Hauer & Lautsch (2011), Kawai *et al.* (2013), Richard, Cattaneo & Rubin (2015) and Warren *et al.* (2015). This can be extended to salmonid populations of the Pacific Ocean (Clark 1992; Nehring & Anderson 1993; Latterell *et al.* 1998, Smith 2000) including sea-migratory populations (Sakuramoto 2005). All these studies suggest that environmental (hydrological) determinants of recruitment are the rule with apparently only one exception, the British BBB population.

Accumulating evidence implies that, relative to the temporal stability and persistence expected to occur in populations regulated by negative feedback mechanisms, in environmentally determined populations and independently of the life-history mode, geological/climatic conditions and population-specific genotype, recruitment fluctuates over time, tracking the randomness of the rainfall/discharge conditions. And given that recruitment is a major determinant of year-class strength and hence of population size, all these populations are expected to be temporally unstable over time, tracking the 'statistically random walk dynamics' that typify environmentally driven populations (Andrewartha & Birch 1954).

Population instability caused by the temporal randomness of the rainfall/discharge conditions provide further insight into several confusing patterns frequently observed in the wild. These include not only the overwhelming year-to-year variation in density observed in practically all populations, but also the inexplicable collapses and new recoveries recurrently observed in numerous salmonid populations (Lobón-Cerviá 2009a). The ascent/descent, threshold-like patterns highlighted for all study populations predict that springs with intermediate discharge conditions determine the highest recruitment levels. Consequently, the maximum number of recruits possible at the scale of a stream or a stream site will never attain magnitudes above those thresholds. At the opposite extreme, unfavorable years either excessively dry with lowest discharge or too rainy with highest discharge induce the weakest recruitment and subsequent weak year-classes. These patterns also predict risks of population extinction at variable geographical scales if and when unfavorable rainfall/discharge conditions persist over prolonged time periods and/or when combinations of very rainy *versus* very dry years alternate each other over several successive years.

Recently, several authors have claimed that an ecological imperative and managing challenge is to forecast population status concurrent with their habitats (Clark *et al.* 2001). The need to forecast population status is widely recognized for the design of management strategies of exploited populations and it is frequently articulated as a primary objective of research programs (Pace 2001). However, despite decade long, intensive efforts, little advances have been observed. A major conclusion from this study is that despite the unpredictable character of the rainfall/discharge conditions, annual recruitment strength can be readily predicted from simple measures of stream discharge over the recruitment period. Discharge measures are routinely collected by numerous gauging stations operating along the distributional range of brown trout. And given that recruitment is the major determinant of year-class strength and population size (Lobón-Cerviá 2009b, Lobón-Cerviá *et al.* 2011) forecasting population status may become a routine exercise. This approach appears a promising tool for populations, streams and fishery management and for the accurate quantification of undesirable human-induced alterations and unpredictable natural processes, including potential extinction risks and the threats of the global change.

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14

Population Dynamics of Juvenile Brown Trout (*Salmo trutta* L.), Recruitment, Mortality, Biological Production and Smolt Yield in Two Danish Baecks

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Introduction

Long-term studies involving density assessment of fry and parr on brown trout population dynamics in running waters are rather few (e.g. Elliott & Elliott 2006; Lobón-Cerviá 2003, 2004 & 2005; Lobón-Cerviá & Rincón 2004; Carline 2006). In contrast there are many short-term studies, working through a few years in the same study area. Long-term studies are costly and may explain why there are so few. The main problem with short-term studies is a lack of a baseline, from which to assess the relevance of the results (Elliott & Elliott 2006).

The only published long-term study from Denmark was made in a small baeck (Lobon-Cervia & Mortensen 2005) covering a period of 17 years. Short-term studies in Denmark usually cover up to three years (Mortensen 1977a + b + c & 1982; Rasmussen 1986a + b). Such studies can be useful to answer specific questions, e.g. growth and mortality in relation to brown trout density and water temperature, calculation of production rates and feeding studies. One of the weaknesses of short-term studies is the lack of natural variation of results. Mostly because the true natural range of recruitment (i.e. the year class of fry from spawning redds in spring that starts a new cohort) is not known; this requires long-term studies.

Brown trout belong to 'equilibrium strategists' (Winemiller and Rose 1992). This is an intermediate-sized fish species that inhabits relatively stable environments, produces small numbers of large eggs compared to most other fish species, and provides high parental investment in their young (Rose *et al.* 2001).

Density of trout fry during spring depends on the number of eggs spawned, and apparently also on the variation of stream flow (discharge) during and shortly after emergence (Daufresne *et al.* 2005; Daufresne & Renault 2006; Lobon-Cervia 2004; Lobon-Cervia & Mortensen 2005; Lobon-Cervia *et al.* 2016). Density dependent processes such as growth, survival and movement are compensatory factors and regulate

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density (Rose *et al.* 2001). These compensation factors are difficult to measure in the field and to realize their importance demands long-term studies.

As described in Larsen (1972), Rasmussen & Geertz-Hansen (1998, 2001) and Rasmussen (2006, 2016), stock enhancement with first generation (F1 – offspring of wild parents) hatchery-reared brown trout fry, parr and smolt has taken place for many decades in Denmark. The stocked smolts represent the most expensive part compared to the values of stocked fry and parr. The question of smolt production is important, so it is obvious to ask the question: what is the size and range of wild smolt production in Danish streams and rivers in the different geographical areas? And which parameters, either biotic and/or abiotic (i.e. density dependent vs. density independent factors) regulate the variation? Mortensen (1977c) stated after two years of study in Bisballe Baeck, a small baeck with lake-run brown trout, that the annual smolt production (calculated from density and mortality) probably was only about 4 smolts per 100 m^2. Rasmussen (1986b) stated in a three-year study from Brandstrup Baeck that the annual smolt production (trap catching) was from 15 to 20 smolts per 100 m^2; a relatively high figure. It is important for economic reasons to calculate the optimal number of supplemental stocking of trout smolt in rivers, where stocking of brown trout fry and parr also takes place (Rasmussen 2016). Based on short-term studies of parr densities and mortality a 'rule of thumb' stated that smolt production in all Danish waters across geographical areas is about 7.5 smolts per 100 m^2. Smolt production in Denmark, before human impact on rivers, was estimated to be 2.5 to 3 million annually (Rasmussen 2006, 2016). This figure has been used for several years to calculate the size of supplementary smolt stockings in Danish rivers (op. cit.). Routine monitoring of streams showed, however, that parr density varied between geographical areas, probably as a combination of recruitment, survival and carrying capacity. Thus, smolt production is also expected to vary as a function of these variables (op. cit.). Recruitment is a function of number of spawners and environmental determinants as: (1) quality of spawning and rearing habitats and (2) hydrological conditions e.g. discharge in spring (e.g. Lobon-Cervia *et al.* 2016). Survival and growth after the recruitment period is most probably a function of quantity and quality of the food, water temperature, and density of the year-class and most probably a function of interaction between year-classes in the stream (Rasmussen 1986b; Elliott 1994 & 2006).

It was therefore decided in the late 1970s to start a long-term study in smaller baecks, where recruitment, growth and survival of brown trout could be regularly monitored by electrofishing, and where the smolt run could be determined by setting up a trap to collect all migrating smolt.

Brandstrup Baeck and Tjaerbaeck in mid-Jutland, Denmark were selected because previous short-term studies have been conducted in the two baecks (Larsen 1955; Mortensen 1978; Rasmussen 1986b). Electrofishing is affordable and because of their smaller size, a smolt trap can be installed at the lower part of the two baecks.

Electrofishing surveys started in 1978 and ended in 2008. The smolt traps were running in the period 1982 to 1992 and 1997 to 2001 in Brandstrup Baeck and in 1982 to 1992 in Tjaerbaeck.

This chapter describes: (1) The localities and physical description of two smaller baecks in Jutland, Denmark, where the population dynamics of brown trout was studied by electrofishing in spring and autumn; and where smolt traps were established during spring. (2) Number, density and mortality, growth and relationship between growth and density through the years. (3) The resulting smolt production and number of autumn recruits. (4) The biological production rates in relation to recruitment, which is discussed in the context of results.

Study Area and Field Sampling Methods

Localities and Physical Description

The Brandstrup Baeck and Tjaerbaeck in the Gudenaa river system (Figure 14.1) was described by Larsen (1955), Brandstrup Baeck by Mortensen (1978), Nielsen (1986) and Rasmussen (1986b), and a short summary will be given here. Both baecks go through a hilly moraine landscape. Besides rainfall, they are fed more or less by seeping groundwater all over their upper and middle course. Therefore, they can be characterized as cold water baecks. River Gudenaa is Denmark's longest river (160 km) with outlet into the 30 km long Randers Fjord, which enters into the Kattegat on the east coast of Jutland. A fishery for salmon and sea trout (i.e. commercial and recreational) takes place in the fjord and recreational (rod and line) in the main river. The recreational fishery has increased in the river and fjord since stocking of Atlantic salmon (*Salmo salar*) smolts started in the 1990s in order to rehabilitate the original, but now lost (in the 1920s) salmon stock in river Gudenaa. Recreational catches of salmon and sea trout in the fjord and river are not recorded, but may have a significant influence on the size of the spawning run of sea trout into the Gudenaa, including the two inlets Brandstrup Baeck and Tjaerbaeck. There is no recreational fishing in the two small baecks. Mammalian predators like the non-native American mink (*Neovison vison*), the European otter (*Lutra lutra*) or piscivorous bird species were never seen in the baecks during the study period. Larger brown trout parr had trout eggs in their stomachs during spawning time and sometimes smaller brown trout parr in their stomachs (Lousdal *et al.* 2002; DTU-Aqua non-published materials). However, the regulatory effect from predation on recruitment and population dynamics is unknown. Aquatic and terrestrial invertebrates constitute by far the largest part of the diet of the trout in the baecks (*op. cit.*).

Habitat

Brandstrup Baeck

Brandstrup Baeck (Figure 14.1) is a 4.5 km long productive (about 450 μS cm^{-1}) baeck (Northing: 6250456, Easting: 550508) tributary to the river Gudenaa, about 22 km upstream from Randers Fjord. It rises from small springs at a high of about 56 m a.s.l. and has a slope of about 1% throughout its length. Catchment area is about 10.9 km^2 (Favrskov Municipality). The baeck from the upper electrofishing site BRB62-63 and down to the smolt trap BRB02-03 is 0.75–2.95 m wide, shallow with mean depths varying from about 16 to 27 cm and with maximum depths up to about 0.4 m. Water velocities vary from fair to very fast. The baeck bed consists of a mixture of sand (dominating), gravel and stones with patches of phanerogamic vegetation, mainly *Berula erecta*. Branches, twigs, undercut banks and overhanging vegetation offer hiding places for the fish. The surroundings of the baeck are a mixture of deciduous forest, mainly *Alnus glutinosa* and cattle and horse pasture. Some of the baeck stretches have been regulated for many years, and other stretches are probably left unregulated. Between sites

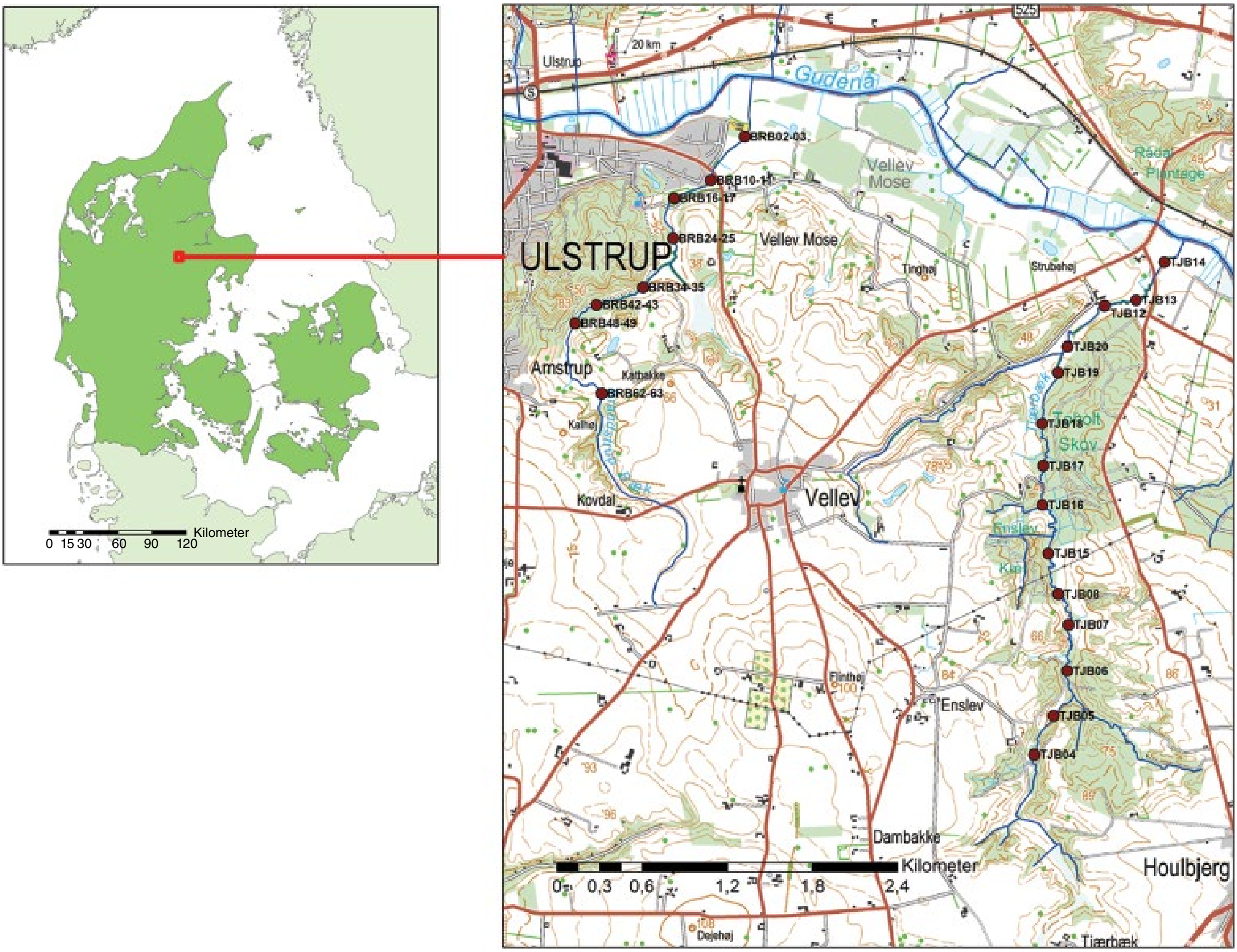


Figure 14.1 Research localities: Brandstrup Baeck and Tjaerbaeck.

BRB34-35 and BRB24-25 the baeck receives a little inlet from swampy areas. There are no brown trout in this inlet, but the water from this inlet possibly slightly influences the water temperature at site BRB02-03, i.e. relatively colder during winter and warmer during summer (Figure 14.2). Brown trout are the dominating fish species, but occasionally other fish species are found. The baeck was part of a genetic population analysis of Danish trout streams (Hansen *et al.* 1993) and most probably the trout in Tjaerbaeck are of the same genetic strain. A study was made on the physiological status of pre-smolt, smolt and non-descending parr in the baeck. The fish caught in the smolt trap were characterized as parr, pre-smolts or smolts based on morphological criteria

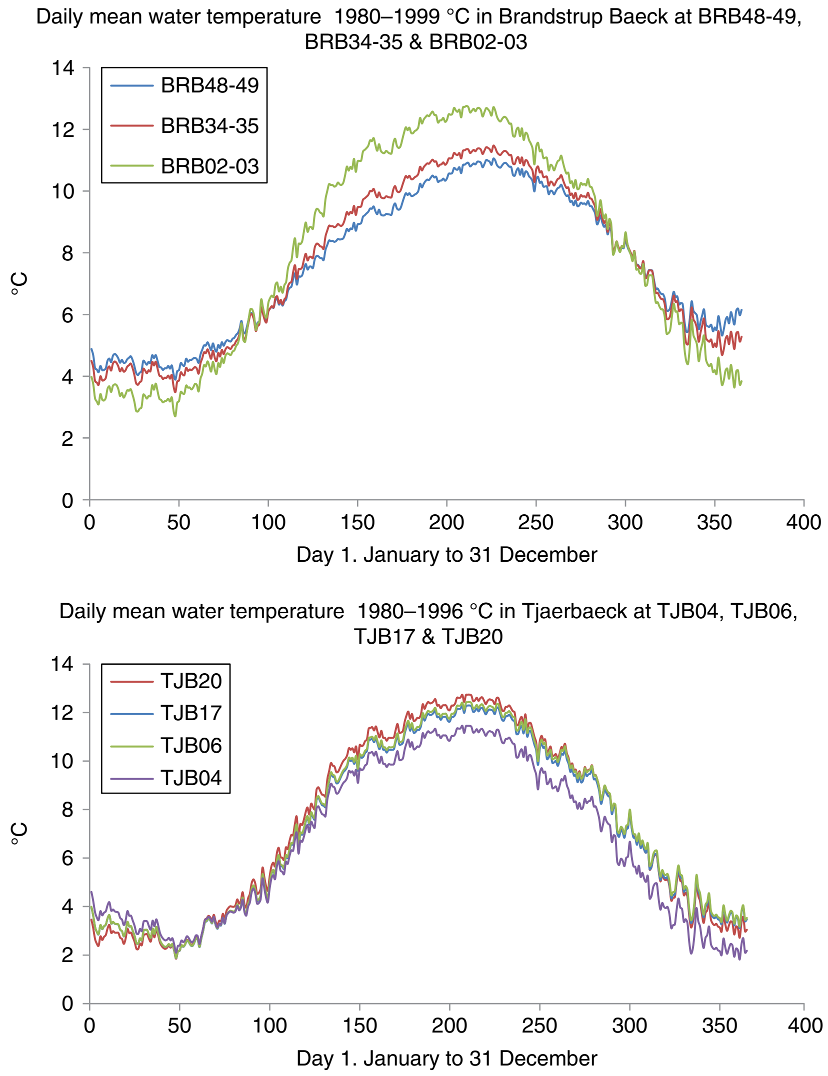


Figure 14.2 Daily mean water temperatures °C in Brandstrup Baeck (three stations) and Tjaerbaeck (four stations).

(Johnston & Eales 1967). Pre-smolts and smolts were characterized by relatively high gill Na+/K+ ATPase activity compared with brown trout judged as parr (Nielsen *et al.* 2006). Trout 0+ taken (about 50% of the total 0+ stock) from Brandstrup Baeck 1985–1989 was used in several stocking experiments (i.e. mortality, migration and smoltification rate) in other brown trout baecks in the Gudenaa river system (Berg & Jørgensen 1991, Jørgensen & Berg 1991).

Around the year 2000 the land owner upstream of the baeck of the brown trout producing area drained minor surrounding areas. This created a heavy increase in the amount of sand to the baeck, covering the baeck bed of the upper sections with drifting sand. The result in the following years was a decrease in spawning activity at all sites (BRB62-63 to BRB02-03) and a decrease in the total brown trout stock. A small number of electrofishing operations in 2013–2015 (not presented here) showed that trout were only present in low numbers at the lower sections of the baeck because spawning areas upstream were still covered by sand. The smolt trap was established at site BRB02-03.

Tjaerbaeck

Tjaerbaeck (Figure 14.1) is a 7.4 km long productive (about 450 µS cm^{-1}) baeck (Northing: 6249307, Easting: 553556) with an outlet to the river Gudenaa about 4 km downstream from the outlet from Brandstrup Baeck to the Gudenaa river. It rises from small springs at a high of about 60 m a.s.l. and has a slope of about 1% throughout its length. Catchment area is about 12.9 km^2 (Favrskov Municipality). The baeck from upper electrofishing site TJB04 and down to the smolt trap TJB20 is 1.05–3.16 m wide, shallow with mean depths varying from 15 to 26 cm and with maximum depths up to 0.6 m. Water currents vary from fair to very fast. Just upstream of the smolt trap at site TJB20 the baeck receives a little inlet with no trout during the study period. However, the water from this inlet possibly slightly influences the water temperature at site TJB20, i.e. relatively colder during winter and warmer during summer (Figure 14.2). The baeck bed consists of a mixture of sand (dominating), gravel and stones, and at the middle and upper stretches with patches of *Fontanalis antipyretica.* At the lower stretches there are patches of phanerogamic vegetation, mainly *Berula erecta.* Upstream the upper fishing site TJB04 iron compounds (Geertz-Hansen & Rasmussen 1994) leak out together with the ground water. Therefore, downstream to the middle fishing sites the baeck bed has small iron compound deposits in varying amounts depending on weather and discharge conditions. Branches, twigs, undercut banks and overhanging vegetation offer hiding places for the fish. The surroundings of the baeck are a mixture of deciduous wood, mainly *Alnus glutinosa* and *Fraxinus excelsior,* which create a canopy with very little sunshine at the baeck bed, and cattle pasture. Some of the upper stretches above the research section (above site TJB04) have been regulated for many years. Other stretches are more or less unregulated. Fallen trees and branches create obstacles and might create problems for up-migrating sea trout. However, during high discharge sea trout are able to pass, but it is not known how much the passage is hindered. Brown trout is the dominating fish species, but occasionally other fish species are found.

1.3 km upstream of the outlet to the river Gudenaa an old mill weir (height about 1.5 m) was re-established in the 1960s for the intake of water to a rainbow trout (*Oncorhynchus mykiss*) farm. When the monitoring started in 1981 the fish farm was closed; but the concrete weir, which had in its middle a cutting (width: 42 cm, depth: 16.8 cm), still existed. Larsen (1955) assessed that the weir is impassable for mature sea trout. During high water discharge, mature sea trout might be able to pass the weir, and spent sea trout were caught in the smolt trap during spring.

Here, the smolt trap was established at site TJB20 in connection and below the weir.

Water Temperature and Discharge

Water temperature (Figure 14.2) in both baecks was measured during the first six study years with a min–max thermometer; thereafter from 1984 it was replaced by loggers (±0.2 C°, logging every hour). In Brandstrup Baeck loggers were established at site BRB48-49 (upper), BRB34-35 (mid) and BRB02-02 (lower; at the smolt trap). In Tjaerbaeck the loggers were established at the upper (TJB04 and TJB06), middle (TJB17) and lower part of the baeck (TJB20, at the smolt trap) and one logger below the studied area. Data from this logger was only used to correct for missing data upstream, and will not be considered here. An air/water temperature relationship: logistic regression (Caissie 2006) with an estimated correction for hysteresis (Mohseni *et al.* 1998) was established for the several stream sections from air temperature data from a nearby station (Tirstrup, Danish Meteorological Institute) and used to calculate water temperature per day for missing data (i.e. lost logger, breakdown of logger) and for the period with min–max temperature before 1984. A logger in air close to site TJB20 showed that the daily mean water temperature could be precisely calculated on a daily basis from the surrounding air temperature. Water temperature at stations without a logger between the logger stations was calculated by simple linear (length of stream) interpolation between loggers. In both baecks the mean daily water temperatures vary from a little above 3 to 4 °C during winter, and mean daily temperature during the warmest period in July–August is up to about 12 °C. The highest hourly summer temperatures ever measured in the whole study period with data loggers was 19.9 °C in Brandstrup Baeck and 17.0 °C in Tjaerbaeck, and the lowest hourly winter temperature measured was –0.1 °C in Brandstrup Baeck and 0 °C in Tjaerbaeck. During cold periods the water temperature can be a little above zero at times, and the water surface of the baecks could be ice covered.

Water discharge (Figure 14.3) in both baecks was measured for several years and seasons at the smolt traps (BRB02-03 and TJB20) by the NaCl method or integration method. That is, a certain amount of NaCl is added to the baeck and the conductivity is measured during the following time at fixed intervals. Q/h (i.e. discharge L sec^{-2} vs. water level cm) was established for BRB02-03 and TJB20 and the daily mean discharge in the two baecks since year 1980 was established from the nearby (20 km apart) Moelballe (gauging station 211663 in the Gudenaa river system) that reports discharge in m^3 sec^{-2}.

The mean annual discharge in Brandstrup Baeck (Figure 14.3) at the smolt trap was about 60 L sec^{-2}. Mean discharge varied from about 55 L sec^{-2} during summer to 70 L sec^{-2} during winter and spring and with annual mean max values of about 85 L sec^{-2} and mean min values about 45 L sec^{-2}. During the whole year sudden high increases in discharge took place, mostly during snow melting and summer thunderstorms.

The mean annual discharge in Tjaerbaeck (Figure 14.3) at the smolt trap was about 105 L sec^{-2} and mean discharge varied from about 90 L sec^{-2} during summer to 110 L sec^{-2} during winter and spring and with annual mean max values of about 150 L sec^{-2} and mean min values about 80 L sec^{-2}. During the whole year, sudden high increases in discharge took place, mostly during snow melting and summer thunderstorms.

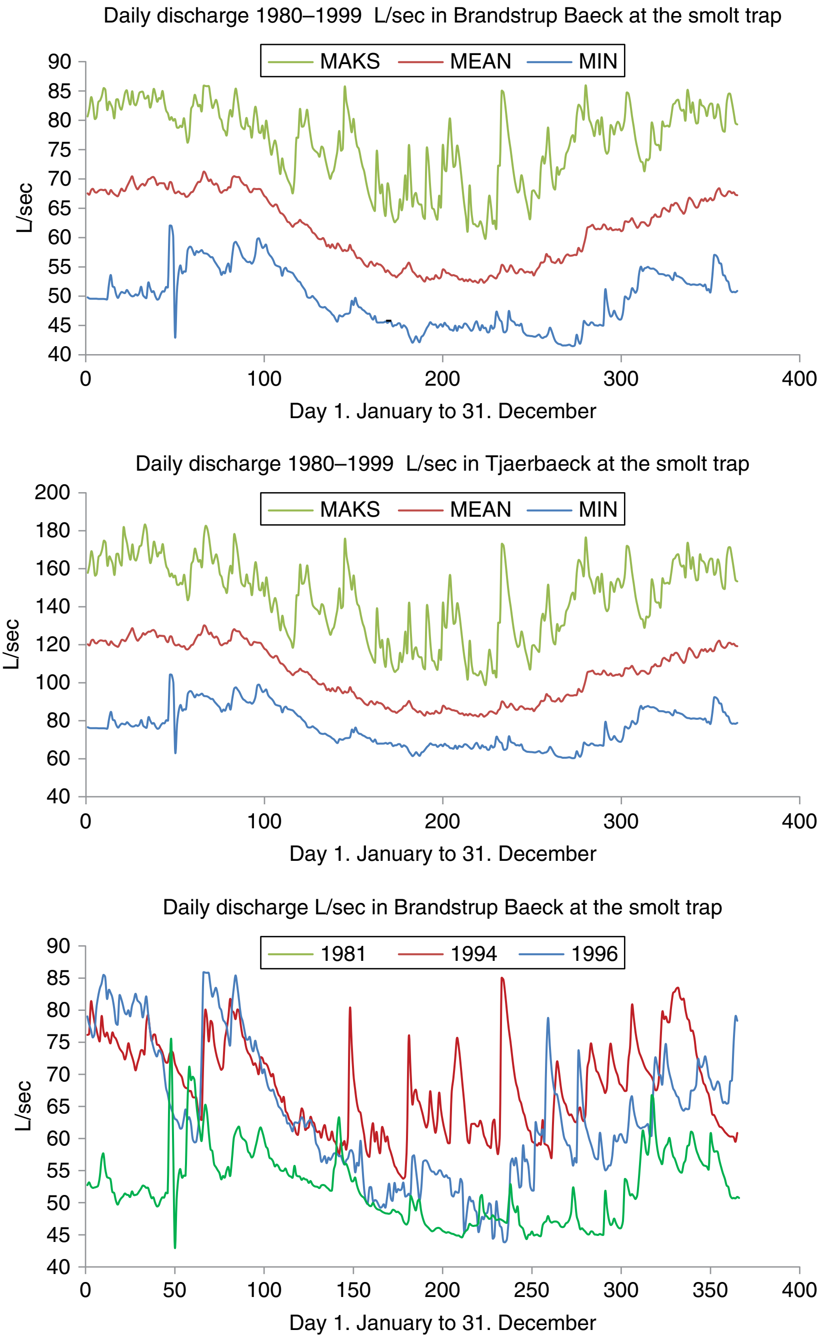


Figure 14.3 Water discharge L/sec in Brandstrup Baeck and Tjaerbaeck.

Production Area

The mean width of the total production areas of the baecks was calculated from measurements of every 50 m stretch from BRB02-02 to BRB62-63 and TJB04 to TJB20. The mean width of the electrofishing sections in both baecks was calculated from measurements of every 5 m stretch. The spawning and smolt producing part of the Brandstrup Baeck from the upstream start BRB62-63 down to the smolt trap BRB02-02, is 3.6 km long, with a mean width of 1.276 m giving a total smolt producing area of 4,594 m^2. The spawning and smolt producing area of the Tjaerbaeck from the upstream start TJB04 and down to the smolt trap TJB20 is 4.4 km long, and with a mean width of 1.813 m to giving a total smolt producing area of 7,950 m^2.

Brown Trout and Other Fish Species

Mature sea brown trout, dominated by 22.5 cm–68.0 cm fish have been captured during electrofishing, and can be found in the baecks from late October; spawning takes place in November and December, occasionally in the beginning of January. Most of the sea trout leave the baecks shortly after spawning. The last sea trout leave the baecks during the smolt run in spring when they are caught in the smolt traps. Very few non-migrating mature females and few non-migrating males spawn in the baecks, so the majority of spawning, egg deposition and the subsequent recruitment is from sea-run brown trout. Eel (*Anguilla anguilla*), three-spined stickleback (*Gasterosteus aculeatus*), burbot (*Lota lota*) and lamprey larvae (*Lampetra planari*) are occasionally found in the baecks.

Sampling and Data Analysis

Electrofishing

Brandstrup Baeck

In 1978 only two sites in Brandstrup Baeck were electrofished (DC), from 1979 to 1990 every second 50 m stretch (a total of 36 sections) from the start of the production area down to the smolt trap had their population estimated by electrofishing once a year in November. Of these a total of eight stretches were fished twice. Testing the mean brown trout density by comparing the 28 sections with the eight sections was not significantly different. So, from 1991 to 2008 electrofishing took place only on the eight stretches (Figure 14.1) (a total of 400 m baeck length) with two removal electrofishing events covering 11.1% of the total production area. Electrofishing for fry and parr also took place on the eight sections before and after the smolt run to: (1) control the catches of smolt in the trap with the change in population density before and after the smolt run; and to (2) identify the size of recruitment, i.e. the fry that start a new cohort.

Tjaerbaeck

A total of eleven 100 m sections (TJB04 to TJB20) above the smolt trap (Figure 14.1) were electrofished (DC) in the period 1981 to 1996 in October/November, covering 1,100 m baeck length and covering 27.3% of the smolt production area upstream the smolt trap. Electrofishing was also made before and after the smolt run to control the catches of smolt in the trap with the change in population density before and after the smolt run and to identify the size of recruitment.

Calculations from Electrofishing

Bohlin *et al.* (1989) and extensions of some of these formulae were used to calculate the total number of brown trout in the different years and sections. From these the total number of trout in the different years in the total production areas was calculated for both baecks.

All densities, length and weight, mortality, smolt- and biological production given here are therefore calculated from the pooled number of trout from the respective sections in the two baecks divided by the total electrofished area to an area of $100\,\mathrm{m}^2$ (i.e. density, smolt and production rate). Only the examples of density dependent growth in Brandstrup Baeck (see Figure 14.7) are given for the eight separate fishing sites.

Recruitment of Fry

In the period April 1978 to April 1981 two sections were fished every six weeks in Brandstrup Baeck, and this fishing combined with the later fishing during the following years in spring enabled determination of the period when the fry recruited from the spawning redds (here set to mid-April), and the establishing of an empirical relationship:

$$0+ = \mathrm{PARM1} \bullet \mathrm{Recruits} \bullet \exp\left(-\mathrm{PARM2} \bullet \mathrm{Recruits}\right) \text{between number per area of recruited fry in mid-April and number per area of } 0+ \text{ in November; and where PARM1 and PARM2 are parameters to be established.}$$

This relationship was calibrated to observations and parameters estimated so that the maximum observed number of 0+ (Brandstrup Baeck; year class 1989) during 30 years of monitoring equals the number of recruits R, when the differential: $d(0+)/dR = 0$ (i.e. the maximum of the equation). Therefore, all observations of recruits and numbers of 0+ lie at the ascending part of the mathematical relationship.

This equation and calibration and estimation of new parameters were also found in Tjaerbaeck, so that the maximum observed number of 0+ in late October (year class 1987) in Tjaerbaeck establishes the parameters PARM1 and PARM2 in the equation. All observations of recruits and number of 0+ lie at the ascending part of the mathematical relationship.

Age, Length and Weight and Kcal

All brown trout parr and smolt were, from 1978 to 1994, measured to 0.5 cm fork length, from 1995 to 2008 measured to total length (total length = $-0.097 + 1.059 \bullet$ fork length, $R^2 = 0.9968$; N = 39; 6.3 cm–15.0 cm). Scales were collected during sampling, if possible covering 10 fish within each one cm length group. This was not possible for the oldest year-classes in low numbers. All lengths for parr and smolt are given here as total length (some length distributions of smolt are given in fork length, later in Figure 14.10).

The scales were aged; an age–length matrix was established for each electrofishing event and for each baeck. From these matrixes, the number of trout from each section was assigned to age/year-class, number and length. Relationship was established between total length of fish L (cm) and wet weight/mass of fish W (g) (i.e. $W = a \bullet L^b$)

and length and energy (Kcal) of fish. The fish were collected over several years covering all seasons. Energy was calculated using a Gallenkamp CB-70 ballistic bomb calorimeter (From & Rasmussen 1984).

$$\text{Brandstrup Baeck: wet weight} = 0.0105 \bullet \text{total length}^{2.9596};\ R^2 = 0.9878;\ N = 155;$$
$$\text{range}: 2.8\,\text{cm} - 22.9\,\text{cm}.$$

$$\text{Brandstrup Baeck: cal} = 0.0081 \bullet \text{total length}^{3.0785};\ R^2 = 0.9751;\ N = 153;$$
$$2.8\,\text{cm} - 22.9\,\text{cm and from these, Kcal / wet weight} = 0.7039 \bullet \text{total length}^{0.1524}.$$

The energy content (Kcal/wet weight) varies on an annual basis (details not shown here): lowest in mid-March, highest in August and thereafter decreases to low value in mid-March. Probably this is related to feeding conditions (amount and quality of food items) and might influence smolting rate (Näslund *et al.* 2015). It is assumed that the relationship between Kcal/wet weight found in Brandstrup Baeck can also be used in Tjaerbaeck, but these results are not used further in this chapter.

$$\text{Tjaerbaeck: wet weight} = 0.009548 \bullet \text{total length}^{3.04103};$$
$$R^2 = 0.9944;\ N = 123;\ \text{range: } 4.0 - 17.1\,\text{cm}.$$

Comparing the two relationships and assuming a common parameter b in the length–weight relationship between the two baecks: $b = 2.9950$; ($P < 0.0001$) we get:

$$\text{Brandstrup Baeck: } a = 0.009577;\ \text{Tjaerbaeck } a = 0.010527;$$

which means that the brown trout in Tjaerbaeck is 10% heavier (wet weight) than brown trout in Brandstrup Baeck for a given length. Most probably this is because of the lower relative recruitment and parr density (Tables 14.1 and 14.2) and higher growth rate (Tables 14.3 and 14.4) in Tjaerbaeck compared to Brandstrup Baeck.

Smolt Trap

Smolt traps (Wolf 1951) were set up late February and were running until the beginning of June, when the smolt run ended. The trap was running in 1982–1992 and 1997–2001 in Brandstrup Baeck and in 1982–1992 in Tjaerbaeck. The trap was tended every day, or every second day (depending on number of fish). The fish were categorized (Johnston & Eales 1967) as parr (non-smoltified), pre-smolt (not fully smoltified) and silvering smolt. Pre-smolt and silvering smolts are pooled here in the results as smolts. The trout were length measured and scales were collected and aged, covering if possible 10 fish within every one cm length group every sampling week. Dead smolts were aged and sexed in Brandstrup Baeck (a total of 370 trout; female to male; 3:1, Rasmussen 1986b). Only a small number of fish were sexed in Tjaerbaeck and not shown here. On occasions following sudden snow melting and very heavy rains, the traps were overloaded and/or filled with sand, twigs and leaves, toads (*Bufo bufo*) and occasionally rats (*Rattus norwegicus*). The smolts could not be sampled precisely in these periods. No correcting factor is present, so the presented smolt estimates (Table 14.5) are slightly underestimated.

Table 14.1 Brandstrup Baeck. Number 100 m^{-2} of recruits in April and 0+, 1+, 2+, 3+ and 4+ in November the following years of the same year class. As electrofishing stopped in year 2008 some older age groups are NA. In years 1985 to 1989 the number of 0+ was reduced by 50%. Mortality (Table 14.6) from 0+ to 1+ is calculated from the reduced number of 0+.

	April	**November**	**November**	**November**	**November**	**November**
	Recruits	**0+**	**1+**	**2+**	**3+**	**4+**
Year-class						
1978	307.8	150.5	62.5	30.9	4.8	2.1
1979	37.4	24.9	21.5	12.5	9.2	1.8
1980	114.4	69.7	43.2	14.8	4.7	1.5
1981	128.1	76.9	43.5	12.6	7.8	1.6
1982	147.8	86.7	48.8	19.0	5.6	0.3
1983	216.5	117.4	56.8	22.4	4.0	1.2
1984	169.7	97.1	37.1	19.7	3.7	0.3
1985	414.5	179.4/89.7	60.2	20.6	0.9	0.1
1986	177.0	100.4/50.2	47.1	15.5	3.2	0.1
1987	196.9	109.2/54.6	45.1	13.1	1.5	0.6
1988	422.8	181.3/90.7	67.4	13.6	2.3	0.0
1989	819.7	223.7/111.8	79.9	12.6	2.5	0.1
1990	275.7	139.8	60.8	20.7	1.8	0.0
1991	418.3	180.3	71.2	33.2	2.4	0.5
1992	292.6	145.5	76.5	30.2	3.9	0.2
1993	228.4	122.2	49.7	17.9	2.6	0.2
1994	124.4	74.9	34.7	14.1	3.3	0.0
1995	289.0	144.3	73.7	20.9	10.0	4.2
1996	352.0	163.6	74.8	25.5	6.7	0.3
1997	226.4	121.4	44.9	20.3	5.1	0.0
1998	211.8	115.5	44.7	20.8	0.0	0.0
1999	112.3	68.6	29.7	8.2	2.4	1.0
2000	60.6	39.3	14.6	12.4	1.4	0.0
2001	108.0	66.3	7.4	6.2	0.0	0.0
2002	58.4	37.9	7.5	9.5	0.2	0.0
2003	316.5	153.2	9.4	2.3	1.2	0.0
2004	155.8	90.6	23.3	9.1	2.5	0.0
2005	48.9	32.1	11.1	7.3	0.0	NA
2006	31.7	21.2	20.3	4.2	NA	NA
2007	106.8	65.7	9.5	NA	NA	NA
2008	119.6	72.4	NA	NA	NA	NA

Table 14.2 Tjaerbaeck. Number 100 m $^{-2}$ of recruits in April and of 0+, 1+, 2+, 3+ and 4+ in October/November the following years of the same year class. As electrofishing stopped in year 1996 some older age groups are NA.

	April	**October/ November**	**October/ November**	**October/ November**	**October/ November**	**October/ November**
	Recruit	**0+**	**1+**	**2+**	**3+**	**4+**
Year- Class						
1977						0.3
1978					3.1	0.6
1979				6.0	2.7	0.3
1980			15.8	7.4	2.1	0.3
1981	21.4	14.5	13.0	5.8	2.0	0.4
1982	34.4	23.0	22.6	7.9	2.5	0.8
1983	32.7	21.9	16.6	6.4	1.4	0.1
1984	44.1	29.1	20.4	7.5	2.6	0.3
1985	54.6	35.6	20.9	5.4	1.9	0.4
1986	57.3	37.2	21.0	4.3	3.0	0.1
1987	83.0	52.4	29.9	9.1	3.1	0.2
1988	26.9	18.1	15.2	5.7	2.6	0.1
1989	37.7	25.1	17.6	6.6	2.8	0.1
1990	19.1	13.0	9.8	8.3	2.6	0.3
1991	36.5	24.3	12.4	6.2	2.3	0.0
1992	10.7	7.3	6.0	3.1	1.9	0.3
1993	15.3	10.5	8.3	5.1	2.1	NA
1994	9.0	6.2	4.4	2.8	NA	NA
1995	36.7	24.4	16.2	NA	NA	NA
1996	32.0	21.4	NA	NA	NA	NA
Mean	34.5	22.8	14.7	5.4	1.9	0.2

Growth, Mortality and Production

Brown trout densities and mean length/mass were only established in spring and autumn in both baecks. Growth rate of salmonids is primarily dependent on fish size, temperature, amount of food and probably also fish densities, e.g. From & Rasmussen 1984; Rasmussen & From 1991; Lobon-Cervia 2005, and Elliott 2015. From the daily water temperatures, a growth model (Rasmussen 1986b; Elliott *et al.* 1995) was fitted to the observed successive mean wet weights (i.e. converted from length), starting from a size of 0.1581 gram (i.e. converted from a size of 2.5 cm for recruited fry in mid-April)

Table 14.3 Brandstrup Baeck. Observed total length cm and calculated wet weight g for five age classes 0+, 1+, 2+, 3+ & 4+ in November 1978 to 2008. The growth trajectory should be read as follows: Year class 1978 has a mean length as 0+ of 6.3 cm in November 1978, as 1+ in November 1979 of 11.8 cm, as 2+ the following November of 16.6 cm, as 3+ of 20.6 cm, as 4+ of 23.6 cm, and so on.

	Total length cm					**Total weight g**				
Year	**0+**	**1+**	**2+**	**3+**	**4+**	**0+**	**1+**	**2+**	**3+**	**4+**
1978	6.3					2.4				
1979	6.6	11.8	15.4	20.8	24.8	2.8	15.6	34.5	83.8	141.1
1980	6.5	12.1	16.6	20.5	23.9	2.7	16.9	43.2	80.5	126.4
1981	6.8	12.3	16.7	20.6	28.3	3.1	17.6	43.9	81.3	208.7
1982	6.0	11.4	14.7	18.5	23.6	2.1	14.0	29.7	59.5	122.0
1983	6.3	11.2	14.8	18.4	23.8	2.4	13.3	30.5	58.4	124.8
1984	6.3	11.0	14.9	18.6	24.0	2.4	12.7	30.9	59.6	127.5
1985	6.1	11.1	15.1	18.9	23.8	2.2	13.0	32.5	62.6	124.7
1986	6.1	11.1	14.7	19.4	26.6	2.2	13.1	30.0	68.2	172.7
1987	6.4	11.5	15.5	19.7	24.2	2.5	14.6	34.9	70.6	130.6
1988	6.0	11.7	16.5	18.9	29.2	2.1	15.1	42.1	63.3	228.2
1989	6.1	11.4	16.0	20.3	27.3	2.2	14.3	38.6	78.3	186.1
1990	6.2	10.8	15.7	21.0	28.0	2.3	12.1	36.1	86.3	200.8
1991	6.0	11.5	15.7	19.5	22.0	2.1	14.4	36.2	69.5	98.2
1992	5.9	10.6	13.9	19.9	NA	2.0	11.3	25.3	73.3	NA
1993	6.1	10.6	14.7	20.7	26.6	2.2	11.2	30.2	82.5	172.2
1994	6.1	10.4	13.9	20.1	NA	2.2	10.6	25.4	75.2	NA
1995	6.4	12.0	15.4	18.8	22.8	2.6	16.5	34.3	61.6	110.2
1996	5.8	11.5	15.8	20.1	25.5	1.9	14.4	37.2	76.0	152.8
1997	5.7	10.5	14.5	16.6	23.5	1.8	11.1	28.9	42.9	120.0
1998	5.9	10.7	14.3	17.3	21.4	2.0	11.6	27.6	48.7	91.0
1999	6.1	10.2	13.6	17.2	21.0	2.3	10.0	23.6	47.4	86.1
2000	6.8	9.6	13.0	17.6	20.5	3.1	8.6	20.7	50.9	80.1
2001	6.7	10.1	13.6	NA	NA	2.9	10.0	24.0	NA	NA
2002	7.4	11.5	14.3	19.3	NA	3.8	14.3	27.4	66.5	NA
2003	6.5	11.6	13.8	17.0	19.8	2.7	14.8	24.9	46.0	72.3
2004	6.8	11.1	14.1	0.0	NA	3.1	12.9	26.6	0.0	NA
2005	7.2	11.6	15.7	20.5	NA	3.6	14.9	36.3	80.1	NA
2006	7.7	10.1	15.1	19.7	NA	4.5	9.8	32.7	70.8	NA
2007	6.6	9.3	14.2	18.5	NA	2.8	7.7	27.3	59.1	NA
2008	7.3	NA	NA	NA	NA	3.7	NA	NA	NA	NA
Mean	6.4	10.7	14.4	17.3	17.0	2.6	12.5	30.5	60.1	95.9

Table 14.4 Tjaerbaeck. Observed total length cm and calculated wet weight g for five age classes 0+, 1+, 2+, 3+ & 4+ in October/November 1981 to 1996. The length trajectory should be read as follows: Year class 1981 has a mean length as 0+ of 6.9 cm, as 1+ of 12.7 cm, as 2+ of 17.1 cm, as 3+ of 21.4 cm and as 4+ of 23.2 cm, and so on.

	Total length cm					**Total weight g**				
Year	**0+**	**1+**	**2+**	**3+**	**4+**	**0+**	**1+**	**2+**	**3+**	**4+**
1981	6.9	12.4	17.4	21.5	27.2	3.4	20.1	56.3	107.4	220.1
1982	6.6	12.7	17.1	21.6	24.8	3.0	21.8	53.2	108.6	166.1
1983	6.6	12.0	17.1	21.4	23.7	3.0	18.2	53.2	105.4	144.1
1984	6.5	12.0	17.0	21.4	24.2	2.8	18.1	52.8	104.9	154.3
1985	6.7	12.2	16.8	20.8	23.2	3.1	19.0	50.6	96.4	135.0
1986	6.2	11.9	16.3	20.9	24.4	2.4	17.9	46.1	98.5	157.2
1987	6.4	12.1	16.7	20.8	26.1	2.7	18.6	49.6	97.0	192.3
1988	6.4	11.4	16.3	20.4	26.9	2.7	15.6	46.5	91.8	211.8
1989	7.5	11.7	16.1	20.6	27.6	4.3	17.0	44.8	94.5	228.1
1990	6.8	11.7	15.8	20.4	27.3	3.2	17.0	42.1	90.7	222.1
1991	7.1	11.8	16.3	20.9	28.8	3.7	17.4	46.3	98.3	259.9
1992	6.9	11.7	15.3	20.6	27.5	3.3	16.7	37.9	94.3	227.4
1993	7.4	12.5	16.4	20.6	26.3	4.1	20.4	47.4	94.5	197.0
1994	7.3	12.9	17.7	21.2	25.4	4.1	22.8	58.9	102.2	178.3
1995	8.0	13.9	18.9	24.5	NA	5.3	28.7	72.1	159.0	NA
1996	7.0	13.4	17.7	21.5	25.8	3.5	25.1	59.7	106.7	187.1
Mean	6.9	12.3	16.8	21.2	24.3	3.4	19.6	51.1	103.1	180.1

of the different year classes in spring and autumn until extinction of the year class. The observed growth rates of the different year classes were compared with Elliott *et al.* (1995), which gives the maximal growth rate for a single trout feeding optimally at the prevailing temperatures. By re-arranging the equations in Elliott *et al.* (1995), the proportion between observed growth and maximal growth (*sensu* Elliott *et al.* 1995) can be calculated by an iterative process.

From the number of recruits in mid-April and density in late-October/mid-November the mortality or loss rate was calculated for the different year classes or cohorts until extinction of each year class. Total mortality Z or 'loss rate' (*sensu* Elliott & Elliott 2006) consists of: (1) true natural mortality (death of fish because of starvation and predation) in the baecks; (2) smolt loss in spring from the baecks; and (3) out-migration loss from the baecks by parr, either during the smolt run period or at other times. The brown trout parr that left the baeck during the nine months (June to February) when the smolt trap was not functional, could not be accounted for. However, the emigration rate in this nine-month period can be calculated as the difference between the observed natural mortality and the expected true natural mortality deducted from the mean mass of each

Table 14.5 Numbers of smolt and parr caught in traps in Brandstrup Baeck and Tjaerbaeck. Results are given for year of trapping and year-classes. Yield % is calculated as the proportion of total catch of smolt and parr to number of recruits and 0+, respectively.

Trap Year	Smolt total 1+ to 4+	Parr total 1+ to 4+	Smolt + parr total 1+ to 4+	per 100 m^2	Year class	Smolt + parr total 1+ to 4+	Smolt + parr per 100 m^2	Yield% from recruits %	0+ %
Brandstrup Baeck									
1982	835	85	920	20.02	1978	717	15.61	5.07	10.38
1983	906	69	975	21.22	1979	206	4.47	11.96	17.98
1984	760	77	837	18.22	1980	791	17.21	15.05	24.70
1985	733	43	776	16.89	1981	1019	22.18	17.31	28.85
1986	559	29	588	12.81	1982	973	21.18	14.33	24.43
1987	349	15	364	7.93	1983	710	15.45	7.14	13.16
1988	89	7	96	2.09	1984	523	11.39	6.71	11.73
1989	893	76	969	21.10	1985	340	7.41		8.25
1990	1453	123	1576	34.31	1986	269	5.85		11.64
1991	1024	107	1131	24.62	1987	797	17.35		31.77
1992	505	35	540	11.75	1988	1585	34.51		38.06
1997	359	36	395	8.60	1989	1218	26.50		23.70
1998	911	36	947	20.62	1995	663	14.43	4.99	10.00
1999	859	103	962	20.94	1996	1042	22.68	6.44	13.86
2000	717	70	787	17.13	1997	870	18.94	8.37	15.60
2001	595	27	622	13.53					
Mean	**200.5**	**16.3**	**217**	**16.99**		**217.1**	**17.01**	**9.74**	**18.94**
Largest/smallest			10.1			7.7		3.5	4.6
CV%				44.7			47.0	46.5	48.0

Tjaerbaeck									
1982	259	23	282	3.55	1981	270	3.40	15.84	23.39
1983	288	38	326	4.10	1982	664	8.35	24.63	36.89
1984	521	44	565	7.11	1983	402	5.06	15.99	23.87
1985	396	35	431	5.42	1984	674	8.48	19.67	29.75
1986	641	71	712	8.96	1985	629	7.91	13.76	21.16
1987	583	24	607	7.63	1986	729	9.17	16.02	24.63
1988	686	33	719	9.04	1987	1044	13.13	15.83	25.06
1989	910	89	999	12.57	1988	320	4.03	14.98	22.25
1990	320	68	388	4.88	1989	363	4.57	12.11	18.21
1991	289	60	349	4.39					
1992	139	27	166	2.09					
Mean	**457.5**	**46.5**	**504**	**6.34**		**566.1**	**7.1**	**16.54**	**25.02**
Largest/smallest			6.0			3.9		2.0	2.0
CV%				48.1			44.0	22.1	21.7

	Distribution% of smolt and parr age classes, and mean smolt MSA and mean parr MPA ages									
	1+		**2+**		**3+**		**4+**			
	smolt	**parr**	**smolt**	**parr**	**smolt**	**parr**	**smolt**	**parr**	**MSA**	**MPA**
Brandstrup Baeck	2.8	11.6	74.5	69.5	21.9	17.8	0.8	1.1	2.21	2.08
Tjaerbaeck	2.6	9.1	83.6	65.7	13.8	25.0	0.0	0.2	2.11	2.16

different age group. True natural mortality of fish species is a function of individual body mass (Ursin 1967, Lorenzen 1996), which means that true natural mortality is decreasing with increasing mass. Observed natural loss (i.e. true natural mortality plus out-migration loss of brown trout parr) is calculated from the (November) density of the smolt producing year class the year before the smolt run and the density of the same year class after the smolt run in the following November. This assumes that the smolt run takes place in the months March to May. Knowing from the smolt trap the number of the different year classes of parr and smolt in a single smolt run year, the observed natural loss can be calculated by an iterative process (Rasmussen 1986b). An empirical 'rule-of thumb' from many electrofishing surveys states that a trout of length X in general requires 2 • X depth of the baeck. Because both baecks are rather shallow it is anticipated that larger trout gradually move away from the baeck to the main course of river Gudenaa. This could take place during the smolt run as parr caught in the trap (these fish are accounted for as explained above), but also at other times (i.e. from June to February) when the traps were not in use. It is not known if these migrating parr (during and outside the smolt run) become residents in river Gudenaa or if they contribute, the same year or a later year, to the smolt production, possibly a combination. Only a full-time running trap, where the brown trout are tagged and recaptured, can solve this and it is highly needed in population dynamic studies, including smolt production and fishery yields of migrating brown trout.

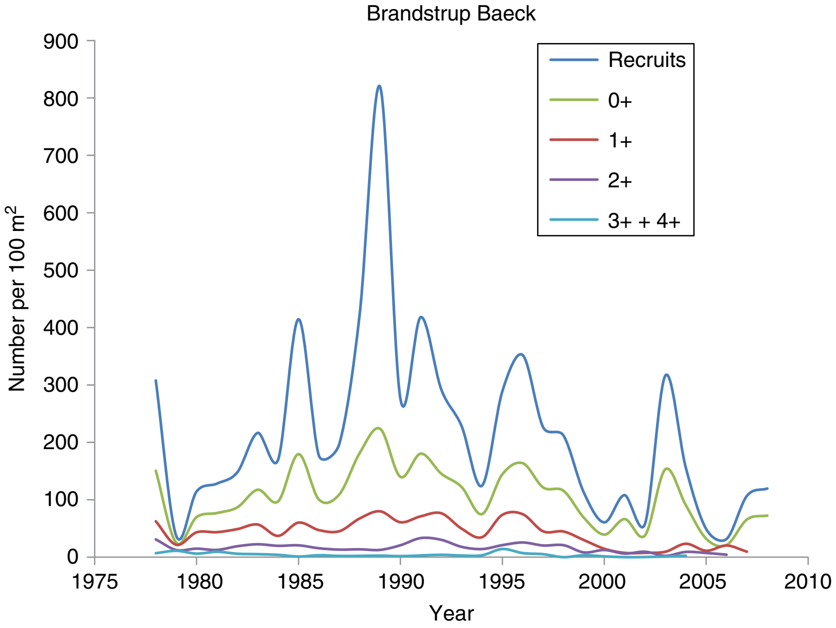
Biological production rates integrate the number of trout from recruitment, growth and mortality data (Hayes *et al.* 2007). Production rate is calculated on a daily basis for each year-class starting with: (1) the number of recruits at mid-April; (2) the daily growth rate $\Delta w/\Delta t$, calculated from the growth model; and (3) the calculated daily number (density) of the same year class using the estimated natural loss (true natural mortality + the estimated migration loss of parr outside the smolt period) until extinction of the year class. The numbers of parr and smolts from the traps are not included in the production and are therefore subtracted from the calculations during the smolt run period. Year class production rate and P/B rates of the age classes (i.e. recruits to 0+, 0+ to 1+ until extinction as 4+) and total production of a year class are calculated from these daily calculations. Because many year classes contribute to the calculations, it is expected that the total production rates of each year class from recruits to extinction represent more or less the annual production rates (i.e. contributions from five year classes in a single year). Food consumption Kcal can easily be calculated (Rasmussen 1986b) but is not presented here.

Results and Discussion

Numbers and Density

Brandstrup Baeck

Table 14.1 and Figure 14.4 show the number of recruits in mid-April and the size of age classes 0+, 1+, 2+, 3+ and 4+ in November for the year classes 1978 to 2008. The possible decrease in recruitment after year 2000 is mostly because of a sediment load that covers the spawning redds. A total of five age classes can be found each year in the baeck, but fish of age classes 3+ and 4+ are relatively rare. This, in combination with



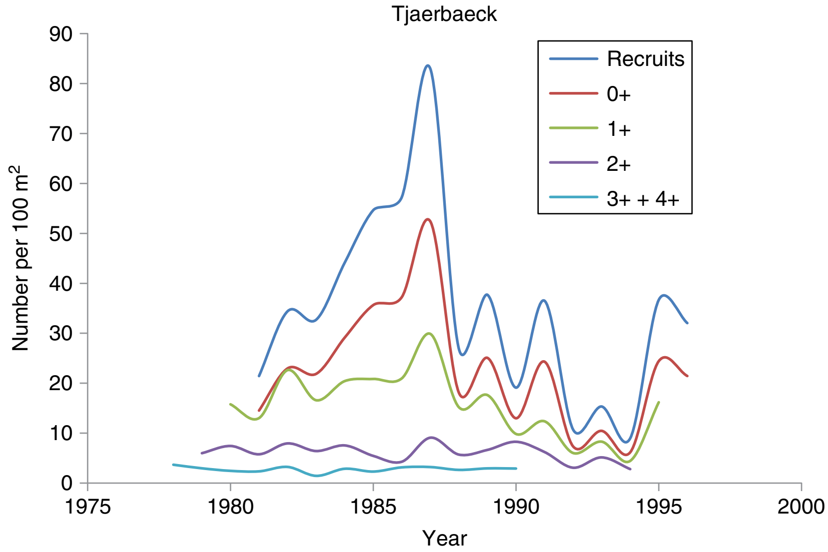


Figure 14.4 Number of recruits, 0+, 1+, 2+ and 3+/4+ per 100 m^2 in 1978–2008 (Brandstrup Baeck) and 1979–1996 (Tjaerbaeck).

the smolt loss (Table 14.5) and emigration mortality outside the smolt run period (see Table 14.8) supports the assumption that the baeck is too shallow for bigger brown trout, and that these migrate out to the river Gudenaa; mostly outside the smolt run period. Numbers of recruits in the period 1978–2008 vary from 0.32 (year 1979) to 8.2 (year 1989) with a mean of 2.16 per m^2. In the period 1978 to 1999 the density of recruits was 0.37 to 8.2 with a mean of 2.58 per m^2. The minimum number of recruits in the period 1978 to 1999 and 0+ was in 1979, most probably because of a very heavy discharge following sudden snow melt in the beginning of March. Sand from surrounding fields more or less covered the whole baeck.

Tjaerbaeck

Table 14.2 and Figure 14.4 show the number of recruits in April and the size of age classes 0+, 1+, 2+, 3+ and 4+ in October/November in the years 1981 to 1996. Numbers of recruits vary from 0.11 to 0.83 with a mean of 0.34 per m^2. The lowest recruitment was in 1994 and the highest in 1987. Mean density of recruits in Tjaerbaeck was only 13.2% of that in Brandstrup Baeck.

Comparing the Two Baecks

Basically, the number of recruits depends on the number of sea trout spawners. This number is not known except for a single year 1984 in Brandstrup Baeck (Rasmussen 2016). The sea trout fishery during the main research period in river Gudenaa and Randers Fjord is more or less the same. So, the most plausible explanation of the high variation in number of recruits is probably a combination of varying smolt production (as a consequence of this a varying number of spawning sea trout) and environmental factors. Of these the most important is probably varying water flow during the period when the numbers of recruits are established. This is documented for brown trout by (Lobón-Cerviá & Rincón 2004 in Northern Spain, Daufresne *et al.* 2005, Daufresne & Renault 2006, Lobon-Cervia & Mortensen 2005 and Lobón-Cerviá *et al.* 2016). Lobón-Cerviá *et al.* 2016 compared recruitment versus discharge in several streams in Spain, UK and Denmark. The smolt production in Brandstrup Baeck and Tjaerbaeck vary less than the recruitment. This supports the idea that environmental factors such as discharge in spring are key factors. So, given a certain (sufficient) number of spawners, discharge in spring during the recruitment period regulates the number of recruits and therefore subsequently the number of smolt and sea trout and vice versa. Daufresne & Renault (2006) propose that density-dependent and density-independent processes act in combination on population density at equilibrium (limitation process).

For the same years 1981 to 1996 there are coinciding estimates of recruits from both baecks. The mean density of recruits in Tjaerbaeck is about 12% of the mean density of recruits in Brandstrup Baeck. When we compare the density of 0+ in the two baecks for these coinciding years we have about 17%. If we compare the proportion of the largest to smallest number of recruits and 0+, respectively, in Tjaerbaeck we have 9.3 and 8.5, respectively. For Brandstrup Baeck for the same period we have for recruits and 0+ values of 6.6 and 3, respectively.

The results indicate that because of the relative low recruitment in Tjaerbaeck the total mortality from recruits to 0+ is lower in Tjaerbaeck compared to Brandstrup Baeck. Whereas in Brandstrup Baeck with a much higher relative recruitment, the number of 0+ is probably regulated by higher density dependent mortality in the period after recruits to 0+. This is further discussed below.

The two baecks are more or less similar in regards spawning and rearing habitats. Water temperature and discharge variation are also quite similar in the two baecks. One explanation for the difference in recruitment between the two baecks and the substantial lower recruitment in Tjaerbaeck is most probably the problem for sea trout passing the weir and maybe natural obstacles like fallen trees in Tjaerbaeck. Which factor is most important remains to be identified.

Length and Weight

Tables 14.3 and 14.4 show the observed mean length and calculated mean wet weight of age classes 0+, 1+, 2+, 3+ and 4+ in the two baecks in October/November (Tjaerbaeck) and November (Brandstrup Baeck) from 1978 to 2008. The water temperatures in the two baecks are quite similar. But the growth rate in Tjaerbaeck is higher compared to Brandstrup Baeck. Comparing the mean weight ratio of Tjaerbaeck to Brandstrup Baeck we get the following: 0+ = 1.4, 1+ = 1.6, 2+ = 1.6 and 3+ = 1.6. The differences are most probably a consequence of recruitment differences, density dependent growth and different mortalities. This is further discussed below.

Density, Body Size and Variation

It is documented that density of salmonids regulates the growth rate and size of young of the year, but published results are divergent. Growth of salmonid fishes is highly plastic and is affected by both density-dependent (e.g. Jenkins *et al.* 1999; Grant & Imre 2005; Lobón-Cerviá 2007; Vøllestad & Olsen 2002; Vøllestad & Olsen 2008; Kaspersson & Höjesjö 2009; Kaspersson *et al.* 2012; Bærum *et al.* 2013; Richard *et al.* 2015) and density-independent factors of e.g. water temperature (Rasmussen 1986a + b). The general prediction for density dependent effects is that growth should be depressed at high densities due to decreased food availability as resources are depleted (Sinclair 1989). Therefore, the observed growth-density relationship is consistent with exploitation composition (Imre *et al.* 2010). But Ward *et al.* 2007 suggested that competition (agonistic behaviour) for space could also be a potential mechanism for the observed growth–density relationship. Furthermore, the effect of density on growth is expected to follow a negative power curve with per capita foraging decreasing as 1/N (N = number of competitors, i.e. here N in the two baecks is other brown trout (e.g. Grant & Imre 2005; Lobon-Cervia 2007)). Detecting density effects on growth in relatively dense natural populations can be difficult, e.g. Elliott 1985 & 1988 & 2015. Density effects appear to be very important for early stages (Lorenzen & Enberg 2002), but are also observed at later life stages (Bohlin *et al.* 2002). The effect of density on growth could also depend on other variables such as food quality and possible habitat and environmental constraints (e.g. refuge availability and temperature).

The results (i.e. all fishing sites pooled (Tables 14.1 and 14.2)) from Brandstrup Baeck and Tjaerbaeck are here given as examples of density growth (i.e. size of 0+ as a proxy for growth rate) in relation to density of age groups in the baecks. Analyzing and comparing the relationships between the lengths of 0+, 1+, 2+ and 3+ vs. density of the same age groups showed no significance ($P > 0.25$) for age groups 1+, 2+ and 3+ (this contrasts with Bohlin *et al.* 2002), whereas the relation for 0+ was highly significant ($P < 0.0001$). Figure 14.5 shows the relationship between the lengths of 0+ vs. density of age group 0+ ($P < 0.0001$), vs. density of age group 1+ ($P < 0.0001$), vs. density of 2+ ($P = 0.0006$), vs. 3+ ($P = 0.042$) and vs. density of 4+ ($P = 0.4$). This means that densities of all year classes (except of 4+ probably because they are so few in number) influence the length of 0 + .

Figure 14.6 shows the significant relationships between length of 0+ and total density of Σ (0+ … 4+) per 100 m^2 for Brandstrup Baeck ($P < 0.0001$) and Tjaerbaeck

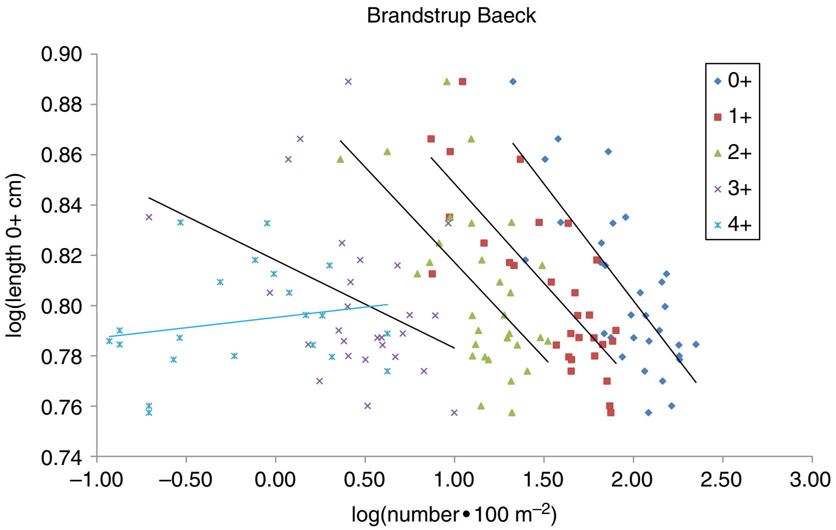


Figure 14.5 Log (length 0+ cm) vs. log (density) of 0+, 1+, 2+, 3+ & 4+, respectively per 100 m^2 in Brandstrup Baeck.

($P < 0.0001$). Figure 14.7 shows an example the same relationships for the eight fishing sites vs. density Σ (0+ … 4+) per 100 m^2 in Brandstrup Baeck. Sites BRB02-03, BRB10-11, BRB16-17, BRB24-25, BRB34-35 are not significantly different ($P >> 0.05$) compared to each other, whereas at the three upper most sites the lengths of 0+ are significantly higher ($P < 0.001$) for a given density of Σ (0+ … 4+). Why this is the case is not clear, but probably has to do with the quality (probably habitat) of these stretches as growth-up areas in contrast to the other stretches. Nevertheless, the result shows that even in a short baeck like Brandstrup Baeck with more or less the same water temperature, sections differ in quality as growth-up areas.

The relatively few publications showing log length vs. log density (see references above) always show the relationship as one straight line as here in Figures 14.5 and 14.7. A further analysis requires a very high number of data. Extrapolating for example the regression in Figure 14.6 to a total density of Σ (0+ … 4+) close to zero in Brandstrup Baeck gives a mean length of about 11.2 cm (13.4 g wet weight). This could be interpreted as a theoretical mean maximum length of 0+ in the autumn, when growth stops below water temperature of 3–4 °C (Elliott *et al.* 1995), and with an extreme low density of brown trout. Figure 14.8 shows all the mean lengths in autumn of 0+ vs. density of Σ (0+ … 4+) per 100 m^2 for all fishing sites during the research years in the two baecks. Visual inspection of the observations (Brandstrup baeck) indicates three regression lines. Split line regression (Perry 1982) to the data shows a mean 0+ length of 7.9 cm (4.8 g wet weight) from close to zero density and up to a total density of 29.8 brown trout per 100 m^2. From here and up to 134.1 brown trout per 100 m^2 the mean length of 0+ decreases from 7.9 cm down to a length of 6.1 cm (2.2 g wet weight) and from here at increasing density the mean length is constant 6.1 cm. As far as is known this (i.e. two thresholds of mean length vs. density) has not been presented before in the literature. An explanation of the results could be,

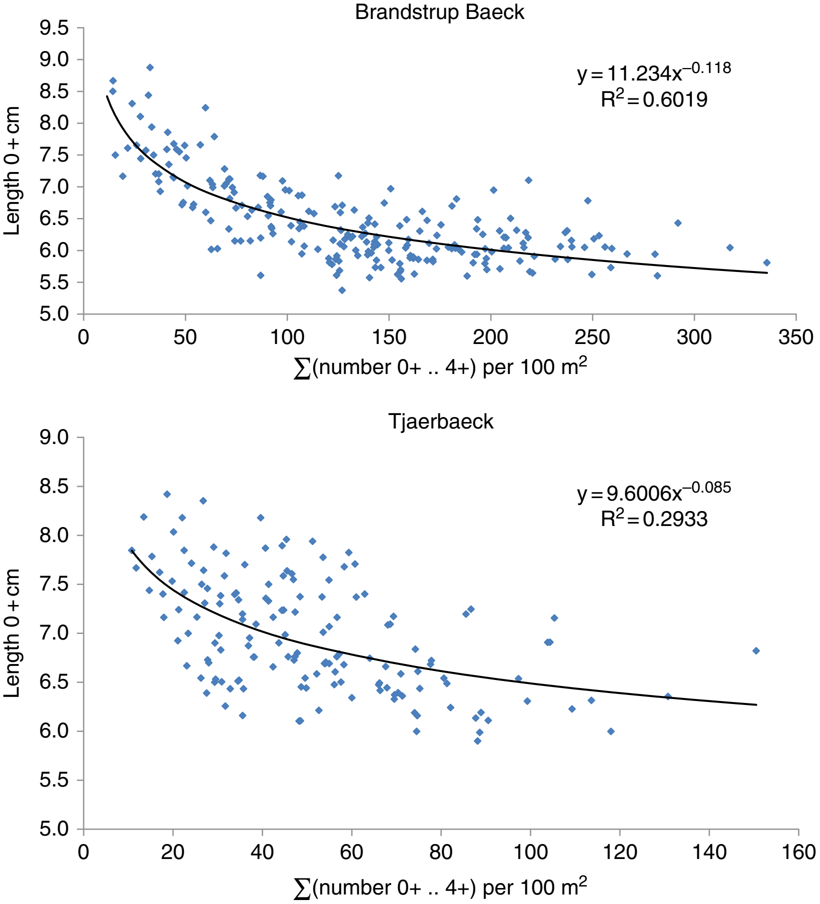


Figure 14.6 Relationship between length 0+ cm and total number of 0+, 1+, 2+, 3+ & 4+ per 100 m^2 in Brandstrup Baeck and Tjaerbaeck for all fishing sites.

that at densities up to the first threshold (density of 29.8 brown trout per 100 m^2) the number of habitats in the baeck probably ensures maximal growth at the prevailing water temperatures from recruits to 0+ (observed growth calculated to 89% of maximal growth *sensu* Elliott *et al.* 1995). At the length trajectory from first threshold down to the second threshold (density of 134.1 brown trout per 100 m^2) the habitats are increasingly filled with competing brown trout. The mean length is decreasing down to the second threshold where the 0+ grow only 60% of maximal growth. That is a decrease in growth from 89% to 60% of maximal growth *sensu* Elliott *et al.* 1995. From the second threshold no further decrease in growth rate is observed, but the observations of mean lengths of 0+ are extremely varied and probably represent differences in the qualities of the different fishing sites (Figure 14.7). The highest observed mean length of 0+ in the whole data set from all years and fishing sites was 8.9 cm at a density of 3.1 trout (i.e. Σ (0+ … 4+) per 100 m^2), and these 0+ grew at the maximum growth rate (i.e. 100% *sensu* Elliott *et al.* 1995) from recruits to 0+. At this low density the fish probably do not interact at all and can be compared to Elliott's

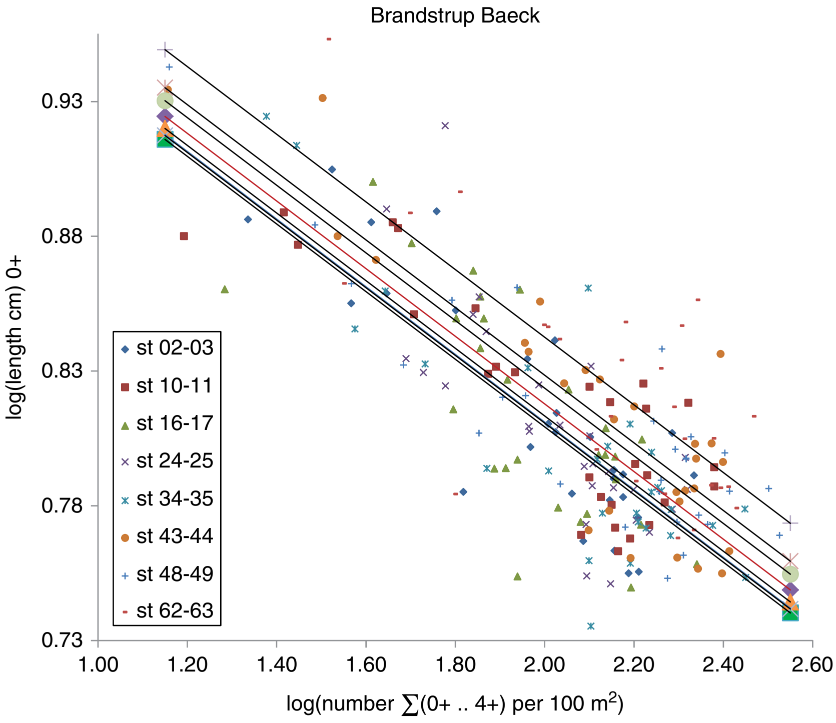


Figure 14.7 Log (length 0+ cm) vs. log density ∑ (0+, 1+, 2+, 3+ and 4+) per 100 m^2 for the eight fishing sites in Brandstrup Baeck.

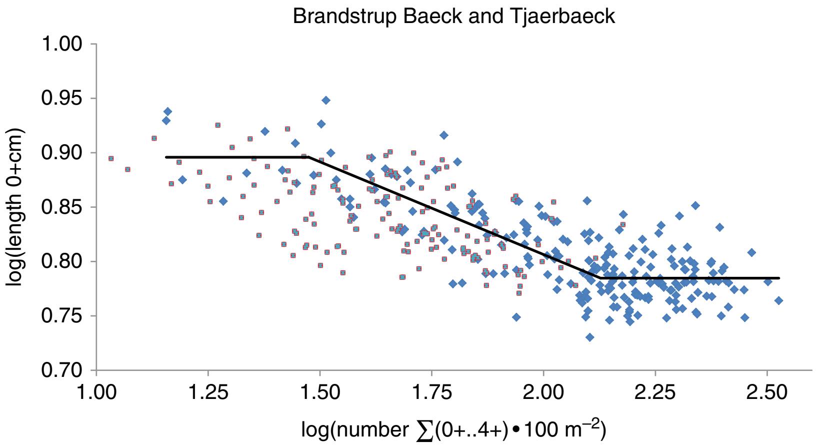


Figure 14.8 Log (Length 0+ cm) vs. log density ∑ (0+, 1+, 2+, 3+ and 4+) per 100 m^2 for all fishing sites. Brandstrup Baeck (diamond) and Tjaerbaeck (square). The regression lines are shown for Brandstrup Baeck; observations from Tjaerbaeck.

single fish eating studies; see next fourth paragraph. It should be noted that split line regression and two fixed thresholds is only an approximation to growth changes vs. density, and in the wild there is probably a gradual decrease in length around the thresholds at increasing parr densities.

The coefficient of variation (CV%) is a measure of the individual variation in trout and used to demonstrate density dependent growth (e.g. Elliott 1994 & 2015, Jenkins *et al.* 1999, Lobón-Cerviá 2010, Richard *et al.* 2015).

Figure 14.9 shows the CV% vs. length of 0+ and density of Σ (0+ … 4+) respectively in the two baecks. An increase in length of 0+ means a decrease in CV%. Thus, a decrease

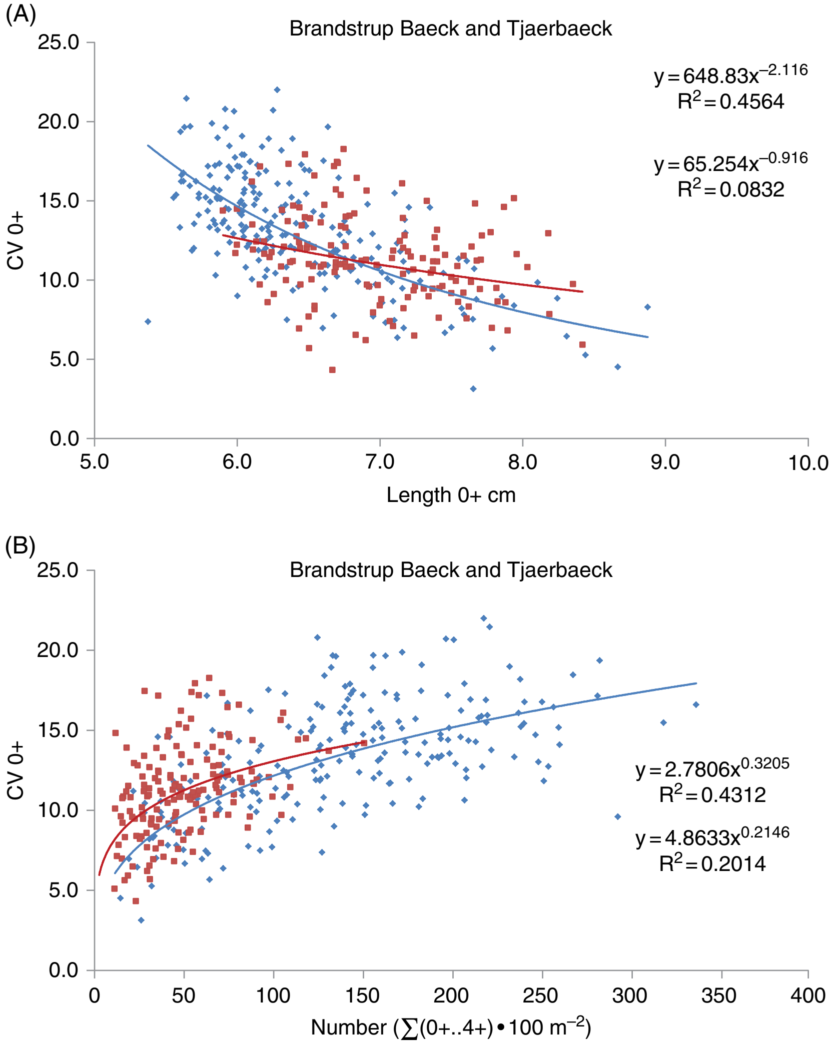


Figure 14.9 CV% vs. length 0+ cm and density (Σ(0 + ..4+) per 100 m^2 in Brandstrup Baeck and Tjaerbaeck. (A) Brandstrup Baeck (diamond) and Tjaerbaeck (square). (B) Brandstrup Baeck (diamond) and Tjaerbaeck (square).

in interaction between the parr and at the same time an increase in food availability, whereas the opposite takes place when mean length of 0+ decreases. The same processes take place when the density of Σ (0+ … 4+) increases: the food availability decreases and increased food competition between 0+ parr and older parr results in an increase of CV% (Figure 14.9). The results are in accordance and confirm with the cited references above.

Elliott (1985, 1988) suggests that mean size or mean growth rates in Black Browse Beck, Lake District, England were not density dependent at any stage in the life-cycle, but when later re-analyzing the same data set Elliott (2015) concluded, that growth in terms of mean length was density independent. In contrast individual variation in trout growth was density dependent, this being highest at low density and lowest at high density of trout.

Applications of Elliott's bioenergetics growth model for brown trout in streams have been discussed by, for example, Edwards *et al.* 1979, Jensen 1990, Jensen *et al.* 2000, Lobón-Cerviá & Rincón 1998, and Elliott 2009. The general impression is that wild brown trout grow less (from about 60% up to about 90% of maximal growth *sensu* Elliott *et al.* 1995). Only in rather cold streams (annual mean water temperatures below 5.1 °C) are there higher observed growths than calculated using the growth model. This could be a genetic adaption to cold water (Jensen *et al.* 2000). The results (i.e. lower growth rate than maximum) in Brandstrup Baeck and Tjaerbaeck are in accordance with the cited reference, but the primary reason for lower growth rate than expected at the prevailing temperatures is basically that the growth rate of wild brown trout is density dependent. Density is not mentioned explicitly in the cited references as the most possible reason when Elliott's bioenergetics growth model was evaluated. Elliott (1975) estimated the parameters in the growth model with single hatchery brown trout food intake, but growth rate of salmonids is higher for single fish vs. several fish interacting (From & Rasmussen 1984; Rasmussen & From 1991). Therefore, when using single-fish growth model in streams it is necessary to include density of brown trout when comparing observed vs. calculated growth rate. Only at very low density of brown trout in streams the growth rate is similar to Elliott's single fish brown trout model.

Smolt Production

The initiation and timing of smolt migration and related physiological changes is under the influence of environmental cues, as increased photoperiod (Hoar 1988), water temperature (McCormick *et al.* 2002; Sykes and Shrimpton 2010) and water flow, often in combination with temperature increases (Bohlin *et al.* 1993; Hvidsten *et al.* 1995; Hembre *et al.* 2001 and Aldven *et al.* 2015). The initiation and cessation of the actual smolt migration have been shown to occur earlier at a faster temperature increases. But rather than a specific temperature threshold, the initiation and cessation of migration appears to be controlled by a certain number of degree-days°C, the experienced cumulative temperature over time (Zydlewski *et al.* 2005; Sykes *et al.* 2009; Sykes & Shrimpton 2010). Boel (2012) showed for brown trout in a small Danish baeck, that the onset of the main migration (evaluated from at least 10% of total smolt number) as a function of day of the year varied from year to year. Whereas presented as a function of degree-days about 500 degree-days°C seemed to initiate the main migration. Availability of food during autumn before smoltification probably also affect the onset of smoltification in juvenile brown trout (Näslund *et al.* 2015).

Table 14.5 shows the annual smolt and parr production in the traps in Brandstrup Baeck and Tjaerbaeck. The migrating parr (no apparent silvering *sensu* Johnston & Eales 1967) represents less than 10% of the total catches. In both baecks two and three years old smolt dominate the run and the MSA (mean smolt age) is 2.21 and 2.11 respectively. The parr are of the same age more or less. Hourly control of the trap on several days from 8th April to 23th April 1986 showed (the full results not presented here) that the smolt run in this period was mostly nocturnal.

Brandstrup Baeck

The mean annual smolt production (Table 14.5) in Brandstrup Baeck is about 17 smolts per 100 m^2 and varies from about 2.1 to 34.3 per 100 m^2 with a factor (i.e. largest/smallest) of about 16. The highest trap catch year was in 1990 (dominated by the 1988 year-class). The next highest trap catch was in year 1991 (dominated by the 1989 year-class) and the third highest trap catch was in year 1989 (dominated by the 1987 year-class). But as seen in Table 14.5 the preceding year classes of 0+ were rather small because of the 50% reduction of 0+ in years 1985–1989. Therefore, the survival of the remaining parr was simply higher and thus also the number of smolt migrating was higher. So, these combinations are responsible for the high observed smolt run in 1989, 1990 and 1991. This corroborate the claim that it is important to have knowledge of densities of either recruits and/or number of 0+ over several years and corresponding density dependent mortalities to predict smolt production from number of recruits or 0+ parr. The percentage contributions of 0+ to smolt of year classes were also high for the mentioned year classes and document the high survival of 0+ until smolting the following years. The mean percentage number of smolt yield from recruits and 0+ are 11% and 19% (median = 15.6%), respectively, and vary with a factor (i.e. largest/smallest) of about 4 and 5, respectively.

Figure 14.10 shows examples of length distributions of smolt (excluding the parr) divided on age classes. The mean length of age classes varies from year to year, probably because of varying recruitment, effects of density both within and between year classes and minor varying water temperature.

In general, the older (three and four years) smolts start migration a little earlier than the younger age classes (Rasmussen 1986b). One question could be: within an age class do the larger smolts start migration earlier than the smaller one? The mean length in March, April and May of two year-old smolts in 1990 were tested, but there was no statistical difference ($P = 0.25$). In the same way three year-old smolts in 1999 showed no differences ($P = 0.42$). The mean water temperature from March and onward is above the lower limit 3.6 °C for growth (Elliott *et al.* 1995). Dead smolt in the trap were visually examined for food items that showed, that the fish were feeding on invertebrates (results not shown here). So, there is likely temperature dependent growth in the smolt run period. A possible conclusion is therefore, that the bigger trout within an age class start migrating earlier than the smaller one, so that the mean length in the trap of the same age class during the smolt run does not change. Whether this result is coupled to the physiological status of the fish is not known, but probably.

Figure 14.11 shows examples of catches of smolt (excluding the parr), water temperature and discharge during the smolt run in Brandstrup Baeck. The smolt run in 1987 is very different from all the other years (1990 and 1998 in the figure), where the smolt run starts in the end of February with a few smolt (mostly three years old)

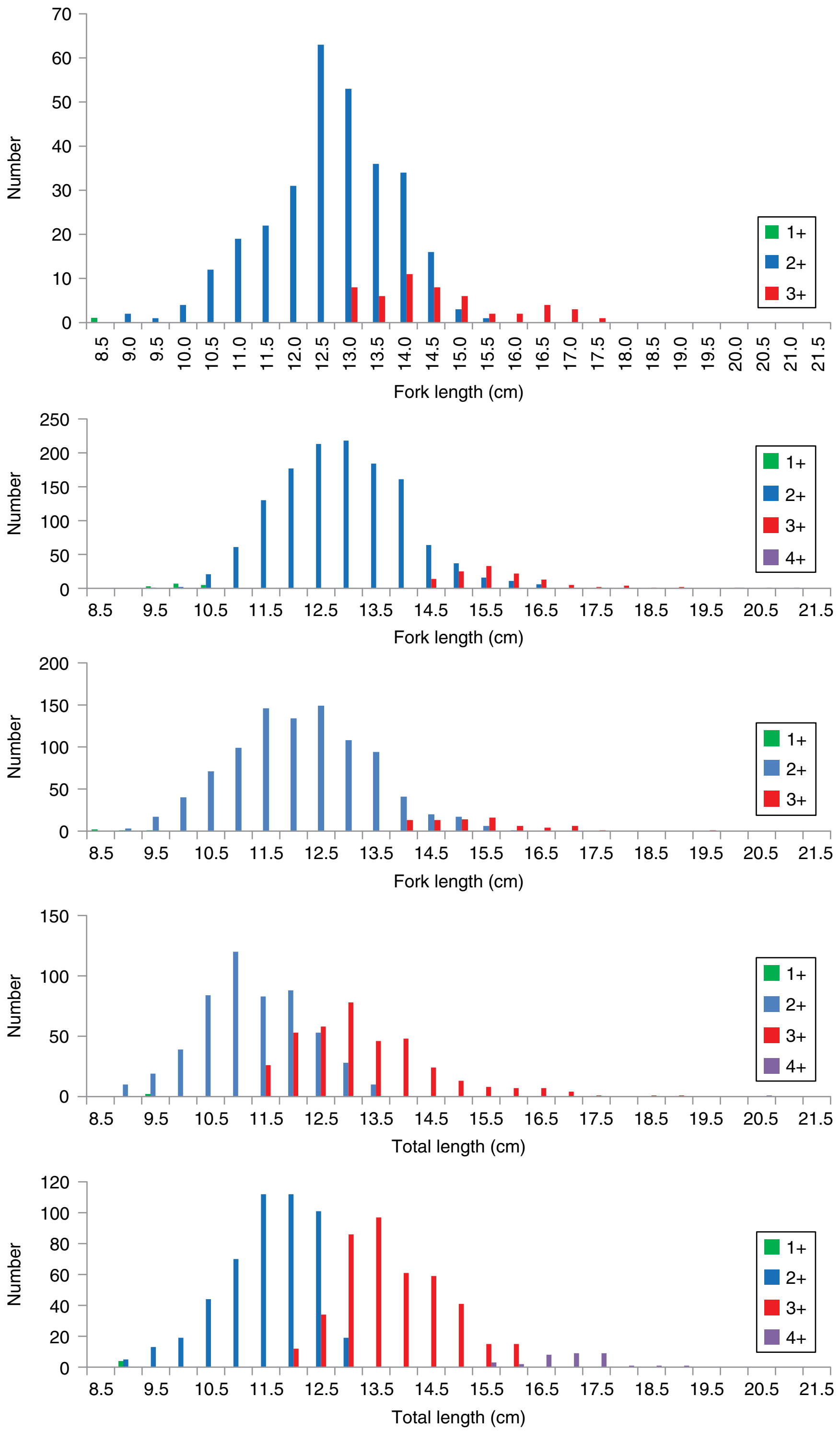


Figure 14.10 Brandstrup Baeck. Length distribution of smolt; years: 1987, 1990, 1991, 1998 and 1999.

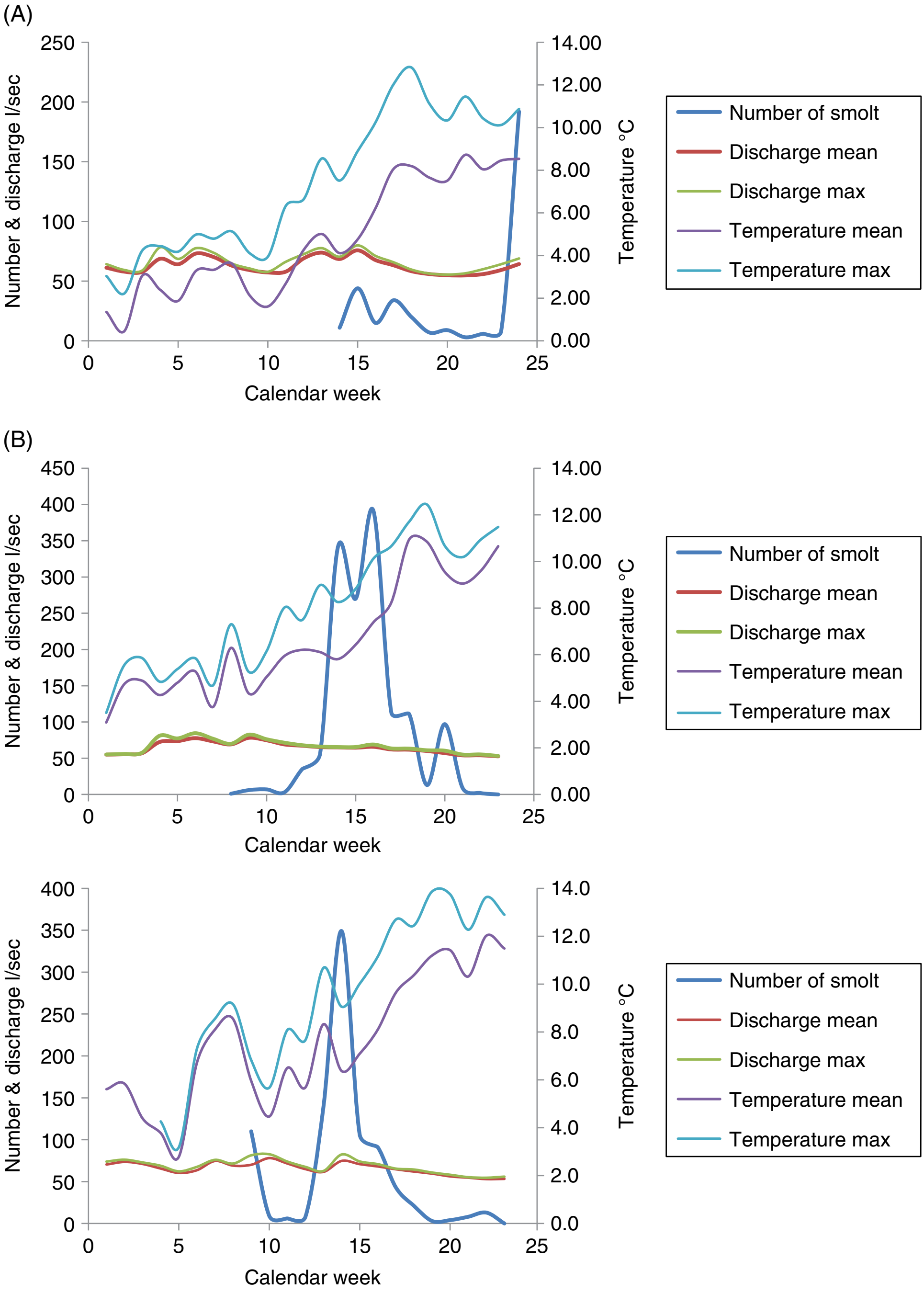


Figure 14.11 Brandstrup Baeck. Number of smolt per week, discharge L/sec and temperatures°C. A: 1987; B: 1990 and C: 1998.

(Rasmussen 1986b), have its maximum in mid-April (weeks 14–16) and ends in May. Year 1987 was a cold spring and the max water temperature below 8 °C until week 13. Two weeks later the smolt run started, maybe in combination with an increase in water discharge. The max water temperature increased up to about 12.8 °C in week 18, but in the same period the water discharge decreased to a very low level for the whole spring period. The smolt run more or less stopped until week 24 (mid-June), when most (60% of the total smolt run) of the smolt migrated.

Figure 14.12 shows as examples the cumulated smolt (excluding the parr) run for five years in Brandstrup Baeck as a function of degree-days°C and day of year. Smolt run in years 1990, 1991, 1998 and 1999 behave more or less as expected and about 50% have migrated when degree-days is about 500 °C, and all smolts have migrated when degree-days is about 800 °C in accordance with the literature. The year 1987 is very different; here most smolts suddenly migrate within a very short period when degree-days are about 800 °C. The conclusion from these examples is that photoperiod in combination with degree-days (which cumulates water temperature) is the dominating factor and that water discharge can have a regulating influence on the smolt run (Aldvén *et al.* 2015). But probably more has to be done on this topic.

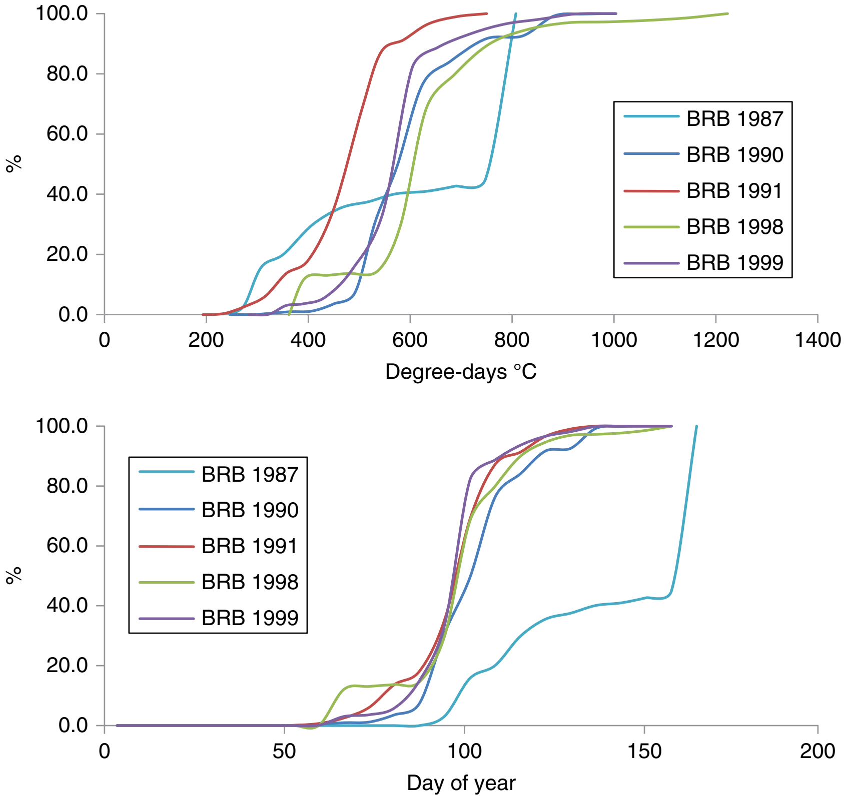


Figure 14.12 Brandstrup Baeck. Percentage accumulated number of smolt per week vs. degree-days °C and day for years: 1987, 1990, 1991, 1998 and 1999; in each year catches of one to four year old smolt and observed and calculated smolt production.

Figure 14.13A shows the number of smolt in Brandstrup Baeck vs. number of recruits from 15 year classes (i.e. 1+, 2+ and 3+ excluding the very few 4+ smolt) and the calculated number of the same age groups of smolt vs. number of recruits. This calculation can be made based on the estimated mortalities of total mortality Z and natural mortality M, and from these the calculated smolt loss. The observations of 1+, 2+ and 3+ smolt catches are

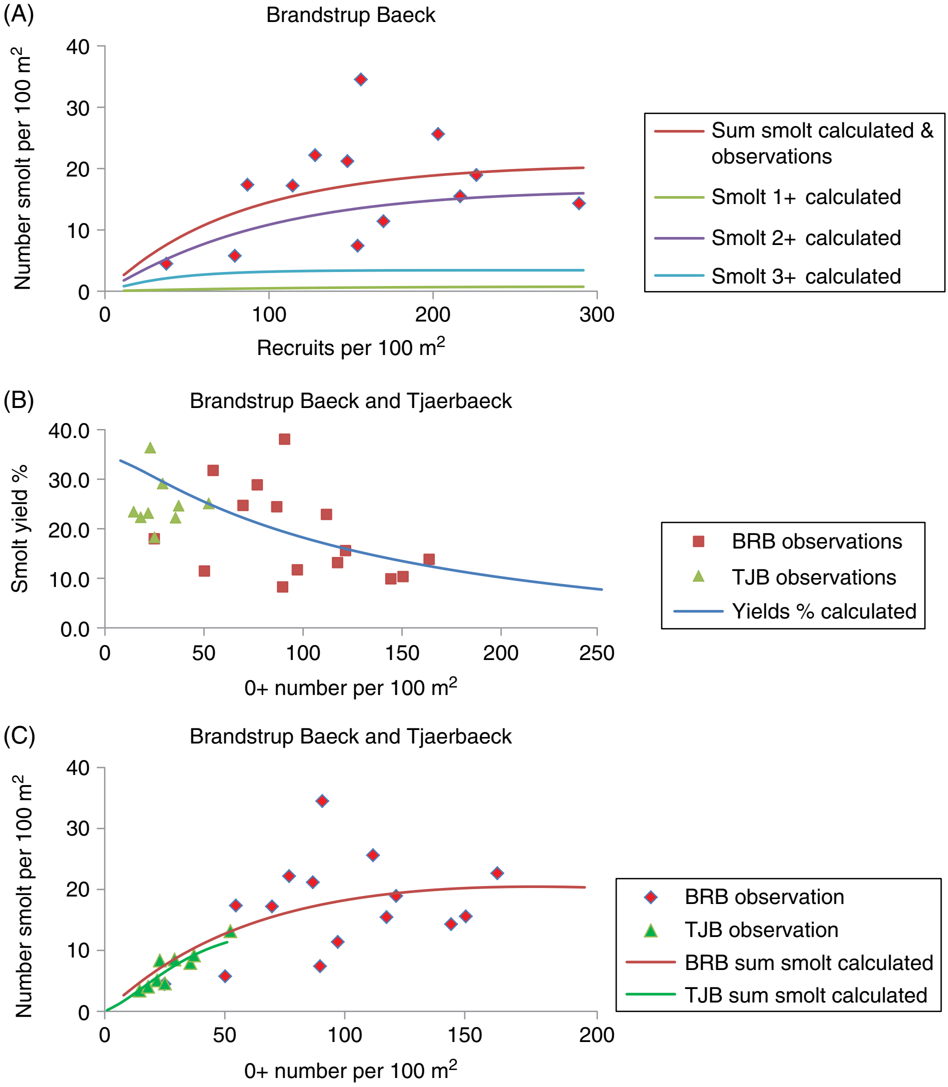


Figure 14.13 A: Observed number of year classes caught in traps (smolt + parr; Table 14.5) and calculated number of year classes (smolt + parr; 1+, 2+ and 3+ fish) vs. number of recruits. The density dependent mortality of the very few 4+ smolt and parr could not be calculated vs. number of 3+ parr for the separate year classes; 4+ fish in BRB was about 1% and in TJB close to zero% (Table 14.5). B: Smolt (smolt + parr; Table 14.5) yield% vs. number of recruits. C: Total observed number of year classes caught in traps (smolt + parr; Table 14.5) and calculated total number of year classes (smolt + parr; 1+, 2+ and 3+ fish) vs. number of 0+ per 100 m^2.

not shown on the figure. There is good agreement between observation and calculated values of total number of smolt. The highest observation is the 1988 year-class, and the most possible explanation is that the proceeding number of 0+ of year classes 1985, 1986 and 1987 was reduced by 50% (see above and Table 14.1). Therefore, the survival of year class 1988 was relatively higher than all other year classes and the smolt production of the year class sizable higher than the other year classes. This shows the importance of density of brown trout parr and the interaction between age classes on mortality rates and from these population regulations. The observations and calculations from mortality shown in Figure 14.13C suggest a maximum smolt production in Brandstrup Baeck of about 20.4 smolts per 100 m^2 at a density of about 180 0+ per 100 m^2. Using the mortalities to calculate smolt production there is a decrease in smolt production at densities above 180 0+ per 100 m^2. This is only a theoretical consequence of using the mortality figures, because we don't have higher observations of 0+ densities. The highest 1989 year-class might have answered this question, but unfortunately the number was reduced by 50% during electrofishing in autumn 1989; see Table 14.1. The most probable answer is that the maximum smolt production is controlled by the number of recruits, density dependent mortality and the carrying capacity of habitat. So, a theoretical decrease in smolt production at increasing densities of 0+ is not possible. This indicates that spawning activity (number of eggs deposited) is not the regulating factor.

Tjaerbaeck

The mean annual smolt production in Tjaerbaeck is 6.3 per 100 m^2, but varied from 2.1 to 12.6 with a factor between highest and smallest of 6 (Table 14.5). The proportion of smolts from recruits and 0+ are 16.5% and 25.0%, respectively, and varied with a factor of 2, respectively. The percentage smolt production in Tjaerbaeck is higher compared to Brandstrup Baeck, but this is because density of recruits and 0+ is much lower in Tjaerbaeck. When comparing the two baecks within the same recruitment level the relative smolt production in Tjaerbaeck is a bit lower compared to Brandstrup Baeck.

Comparing the Two Baecks

Electrofishing within the Danish monitoring program (Rasmussen 2016) takes place during late summer and early autumn when the 0+ age class can be caught with relative high efficiency. These results might give an indication of the expected smolt yield one to four years after monitoring of 0+ parr. Figure 14.13B shows the smolt yield in Brandstrup Baeck and Tjaerbaeck as a percentage of number of 0+ for observed and calculated data for Brandstrup Baeck (i.e. using the mortality rates for Brandstrup Baeck). As shown, low density of 0+ gives low number of smolt, both observed and calculated (Figure 14.13C), but low density of 0+ gives a much higher percentage smolt yield (about 35%) compared to increased density of 0+, which gives about 10% (Figure 14.13B). A mean figure of 16% has been used by Rasmussen 2016 to estimate the present Danish smolt production. This figure of 16% can only be 'a rule of thumb', because densities of 0+ vary very much between river systems and between geographical areas (*op. cit.*). Visual inspection (Figure 14.13B) shows that the observed data from Tjaerbaeck mostly lie below the calculated curve for Brandstrup Baeck (see next paragraph). Aldvén *et al.* 2015 trapped trout smolt in a small stream (Himleaaen) on the Swedish west coast going to the Kattegat and compared the trap catches with calculated number of smolts (30% of 1+ is assumed to become smolt, Bohlin 1981) from number of 1+ parr (mean 23.8 per 100 m^2; calculated from Aldvén *et al.* 2015) from electrofishing. Even including migration mortality in the Swedish baeck (not done in Brandstrup Baeck) the calculated smolt production was 18–19% higher than the number of actually trapped smolt. Using the estimated density dependent mortality in Brandstrup Baeck the relative low density of 23.8 parr (*op. cit.*) equals 27.5 0+ per 100 m^2 in the Swedish baeck. So, from Figure 14.13B the percentage smolt yield is 29.1% and very close to the factor 30% (Bohlin 1981) with no migrating mortality. The result and similarity between the two baecks (i.e. Brandstrup Baeck and Himleaaen) is rather surprising. Aldvén *et al.* (2015) discuss why their electrofishing data gives about 20% higher values compared to the trap results and mention underestimation of trap catches, fixed value of migration mortality and most probably, an overestimation of parr density because the fishing sites were done in order to study Atlantic salmon recruitment.

Figure 14.13C compares the total calculated smolt production *vs.* density of 0+ in Brandstrup Baeck and Tjaerbaeck. Comparing the two calculated trajectories (i.e. observations in both baecks below 60 0+ per 100 m^2) the relative smolt production Tjaerbaeck is lower (22%) than Brandstrup Baeck. Density is lower and growth rate is higher in Tjaerbaeck compared to Brandstrup Baeck, and both total mortality Z and natural mortality M is higher in Tjaerbaeck (Figure 14.14), but the true natural mortality is lower in Tjaerbaeck compared to Brandstrup Baeck (see Table 14.8). Therefore, the most probable reason why relative smolt production is lower in Tjaerbaeck is the higher parr emigration loss from Tjaerbaeck (see Table 14.8). Why the brown trout emigrate in higher proportion from Tjaerbaeck is not known, but is discussed in the section on Mortality.

Comparing the two baecks it is evident that in the low recruited Tjaerbaeck the smolt production is lower per area and because of higher growth rate a higher emigration loss from parr. The percentage smolt production from recruits and 0+ is lower and the variation between years and year classes is much lower, which is also corroborated by the lower true natural mortality in Tjaerbaeck than in Brandstrup Baeck.

Rasmussen 2016 (Tables 19.1 & 19.2, Chapter 19) collected all results of smolt production in Denmark; either from trap catches or from monitoring of 0+ parr converted to smolt using a fixed factor of 16%, which from the results (Figure 14.13B) in the two studied baecks can only be used as an approximation.

Mortality

Tables 14.6 and 14.7 show the calculated instantaneous natural mortality M (i.e. true natural + emigration mortality from parr) and instantaneous total mortality Z from recruits to 4+, that is over a period of 4½ year. Natural mortality M can only be calculated for the year classes with smolt catches. Figure 14.14 shows the relationship of total M and total Z vs. density of recruits, which is the accumulated mortality from recruits up to 1,200 days to compare with the results from Bisballe Baeck, Denmark (Lobón-Cerviá & Mortensen 2005). The relationships between localities are significantly different ($P < 0.001$) for both total M and total Z. Because of the smolt run the total mortality Z increases through age classes (Tables 14.6 and 14.7). But more interesting, the natural mortality M (Tables 14.6 and 14.7) also increases from age classes 0+ to 4+; especially from 3+ to 4+, when the parr have a length above 20 cm.

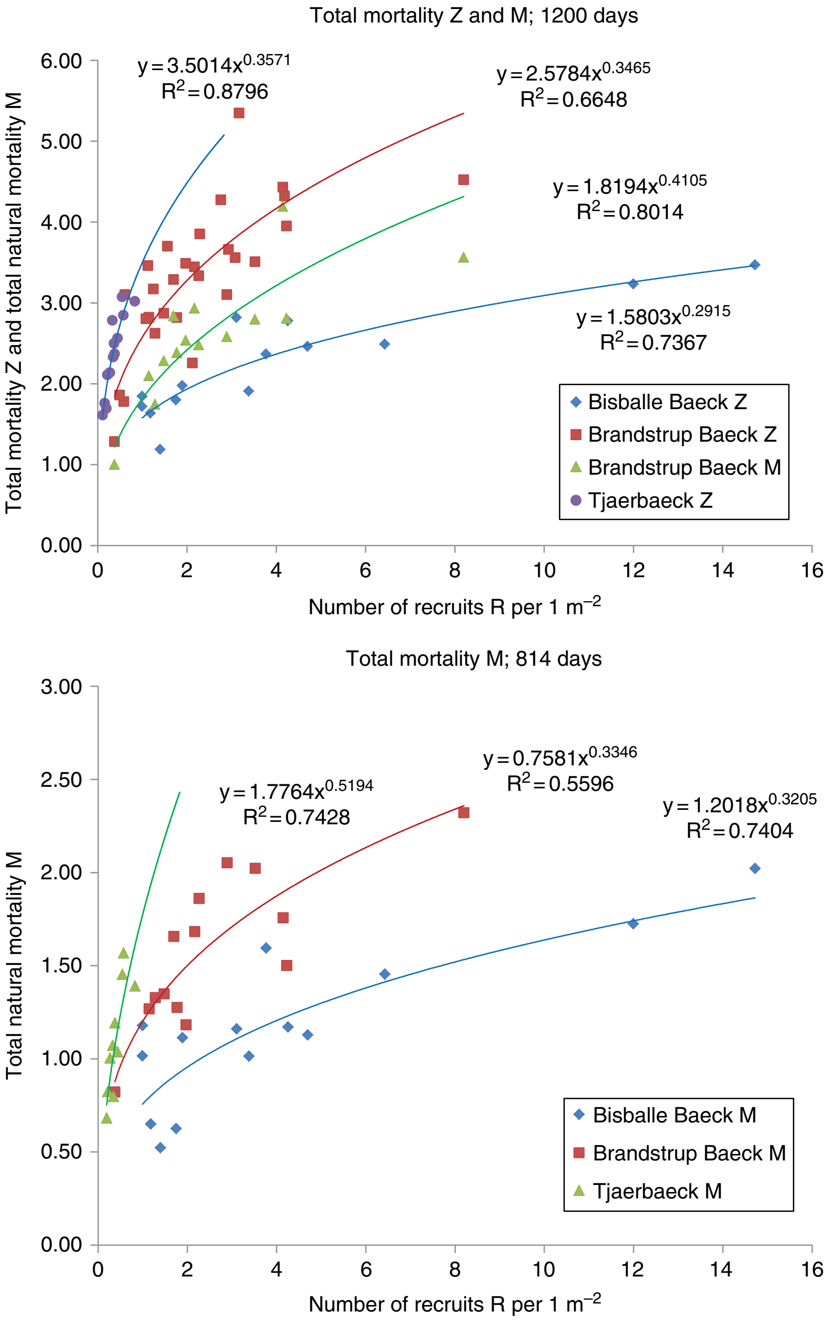


Figure 14.14 Total mortality Z and M (1200 days) and total natural mortality M (814 days) vs. number of recruits per 1 m^{-2}. Mortalities in Bisballe Baeck have been calculated from Lobón-Cerviá *et al.* 2011.

Table 14.6 Brandstrup Baeck. Instantaneous total mortality Z and natural mortality M per day for year classes 1978 to 2007 and total Z and M for 1200 days (0 to 3+). 1200 days is chosen to compare with Lobón-Cerviá & Mortensen, 2005. The period from day of recruitment to day of 0+ is 214 days, from 0+ to 1+ and 1+ to 2+ is 365 days respectively, and from 2+ to 3+ is 256 dayse

Year class	Recruits per 1 m^2	Z = M 0/0+	Z 0+/1+	M 0+/1+	Z 1+/2+	M 1+/2+	Z 2+/3+	M 2+/3+	Z 3+/4+	M 3+/4+	Total Z	Total M
1978	3.08	0.0033	0.0024		0.0019		0.0051				3.6043	
1979	0.37	0.0019	0.0004	0.0004	0.0015	0.0013	0.0008	0.0001			1.3104	1.0271
1980	1.14	0.0023	0.0013	0.0013	0.0029	0.0014	0.0032	0.0025			2.8541	2.1275
1981	1.28	0.0024	0.0016	0.0015	0.0034	0.0014	0.0013	0.0009			2.6568	1.7775
1982	1.48	0.0025	0.0016	0.0015	0.0026	0.0012	0.0033	0.0030			2.9062	2.3155
1983	2.17	0.0029	0.0020	0.0020	0.0025	0.0017	0.0048	0.0040			3.4841	2.9705
1984	1.70	0.0026	0.0026	0.0026	0.0017	0.0008	0.0046	0.0042			3.3235	2.8720
1985	4.14	0.0039	0.0011	0.0011	0.0029	0.0024	0.0085	0.0083			4.4831	4.2448
1986	1.77	0.0026	0.0002	0.0002	0.0030	0.0029	0.0043	0.0029			2.8542	2.4181
1987	1.97	0.0028	0.0005	0.0005	0.0034	0.0019	0.0059	0.0043			3.5262	2.5729
1988	4.23	0.0040	0.0008	0.0007	0.0044	0.0019	0.0049	0.0042			4.0043	2.8619
1989	8.20	0.0061	0.0009	0.0009	0.0051	0.0033	0.0044	0.0032			4.6032	3.6430
1990	2.76	0.0032	0.0023		0.0030		0.0068				4.3175	
1991	4.18	0.0039	0.0025		0.0021		0.0072				4.3732	
1992	2.93	0.0033	0.0018		0.0025		0.0056				3.7048	
1993	2.28	0.0029	0.0025		0.0028		0.0053				3.8923	
1994	1.24	0.0024	0.0021		0.0025		0.0040				3.2043	
1995	2.89	0.0032	0.0018	0.0018	0.0035	0.0031	0.0020	0.0005			3.1462	2.6238
1996	3.52	0.0036	0.0021	0.0021	0.0029	0.0022	0.0036	0.0019			3.5570	2.8448

(Continued)

Table 14.6 (Continued)

Year class	Recruits per 1 m^2	Z = M 0/0+	Z 0+/1+	M 0+/1+	Z 1+/2+	M 1+/2+	Z 2+/3+	M 2+/3+	Z 3+/4+	M 3+/4+	Total Z	Total M
1997	2.26	0.0029	0.0027	0.0027	0.0022	0.0012	0.0038	0.0018			3.3751	2.5187
1998	2.12	0.0028	0.0026		0.0021		-0.0001				2.2953	
1999	1.12	0.0023	0.0023		0.0035		0.0034				3.4934	
2000	0.61	0.0020	0.0027		0.0005		0.0060				3.1301	
2001	1.08	0.0023	0.0060		0.0005		-0.0001				2.8339	
2002	0.58	0.0020	0.0044		-0.0006		-0.0001				1.8076	
2003	3.17	0.0034	0.0077		0.0038		0.0018				5.3938	
2004	1.56	0.0025	0.0037		0.0026		0.0035				3.7347	
2005	0.49	0.0020	0.0029		0.0012		-0.0001				1.8875	
2006	0.32	0.0019	0.0001		0.0043							
2007	1.07	0.0023	0.0053									
2008	1.20											
Mean	2.16	0.0029	0.0024	0.0014	0.0026	0.0019	0.0037	0.0030	0.0046	0.0044	3.3485	2.6299

Table 14.7 Tjaerbaeck. Instantaneous mortality Z and natural mortality M per day for year classes 1978 to 2005 and Total Z and M for 1200 days (0 to 3+). 1200 days is chosen for comparison with Lobón-Cerviá & Mortensen, 2005. The period from day of recruitment to day of 0+ is 198 days, from 0+ to 1+ and 1+ to 2+ is 365 days respectively, and from 2+ to 3+ is 272 days.

Year class	Recruits per 1 m^2	Z = M 0/0+	Z 0+/1+	M 0+/1+	Z 1+/2+	M 1+/2+	Z 2+/3+	M 2+/3+	Z 3+/4+	M 3+/4+	Total Z 1,200 days	Total M 1,200 days
1978												
1979							0.0022303					
1980					0.0020624		0.0034301					
1981	0.21	0.0020	0.0003	0.0003	0.0022	0.0013	0.0029	0.0026			2.1117	1.6923
1982	0.34	0.0020	0.0000	0.0000	0.0029	0.0016	0.0032	0.0023			2.3319	1.6052
1983	0.33	0.0020	0.0008	0.0007	0.0026	0.0016	0.0043	0.0033			2.7858	2.1630
1984	0.44	0.0021	0.0010	0.0010	0.0027	0.0011	0.0029	0.0025			2.5640	1.8427
1985	0.55	0.0022	0.0015	0.0014	0.0037	0.0020	0.0028	0.0022			3.0763	2.2665
1986	0.57	0.0022	0.0016	0.0016	0.0044	0.0023	0.0009	-0.0001			2.8496	1.7867
1987	0.83	0.0023	0.0015	0.0015	0.0033	0.0015	0.0030	0.0021			3.0219	2.1309
1988	0.27	0.0020	0.0005	0.0004	0.0027	0.0018	0.0022	0.0017			2.1394	1.6852
1989	0.38	0.0021	0.0010	0.0010	0.0027	0.0017	0.0023	0.0019			2.3712	1.9055
1990	0.19	0.0020	0.0008	0.0008	0.0005	0.0001	0.0032	0.0030			1.6955	1.4982
1991	0.37	0.0021	0.0019		0.0019		0.0027				2.5010	
1992	0.11	0.0019	0.0005		0.0018		0.0013				1.6139	
1993	0.15	0.0019	0.0006		0.0013		0.0025				1.7622	
1994	0.09	0.0019	0.0009		0.0013							
1995	0.37	0.0021	0.0011									
1996	0.32	0.0020										
Mean	0.34	0.0020	0.0009	0.0009	0.0024	0.0015	0.0027	0.0021	0.0060	0.0056	2.3711	1.8576

This increase of natural mortality contrasts with the general logical statement that the natural mortality decreases with increase of fish size (see section on Growth, Mortality and Production). The total natural mortality M and Z for 1,200 days is higher in Tjaerbaeck compared to Brandstrup Baeck. The same results are seen with the total natural mortality M for 814 days (Figure 14.14), where 814 days is used to compare with natural mortality in Bisballe Baeck. As described earlier, Z includes true natural mortality (size dependent), smolt loss and migration loss. Actually, the relative smolt production is lower in Tjaerbaeck (Figure 14.13C), and the age specific length/mass higher in Tjaerbaeck (Table 14.4); this should imply that the true size-specific natural mortality is lower in Tjaerbaeck. So, the most probable explanation is that a gradually higher migration loss takes place out from Tjaerbaeck outside the smolt run period compared to Brandstrup Baeck (see section on Smolt Production). Why the natural mortality in Bisballe Baeck is lower compared to Tjaerbaeck and Brandstrup Baeck can only be explained by the fact that the parr migration rate is much lower in Bisballe Baeck, but the reason for this is not known. The estimated smolt production (to Lake Hald with a weir established about year 1175 at the lake outlet, so sea trout cannot migrate back from sea to Bisballe baeck) was estimated to 4 per 100 m^2 (Mortensen 1977c). So, the explanation could be that because the isolated position of this baeck, the parr simply have a lower migration intention: the parr simply stay in the baeck.

Table 14.8 shows the simulated outcome of 1,000 recruits up to 4.5 years after recruitment in Brandstrup Baeck and Tjaerbaeck. Mean weight and mortality has been

Table 14.8 Mean number, mean weight and true natural mortality starting with 1,000 recruits. Brandstrup Baeck in years 1979–1989 & 1995–1997; Tjaerbaeck in years 1981–1990. True natural mortality has been calculated as observed natural mortality – weight specific mortality.

	Mean number	Mean weight	True natural mortality	Dead	Smolt	Emigration
Brandstrup Baeck						
recruits > 1+	586.8	1.68	1.1526	676.4	5.6	11.0
1+ > 2+	186.4	19.99	0.3685	68.7	75.1	60.8
2+ > 3+	54.2	42.72	0.2661	14.4	19.3	44.6
3+ > 4+	11.7	74.35	0.2378	2.8	0.9	16.0
Total			2.0250	762.3	100.9	132.3
%				76.6	10.1	13.3
Tjaerbaeck						
recruits > 1+	708.1	2.64	0.7256	513.8	6.8	0.0
1+ > 2+	302.4	35.15	0.2270	68.6	138.4	97.0
2+ > 3+	110.3	79.12	0.1732	19.1	25.1	67.4
3+ > 4+	25.7	157.07	0.1378	3.5	3.9	49.3
Total			1.2635	605.1	174.2	213.7
%				60.9	17.5	21.5

calculated from the smolt producing year classes and true natural mortality calculated from mean weights. This makes it possible to calculate: (1) the number of fish that die in the baecks because of true natural mortality; (2) smolt loss; and (3) emigration loss.

Following a cohort of recruits in Brandstrup Baeck shows that 76.6% of the original recruits are lost; they die in the baeck, due to true natural mortality. 10.1% of the recruits give a total smolt production of four age classes (1+ to 4+). 13.3% of the recruits migrate out as parr of the baeck, some in the smolt run period and the others outside the smolt run period.

Because the recruitment is much lower in Tjaerbaeck (Table 14.2) the mean weights of the age classes are higher (Table 14.4) in this baeck, and therefore the true natural mortality is lower. A total of 60.9% of the original recruits are dead because of true natural mortality. 17.5% of the recruits give a total smolt production of four age classes (1+ to 4+) and 21.5% of the recruits migrate out of the baeck as parr.

The emigrated parr of the recruits would normally be assumed to have died in the baecks (i.e. they are included in M (true natural mortality plus migration loss of parr)) when calculated from Z. As mentioned earlier we do not know if these emigrated brown trout parr contribute to the sea trout population or stay in the main stem of river Gudenaa. It should be noted that the higher percentage smolt in Tjaerbaeck cannot be compared with the density-dependent smolt production per area.

The most likely explanation based on Table 14.8 is that the parr, as they grow up and become larger, gradually leave the baeck (as some also do in the smolt period, but here they can be accounted for) because of the relative shallow habitats in the two baecks. Only a full year running trap can demonstrate this. Why the emigration of parr in Tjaerbaeck is higher is not known, but because of more or less total darkness from tree canopy on the baeck bed and/or the slight silting with iron compound, the food production is probably lower in Tjaerbaeck. Low food production is believed to be a contributing factor to increased smolt emigration (Olsson *et al.* 2006).

Autumn migration of Atlantic salmon and brown trout has been registered on a few occasions. Pemberton (1975) is probably the first to describe the phenomenon of autumn brown trout recruits in Scotland. Poole *et al.* (1996) registered in Burrishoole, Ireland, an annual downstream migration of unsilvered brown trout which takes place between August and January with peaks in October and November and with sizes from 14 to 28 cm. Winter *et al.* (2016) analyzed autumn migration using PIT telemetry over an eight-month (October to June) period in River Deerness, UK and River Villestrup, Denmark. Those leaving Deerness during autumn–winter represented 46% of all stream-emigrant juveniles in the study period. Whereas, in River Villestrup incidence of autumn migration was only 25%, yet remains higher than that reported by Jonsson & Jonsson (2009) in River Imsa, Norway, which amounted to 18%. In Brandstrup Baeck, smolt and emigrated brown trout parr amounted to 23.4% of recruits and the emigrated parr during June to February represented 57% of all stream-emigrants (smolt + parr). In Tjaerbaeck, smolt and emigrated parr amounted to 29% of recruits and the emigrated parr during June to February represented 55% of all stream-emigrants (smolt + parr). These figures are close to the results from Burrishoole, Ireland, which states that the numbers of autumn-migrating brown trout parr have fluctuated between 18 and 57% of the total annual juvenile downstream migrant count since 1982, Marine Institute (2014).

These results are important when managing trout streams, because the smolt production calculated in the traditional smolt period in spring from traditional trap captures or from recaptures of electronic tagged parr before the smolt run period, will probably underestimate the true migration out from the nursery streams during a whole year. At present we do not know the fate of these out-migrating brown trout parr outside the normal smolt period in spring: do they smoltify later and contribute to the sea trout or do they stay in larger sections of the river?

Biological Production Rates

Table 14.9 gives the biological production rate and P/B from recruitment to age class 4+ (i.e. for a period of 4½ year) in both baecks. The production rate in Brandstrup Baeck is a factor 2.3 higher compared to Tjaerbaeck and primarily determined by the recruitment density and growth rate, because water temperatures are more or less the same in the two baecks. The recruitment in Brandstrup Baeck is a factor 3.8 higher compared to Tjaerbaeck, but the growth rate (Table 14.3) is lower and true natural mortality (Table 14.8) is higher in Brandstrup Baeck compared to Tjaerbaeck. In Tjaerbaeck growth rate (Table 14.4) is higher and true natural mortality (Table 14.8) lower compared to Brandstrup Baeck. This explains why the production in Brandstrup Baeck is only a factor 2.3 higher compared to Tjaerbaeck. P/B is more or less the same in the two baecks. In both baecks the main production takes place during the period from recruitment to 2+ (two and half year). This is shown as an example in Brandstrup Baeck, 1995 year-class, (Figure 14.15A), which also shows that growth and production take place in the period from spring to autumn when temperatures are above 3–4 °C, and the brown trout grow (Elliott *et al.* 1995).

Biological production rate integrates recruitment, survival, growth and water temperatures. Table 14.9 shows the CV% of recruitment and production in both baecks. The relative variation of production is reduced in both baecks compared to the variation of recruitment. This shows that interactions between the size of recruitment and the secondary effects on survival and growth try to reduce the variation in production rate to the carrying capacity of each baeck.

Figure 14.15B shows the relationship between production and recruitment in both baecks, and the effect of increased mortality and decreased growth at increasing density of recruits is clearly seen. The relative production per recruits is lower in Tjaerbaeck compared to Brandstrup Baeck ($P < 0.0001$). If for example the recruitment is 100 per 100 m^2, the calculated total year class production in Brandstrup Baeck is about 1410 g wet wt. per 100 m^2, but only about 851 g wet wt. per 100 m^2 in Tjaerbaeck. Tjaerbaeck is mostly surrounded by trees over its course, so the invertebrate production might be lower here compared to the less shaded Brandstrup Baeck. The recruitment in the two baecks is simply very different and probably the same can be said about the food production rates of invertebrates.

Mortensen (1977 & 1985) reviews the brown trout production in Danish streams with a maximum of 33 g wet wt. per 1 m^2 and the present results are as expected with Mortensen (op. cit.). Rasmussen 1986a compared the annual production (8.5–9.5 g wet wt. per 1 m^2) of brown trout in river Mattrup, Denmark, upstream a rainbow trout hatchery (i.e. no effect from fish farming) with the production of brown trout downstream from a trout hatchery (effect from farming) and the annual production was here

Table 14.9 Number of recruits R (ind. per 100 m^2) and biological production (g wet wt. per 100 m^2) and P/B in Brandstrup Baeck and Tjaerbaeck. Numbers of recruits for year classes 1985–1989 in Brandstrup Baeck have been recalculated in accordance with the 50% reduction of 0+ in years 1985–1989. The true production of R > 0+ is underestimated 65% for years 1985–1989.

	Recruits R	R > 0+	0+ > 1+	1+ > 2+	2+ > 3+	3+ > 4+	Total R > 4+
BRB Year class							
1979	37.4	75.5	315.2	395.7	141.0	203.2	1130.7
1980	114.4	216.4	738.1	175.0	150.0	79.9	1359.3
1981	128.1	270.6	550.0	193.5	137.8	86.8	1238.7
1982	147.8	209.1	650.2	344.9	210.3	162.1	1576.6
1983	216.5	331.5	725.7	513.1	224.0	73.5	1867.6
1984	169.7	265.7	512.9	590.2	511.6	294.3	2174.8
1985	154.0	188.9	737.8	594.5	92.5	42.9	1656.6
1986	79.2	119.0	590.3	456.2	169.5	234.8	1569.8
1987	86.9	146.4	600.1	390.0	95.3	3.7	1235.6
1988	156.0	185.7	891.0	196.7	29.2	0.7	1303.2
1989	203.0	191.0	873.8	391.5	106.2	54.5	1616.9
1995	289.0	454.2	1039.9	441.5	193.0	95.2	2223.9
1996	352.0	383.2	864.2	579.5	143.1	50.7	2020.7
1997	226.4	261.1	605.4	280.9	129.5	9.0	1285.8
Mean	168.6	235.6	692.5	395.9	166.6	99.4	1590.0
Mean%		14.8	43.6	24.9	10.5	6.2	
CV%	50.0						22.7
Mean P/B		2.69	1.77	0.89	0.70	0.70	
TJB Year class							
1981	21.4	51.1	210.6	168.3	100.3	8.3	538.6
1982	34.4	69.5	294.6	217.6	82.9	16.2	680.7
1983	44.1	89.7	313.2	240.1	76.0	27.9	746.9
1984	44.1	84.4	308.7	119.3	99.3	40.6	652.4
1985	54.6	115.4	298.7	120.1	61.9	35.8	632.0
1986	57.3	92.7	335.8	84.9	57.6	34.1	605.1
1987	83.0	146.6	392.7	228.8	103.6	57.6	929.2
1988	26.9	50.1	197.2	205.9	198.2	86.9	738.3
1989	37.7	111.6	215.8	189.0	131.9	52.4	700.7
Mean	44.8	90.1	285.2	174.9	101.3	40.0	691.5
Mean%		13.0	41.2	25.3	14.6	5.8	
CV%	41.2						16.0
Mean P/B		2.89	1.74	0.95	0.68	0.71	

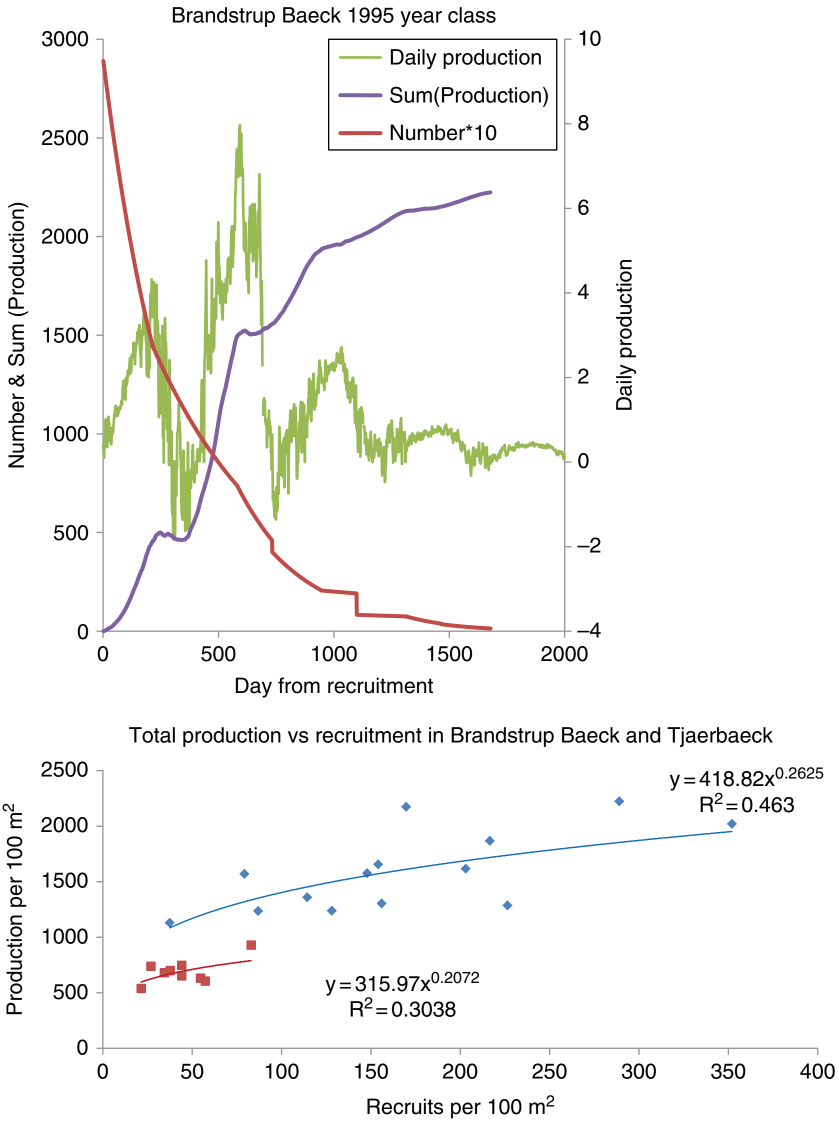


Figure 14.15 Biological production g wet wt. in Brandstrup Baeck 1995 year class and total production of year classes 1979–1989 and 1995–1997 in Brandstrup Baeck (diamond) and year classes 1981–1989 in Tjaerbaeck (square) vs. number of recruits per 100 m^2.

6.5–13.2 g wet wt. per 1 m^2. The brown trout here competed with escaped rainbow trout (*Oncorhynchus mykiss*) with an annual production of 33.1–43.3 g wet wt. per 1 m^2 to give a total salmonid production of 43–49.8 g wet wt. per 1 m^2. Because of the very high production rate of invertebrates and the higher water temperature (effect from the hatchery) the growth of brown trout was higher here compared to the growth of brown trout upstream the hatchery. Below the hatchery the brown trout and rainbow trout ate invertebrates, but also different fish species with a higher energy content compared to invertebrates and their growth rate was higher compared to Brandstrup Baeck and Tjaerbaeck. So, the conclusion is that besides recruitment the biological production of brown trout depends on water temperature and quality (energy) of food items.

The proportion between production P and biomass B (P/B) is an index of turnover rate and is more or less the same in the two baecks, and it is as expected to be highest for the production from recruits to 0+, and hereafter decreases with increasing age.

General Conclusions and Recommendations

This study is one of very few covering a period of several years (i.e. 31 years) on population dynamics of brown trout in running waters and illustrates the value of long-term studies (Elliott & Elliott 2006). The analysis showed that the recruitment and subsequently the density of parr varied greatly from year to year. This was most probably because of the effect from discharge in the short period, when cohorts establish as recruits in spring after emergence from spawning gravel (Lobón-Cerviá *et al.* 2016). The analysis also showed that density of recruits and parr is one of the fundamental drivers of survival, growth rate, smolt production and biological production. It was shown that after stabilization of the initial number of recruits, density dependent mortality regulates the survival of the cohort from recruits to the last trout several years after: low density–high survival; low density–high growth and vice versa; low recruitment–low smolt production; low recruitment–low biological production and vice versa.

Water temperature (in combination with food production) and densities of the different number of age classes regulate the growth rate of 0+ parr in the period from recruits to half-yearlings (i.e. 0+) as shown in this study. Therefore, very low density of brown trout parr means a growth rate where the brown trout grow at the maximum when compared to a bio-energetical single-fish fed growth model (Elliott 1975). Water temperature and food production only regulate the growth rate of older trout in this study, so that growth rate is not density dependent for older parr.

Trapping smolts is expensive, and it was only because smolt from many year classes were trapped in this study, that it was possible to calculate natural mortality and split it up into true natural mortality and emigration loss. Compared to the rather few references above (see section on Mortality) most probably this can be considered as an autumn migration. The latter showed that true smolt production might be at least twice the number of smolt trapped if the migration parr go to the sea.

In management terms this topic should be studied further, as done recently in Winter *et al.* (2016) and with individual PIT tagging of parr before the 'normal' smolt run in spring and with PIT antenna established during whole years after tagging. The emigration out from smaller streams can thus be divided into true smolt and parr, and these can later be separated into sea migrating parr and parr migrating to larger river sections when they return to spawn in the same streams.

It is highly recommended that long-term studies on the population dynamics of brown trout should be continued in Denmark (as well as in other brown trout countries). It would be preferable to include bigger river systems compared to the two small becks in this presentation. Also, further studies should preferably use a combination of traps and electronic tagging of smolt, parr and sea trout kelts to obtain a much better understanding of the variable life strategies of brown trout.

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15

Foraging Behaviour of Brown Trout: A Model Species For Linking Individual Ecology to Population Dynamics?

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Introduction

Much recent research on stream fish ecology has focused on large-scale processes such as populations, communities, ecosystems (Gido & Jackson, 2010), and even social-ecological systems (see e.g., Bottom *et al.*, 2009). This focus is probably justified given the crisis of anthropogenic extinction facing freshwater organisms in the 21st century (MEA, 2005). One might argue, however, that research on the behaviour of individual organisms ought still to play a major role in ecology; after all, it is largely upon the individual that natural selection acts (Darwin, 1859). Observing individual fish behaviour, therefore, ought to lead to robust conclusions about the costs and benefits that animals must trade-off in order to maximize fitness. And ultimately, those individuals that achieve the greatest fitness ought to drive the population-level processes that have attracted so much of stream fish ecologists' attention in recent years. The argument therefore, is that if we do not understand *why* fish select the habitats that they do (Hughes & Dill, 1990), we will be in a very poor position to predict the results of either habitat degradation or restoration. One very promising means of understanding the short-term fitness needs of individual stream fish is to estimate their net energy intake (NEI) by measuring the costs and benefits of foraging (Fausch, 1984; Hill & Grossman, 1993; Hughes *et al.*, 2003; see Piccolo, Frank & Hayes, 2014 for a review).

In linking behavioural- to population-level ecology, we are in luck when it comes to the brown trout – there is probably no individual stream fish species whose population ecology is better quantified (Elliott, 1994; Jonsson & Jonsson, 2011); nor are there many species that have attracted more attention from behavioural researchers over the past 75 years (Kalleberg, 1958; Frank, Piccolo & Baret, 2011; Piccolo *et al.*, 2014). The brown trout, then, might be considered as an excellent model species for developing the ecological understanding of how natural selection (i.e., individual, fitness-based decisions) acts to regulate stream fish populations. Because foraging efficiency determines the net 'income' of individual fish, i.e., the amount of energy they have to grow and reproduce, a thorough understanding of the foraging behaviour of trout is warranted.

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

In this chapter we review and synthesize the literature on brown trout foraging experiments that have taken an NEI approach, with an eye towards identifying the knowledge gaps that remain to be filled in order for ecologists to quantify the fitness costs and benefits of foraging behaviour. We first give a brief summary of NEI modelling research. We then review the NEI-related research on brown trout by breaking it down into various aspects of the foraging maneuver sequence. We conclude with a brief section on how NEI modelling can contribute to stream fish conservation by generating quantitative predictions of the relationship between organisms and their habitat.

The Net Energy Intake (NEI) Modelling Approach

> *Why do fish select one position over the multitude of alternatives?*
>
> Hughes and Dill (1990)

Consider what is at stake for a trout when it chooses a foraging position: it must trade-off energy gain versus prey capture costs and at the same time it must avoid being preyed upon. What 'decisions' (in evolutionary terms) does the fish need to make? It 'knows' that it ought to maximize its growth rate – larger fish should have higher fitness: they usually win the best territories, they are faster swimmers, they reach reproductive age faster, and they produce more gametes. Through a complex series of physiological feedbacks, larger fish are able to use faster, deeper habitats, where NEI potential is greater, leading for further increases in growth rate, further ontogenetic niche shifts and higher likelihood of accruing fitness benefits. Depending on the life history strategies available in the given habitat (e.g., migratory, sea-run, resident), selective pressure for fast growth will vary, of course. Nonetheless, for juveniles 0–2 years of age maximizing growth rate (while avoiding being eaten) would be the expected strategy. Considering that mortality rates are often very high during the first year, any slight advantage in foraging ability should be highly adaptive (the accumulation of such slight advantages was, in fact, Darwin's main thesis). In short, trout need to eat and to avoid being eaten, and gaining clear insights into how they accomplish this ought to be of overriding interest to ecologists.

And yet, *much* more attention has been given to *where* trout are found (depth, velocity, cover, substrate) than to *why* they are found there. This is probably because it is much easier to measure and predict changes in physical habitat than it is to quantify NEI potential through estimating invertebrate prey availability and fish feeding performance. The past 20 years have seen major advances in foraging-based habitat quality theory, but we are just now beginning to see widespread attempts to apply these to stream management (e.g., Railsback *et al.* 2012; Hayes *et al.* 2016).

Elliott (as summarized in 1994) laid the groundwork for an inclusive energetics-based understanding for habitat selection and habitat quality through careful development of the energetic budget for brown trout. He noted (1994), however, that at that time there had 'been little attempt to develop general equations' that could describe the complex relationships among variables that influence food intake, 'the income for the energy budget' of the fish. This is thankfully no longer the case for drift-feeding salmonids due to the ensuing 20 years of research on foraging theory. We are now at the point that the mechanistic foraging models first proposed in the 1980s–1990s have been ground-truthed enough to say we do have some 'general' equations for food intake of drift-feeding salmonids. But we have a long way to go in testing and improving these models, developing species-specific models, and in particular, estimating the energetic availability of invertebrate prey (see Piccolo *et al.*, 2014; Rosenfeld *et al.*, 2014; Hayes *et al.*, 2016). As regards the brown trout, although it has been the species with the only specific model and test of drift-feeding (Hughes *et al.*, 2003), we do not have empirical data for some of the key model inputs, as outlined in the section below.

The majority of stream-living brown trout drift feed, holding a foraging position in the stream and capturing invertebrate prey that is delivered by the water current (Bachman, 1984; Fausch, 1984; Hughes *et al.*, 2003). Stream trout may also search-forage for benthic invertebrates (Gunnarsson & Steingrímsson, 2011; Harvey & Railsback, 2014), and they may prey on other fishes when they grow to a large enough size. In the present chapter we focus on drift feeding both because it appears to be the most common behaviour and because it has received by far the most research attention. Many stream fish species may drift feed (Grossman *et al.*, 2002; Grossman, 2014), but salmonids have been the subject of virtually all drift-feeding research. Early drift-feeding research focused on brown trout and the species has been among the widely and carefully studied drift feeders to date (Fausch, 1984; Hughes *et al.*, 2003; Piccolo *et al.*, 2014). Still, much remains unknown about the mechanisms of drift feeding.

Although early researchers noted the importance of trout habitat selection in terms of the energetic costs and benefits, Bachman (1984) and Fausch (1984) developed the first quantitative cost-benefit models for drift-feeding trout (Faush also included other species). Hughes *et al.*'s (2003) model remains by far the most detailed drift foraging model and test for any salmonid species, and this model was developed for brown trout. Both the Fasuch and Hughes *et al.* models rely on a wealth of behavioural and physiological research on brown trout and other salmonid species, which has been conducted over the past half century. In simple terms, a fish's net energy intake (NEI) equals its gross energy intake (GEI) minus the energetic costs of swimming to hold position and capture prey (SC):

$$\mathrm{NEI} = \mathrm{GEI} - \mathrm{SC}$$

The GEI parameter consists of a series of measures or estimates, including the number of prey detected (PD), the number of prey captured (PC), and the energetic content of the prey (EC). The cost of swimming includes periods of sustained swimming to hold the focal position, plus periodic increased costs to attack prey and return to the focal point. Most NEI models to date have ignored additional prey capture costs and estimated SC the cost of holding position (but see *Prey capture costs* below). For stream salmonids in general, NEI models have proven effective theoretical tools for improving the understanding of habitat selection (see Piccolo *et al.* 2014 for a review). Furthermore, the most advanced NEI-based models have been developed for brown trout in particular (Hayes, Stark & Shearer, 2000; Hughes *et al.*, 2003; Hayes, Hughes & Kelly, 2007).

The NEI-based brown trout models have been successful at accurately predicting habitat selection and fish production and individual-fish and stream-reach scales. These models are among the most complete efforts to date to incorporate the fitness-based logic of NEI into stream fish management. Parallel efforts on other salmonid species are also underway (see e.g. Piccolo *et al.* 2014 and articles therein). Thus the brown trout is an excellent species to serve as a model for improving our ability to use a fitness-based approach to develop accurate predictive models of stream fish production. Such fitness-based models have the potential to supersede the habitat-based models of the previous generation of fisheries management. These fitness-based models may help to explain the tremendous variation often seen in such stock-recruit relationships as those that predict smolt production from the number of spawners. Improvements in such predictive models are also needed to understand the results of habitat and fish passage restoration, and predict future changes such as climate-induced habitat changes.

The Foraging Maneuver Sequence

To complete a successful foraging maneuver sequence, drift-feeding trout need to (1) hold a position by swimming against the current to maintain a focal point (typically also defending a territory); (2) detect a drifting prey (3) swim towards the prey; (4) align the snout linearly with the prey; (5) attack the prey with a burst of swimming; (6) perform a sequence of jaw, opercular and branchiostegal movements, sucking the prey into the buccal cavity, (7) manipulate the prey to finally prepare it for ingestion; (8) ingest the prey and (9) swim to return to the focal point (Ringler, 1985) (Figure 15.1). At a basic level, the physical processes and energetics of foraging maneuvers have been fairly well-established for salmonids in general (Hughes and Kelly 1996), but specific knowledge for various components is lacking for many species, including brown trout. For example, Hughes *et al.* (2003) did not include species-specific data for either swimming costs or prey detection/capture capabilities). Here we describe each component of the foraging maneuver, with special attention to brown trout and specific knowledge gaps.

The Focal Point

Stream-living brown trout, like many salmonid species, defend feeding territories throughout much of their fluvial lives. Much has been written about territoriality in brown trout, all of which is inextricably linked to drift feeding. This will not be reviewed here. From a theoretical perspective the foraging area should be selected in order to maximize NEI, that is maximizing the difference between the GEI and SC (Figure 15.1). In reality, however, fish must also weigh predation risk and the cost of defending the territory, issues that have only partly been addressed in foraging theory (Kawai *et al.*, 2014). Under certain circumstances, however, NEI potential alone has been shown to be a good predictor of position choice for other salmonid species (Hughes & Dill, 1990) and of the rank order of territories for drift feeders (Hughes 1992). Hughes (1990) found that NEI potential predicted focal point locations of Arctic grayling (*Thymallus arcticus*) in an Alaskan stream.

Fish size plays an important role in habitat (i.e., focal point) selection. Larger fish have better swimming ability, better vision, more foraging and social experience, and different energy budgets than do smaller fish. In general, drift feeders move into faster and deeper water as they grow, and their territory size increases. Prey availability, however, can strongly affect choice of focal point, size of foraging territory, diurnal and seasonal foraging behaviour, and migration.

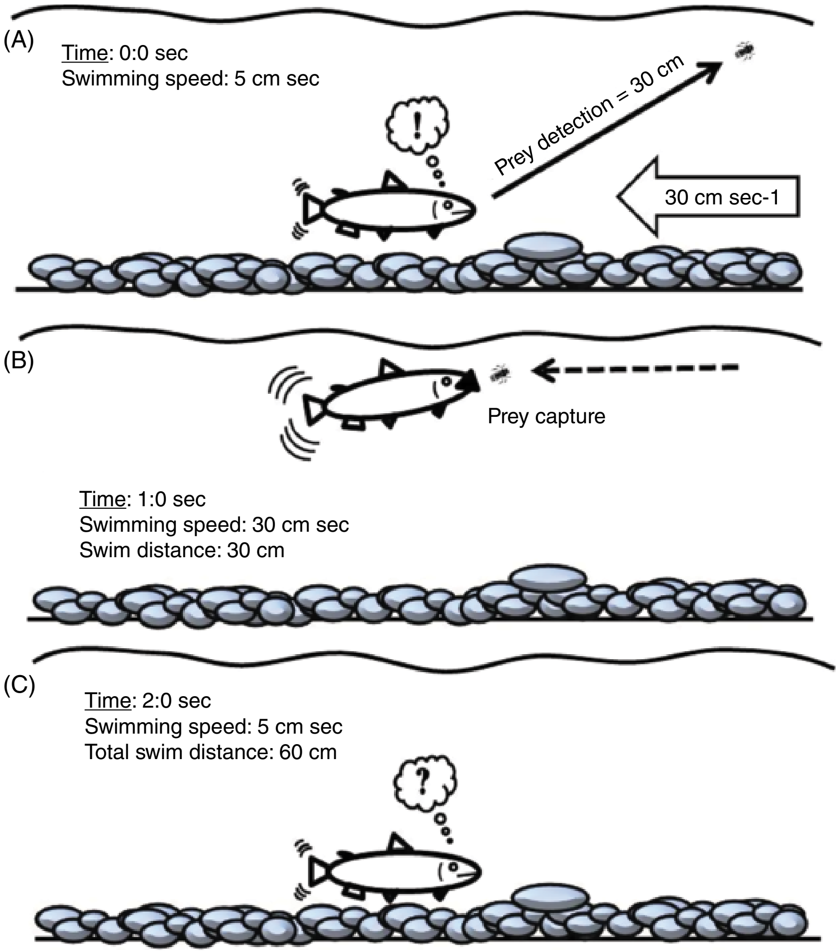

Figure 15.1 The drift-feeding maneuver sequence with a rough approximation of times and distances. See text for more literature with more detailed descriptions. (A) The fish holds a focal position and searches for prey. (B) The fish has detected a prey and swims to catch it. When it leaves to focal point and enters faster water it must increase its swimming speed to maintain a position equal to the focal point. (C) The fish has returned to the focal point is begun searching for prey again.

Prey Detection

The ability of a foraging fish to detect prey depends upon both its internal state and the environment surrounding it. The fish's visual acuity and its cognitive ability determine which prey it is able to detect. Prey detection is further limited by complex interactions among debris load in the stream, ambient light levels, prey size and distance from the focal point, water colour and velocity, temperature, and even chemical cues. Social interactions with other fish also play a role (e.g., Shannon and Gowan 2014, Hart *et al.* 2014). Early foraging models assumed that all prey were detected at their maximum reaction distance (e.g., Hughes and Dill 1990). More recent models (e.g. Hayes *et al.* 2016) account for the fact that prey are detected throughout the reaction volume (Hughes *et al.* 2003, Piccolo *et al.* 2007, 2008a). The most advanced prey detection model to date has been developed for adult brown trout in New Zealand (Hayes *et al.* 2016),

In general, our lack of understanding of prey detection ability is one of the main limiting factors in quantifying NEI (Hughes *et al.* 2003, Neuswanger *et al.* 2014, Piccolo *et al.* 2014). It should be noted that in many experiments the number or percent of prey detected is not known but is assumed from the number of prey attacked (see *Prey capture* below). Thus, studies that assume that the number of captured is equal to the number of prey detected may underestimate prey detection and potentially prey availability. For brown trout, Hughes *et al.* (2003) note that the best current drift feeding model made poor predictions of prey detection (Piccolo *et al.* 2014). There is much scope of research that improves our ability to understand prey detection for drift feeders. Careful observation of the fish's eye is required to note when it fixes on a potential prey, and in most cases this is not possible. Piccolo *et al.* (2008a) report some prey that we detected and not pursued (Pacific salmonid species).

Prey Capture

Once a prey is detected and a fish has decided to attack it, the fish swims to catch it. To our knowledge, the theory that fish minimize prey capture distance by anticipating the shortest geometric line has not been tested. Brown trout adults intercept prey at a variety of swimming speeds, not at the predicted maximum sustainable swimming speed (Vmax) (Hughes *et al.* 2003). No data exists for juvenile brown trout, an area ripe for increased research effort. Juvenile steelhead (*Oncorhynchus mykiss irideus*) and coho salmon (*O. kisutch*) have been shown to intercept prey at Vmax (Piccolo *et al.* 2007, 2008a), and the difference between adults and juveniles is likely related to differences in energy budgets and growth trajectories. The percent prey capture success for juvenile brown trout now exists for different water temperatures and light levels (Watz and Piccolo 2011, Watz *et al.* 2012).

Swimming Costs

The prey capture maneuver includes the cost of swimming to both hold a focal point position and to swim to capture prey (Figure 15.1). Early drift feeding models ignored the increased swimming costs of capturing prey despite the knowledge that this assumption was invalid (Hughes and Dill, 1990). Various models have attempted to rectify this to some degree. The latest model of prey capture was developed for adult brown trout within Hayes *et al.*'s (2016) habitat quality model. It incorporates a number of improvements over earlier models, including a function for prey capture maneuver costs. Many of the parameters of Hayes et als (2016) swimming cost model component still rely on data for other species or fish sizes. Thus, there remains a broad scope for new research on brown trout foraging energetics for both juvenile and adult life stages.

The Physical Factors Affecting Prey Capture and NEI

Water Velocity: The Basis for Net Profitability and NEI Theory

Water velocity is a key physical variable affecting drift feeding because it influences swimming costs (SC), prey capture ability (i.e., GEI), and prey availability (also GEI). Hence the dome-shaped curve of NEI vs. water velocity is a result of the relationship between swimming costs and prey capture success (Hill and Grossman 1993, Piccolo *et al.* 2008b). Brown trout were the first species to be observed from a drift-foraging standpoint (Kalleberg, 1958) but NEI theory began with Fausch's (1984) oft-cited paper on 'net profitability', which included juvenile brown trout (non-native) among other species (see Fausch, 2014 for an historical account with many background references). A major knowledge gap is that the NEI curve has not been tested empirically for brown trout as it has for other salmonid species (Hill and Grossman, 1993; Piccolo *et al.*, 2008). Given our good knowledge of the physiology and ecology of brown trout, it would be desirable to develop and test of a new theoretical foraging NEI model that incorporates knowledge of all aspects of the prey capture maneuver.

There are no published studies that have specifically investigated the effects of water velocity on prey detection or capture by brown trout. Hayes *et al.*'s (2016) model for brown trout incorporates velocity-dependant reductions in prey capture efficiency, but this relies on data from other species. Increased water velocity has been shown to decrease prey capture success for juveniles of other species (Hill and Grossman, 1993; Piccolo *et al.*, 2008a); no known studies have investigated adult salmonids, probably because of the logistic difficulties of working with large volumes of fast-flowing water. Because fish size plays a major role in how water velocity interacts with prey capture (and hence NEI) experimental studies with several size classes of brown trout should be a research priority.

Water Depth

Brown trout are known to prefer pools, which are the deepest segments of streams. The fish's choice of position in a pool is important in terms of NEI, because the decreased water velocity reduces prey encounter rate and increases prey settling rate. Therefore, the best foraging position is at the upstream head of the pool where prey is delivered. In theory, increased water depth can offset some of the loss of prey encounter rate due to decreased velocity because a fish can have a greater prey detection area. Piccolo *et al.* (2007) tested the effects of water depth for juvenile salmon and steelhead, but there are no specific studies for how depth affects brown trout foraging efficiency. Because brown trout seem to prefer slower and deeper water than do Atlantic salmon, comparative studies on the effects of water depth are warranted for both species.

Water Temperature

Physical performance of fish scales with water temperature, and the relationship between e.g. swimming ability and temperature (Butler, Day & Namba, 1992) has implications for the prey capture ability of drift-feeding fish. Temperature influences the time it takes to complete the sequence of behaviours of which the prey capture maneuver consists. For instance, Watz & Piccolo (2011) measured the prey capture maneuver time of brown trout in a laboratory stream and the whole prey capture maneuver sequence took about 1 s in 14 °C. This time increased with decreasing temperature and was about 50% longer at 6 °C. The effect of temperature has also been investigated separately for several of the components of the prey capture maneuver. Data from Atlantic salmon show a relationship between temperature and maximum velocity at which a fish can hold its position in the current (Rimmer, Saunders & Paim, 1985; Graham, Thorpe & Metcalfe, 1996). However, Atlantic salmon and brown trout tend to hold position differently; Atlantic salmon clings to the bottom substrate, whereas brown trout like many other salmonids often hold position by means of active swimming (Höjesjö, Kaspersson & Armstrong, 2015). Since temperature influences swimming endurance (Ojanguren & Brañta, 2000), it is possible that the effect of temperature on brown trout position holding performance is even larger than that reported for Atlantic salmon by Rimmer *et al.* (1985).

It has not been investigated whether or not temperature affects prey detection. However, it has been shown that reaction distance is positively related to temperature in the temperature range of 3 to 11 °C (Watz *et al.*, 2014b). This positive relationship could either be caused by an effect of temperature on either on prey detection or on reaction time, i.e. the time the fish needs to process visual cues and decide to initiate an interception of the prey.

Also, the capacity to accelerate to maximum burst swimming speed is positively related to temperature (Webb, 1978), affecting the ability to intercept drifting prey, in particular in high water velocities, where the time window for the prey capture is short. Furthermore, the ability of trout to perform the jaw movements needed to suck the prey into the buccal cavity after interception might be positively related to temperature. Environmental effects on this ability have not been investigated in drift-feeding fish, but the effect of temperature on jaw movements related to prey capture has been shown for other freshwater fish species, such as largemouth bass, *Micropterus salmoides*, (Devries & Wainwright, 2006) and bluegill, *Lepomis macrochirus*, (Wintzer & Motta, 2004). It is possible that the observed negative effect of temperature on prey handling time of brown trout (Watz *et al.*, 2014a) reflects a temperature-dependent ability to efficiently perform the jaw movements necessary for prey manipulation and ingestion.

All in all, temperature dependence of the different components of the prey capture maneuver combines into an effect of temperature on the prey capture ability. For brown trout drift feeding at temperatures near its growth optimum, 14 °C (Elliott, Hurley & Fryer, 1995), prey capture ability remains relatively unaffected by temperature, but is markedly reduced at low temperatures (Watz & Piccolo, 2011). For example, the prey capture ability of brown trout drift feeding in an artificial stream at 2 °C was about 60% of their capture ability at 11 °C (Watz *et al.*, 2014b). The effect of temperature on prey capture seems to differ for fish using different foraging tactics (Watz *et al.*, 2012), with a larger effect on mobile cruise feeders, foraging in the water column or from the surface ('movers' sensu Grant & Noakes, 1987), than on stationary, sit-and-wait feeders ('stayers').

Light and Turbidity

Salmonids are primarily visual hunters (Rader *et al.*, 2007; Elliott, 2011), and low light intensities and turbidity reduce visibility and consequently limit detection distance and reduce foraging success (Tippets & Moyle, 1978; Robinson & Tash, 1979; Barrett, Grossman & Rosenfeld, 1992; Metcalfe, Valdimarsson & Fraser, 1997). For example, prey capture ability under low light conditions (~0.1 lx at the surface, corresponding to moonlight) is estimated to be somewhere in the range from 10 to 35% of that in daylight (Fraser & Metcalfe, 1997; Watz *et al.*, 2014b). Therefore, it has been suggested that drift-feeding salmonids may change from a sit-and-wait foraging tactic to mobile epibenthic feeding when feeding ability or prey encounter are low due to poor visibility at night or in turbid waters (Fausch, Nakano & Kitano, 1997; Amundsen *et al.*, 2000; Sweka & Hartman, 2001; Linnansaari & Cunjak, 2013).

The Biological Factors Affecting Prey Capture and NEI

The biological factors that influence NEI include characteristics of invertebrate prey, intra- and inter-specific competition, predation, and even parasitism. There is a large body of literature that has investigated how these various factors affect brown trout. Thus, there is great potential to develop NEI models for brown trout that incorporate various aspects of these biological factors. To date, however, NEI models for brown trout have specifically incorporated only the aspects of prey size and drift density. Intraspecific competition has been modelled simply by upstream fish depleting potential prey from fish further downstream (Hayes *et al.* 2016); interspecific competition, predation risk, and parasitism have yet to be accounted for in any NEI model for brown trout. Expanding NEI models to include these extrinsic biological factors will be challenging, but they should reward us with increased understanding of how stream ecosystems function.

The Role of Foraging and Habitat Modelling in Brown Trout Conservation

Although ecologists and fisheries scientists have made great strides in understanding behaviour and population dynamics we still have much work to do. Without improving our predictive capacity, we will be less effective at conserving and restoring brown trout populations. Individual-based models for trout have the potential to contribute to conservation efforts by generating testable hypotheses about the *processes* that underlie population dynamics. At the heart of these IBMs are foraging models that can accurately predict net energy intake. In this chapter we have summarized the current status of brown trout foraging models and suggested some directions for future research. A consolidated effort to develop and test NEI models ought to be of use in furthering conservation efforts.

There is an immense body of literature on brown trout diet, habitat selection and growth from both manipulative field and lab experiments and from observational studies (see chapters this book; Elliott, 1994; Jonsson and Jonsson, 2009). This literature is matched by an equally large body of physical habitat modelling literature (Frank *et al.*, 2011). Surprisingly little of this literature has taken into account fitness-based foraging theory (but see Hayes *et al.*, 2016 for an excellent summary). Future research that bases field and lab experiments on the principles of such fitness-based theory ought to have the long-term result of unifying, through the development of testable hypotheses, our ecological understanding of the processes that underlie fluctuations in brown trout abundance and survival. Without making continuous progress toward linking individual behaviour to population processes through asking the question '*Why do fish select one position over the multitude of alternatives*?' (Hughes and Dill, 1990) ecologists will miss the opportunity apply the vast amount of knowledge about brown trout to basic eco-evolutionary questions that can help solve conservation problems.

Despite its success as an introduced species worldwide, innumerable endemic brown trout populations across their native range have been extirpated by anthropogenic causes; many more endemic populations are currently threatened (Lobón-Cerviá, Introduction, this volume). These remaining populations harbour a multitude of local adaptions that provide ecosystem services and are of immeasurable intrinsic value (Piccolo 2015; Piccolo *et al.,* Chapter 25, this volume). Thus, there is no time to wait for full scientific knowledge of their ecology–all endemic trout populations ought to be protected from overharvest and habitat degradation as completely and quickly as possible. Restoration of depressed populations should also proceed immediately.

Despite the broad scope for improvement of NEI foraging models, the current state of NEI models represent a substantial predictive advance over habitat-based models alone (see Hayes *et al.*, 2016 and references therein). Thus, the past 30 years of the development of NEI-based theory (see Piccolo *et al.*, 2014) is beginning to yield fruit in the scientific quest to link individual behaviour to population-level processes. NEI-based models have an immediate and important role to play in predicting the carrying capacity of stream habitat for conservation and restoration purposes. In the future, hypothesis-driven research based on a mechanistic understanding of drift feeding, as illustrated in this paper, can continue to improve the predictive capacity of NEI-based habitat quality models.

The long and rich history of ecological research on brown trout means that the species can serve as an excellent model for linking individual to population processes. The development of theoretically-sound drift-feeding NEI theory offers a unique opportunity for ecologists to directly test energetics-based fitness models. The successes and failures of such predictive models developed and tested for brown trout can inform conservation efforts for other fluvial species, many of which have lesser-known ecology. Furthermore, the ecological knowledge gained from such fitness-based models and tests should have broad eco-evolutionary implications that extend far beyond the stream banks.

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16

Competition Within and Between Year Classes in Brown Trout; Implications of Habitat Complexity on Habitat Use and Fitness

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Introduction

Brown trout is spread all over the world and can be found in a variety of habitats; from landlocked small streams and lakes to migratory populations. The spawning generally takes place in streams where the quality and abundance of suitable spawning areas for adult fish and nursery habitats for juvenile fish sets the limit of population size (Elliot 1994; Chapman 1966). The effects of habitat complexity and quality on population density of salmonids were already visualized in the classical paper by Kalleberg in 1958 in which he demonstrated how the size of the territory decreased with number of stones (Figure 16.1).

Since then, there has been an extensive amount of research investigating habitat preference and utilization of habitats in salmonids (reviewed in Armstrong 2003; Heggenes 1990; Fausch 1984). Generally, habitat utilization of stream salmonids can be described as multiple layers of filters where clearly habitat preference and utilization (realized niche) might differ substantially from each other (Höjesjö *et al.* 2015). First, the size- and species-specific swimming performance of fish will exert a primary control on the area of available habitat for each cohort. Thus, the first constraint or filter is environmental and is mainly determined by a combination of depth, velocity, substrate composition, in-stream structure and bank-side cover (Heggenes *et al.* 1999), and an individual fish is likely to respond to a combination of these variables (Armstrong *et al.* 2003). Together, this defines the fundamental niche and based on the energetic cost of foraging in a certain area and swimming abilities there will be a limited number of optimal as well as suboptimal foraging sites (Fausch 1984; Hughes *et al.,* 2013) for each individual fish. Secondary constraints include a broad range of local biological factors, including social interactions both within and between cohorts as well as species, predation risk and energy value of a patch, which collectively will define the realized or utilized niche (Figure 16.2).

For newly emerged salmonids, there is an intense density-dependence observed at the point of emergence (Einum *et al.* 2008), most likely due to a limited number of available habitats for the juvenile fish. At emergence, salmonid fry generally establish small territories

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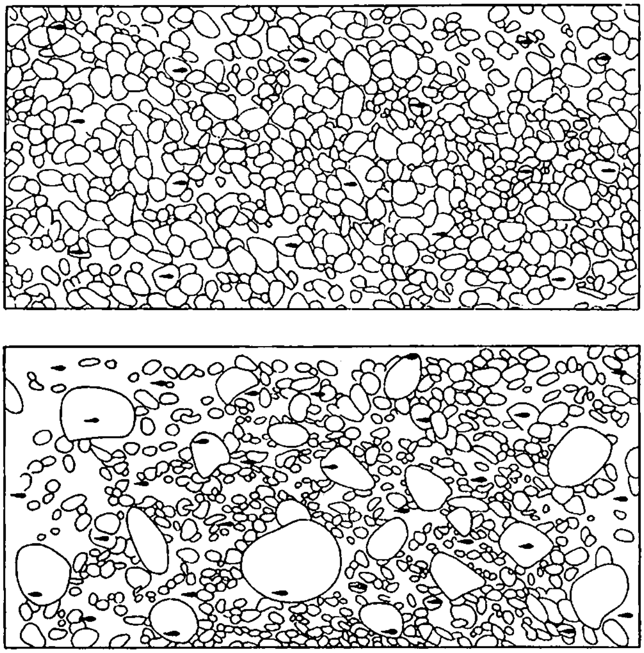

Figure 16.1 An illustration showing how habitat complexity decreases the size of the territory. For a fixed area (80 × 170 cm) the average size of the territory of salmon fry decreased with increasing complexity from 9.2 dm^2 (upper panel) to 4.5 dm^2 (lower panel). Modified after Kalleberg (1958).

(Grant *et al.* 1998), in shallow (<10 cm) habitats close to the stream-bank where the water velocity is low (Heggenes *et al.* 1999; Nislow *et al.* 1999) and the bottom substrate mainly consists of coarse gravel (Heggenes 1988). When fry outgrow these habitats they usually move further away from the spawning areas where they emerged and establish territories in deeper water with a sufficient numbers of structures such as larger stones and dead wood that gives relaxation from the water current, visual isolation (e.g., reduced numbers of aggressions) and protection from predators (Bardonnet & Heland 1994; Imre *et al.* 2002).

Generally, deep habitats of streams and rivers are often assumed as more profitable than shallow, marginal, areas. For example, deep areas may provide a better environment to find and forage on drifting food items through their larger area (Hughes & Dill 1990) and lower risk of predation from bank-side predators, such as heron (*Ardea cinerea*) and mink (*Mustela vison*) (Heggenes & Borgstrom 1988; Lonzarich & Quinn 1995). Deep habitats, in the centre of the stream-channel, may also have higher water velocity relative to marginal areas, resulting in a greater availability of invertebrate drift (Hill & Grossman 1993), an important food source of juvenile salmonids (Keeley & Grant 1995; 1997).

Hence, the question arises why do juvenile salmonids still use shallow, and presumably less beneficial habitats, during their first year? There seems to be at least three plausible explanations for this pattern: (1) Size-dependent habitat availability where the ability to swim and capture drifting food items increases with body-size (Nislow *et al.* 1999; Fasuch 1984); (2) Size-dependent predation risk; where movement of smaller individuals to deeper habitats may be more restricted due to the presence of piscivores such as northern pike (*Esox lucius*) or bullhead (*Cottus gobio*) (Greenberg *et al.* 1997;

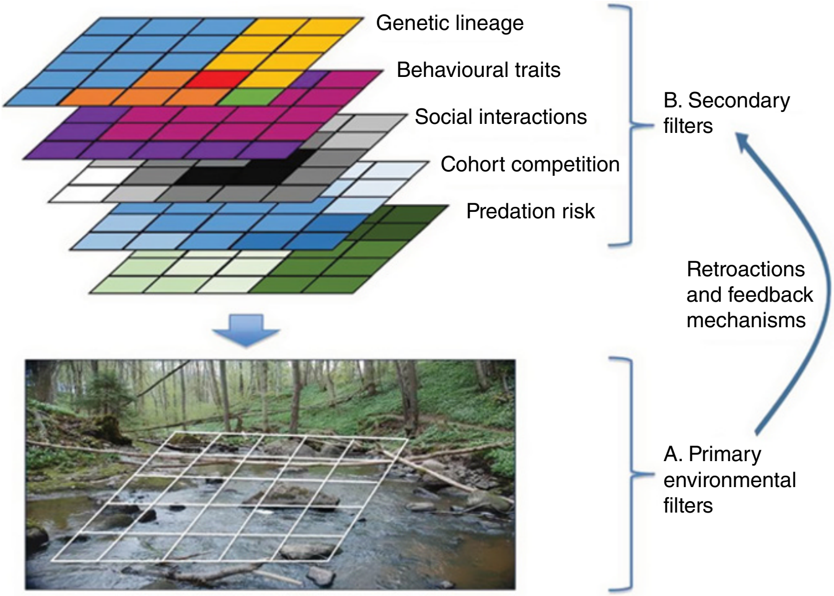

Figure 16.2 Habitat utilization of stream salmonids is first determined by a primary filter (A) where mainly abiotic factors such as depth, velocity, substrate composition, in-stream structure and bank-side cover will determine the range of available habitat for each cohort. Due to size-related and species specific swimming performance there will be a limited number of optimal foraging sites within these fundamental niches. Secondary constraints or filters (B) then includes a broad range of habitat specific filters such as predation risk, social interactions, individual behavior trait and energy value of a patch as well as genetic lineage which collectively will define the realized or utilized niche. The different colours in each of the secondary filters illustrate the numbers of possible combinations or variations. Clearly, all these filters will interact with each other as well as causing an interaction and feedback mechanism from the primary filter (A).

Roussel & Bardonnet 1999). Finally, (3) competitive exclusion (Hardin 1960) where young-of-the-year trout are excluded to shallow less preferred habitats, through intraspecific competition from older, more dominant, individuals (Armstrong 2005).

If older cohorts have prior access to the most profitable resources through their higher dominance rank and that cohorts of salmonids overlap in the preference for resources one would indeed expect a negative effect of older cohorts on young-of-the-year performance. In this chapter I will therefore try to summarize the current knowledge of how competition between and within year classes in brown trout (*Salmo trutta* L.) interacts with habitat complexity and how it may affect habitat utilization and fitness.

Evidence of Inter-Cohort Competition

Relatively few studies have investigated inter-cohort competition, in the context of resource use and behavioural interactions in fish, and has also almost exclusively focused on the effects from older cohorts. Some data has been provided though from coral-reef fishes, where young-of-the-year damselfish used feeding sites with lower food availability and increased risk of predation, in sympatry with older cohorts

(Webster 2004; Holbrook & Schmitt 2002). Further, small-sized individuals of the fairy basslet experienced 60% lower feeding rates in presence of larger, more dominant, conspecifics (Webster & Hixon 2000) and young-of-the-year individuals of the marine tidepool sculpin (*Oligocottus maculosus*) both reduced their use of predator-safe shelters and foraging activity in sympatry with older cohorts (Szabo 2002).

In populations of stream-living salmonids, several cohorts often coexist within a relatively confined area (Elliott 1994) which suggests a potential for intense inter-cohort interactions. Nevertheless, relatively few studies have explicitly investigated inter-cohort competition in salmonids and conflicting results have been reported. To my knowledge there are relatively few papers explicitly examining this effect in brown trout; no evidence of inter-cohort competition was provided based on observational time-series data on brown trout in the Black Brow's Beck (reviewed in Elliott 1994) and his influential work led to the conclusion that sympatric cohorts of salmonids experience low niche-overlap. However, this is a small and homogenous stream with a high density of fish and may not be representative of all streams and other studies have indeed indicated that competition between cohorts can be substantial, both reflected in altered space use, decreased growth and mortality; Bohlin (1977) for example, detected that young-of-the-year brown trout used riffles to a greater extent in sympatry with yearlings (1+) and later Vehanen *et al.* (1999) showed that older cohorts (>1+) excluded young-of-the-year trout (0+) from preferred velocity shelters. Further, Nordwall *et al.* (2001) detected that experimentally reduced densities of yearling and older (>1+) in natural stream resulted in increased apparent survival of age-0, age-1, and age-2 fish in the subsequent year. Similarly, Kaspersson *et al.* (2009, 2011) detected that young-of-the-year brown trout grew significantly better and selected deeper habitats when the density of older trout (>1+) experimentally was reduced.

Intuitively, negative effects of smaller less competitive cohorts on the performance of older conspecifics appear to be less likely. Nevertheless, Kvingedal and Einum (2011), detected a negative effect of local underyearling density on body mass of older brown trout (1+) to the same extent as from their own. Hence, despite their ability to change habitat, yearlings did not appear to prioritize growth rate per se as a cue in movement decisions and instead mainly distributed themselves according to preferred abiotic variables. Here, the yearlings were facing competition in some of the preferred habitat due to patchily distributed young-of-the-year fish (e.g. Kvingedal and Einum (2011)). A mechanistic explanation for this phenomenon was given by Kaspersson *et al.* (2010) in controlled experiments where yearling trout made significantly more unsuccessful foraging attempts and adopted a darker body coloration with increasing young-of-the-year densities. This indicates how the cost of defence may increase with under-yearling density, probably as a consequence of stress from interference with under-yearlings employing alternative competitive strategies.

Density Dependence and Ontogenetic Development in Performance

The carrying capacity of salmonid streams in terms of densities of brown trout is influenced by both environmental abiotic factors (e.g., flow, nutrients and temperature) as well as biotic conditions such as variation in predation, feeding opportunities and competition within or between species (Bohlin *et al.* 2002; Sundström *et al.* 2013) (Figure 16.2). As the population size approaches the carrying capacity of the area, emigration and mortality usually increase (Einum and Nislow 2005). Since all fish produce a large number of eggs, greatly exceeding the carrying capacity of the local habitat (Sinclair 1989), density-dependent mortality are generally substantial during the juvenile phase. Among stream-living salmonids this is especially apparent during the Early Critical Period (ECP) as the fry switches from maternal provisioning to external feeding. This has been demonstrated to be an important bottleneck in brown trout and mortality rates between 65% and over 90% during the first months after emergence have been reported (Einum & Fleming 2000; Elliott 1994). Spatial variation in initial densities during emergence has been shown to primarily influence mortality rates with little effects on growth or dispersal of those that survive but as the summer progresses, spatial variation in density becomes more likely to influence growth rates (Einum *et al.* 2006) which also is the pattern found in many natural populations (Jenkins *et al.* 1999; Grant and Imre 2005). Local competition may also to a larger extent cause increased dispersal away from areas of high density, suggesting an ontogenetic increase in dispersal abilities (Einum *et al.* 2006).

Two main models have been developed aiming to establish the relationship between the number of fish spawning (parental stock) and the number of recruits. The first model (Ricker 1979) describes a dome-shaped correlation between egg density and density of survivors a fixed period after emergence. Although the Ricker curve model has been proven to be correct in some streams (Gardiner and Shackley 1991; Kennedy and Crozier 1993; Crozier and Kennedy 1995; Dumas and Prouzet 2003), the second alternative asymptotic Beverton-Holt model (1973) suggesting that the offspring density reaches a maximum at a certain parental stock and then remains at this level despite an increasing parental stock has also proven to be correct (Poole *et al.* 2006; Chadwick 1985). Clearly, this suggests that increased density might affect mortality and growth to a different extent in different rivers. A high rate of mortality can be due to size-dependent habitat availability where newly emerged fry are restricted to marginal habitats with low food availability and high predation risk due to their reduced swimming capacity and maneuverability (Nislow *et al.* 1998; Armstrong & Nislow 2006). Alternatively, the presence of older cohorts could exclude newly emerged fry to less favorable, marginal, habitats, in the same way as size-dependent swimming capacity. Hence, although these theories provide different underlying mechanisms, both highlight the importance of marginal fry habitat in determining the intensity of density-dependence at the ECP (Einum *et al.* 2008; Nislow *et al.* 2004). As the fry grow, however, the availability of favorable habitats is assumed to increase no matter the underlying mechanism and will subsequently also lessen the constraints on population growth (Armstrong & Nislow 2006).

Density-dependent mortality and emigration seems to be most prevalent at high densities during emergence which could explain the lack of response on growth in high density population such as the population in Black Brow's Beck (Elliot 1994). In agreement, evidence for density-dependent growth has been provided primarily from low-density populations after the ECP (Grant & Imre 2005; Lobón-Cerviá 2005; Jenkins *et al.* 1999). A theory has therefore put forward suggesting that salmonid populations may be regulated via two mechanisms; exploitation competition for drifting food items at low densities, reducing the individual growth rate, and interference for limiting territories at high densities, reducing the survival rate. Hence, this would explain the lack of response on growth in high-density population (Elliott 1994) and support for this theory has been provided in several papers (Grant & Imre 2005; Imre *et al.* 2010; Jenkins *et al.* 1999). By adding small or large individual to a stream, Kaspersson *et al.* (2013) very nicely demonstrated how interference competition acts as the primary mode of competition in juvenile brown trout. They found a reduced growth rather than an increased mortality and movement when adding large individuals and argued that this might be due to exclusion from optimal habitats or increased stress levels among inferior individuals. In addition, young-of-the-year Atlantic salmon were observed to use several large multi-central territories within the stream habitat, rather than one single foraging station (Steingrimsson & Grant 2008) suggesting that stream habitats may be limiting even at relatively low densities, thus providing an additional explanation for the occurrence of density-dependence at lower densities than expected. Most likely then, interference and exploitation operates simultaneously in complex natural stream habitats, but that the detection of growth may be less obvious in high-density populations with a high mortality rate (e.g., Ward *et al.* 2007 and Lobon-Cervia 2007).

In addition, recent studies also suggest that density-dependent processes may be of importance at later life stages, for example during the first winter, probably influenced by both small body-size and low energy stores at the onset of winter, but also by density-dependent shelter availability and increased predation by mammalian and avian predators on individuals using less profitable habitats (Huusko *et al.* 2007).

Characteristics associated with individual performance, such as resource acquisition often correlates with body-size and individuals of different size- or age-classes tend to undergo ontogenetic niche-shifts; changes in resource use during the course of an individual's life-time (Werner & Gilliam 1984). For fishes, ontogenetic shifts have been attributed to for example size-dependent diet preferences; where small-sized individuals are restricted from feeding upon prey of certain size, or to predation; where juveniles use littoral habitats to avoid piscivorous predation but switch to deeper areas as they increase in size (e.g. Mittelbach 1981; Werner *et al.* 1983). These, size-dependent diet and habitat selection reduces the niche-overlap between cohorts and competition is sometimes believed to occur within cohorts rather than between (Elliot 1994). In agreement, young-of-the-year trout tend to remain in the marginal nursery habitats during the entire first summer, which are actively avoided by older age-classes (Armstrong *et al.* 2003; Heggenes & Borgstrom 1991). The ontogenetic shifts in habitat use or the 'bigger-fish–deeper-habitat relationships' seem to hold for many species of stream-living fishes (e.g. Davey *et al.* 2005; Mullen & Burton 1995) and is an especially common pattern in the distribution of salmonids in nature (e.g. Bohlin 1977; Bremset & Berg 1999; Greenberg *et al.* 1996; Mäki-Petäys *et al.* 2004). The data provided in this chapter suggest that this pattern to a large extent is influenced by the competition from older cohorts.

Habitat Complexity and Inter-Cohort Competition

Several papers have demonstrated how densities of fish increase with habitat complexity (Fausch & Northcote, 1992; Roni & Quinn, 2001; Lehane *et al.*, 2002; Zika & Peter, 2002; Degerman *et al.*, 2004; Sweka & Hartman, 2006). Generally, this phenomenon is explained by an increase in visual isolation from both predators and conspecifics, thereby decreasing the size of the territory as well as amount of aggressive interactions between fish (Kalleberg, 1958; Sundbaum & Näslund, 1998; Imre, Grant & Keeley, 2002) (Figure 16.1). Structural elements such as large stones, blocks and large woody debris will also alter the hydro-morphology of the stream and allow for an individual fish to be positioned immediately up- or downstream of the structure where the current velocity and cost of holding station will be lower (Fausch 1984; Hughes *et al.*, 2013). Generally, a fish should select a location that provide high energy intake whilst minimizing their energy expenditure. Fausch (1984) published the now classical first quantitative cost-benefit model for drift-feeding salmonids and it is now widely accepted that drift feeding represents an energetic trade-off between the costs and benefits of foraging in flowing water (Fausch 2014, reviewed by Piccolo 2014). For salmonids that forage on drifting invertebrates that usually transfers to a focal position that is maintained near the substrate, at relatively low water velocities, while foraging in the faster surrounding current that contains more drifting invertebrates. However, there is an important but generally neglected correlation between habitat complexity and drift foraging energetics. Management is based merely on the space in which fishes live (i.e., physical models that quantify the relative suitability for all habitat variables, such as habitat utilization indices (HSI) (e.g. Bovee 1986; Moir *et al.* 2004). Although these models are relevant to understand the distribution of the fish, it misses the importance of food in influencing fish habitat selection, growth and abundance (Grossman *et al.* 2002; Rosenfeld 2013; Armstrong 2010).

The energetics of foraging in pool and riffle are well-documented; at low discharge the velocities are slower in the deeper pools (Richards 1977; Knighton 1998) but as stream flow increases the velocity has been reported to increase relatively more in pools compared with the riffle (Wilkinson *et al.* 2004) and the pools might switch from being depositional to erosional (Rosenfeld *et al.* 2007). Overall though, the deeper pool areas generally are reported to be the preferred habitat for larger fish since it provides better protection toward predators and have a nearby access to drifting prey items. Individual fish that are able to maintain position in the pool are also expected to grow better because of lower swimming costs and increased prey capture success and supporting evidence of this has also been provided both from the field and controlled laboratory experiments (Hill & Grossman 1993; Harvey, White & Nakamoto 2004; Rosenfeld & Taylor 2009).

Some of the drift feeding models has also reported size-specific patterns where different size classes of fish are predicted to utilize different foraging positions due to size-specific returns in terms of energetic benefits/costs associated with a predicted habitat (Hughes & Dill 1990; Hill & Grossman 1993; Hayes, Hughes & Kelly 2007). Large trout has been reported to prefer pool habitats (Greenberg, Svendsen & Harby 1996; Bremset & Berg 1999; Heggenes, Bagliniere & Cunjak 1999), whereas smaller individuals to a larger extent occupies shallow riffle habitats (Heggenes 1996; Mäki-Petäys *et al.* 1997). In agreement with my reasoning above, the mechanisms behind this partial segregation is believed to be a combined effect of size-dependent preferences/swimming ability, inter-cohort competition and predation (Bohlin 1977; Power 1987; Schlosser 1987; Greenberg, Bergman & Eklöv 1997).

As high densities of woody debris alter the physical characteristics of habitats; generally decreasing mean current velocity, increasing pool frequency and increasing structural complexity (Riley & Fausch 1995; Hilderbrand *et al.* 1997; Keim, Skaugset & Bateman 2002), woody debris may have size-dependent effects on fish foraging. In agreement, Gustavsson *et al.* (2014) found that addition of large wood to a small boreal stream had a positive effect on the growth of large trout (>2+) but no effect on small trout (1+). Similarly size dependent effects of complexity where detected by Höjesjö *et al.* (2014) where the biomass of young-of-the year brown trout (0+) more than doubled and the condition index increased with added complexity. Hence, these studies are in agreement with the paper by Kalleberg (1958) (Figure 16.1), suggesting that the size of the territory decreases with structural complexity and that structure per se, at least for newly emerged fish, increases the number of individuals within an area. Additionally, this positive effect could also be due to an enhanced production of food and protection from predators and/or superior competitive older individuals. A more complex habitat may also allow for algae and subsequently invertebrate prey to settle (Harmon *et al.* 1986; Sundbaum & Näslund 1998). However, in the study by Höjesjö *et al.* (2014) this effect was only present initially after emergence and six week later, there were no effects on density, biomass or condition. Surprisingly, the size of both the young-of-the-year fish (0+) and older fish (<1+) was now instead smaller in the more complex habitats. One possible explanation for this finding could be ontogenetic development where food requirements and competition for space change with size (e.g. Ayllón *et al.* 2010; Wood *et al.* 2012). Here, YOY fish preferred and aggregate in the more complex habitat but with size, the density-dependent competition for limited food/space in the complex treatments apparently increased whereas in more simple habitats initial densities of YOY fish were lower allowing a faster growth rate despite lower habitat quality. Alternatively, since monopolization of resources generally is related to size (Johnsson *et al.* 1999, Kemp *et al.* 2005), it is plausible that increased habitat complexity decreases the ability to monopolies a foraging area.

Bolder individuals could then actively choose to forage in more risky habitats with more predators if competition from conspecifics was lower causing growth rate to be higher in these habitats. This finding is also supported by previous studies where aggressive dominant brown trout have been shown to grow slower in more complex habitats (Höjesjö *et al.* 2002, 2004). In addition, during period of draught, local population density may increase and Stradmeyer *et al.* (2008) experimentally showed that dominance status is even more important during such an event; immediately after dewatering, dominant fish increased their aggression and ceased feeding. However, feeding soon returned to normal for the dominant individual whereas there was an overall reduced average feeding within the group at draughts, increasing the polarization between the top ranking fish and others even further.

If there is a selection for bolder more dominant individuals to grow better in certain areas this might maintain personality differences within the population and lead to coevolution of behavioural, physiological and life history traits, also referred to as the ‘pace of life syndrome’ (POLS, reviewed in Reale *et al.* 2010 and discussed in Zavorka *et al.* 2015). This is indeed an expanding research field and beyond the scope of this chapter but it is important to include personality differences within and between cohorts in order to fully understand the distribution and growth patterns of brown trout in different habitats.

Conclusion and Implications for Management

To summarize, the data provided here suggest that the observed difference in habitat use between young of the year and older brown trout to a large extent is influenced by habitat exclusion from the older cohort. With a large cohort of yearlings, newly emerged fish may then be outcompeted to shallow low velocity habitat with a reduced growth. Increasing habitat complexity on the other hand has been proven to increase the density of fish, but may also act as a refuge from aggressive interaction both within and between cohorts which may alter the population dynamics.

Although strong evidence for inter-cohort competition has been provided here, there is also papers suggesting a lack of competition between cohorts. One reason for the diverging results could be that factors such as food preference and temporal activity patterns might have been overlooked and this may offcourse influence the intensity of inter-cohort competition (Bremset & Berg 1999; Bremset & Heggenes 2001). Generally, there is positive correlation between prey size and salmonid body-size (e.g. Amundsen *et al.* 2001; Bozek *et al.* 1994; Bridcut & Giller 1995; Fahy 1980; Hunt & Jones 1972; Keeley & Grant 1997; Steingrimsson & Gislason 2002) but diet selectivity have also been reported where different cohorts of older trout parr (age 2 and older) forage upon significantly different invertebrate taxa and large salmon parr (12–15 cm) used surface feeding to a greater extent than smaller individuals (10 cm) (Stradmeyer & Thorpe (1987). Nevertheless, there is conflicting results also indicating a potentially large overlap in diet among size-classes and cohorts (e.g. Amundsen *et al.* 2001; Bozek *et al.* 1994; Elliott 1967; Keeley & Grant 1997). Temporal segregation has also been demonstrated under laboratory conditions, where large-sized, dominant, individuals foraged during the beneficial hours at dusk and night while subordinate fish were active at dawn and day, when the risk of predation is higher (Alanärä *et al.* 2001).

Similarly, Zavorka *et al.* (2016) found that individuals with high activity in the laboratory displayed high dispersal and distributed their activity evenly throughout the daily cycle when released in their natal stream. In contrast, trout with low laboratory activity were more active during the night. This suggests that although diet is dictated by the intensity of drifting prey older cohorts may be differentiated also in foraging diet selective behaviour or temporal segregation and clearly more research is needed to elucidate these patterns.

Another important aspect to consider is the species specific difference in habitat preference and distribution among salmonids. Brown trout often lives in sympatry with Atlantic salmon and although they to some extent overlap in their distribution indicating a potential competition of resources they also have species specific characters; Brown trout is usually considered to be more aggressive and dominant compared with salmon (Höjesjö *et al.* 2005). Atlantic salmon on the other hand is better adapted to fast flowing water with their larger pectoral fins that act as hydrofoils enabling them to maintain position at a higher velocity relative the Brown trout (Arnold *et al.* 1991). Hence, salmon yearlings and over-yearlings tend to have their main occupancy in high-velocity habitats (20–60 cm s^{-1}), whereas the distribution of older trout have been reported to be directed towards deep but slow flowing habitats (pools) (<20 cm s^{-1}) (Armstrong *et al.* 2003; Heggenes 1988; Heggenes *et al.* 1999; Näslund *et al.* 1998).

For management purposes, the data provided here clearly suggest that habitat complexity is important for the survival and recruitment of newly emerged brown trout. Although, the importance of shallow low velocity habitats near the spawning sites already is well established and understood the underlying mechanism for this is more likely to be competitive conclusion from older cohorts rather than constrains in maneuverability of the newly emerged fish. For restoration work in rivers these results should indeed be incorporated into strategies aiming to identify limiting factors and prescribing appropriate restoration activities in order to increase the density of brown trout stock in rivers. One of the challenge for the future in order to fully understand habitat partitioning among salmonids will be to assess and quantify all set of hierarchical filters that may affect the distribution in a natural river (Figure 16.2). To increase our understanding of population dynamics, distribution and growth pattern of salmonids in a realistic complex environment it will therefore be important to merge habitat suitability models (Armstrong *et al.* 20003, Milner *et al.* 1998,1993) with drift feeding models (Hughes *et al.*, 1990, 2003, 2013; Piccolo *et al.* 2009, 2014) as well as to includes individual variation in behaviour such as boldness and dominance rank where usually only few despotic individual may choose foraging sites freely.

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17

Brown Trout on the Move – Migration Ecology and Methodology

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Introduction

Readers of this book should not be surprised to learn that the brown trout[1] has an amazing wide range of life histories. Thus, a trout is far from just being a trout; there is a multitude of different ecological types of trout, many of which are related to the behaviour in terms of migrations between habitats.

Studies of trout ecology, especially in terms of migration, started early in the previous century. In many respects, trout has been the 'poor cousin of Atlantic salmon', and much research was focused on salmon. Though the general life-cycles are similar, it was early recognized that there are specific differences between the two species, leading to studies specifically addressing trout. Although much focus has been, and still is, on Atlantic salmon, trout is nevertheless recreationally and economically important in many areas, mainly because it is widely distributed and available for a much wider range of people than the somewhat exclusive salmon fishing.

The first genuine book in English specifically dealing with trout life history, including migration, was probably 'The Life of the Sea Trout' by Nall (1930), but older books exist in other languages (Johansen & Løfting 1919; Dahl 1910). The available methods at that time set limits to what could be studied, principally involving trapping, scale reading and external attachment of small numbered silver plates (an early form of Carlin tags), which are methods most trout ecologists are familiar with even today. The results provided information on growth and general whereabouts of the trout. Based on tagging and recapture studies, it was possible to record movement of trout on a coarse scale, providing the first systematic data of migrations between habitats and movement speeds. However, data based on tagging and recapture are strongly biased by variation in catch per unit effort (CPUE), because there will be no recoveries from areas where

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[1] In the following chapter, hereafter referred to as 'trout'. When we refer to other trout species than *Salmo trutta*, their full species name is given. The term anadromous trout is used when we specifically mention sea-run trout or sea-trout.

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there is no fishing, and it is unknown what the fish did between tagging and recapture. That being said, much important ecological information on trout has been generated based on these methods, including the description of three major migrations: (1) the juvenile downstream migration as smolt; (2) the migrations of immature fish (often termed finnock and whitling); and (3) the migrations of adult fish related to spawning (Allan & Ritter 1977).

The classical research methods are universally applicable, and are still widely used today. However, their limitations coupled with recent technological development have led to a suite of new methods that provide higher resolution data on the behaviour and migration not only on trout, but on animals in general (Hussey *et al.* 2015). In this chapter, we focus on the downstream smolt migration and the upstream spawning migration of mature anadromous trout. We also aim to provide an overview of the most important electronic tag methods, also termed telemetry, which can provide higher resolution data on the whereabouts of the trout during their migrations.

Animal Migration – and the Trout in this Context

There are several definitions of migration, and many of them are adjusted to describe a situation within a single group or taxon (Dingle 1996). A more general approach was suggested by Dingle (1996), defining migration as:

> *a persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence.*

This complex definition illustrates the diverse mechanisms involved in migration in different taxons. A shorter definition was suggested by Taylor & Taylor (1977), when they defined migration as '*a fundamental biological response to adversity*', meaning that an animal migrates when the conditions of the surrounding environment are unfavourable. Northcote (1978, 1984) defined fish migration as '*movements that result in an alternation between two or more separate habitats, occur with a regular periodicity, and involve a large part of the population*'. This definition is based on a view on migration as a way to optimize fitness of individuals by moving between habitats suitable for different purposes (e.g. feeding and reproduction).

In many fish species, migration is a common endeavour (Lucas & Baras 2000). The anadromous salmonids have life-cycles with multiple migrations, starting at the end of the embryonic period, when the fish move through the gravel to the surface of the spawning substrate and shortly thereafter disperse over the nearby streambed (e.g. Thorpe 1988, Thorpe & Moore 1997). These small-scale migrations are followed by much longer ones; from freshwater to seawater, and back to freshwater (e.g. Harden Jones 1968, Thorpe 1988). Within the Salmonidae, the different genera display a diverse pattern of migration, from the obligate anadromous pink salmon (*Oncorhynchus gorbuscha*) to the exclusively non-anadromous Danube salmon (*Hucho hucho*) and lake trout (*Salvelinus namaycush*), undertaking only short migrations within the river or lake (Hoar 1976; Thorpe 1988). The trout has a variable life-cycle, and populations prosper in numerous places without anadromous individuals (Jonsson 1985). Both males and females may stay and complete their life-cycle in freshwater. This particular ability is important for the resilience of the species, because it enables an otherwise anadromous population to survive potential perturbations over time, such as blockage of migration (e.g. beaver dams), but more importantly anthropogenic constructions such as weirs, water mills and hydropower dams. The high degree of flexibility in life history is probably one of the main reasons that trout today are much more common and widely distributed than its close relative Atlantic salmon.

For trout, the first long-distance migration is the downstream movement of juvenile fish (smolt) to the sea, which is believed to be a feeding migration driven by the larger growth potential in the sea. Increased growth enhances fitness of the individual (Gross 1987). Another important migration is the return migration and upstream movement of adult fish to the natal stream for reproduction (Harden Jones 1968; Gross 1987). The trout do, however, sometimes migrate between the sea and freshwater without this being a spawning migration (Le Cren 1985). In autumn and winter, proportions of some anadromous trout populations enter the lower rivers, after spending only a few months at sea and leave again within few months. The majority of these fish are sexually immature, thus the migration is not linked to reproduction (Le Cren 1985). A trout at this particular stage is called a finnock (Allan & Ritter 1977). This type of migration is rarely studied, and the reason for this upstream migration of the immature trout is poorly understood, but it has been hypothesized that the combination of high salinity and very low water temperature force these immature individuals to overwinter in freshwater (Thomsen *et al.* 2007). However, reduced saltwater tolerance seems not to be the sole explanation for the behaviour (Walker *et al.* 1996). This migration can be an anti-predator behaviour, if winter growth potential in the sea is limited, while predation pressure can be high.

Benefits of Migration

Migration is one of the most complex, fascinating and yet fundamental biological phenomena in the animal kingdom, and is observed in a wide variety of taxa (Dingle 1996). Animals are thought to engage in movements or migrations to optimize fitness. This can be achieved through a number of ways, including: (1) increased survival probability (moving to low-risk areas); (2) increased growth (higher fecundity, competitive ability); and (3) increased chance of mating (finding potential mates and spawning grounds). These three purposes can explain most trout migrations. To maximize its chance of survival, a trout should ideally stay in the stream close to where it was hatched throughout its life. This is indeed what some individuals do, and under some circumstances, this may be the best choice. For instance, in a river with low connectivity, this may be the optimal strategy. However, if there is a possibility to undertake migrations between habitats and actually return to the natal stretch, or colonize other suited spawning areas, migration may be a superior strategy. If an individual takes the risk of moving to another habitat, be it a larger river, a lake or the sea, the benefit of more food can often compensate for a potential increased mortality risk. With more food, they achieve faster growth, larger body size, more eggs, better competitive ability and thus more offspring. The relationship between body size, egg size and fitness in terms of viable offspring is well documented for female salmonids (Einum & Fleming 1999), whereas the relationship in males remains more ambiguous, but there is evidence that very large males do have high reproductive success.

One way of studying such mechanisms in the field is by monitoring trout populations in low connectivity streams for a number of years, then restore connectivity by removing obstacles and continue the monitoring. We have done so at several sites in Denmark and have observed a swift increase in abundance of juvenile trout as a response to restored connectivity (own unpublished data). Studies in low connectivity Austrian Rivers have revealed a general trend of higher fish biomass per area with increased connectivity, measured as distance between barriers up- and downstream (N. Schotzko, pers. comm.). It may not be surprising that the ability to move relatively freely and safely between different habitats is an asset, and for trout, it is evident that populations inhabiting free-flowing streams with access to large lakes or the sea are more productive than populations restricted in movement. Besides the benefit gained in terms of growth, the possibility to escape dangerous conditions like extreme cold, dry-out periods, high predation events, warm water, low oxygen levels, pollution, low food availability and parasite loads is beneficial.

The advantages associated with migration are well documented, and if an individual can make the right decisions, it may hit the jackpot and experience High growth at minimal risk. But how can an individual make these right decisions? A trout staying in one restricted reach of a stream may achieve information about its surroundings to gain experience enough to make local decisions. However, how can a trout in a small stream get information about crucial factors like sea temperature, predation risk in an estuary, food availability along the coast and the number of obstacles to pass before reaching the sea? Such information is crucial for a trout that are to make the decision of staying or going–to choose a resident or anadromous life history. When an adult trout are to decide when to return to the natal stream to spawn, the same problem arises. A trout may play it safe and enter the river many months before the spawning period. In that way, it will be sure to get there in time and maybe occupy an attractive holding site in the stream. On the other hand, staying in the sea or lake for several more months feeding will greatly increase body size, thus improving both fecundity and competitiveness. The truth is probably, it cannot. Individual trout must rely on some evolutionary shaped indices embedded in genetic or epigenetic fabric of the individual. We do not yet understand the mechanisms involved in the decision making of trout, but the importance of these decisions is high, and they are based on sparse information.

Trout Migrations are not Easily Categorized

Trout parr in a small tributary as well as large anadromous trout in the sea have no way that we know of to obtain information on other habitats than where it stays to aid the decision-making. The mechanisms that do in fact regulate this decision-making are both interesting from a scientific point of view and relevant from a management perspective. Through field and laboratory studies of wild fish, often using telemetry methods, we have learned considerably more about individual fish movement and timing of migration, which is addressed in detail in this chapter. Not long ago, there was consensus that smolt outmigration was a coordinated event, where fish would benefit of being part of a large group and thus try to migrate out during a relatively short smolt migration period. Likewise, it was believed that sea-trout spawning migration occurs mainly in summer/autumn, and that fish observed earlier or later were exceptions and outliers. Telemetry studies have provided detailed information on individual fish movements and made it clear that trying to categorize trout behaviour from the mean values of observations made little sense, whereas the variation in behaviour provided useful insight. We have learned that in many instances the outliers and 'abnormal' behaviour was the rule rather than the exception. Today, it is safe to conclude that trout migrations are highly flexible and not easily categorized.

Smolt Downstream Migration

The seaward smolt migration is believed to be a movement towards more favourable habitats for feeding and growth, which ultimately enhance fitness (Gross 1987; Jonsson & Jonsson 1993). Residing and growing in a stream, juvenile trout basically have three alternatives at the individual level, linked to the growth potential: (1) stay in the stream, mature and participate in reproduction if they have had sufficient growth; (2) smoltify and migrate downstream the following spring; or (3) remain as immature fish one more year in the river (Thorpe 1987). When and how these decisions are made remains unclear.

One hypothesis, developed for Atlantic salmon, suggests that the developmental path of the individuals is taken in late summer, several months before the actual event of migration (Thorpe *et al.* 1998). At this critical point in time, inherited reaction norms will be balanced against the current growth status, and the outcome will be a choice of developmental path. If the path is smoltification, hormonal changes will spur a number of changes in the trout, ultimately leading to downstream migration. Initially, the fish grow faster than conspecifics that will be resident another year (because the latter group decreases appetite), leading to different length distributions between the two groups in autumn. Maturation and smolting have been described as physiologically reverse processes, as maturation in both sea trout and salmon parr has been shown to delay and even inhibit smolting the following spring (Dellefors & Faremo 1988; Berglund *et al.* 1991). The smoltification process in trout is reversible, and smolts kept in freshwater can desmoltify and again attain the characteristics of a freshwater resident (Hoar 1976).

Age, Size and Sex of Trout Smolt

The age of trout smolts has been found to vary from one to eight years (e.g. Okland *et al.* 1993; Anonymous 1994), with mean smolt age being related to growth rates (Jonsson 1985). There is a positive correlation between increasing latitude and mean smolt age, probably reflecting the generally poorer growth potential in northern climates related to colder temperatures and shorter day length (Elliott 1975; Egglishaw & Shackley 1977; L'Abee-Lund *et al.* 1989). For example, the mean smolt age for trout in France is 1.1 to 1.6 years, with 3 y old smolts being the exception (Euzenat *et al.* 1999). In Lake Ijsselmer in the Netherlands, 75% of the trout captured at sea had reared for only one year in freshwater before migrating to sea, with 20% migrating at two and 5% at three years of age (de Leeuw *et al.* 2007). In Denmark, the mean smolt age for trout is between

1.8 and 2.2 years (Christensen *et al.* 1993). Mean smolt age in Norway varies between 1.5 and 5.6 years depending on latitude (L'Abee-lund *et al.* 1989).

The mean length of trout smolts in different populations vary between 12 and 20 cm (Anonymous 1994) and between 10.7 cm and 25.2 cm, with an individual range from 6 to 32 cm (Jonsson & L'Abée-Lund 1993). Generally, the reported variation is lower on the British Isles (15–23 cm, Fahy 1980; Pratten & Shearer 1983), and in Irish rivers (17–25 cm, Went 1962a). Mean smolt size increased with latitude along the Norwegian coast, but such a pattern was not found in a broader study area (Jonsson & L'Abée-Lund 1993). However, most of these data are obtained from trap catches and thus subjected to variation in terms of trap efficiency versus size of the trout. Therefore, care should be taken before making comparisons among studies.

The sex ratio of trout smolts is usually in favour of females, typically 60% to 70% females (Christensen *et al.* 1993; Euzenat *et al.* 1999; Knutsen *et al.* 2004; Olsen *et al.* 2006; Solomon 2006). However, there are exceptions, where equal ratios between females and males have been observed (Le Cren 1985; Elliott 1993). The reason for this overrepresentation of females can be explained as a trade-off between survival and fecundity, as the investment in one reproductive unit (egg and semen) is considerably higher in females than in males. Therefore, the potential gain of increased growth opportunities by smolting and migrating to the sea is believed to favour females compared to males (e.g. Gross 1985).

Seasonal Timing

The main smolt migration occurs in the spring and early summer (Jensen 1968; Gargan *et al.* 2006; Jonsson & Jonsson 2009; Jensen *et al.* 2012; Rasmussen 1986). As with smolt age, there is a correlation between latitude and the time of migration, with later migration at higher latitudes (Hansen 1990; Anonymous 1994). In Southern reaches like Galicia in Spain, the smolt migration period is from March to May (Caballero *et al.* 2006). In Denmark, the trout smolt migration takes place from mid-March to late May (Christensen *et al.* 1993), usually with a peak migration in the middle/last part of April and early May (Rasmussen 1986; Nielsen *et al.* 2006). The same pattern has been observed in Scottish rivers, with smolt migration from the end of March to mid-May, but peak run timing vary among years, from early April to first half of May (Pemberton 1976). In the most northern parts of the distribution range, the main migration starts as late as June, with some median migration dates well into July (Jensen *et al.* 2012). Timing of migration does not only change with latitude, but there is also local variation dependent on environmental conditions. The main trout smolt run may last for one or two months, and in comparison to salmon, the migration period is longer, and may occur more erratic over the season (Thorstad *et al.* 2011; Thorstad, Whoriskey *et al.* 2012).

Smolt size and age seem to play a role in the timing of migration, as the largest and oldest smolts tend to migrate earlier in the season than smaller and younger smolts (Rasmussen 1986; Bohlin *et al.* 1993; Bohlin *et al.* 1996; Gargan *et al.* 2006). However, individual growth is probably the underlying reason as there is no critical length determining migration (Økland *et al.* 1993), and timing of downstream migration depends on body size, not age (Bohlin *et al.* 1996). Acolas *et al.* (2012) found growth rate to be a better predictor than body size. Later migrating smolts have often grown considerably during spring, a growth termed 'b-type growth' (Fahy 1980).

Time of Day

Most studies have found trout smolt migration to be nocturnal (e.g. Moore & Potter 1994; Aarestrup *et al.* 2002). A few studies in northern regions have described salmon smolt migration to occur during daytime (e.g. Bakshtanskiy *et al.* 1980), which may be due to the near 24-h daylight during smolt migration in these regions. Furthermore, studies have shown that late in the smolt period, an increasing number of salmon smolts migrate during daytime (Hansen 1990). This has been interpreted as a response to increased water temperature as the season progresses, making the fish more active during daytime (Thorpe & Moore 1997) and having a better escape response to predators (Rikardsen *et al.* 2006). None of these observations have been described in detail for trout, but will likely also apply for trout smolts. Substantial daytime migration, in the middle of the main smolt run, has been observed probably as a consequence of a rapid water temperature increase (Aarestrup *et al.* 2002). The proximate stimuli initiating the nocturnal migration pattern has been explained by smolts losing visual cues, and thereby, responding to low light levels by moving up in the water column and passively migrating downstream (Moore *et al.* 1998). The ultimate factor explaining this behaviour may be survival optimisation by reducing predation risk (Moore *et al.* 1998), a plausible explanation considering recent reports of very high predation pressure on migrating smolt (see below).

Preparatory Changes

Change in photoperiod has been described as the major factor initiating the physiological changes associated with the smolting process in salmonids, with temperature as a co-factor via inhibition of prolactin (McCormick & Saunders 1987). During the smoltification process, the fish undergo a number of preparatory morphological, biochemical and physiological changes to adapt to the life in high salinity water (reviewed by Hoar 1988, Boeuf 1993). The morphological changes include a slimmer body form, darkened fins and a silvery appearance (Figure 17.1).

Figure 17.1 Five juvenile trout caught on the same day, showing different degrees of smoltification, ranging from non smoltified (uppermost fish) to fully smoltified (lowermost fish). Photo: Finn Sivebæk.

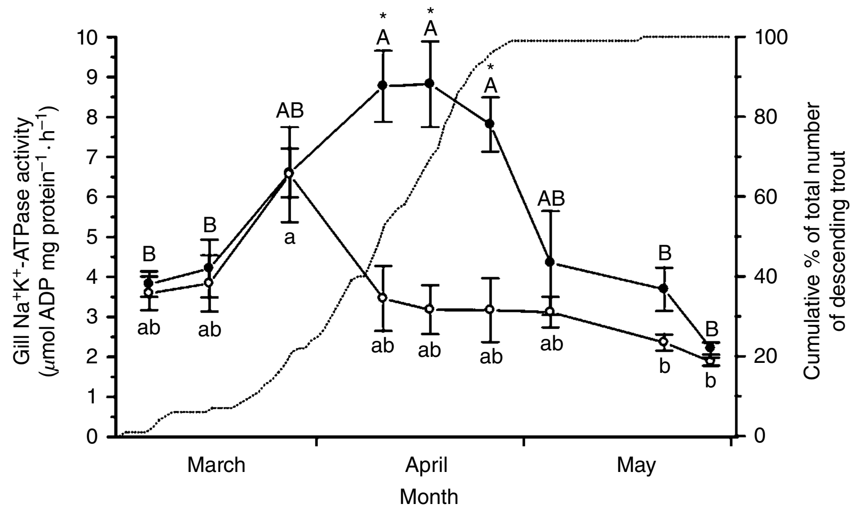

Figure 17.2 Spring changes in mean gill Na+, K+-ATPase activity in wild brown trout caught in a trap (filled circles) and by electrofishing (open circles). Dotted line shows cumulative catch in percent of the total number of descending trout caught in the trap. Na+, K+-ATPase activities are mean values ± SEM of eight to ten fish, and values with shared letters are not significantly different ($P > 0.05$). Capital and lower-case letters are used for trout caught in the trap and by electrofishing respectively; asterisks indicate significant difference in Na+, K+-ATPase activity between trout caught in the trap and trout caught by electrofishing on a particular sampling date. From Nielsen *et al.* (2006).

Physiological changes include a decrease and change in composition of body lipids, loss of glycogen from the liver and increased gill Na+,K + -ATPase activity (Hoar 1976). Na+,K + -ATPase is believed to generate the ionic and electrical gradients, which drives the active salt excretion necessary when the fish is in a saline environment. The increase in gill Na+,K + -ATPase activity is considered to be a reliable indicator of the smolting status of salmonids (e.g. Boeuf 1993), and further has the advantage that a live-biopsy can be taken, enabling the possibility for monitoring behaviour of individual fish with known levels of ATPase. Increases in gill Na+,K + -ATPase activity are reported to temporally coincide with changes in plasma level of growth hormone (GH), prolactin, cortisol and thyroxine (T4) (see reviews by Barron 1986, Boeuf 1993), indicating that the physiological changes during smolting may be neuro-chemically or hormonally linked to migration.

Little is known about the relationship between individual physiological development and migratory behaviour in the river, which is an area where telemetry provides a powerful method. Coupling telemetry with individual measurements of physiological status have proven successful (Cooke *et al.* 2004) and has been used in several studies combining results from electronic tagging and gill biopsies of individual trout. Aarestrup *et al.* (2000) demonstrated a relationship between smolt status measured as gill Na+,K + -ATPase activity and the subsequent behaviour of two different stocks of hatchery reared trout after release in a river. There was a clear relationship between gill Na+,K + -ATPase activity and the time until initiation of downstream migration. Fish released in March and April predominantly migrated downstream in April, when measurements of gill Na+,K + -ATPase activity were highest. At the third release in

May, when gill Na+,K + -ATPase activity was regressing, the fish started to migrate downstream immediately, but in lower numbers than the two previous releases. The coupling to gill activity was further corroborated in Nielsen *et al.* (2004), where gill activity was shown as a reliable predictor of future migratory behaviour, and in Nielsen *et al.* (2006), where a comparison between migratory and resident fish was made in a wild population (Figure 17.2).

Initiation of Migration

The smolt migration seems to be synchronized by increasing day-length (Hoar 1988). A proximate stimulus is needed for migration to be initiated (Hoar 1976). Smolts of Atlantic salmon and trout respond similarly to the abiotic factors (i.e. temperature) that initiate migration (Leonko & Chernitskiy 1986). Generally, initiation of migration is correlated with an increase in water temperature and/or flow in the river (Jonsson & Gravem 1985; Bohlin *et al.* 1993; Aarestrup *et al.* 2002; Jensen *et al.* 2012; Aldvén *et al.* 2015a), with relative importance of water discharge and temperature varying among years (Hembre *et al.* 2001). Large numbers of migrating smolts early in the season are often coinciding with high flow events (Pemberton 1976).

The correlation between migration, temperature and flow is complex and differs among systems. Studies on trout in Sweden have shown different effects between streams and also different response to temperature depending on the actual temperature level (Aldvén 2016). Studies on salmon in Norway have indicated that downstream migration of smolts correlates well with seawater temperature irrespective of the factor (temperature or water flow) initiating the migration (Hvidsten *et al.* 1998). This suggests that the timing of salmon smolt migration is inherited, population-specific and adapted to meet the most favourable osmotic and feeding conditions at sea outside the native river. This is supported by observations of genetically based differences of the behaviour in fry (Brannon 1972; Kelso *et al.* 1981), juvenile (Taylor 1991) and adult (Hansen & Jonsson 1991) salmonids. However, none of these observations has so far been reported in trout, revealing a clear need for further research.

Behaviour

The downstream migration in Atlantic salmon smolt has been described to be mainly passive by displacement (Fried *et al.* 1978; Hansen *et al.* 1984; Greenstreet 1992), but also active movement has been reported (Kalleberg 1958; Fangstam 1993). Smolts primarily move downstream by following the current, actively selecting the areas of the stream with the highest velocity (Bakshtanskiy *et al.* 1988). The highest velocity is often found in the main flow of the river, and from telemetry studies it has been observed that smolts tend to follow the main flow of the river (Fried 1977).

Behavioural changes of smolts during migration include a decrease in aggression and rheotactic behaviour, which enables the fish to leave the territories on the streambed and form schools (Folmar & Dickhoff 1980). Based on visual observation, Bakshtanskiy *et al.* (1980) concluded that smolt migrate both as individuals and in schools, and that individual fish often group when encountering a site of potential danger. School formation is believed to reduce individual risk of predation, and is therefore a means of increasing the chance of survival (Hansen 1990). None of the above observations has been reported in trout and should be further investigated. Energetic status may also affect the length of the migration. Boel *et al.* (2014) found lower triacylglycerides levels in short-distance migrating trout smolts, indicating that they were more lipid depleted prior to migration than the long-distance migrants, suggesting that the energetic state of individual fish provides a possible mechanism underpinning the migration continuum in brown trout.

The net ground speed in freshwater of migrating Atlantic salmon smolts has been observed to vary considerably. Velocities from 0.2 km/day and up to 28 km/day have been observed (Allen 1944; Mills 1964; Ruggles 1980; Thorpe *et al.* 1981; Hansen & Jonsson 1985; Shearer 1992). Data on trout smolts are scarce. Net ground speed of wild trout smolt through a river has been observed to vary considerably between 1 and 60 km/day (Aarestrup *et al.* 2002). The net ground speed can be considerably higher during flood conditions than under normal flow conditions (Aarestrup *et al.* 2002). Serrano *et al.* (2009) investigated migration of trout smolt through a lower river and estuary and recoded mean speeds between 5.7 km/day and 33.1 km/day, depending on the particular stretch where the net ground speed was recorded. Through lakes, the migration speed is slower than in rivers, but can still attain several km/day (Jepsen *et al.* 1998). The slower migration speed in lakes is probably because of lower current velocities compared with rivers, and/or because smolt to some extent lose their orientation.

It should be noted that the net ground speeds are estimated by different methods, and ground speeds recorded by trap catches, tagging with electronic tags and other methods may be affected in method-specific ways. Traps are typically tended daily, reducing the accuracy of arrival time in the trap. This will lead to underestimations in calculations of migrations speed, as opposed to using loggers recording fish with electronic tags, where often the timing of arrival is measured precisely. Both methods are subject to variation caused by the difference in distance over which the speed is recorded, and of diel variation in the fish behaviour. A smolt moving downstream 24 h per day will migrate faster than a smolt migrating only nocturnally.

Further studies of trout migration behaviour and speeds are needed. For example, knowledge on heritability of the response of trout smolts to factors initiating migration is lacking. A comparison of trout smolts from rivers with different flow regimes, and of smolts from rivers with different light conditions (i.e., with and without 24 h daylight), would also provide basic knowledge of mechanisms influencing the smolt migration.

Smolt Loss

Smolt loss in a river may occur as a direct result of predation, disease or because smolts cease the migration before reaching the sea. Nielsen (1996) compared the mortality of migrating smolts of Atlantic salmon and trout from several studies and found that the mortality of smolts migrating downstream in rivers averaged 1.2% km^{-1} migrated distance for salmon and 1.5% km^{-1} for trout smolts. Gauld *et al.* (2013) showed that low spring flow regime gave significantly higher smolt loss during the downstream migration. Migration of smolts through lakes gave considerably higher mortalities, on average 14.5% km^{-1} for trout smolts and 19.1% km^{-1} for salmon smolts. Low survival through lakes appears to be the norm for trout smolts, with several studies showing survival below 20% (Jepsen *et al.* 1998; Olsson *et al.* 2001). Hence, smolts migrating through one km of river have a considerably higher chance of surviving than smolts migrating through the same distance of a lake, reservoir or impoundment. This difference may be explained by a lower migration speed in the lakes, combined with a high density of predators in lakes compared to the rivers (Jepsen *et al.* 1998; Aldvén 2016). The fate of smolts passing a reservoir was studied by Jepsen *et al.* (1998). The loss of radio-tagged smolts was close to 90% for both trout and salmon. The majority of the loss was predation, where pike (*Esox lucius*) was the most important predator in the lake, eating close to 40% of both the salmon and trout smolts. Besides pike, pikeperch (*Sander lucioperca*) have been reported to eat trout smolts (Carl & Larsen 1994). Also many bird species have been reported to prey on smolts. Predation by grebe (*Podiceps griseigena*) and grey heron (*Ardea cinerea*) was recorded by Jepsen *et al.* (1998), and cormorants (*Phalacrocorax carbo*) have also been documented to be effective smolt predators (Koed *et al.* 2006, Jepsen *et al.* 2010).

The telemetry study by Jepsen *et al.* (1998) indicated potential high-risk areas when passing a reservoir. The predation seemed to be concentrated in the upper part of the lake where it widens out, in the middle part, where the fish have to pass a 25 m culvert, and in the lower end close to the outlet. The preferred route of smolts passing through the lake was in the open parts of the lake. The apparent concentration of predation in three specific areas indicates that predation risk is higher for smolts in areas where conditions, such as current and depth, change. The smolts may respond to changes in current and depth by for instance losing orientation and slowing down migration speeds, leading to an increased predation risk. It may also lead to aggregation of smolts in these specific areas, where predators can have easy access to them. Finally, because of the lower ground speed and resulting delay in lakes, the smolts are exposed to the predators for a longer time period (for further discussion see Jepsen *et al.* 2000). Considering the high rates of predation found in telemetry studies on trout smolts, this seems to be an important factor reducing population size. In combination with the high predation rates encountered at sea-entry (Jepsen *et al.* 2006), predation may often be the factor determining the actual size of the sea-trout run in a river.

Migration at Other Times of the Year

The above description of smolt migration gives a general introduction to the descent of trout juveniles, as can be found in most textbooks. However, this is an incomplete description, because it only covers part of the downstream migration. Juvenile trout may migrate downstream to sea at other times of year. Juvenile salmon parr (pre-smolts) have in several cases been shown to migrate downstream in autumn, and even spend the winter in a brackish estuary (Cunjak *et al.* 1989). Autumn migration in trout pre-smolts is less described, but has been indicated from catches in Scottish sea lochs (Pemberton 1976), and has also been shown in index rivers such as Imsa in Norway and Burrishoole in Ireland (Jonsson & Jonsson 2009; Poole *et al.* 1996), where a considerable proportion of descending trout is caught during autumn. Migration at other times of the year than the spring has furthermore been indicated for trout in the Baltic by scale reading methods (Taal *et al.* 2014). For trout, migration at other times of the year than the usual spring smolt migration period may in many places be the norm rather than the exception. Data from a Danish stream also show that a large proportion of the tagged trout migrated downstream before the smolt season, some in late autumn, but also a

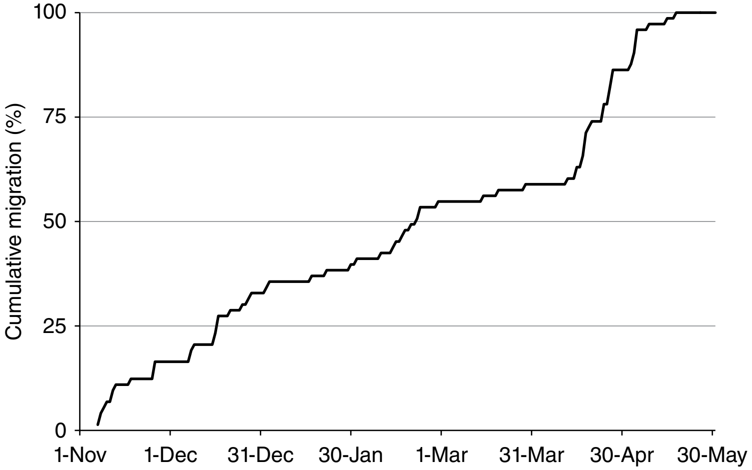

Figure 17.3 Cumulative migration of juvenile trout (range: 12–24 cm) during winter and spring season in Gudsoe Mill stream. Fish were tagged with PIT tags on 3–4 November 2012 and their downstream movement detected at an antenna station 1 km upstream from the outlet of the stream.

considerable part during winter (Figure 17.3). The descending number of smolts per time unit was larger in the spring; however, 50% of the migrants had left the river by 15 March, which is before what is regarded as the smolt migration period in the spring. This pattern has been confirmed in recent studies, showing that a significant proportion of juvenile trout tagged with PIT tags in the autumn had migrated downstream before the smolt season in the spring (Winter *et al.* 2016). Hence, variation in smolt migration timing may be a more general phenomenon than hitherto thought. Potentially, the autumn migration could be related to density dependence, but proximate and ultimate reasons are presently unknown.

In an evolutionary context, the interesting questions about fish migrating outside the smolt period, is whether they will survive, what their physiological status is and if the behaviour offers a positive fitness. According to classic theory, these fish should be poorly adapted to life at sea and also poorly matched with food production in the sea. Poole *et al.* (1996) regarded these autumn migrants as unsmoltified trout based on their lack of silver coloration and low survival (total return-rate of tagged fish migrating in autumn was only 1.7%). Nevertheless, both Jonsson & Jonsson (2009) and Poole *et al.* (1996) have shown the fish to survive and return to the river, suggesting these fish constitute a part of the reproducing population.

Challenge in explaining trout migration arises because the main body of knowledge of smoltification linked to migration and survival comes from research in Atlantic salmon. In Atlantic salmon, there is a link between smolt timing and subsequent survival, generally explained as an adaptation to favourable sea condition in spring. This is due to low salinity tolerance at low winter sea temperature and/or a match/mismatch food scenario (Thorstad *et al.* 2012). This has been assumed to apply to trout as well as salmon. However, this may not always be true for a number of reasons, especially because trout do not necessarily migrate to full strength saltwater like Atlantic salmon (e.g. Davidsen *et al.* 2014). As anadromous trout often stay close to their river of origin, and even may spend the entire marine phase in fjords, immediate tolerance to high salinity water may not be a prerequisite for survival after sea entry. Furthermore, the amount and timing of food availability most likely differ between coastal and oceanic areas. Hence, some trout may well abide to the general relation between smoltification status and migration timing, and some may not. In the low saline Baltic Sea, even 0+ trout have been observed to migrate to sea prematurely, as a consequence of rivers drying out during summertime (Titus & Mosegaard 1992; Landergren 2004). Additionally, recent studies have shown that juvenile trout descending in the spring, classified as parr, survived the marine migration and even had a higher return rate than fish classified as smolts (del Villar-Guerra *et al.* in review).

Marine Migration

Existing knowledge about the movements of trout in marine habitats points towards a complex and flexible behaviour, ranging from staying in the river mouth and estuary to undertaking very long feeding migrations almost like salmon (reviewed by Thorstad *et al.* 2016). Marine residence time also varies considerably. Berg & Berg (1989) reported an average marine residence time of 68 days, with annual means ranging from 54 to 88 days in a Norwegian river. The fish that descended first typically undertook the longest stay at sea, the duration of which increased with sea temperatures. They also observed that when autumn river levels were low, the upstream migration was delayed and the duration of marine migration was accordingly extended (Berg & Berg 1989). Flaten *et al.* (2016) reported an even shorter mean marine residence time of 38 days, with a variation from 22 to 99 days. Males may stay at sea for a shorter period than females (Jensen 1968). Jonsson & Jonsson (2009) recorded a mean duration of the marine migration of 6-9 months for first-time migrants moving to sea between January and June, and of 8–18 months for those migrating to sea between July and December. Mean duration of the marine migration was longer for first-time migrants than for veterans, and individual variation in time at sea ranged from 1 month to 3 years (Jonsson & Jonsson 2009). Trout are frequently recorded in the sea during the winter months in many geographic areas (Svärdson & Fagerström 1982; Pemberton 1976; Knutsen *et al.* 2004; Olsen *et al.* 2006; Jensen & Rikardsen 2008; Jensen & Rikardsen 2012). Latitude will likely affect the time spent at sea. As the ability to osmoregulate decreases in colder water, and may pose a problem when temperatures are very low (Thomsen *et al.* 2007), northern populations may be more inclined to spend the winter in freshwater and hence reduce the length of the marine residency. Once in the sea, some populations stay in near coastal areas during the marine migration, whereas in other populations, some or all fish leave the estuary and enter the sea (Bendall *et al.* 2005). Some populations apparently divide into two categories, with individuals in one category leaving for the sea and those in the other category staying in the brackish estuaries (Chernitsky *et al.* 1995; del Villar-Guerra *et al.* 2014). What leads the individual trout to choose either strategy is unknown. The advantage for trout remaining in estuaries may be feeding opportunities and the shorter migration, potentially leading to lower predation, including the avoidance of some marine predators. Another possible reason could be the lower salinity, which may enable fish to save energy, since they may not be required to adapt physiologically to full-salinity seawater, and they may also avoid sea lice infection (Thorstad *et al.* 2015). However, the physical and biological characteristics of estuaries show considerable variation, and it is therefore difficult to generalize.

Upstream Spawning Migration

Homing

Salmonids are renowned for their precise homing to the river of origin, and results from field studies, and genetic evidence indicates that this homing ability also exists in trout (Stuart 1957; Hansen & Mensberg 1998). Three main theories have been proposed to explain the homing ability of salmonids. The single imprinting hypothesis (smolts are imprinted in a very short period, Hasler & Wisby 1951), the sequential imprinting hypothesis (smolts are imprinted several times during the smolt migration, Harden Jones 1968) and the pheromone hypothesis (adult fish have an inherited ability to detect population specific pheromones released by descending smolts, Nordeng 1977). All hypotheses have olfaction as an important aspect, but over longer distances, other cues are most likely more important, like for instance magnetic stimuli.

Recently, Putman *et al.* (2014) demonstrated that Chinook salmon (*Oncorhynchus tshawytscha*) responded to magnetic fields and may have an inherited 'magnetic map'. Research has largely rejected the pheromone and single imprinting hypotheses, leaving the sequential hypothesis as the most plausible explanation (Jonsson & Jonsson 2011). The learning of how to find the home river seems to occur only at the smolt stage, and to be fixed for the entire life in both Atlantic salmon and trout (Hansen & Jonsson 1994; Stuart 1957). Most studies on the homing ability of trout have reported higher straying rates for trout than for salmon. Trout have also been observed to move between different tributaries (Jensen *et al.* 2015) and return to a different river than the trout was genetically assigned to (Östergren *et al.* 2012). In comparative studies, trout also have a larger fraction leaving the river before spawning than salmon (Gauld *et al.* 2016). Thus, trout may also in this regard have a more flexible homing strategy than salmon, but migrations to other rivers than their natal river does not necessarily mean that they spawn there (Davidsen *et al.* 2014). Clearly, more research on homing and straying in trout, and if strayers actually spawn in the river they entered, is needed.

Age, Size and Sex

Adult maturing trout may return to a river to spawn after a period of one month to five years at sea (Went 1962a; Jensen 1968; L'Abee-Lund *et al.* 1989; Christensen *et al.* 1993; Jonsson & L'Abée-Lund 1993; Euzenat *et al.* 1999; Skaala *et al.* 2014). As with smolt age, the age at return to the river is related to geographic area. Sea age at first maturity typically increases with latitude (L'Abee-lund *et al.* 1989; Jonsson & L'Abée-Lund 1993) and is dependent not on in-river growth rate, but on growth rate at sea (L'Abée-Lund 1994). Similarly, Jonsson & Jonsson (2007) found that higher growth rate during the first year at sea in salmon leads to a later return and maturation in Atlantic salmon. However, no relation between time spent at sea and growth rate was found on an individual level in the Simested River in Denmark (Frier 1994). A higher freshwater age at smoltification may reduce age at maturity (L'Abee-lund *et al.* 1989; L'Abée-Lund 1994). In small coastal streams, Jonsson *et al.* (2001) found mean length and age at maturity to be correlated with mean annual discharge. The number of years spent at sea before maturation may be partly inherited in

Atlantic salmon (Piggins & Mills 1985; Barson *et al.* 2015). Most likely, such heritability also holds for trout, although no studies have been published. The sea age of 50% maturity of trout was 0.5 years in the south and 3 years in the north for European populations ranging between 54 and 70°N (Jonsson & L'Abée-Lund 1993). Depending on the smolt age and the time spent at sea, returning maiden trout will be 2 to 8 years old. Because trout are iteroparous, ie. individuals may spawn two or more times during their lifetime, trout can reach a considerable age (e.g. Aarestrup & Jepsen 2000). They can spawn at least five times according to Went (1962b) and at least seven times according to Euzenat *et al.* (1999). A sea age of up to 13 years has been recorded (L'Abee-lund *et al.* 1989). Scale reading has indicated up to 8 consecutive spawnings (Aarestrup & Jepsen 2000). According to several authors, trout spawn annually (consecutively) after their first spawning (Jensen 1968; Pemberton 1976; Jonsson & Jonsson 2009; L'Abée-Lund 1994), a pattern also demonstrated using acoustic telemetry (Aarestrup *et al.* 2015). Alternate spawners appear to occur rarely. However, Nall (1930) suggested that alternate spawners constituted a part of the spawning population in the River Tweed based on scale analyses, and this has also been suggested for trout in the Vistula River (Borzêcka 1999). The body length of returning trout ranges from 20-100 cm (Anonymous 1994).

The sex ratio in upstream migrating trout reflects the ratio observed in trout smolts and is therefore usually in favour of females (Le Cren 1985; Christensen *et al.* 1993), but has also been observed to be in favour of males (Rubin *et al.* 2005). On average, males often mature at a younger age than females (L'Abee-lund *et al.* 1989; Rubin *et al.* 2005). Moreover, males have a higher mortality associated with spawning, leading to an even more pronounced female biased sex-rate among repeat spawners (Le Cren 1985).

Time of Year

The upstream migration of anadromous trout within a river may occur over several months. Returning trout in the River Imsa (Southern Norway) ascended the river from April to December, but with the majority (72%) between August and October (Jonsson & Jonsson 2002). In a river in western Norway, upstream migration commenced in July and continued until November (Jensen 1968). The same pattern has been observed in Danish sea trout rivers, where spawners usually ascended from August to December (Christensen *et al.* 1993; Johansen & Løfting 1919), but they have also been observed to ascend in larger rivers as early as April and as late as February, close to the end of the spawning season (Aarestrup & Jepsen 1998). In a French study, sea trout ascended from May to January, separated in two distinct runs, and with few trout ascending in August–September. Larger individuals with longer sea residence often enter the river earlier (Hellawell *et al.* 1974; Jonsson & Gravem 1985). However, in small rivers, the opposite has been observed, probably because very small rivers do not offer holding habitat for large trout, or because conditions for ascent from the sea are unfavourable (e.g. low water level) (Jonsson & Jonsson 2011). Sea trout males in France have been observed to enter rivers later in the season than females (Euzenat *et al.* 1999), while the opposite pattern was observed in Norway, where males tended to enter the river earlier than females (Jensen 1968). Overall, timing of return appears population specific and partly inherited (Jonsson *et al.* 2007). Many explanations have been proposed to explain the variation in timing of river entry in salmonids, but at present no satisfactory adaptive explanation exist (Fleming 1996).

Time of Day

Both the migration from sea to river and further upstream migration within rivers for salmonids, including trout, are usually nocturnal (Jonsson 1991; Allan 1966). We found no relationship between time of day and river entry in sea trout entering the River Gudenaa (Aarestrup & Jepsen 1998).

Initiation of Migration from Sea to River

Many studies have found increases in discharge to be an important stimulating factor for river entrance of salmonids, especially in smaller rivers (Banks 1969; Alabaster 1970; Jonsson 1991; Smith *et al.* 1994). Sea trout migrate upstream during increasing flow, but also after the flow has peaked (Banks 1969). Strong onshore winds are reported to concentrate salmon in estuaries and can be a contributory factor for river entrance (Banks 1969). In salmon, Smith *et al.* (1994) observed a stronger correlation between river entry and increases in water flow when the flow was below average compared to the average of the season. River entrance of salmon can be delayed by low discharge (Alabaster 1970; Potter 1988), with larger fish being more dependent on increasing water discharge than smaller fish (Jonsson & Jonsson 2011). In River Imsa, Norway the daily number of ascending trout correlated positively with mean monthly discharge (Jonsson & Jonsson 2002). More specifically, increases in flow early in the season stimulated ascent, but later in the season, no correlation was found. The authors explained the pattern by the difference in flow pattern over the season. Early in the upstream migration season, the river flow is close to the minimum and trout use the freshets to ascend, whereas later in the season, river flow is generally higher and the fish may enter irrespective of freshets.

The dependency on high flows increases even further in very small streams where low flows constrain trout and hence necessitates a delay in the upstream migration until they are almost ready to spawn (Jonsson & Jonsson 2011). At very high flows, the migration activity may decrease and can even be halted (Stuart 1957; Svendsen *et al.* 2004), possibly due to increased energy expenditure (Enders *et al.* 2005) or increased risk of injury of moving upstream during flood conditions. Late in the season, fish have less streamlined bodies and potentially less energy available for swimming because of maturation processes, so earlier migrants may be able to move upstream under more difficult conditions than latecomers.

The river entrance of salmonids has been reported to be related to the tidal regime (Potter *et al.* 1992) and water temperature (Banks 1969). However, the influence of temperature seems to be conflicting and inconclusive (Banks 1969). Jonsson & Jonsson (2002) found a negative correlation between upstream migration and temperature. Most likely, the conflicting evidence arises because changes in water temperature in different temperature intervals (e.g. low versus high water temperature) will elicit different responses by salmonids. A long migration distance typically takes longer time to complete, so if summer temperature in the lower reaches becomes too high (like in some rivers in Southern Europe), spring ascent may be necessary to accomplish the migration and avoid high summer temperatures as well as summer droughts.

Within-River Migration Behaviour

Further upstream migration within the river is often observed to also be stimulated by increases in discharge for both anadromous trout and salmon (Le Cren 1985; Jensen *et al.* 1986; Bagliniere *et al.* 1990; Jonsson 1991; Tenojoki *et al.* 1999; Svendsen *et al.* 2004). However, trout is believed to move at lower discharges than salmon (Le Cren 1985). Moon phase was shown to affect migration in brown trout in a fragmented river system (Slavík *et al.* 2012). For salmon, increasing water temperatures can also stimulate the upstream migration at low temperatures (Jensen *et al.* 1986), but will be negatively affected when water temperatures exceed 19-20 °C and stops when it reaches 24–25 °C (Elson 1969; Alabaster 1990). No such evidence has been reported for trout. We have observed in the River Gudenaa and Karup Aa in Denmark that trout can seek thermal refugees (lower water temperatures) when river temperatures are high (own unpublished data), and this may be a common behaviour strategy for early migrants in watersheds where water temperatures become high.

The dependence on flow as a primary driver for upstream migration both into and within the river in streams and smaller rivers is not surprising. Increased flow will provide better opportunities for passing various obstacles and reduce predation risk as a consequence of the deeper water, higher water current and increased turbidity, especially in smaller rivers and streams, thereby enabling the trout to optimize fitness (Tetzlaff *et al.* 2005; Abrahams & Kattenfeld 1997). In summer, increased flow often means relatively cool and well-oxygenated water, promoting swimming activity and energy conservation.

Upstream migration is often completed within a few weeks depending on the length of the migration (Le Cren 1985; Finstad *et al.* 2005). However, the upstream migration can take different forms depending on the distance to the spawning site and river configuration. Östergren *et al.* (2011) identified three different types of upstream migration; a group with considerable up- and downstream migrations, a group with a stepwise migratory pattern with several holding or resting positions, and a group with a direct continuous upstream migration, i.e. no holding or resting positions except at spawning areas. The different migratory patterns appeared to be related to the distance to the spawning area and stocking practices. In Irish catchments with large lakes, anadromous trout may stay in these for long periods before spawning (Paddy Gargan, personal communication). Net ground speed achieved by trout during upstream migration is reported to vary from less than 1 km · day^{-1} and up to 95 km · day^{-1} (Aarestrup & Jepsen 2000; Bij De Vaate *et al.* 2003; Bartel 1988). Fish entering early in the season migrate further upstream (Östergren *et al.* 2011). Large trout tend to migrate longer within the river than small trout (L'Abée-Lund 1991), probably because of the energy requirement by longer migrations. It is also corroborated by the observation that non-migratory individuals tend to become more dominant further from the sea (Bohlin *et al.* 2002; Jonsson 2006).

Some trout do not display a continuous upstream migration (Finstad *et al.* 2005). Breukelaar *et al.* (1998) observed anadromous trout moving many km downstream in one river branch before continuing the upstream migration in another branch of the Rhine.

Several trout in River Gudenaa also initially moved several km upstream and then downstream before entering their final spawning tributary (Aarestrup & Jepsen 1998). Provided trout display local homing within the watershed, fish following some kind of olfactory cue during the upstream migration may explain this behaviour (termed overshooting, and also observed in salmon (Aarestrup & Jepsen 1998)). The trout may follow the olfactory cue upstream and when the cue is no longer present, the fish drops back in the river until the cue is picked up again. However, such behaviour was not displayed by all trout in the study (Aarestrup & Jepsen 1998).

Gender differences in behaviour have been observed. Males were shown to spend more time in freshwater in the spawning tributary, while females spent most time in the deeper channel of the main river, in a study in the River Gudenaa (Aarestrup & Jepsen 1998). Both sexes presumably optimized spawning success by this behaviour. By spending time on the spawning grounds, males can increase the opportunity to spawn with several females and thereby increase their reproductive success. Females, to a larger extent, depend on their own chance of survival and success in egg deposition. Thus, the time spent on the shallower spawning grounds should be minimised by the females to reduce the predation risk.

Post Spawning Migration

After spawning, surviving trout may return to the sea. This part of the life-cycle has received relatively little interest until recently. Post spawning trout (kelts) may move towards the sea shortly after spawning, or spend an extended period in the river (Bendall *et al.* 2005; Östergren & Rivinoja 2008). In the River Gudenaa, river residence varied between 22 and 163 days (Aarestrup & Jepsen 1998). In the Norwegian River Vardnes, the freshwater stay of trout was considerably longer, due to all fish overwintering in the river (Berg & Berg 1989). Trout repeat spawners in a river in Ireland had a mean residence time of 105 days, with a range from 43 to 362 days (Piggins 1964). This shows that a high degree of variation in the river residence time of trout must be expected, both within and among populations.

In large rivers, kelts may spend the winter in the river or lakes and descend in spring or early summer, whereas in other and smaller systems, trout may descend in winter and use the estuary as overwintering areas (Jonsson & Jonsson 2011) or migrate to sea (Aarestrup *et al.* 2015; Aldvén *et al.* 2015). The downstream migration has been shown to take place both during daytime (Östergren & Rivinoja 2008; Aarestrup *et al.* 2015) and night time (Bendall *et al.* 2005; Aldvén *et al.* 2015). Progression rates through estuaries vary considerably, and fish can exit within one tidal cycle in short estuaries with high tidal influence (Bendall *et al.* 2005), but are generally slower in larger less tidal impacted estuaries (Aarestrup *et al.* 2015; Aldvén *et al.* 2015). Often, the progression decreases in the outer estuaries, possibly because of resumed feeding (Aarestrup *et al.* 2015; Aldvén *et al.* 2015). Estuary residence time ranged from 3 to 38 d in the study of Aarestrup *et al.* (2015), while Aldvén *et al.* (2015) recorded a median time of 2.5 d in the estuary, with a maximum of 106 d. Survival of kelts can be high, and repeat spawners can constitute a large part of the spawning population. Marine survival from 18% to 65% has been recorded in different studies (Berg & Jonsson 1990; Bendall *et al.* 2005; Aarestrup *et al.* 2015; Flaten *et al.* 2016).

Telemetry Methods

Telemetry has become one of the most widely used methods in fisheries science and management. There are several definitions of telemetry, and the word is derived from ancient Greek, where tele means remote and metron means measure, so basically telemetry is measured data transferred from a distance. Here, we use the term telemetry to describe the use of electronic transmitters (Figure 17.4 and see Figure 17.8) and other tags to gain information from free-swimming fish. This includes information on fish movements, and sometimes also information on the physiology and environment of the tagged fish by using different sensors. The methods described include the use of radio transmitters, acoustic transmitters, PIT tags and electronic tags that store data (archival data loggers/data storage tags–also termed bio logging within ecology).

The growing suite of methods is used over a continuum of scales in freshwater and marine environments to address basic biology and a wide range of fisheries management issues. Methods range from hand-operated systems that are used to identify the locations of a limited number of fish weekly, to automatic systems that monitor the position of many individuals in three dimensions in near real-time. For fishes moving over large areas, remote methods such as archival tags or pop-up satellite tags (PSAT), and large networks of acoustic arrays, are also used. Telemetry is, nevertheless, only a tool and cannot address all problems or answer all the questions. As with all studies, it is necessary to identify the specific biological problem and address it with the most appropriate method, which is often a combination of methods. Taking that into account,

Figure 17.4 A collection of different radio and acoustic transmitters used to tag fish. The radio transmitters are those having an antenna, whereas the two cylindrical transmitters without antennas are acoustic transmitters. Acoustic transmitters usually have a cylindrical shape, whereas radio transmitters are produced in both cylindrical and flat shapes. A cylindrical shape is optimal for surgical implantation of transmitters, whereas a flat shape is optimal for external attachment to the fish. Photo: Eva B. Thorstad.

telemetry can be the key to collect fundamental data related to field-based questions, with the principal advantages being multiple observations of the same individual and documentation of individual fate.

In some countries, telemetry has been used as one of the primary methods for obtaining data to address fisheries management related problems for the last 20 years. Telemetry studies often reveal previously unknown behavioural characteristics as well as overturning many dogmas within fisheries science. Such knowledge is crucial for helping to build biologically realistic models and optimize future management. Telemetry can provide behavioural data, which are fundamental for understanding aspects of fish life-cycles, and may be a pre-requisite for successful management of the species. The outcomes of such studies have demonstrated the huge impact the advent of telemetry has had on the management and conservation of fish and fisheries, as well as the general societal benefits that improved knowledge of fish behaviour brings. Two typical examples show how telemetry studies changed views and management of trout in Denmark. Firstly, it was believed that modern fish ladders could provide almost free passage of trout at dams and weirs. Telemetry studies (Aarestrup & Jepsen 1998; Aarestrup *et al.* 2003; Jepsen *et al.* 1998; Aarestrup *et al.* 1999) showed very low success of upstream passage and large mortality of downstream migrating smolts, thus forcing management to remove the barriers, or develop alternative ways of passage. Secondly, it was believed that survival from smolt to adult was dependent on an undefined range of factors in the sea. Telemetry studies (Koed *et al.* 2006) revealed that a high level of mortality (often > 50%) occurred in the transition between freshwater and the sea and that this was mainly caused by predation from cormorants, leading to enhanced management aiming at reducing this predation.

In the following, the principal telemetry methods are described, ranging from passive tags such as data storage tags (DST, also called archival tags) and PIT telemetry, to active tags such as radio and acoustic transmitters, and combinations thereof. We will then describe the important factors to consider when selecting a method for studying the different aspects of trout movements. As telemetry is a rather expensive technology, it is our hope that besides demonstrating the breadth and applicability of electronic tags, this chapter can be used as a practical guide when designing studies on trout movements, and that it will help trout researchers avoiding some of the pitfalls of telemetry.

PIT tags, radio transmitters and satellite tags transmit signals through the electromagnetic spectrum, but via very different parts of the spectrum. The specific properties of water (density and chemistry) make electromagnetic wavelengths shorter than 1 m practically useless in water, limiting the spectrum to lower frequencies. While PIT tags transmit typically in the 100–150 kHz range, radio transmitters operate in the 30–200 MHz (VHF band) also used for a number of other applications (radio stations and various communication devices), and satellite tags in the 400 MHz range (ARGOS satellites transmit at 401.650 MHz). The signals are transmitted by the speed of light (300.000 km/s). Signals propagate through water and air, but the different properties of the electromagnetic spectrum limit the range. Generally, the lower the frequency, the lower the range.

PIT Tags

Passive Integrated Transponder tags (PIT tags, also called radiofrequency identification technology, RFID) operate at lower frequencies than radio transmitters and satellite tags, and have the most limited range. A PIT tag is essentially a radio transponder with no battery, but containing a unique 10 or 15 digit alpha-numeric identification number. This allows individual fish tagged with PIT tags to be detected and identified. Unlike acoustic and radio transmitters that actively transmit a signal, PIT tags are passive and do not require a battery. Instead, the antenna (tag reader) emits a magnetic charge signal on a specific radio frequency, and when a PIT tag is within range, the tag will be charged and relay the identification code back to the receiver, enabling detection and recording of the animal. The lack of a battery makes the tags small compared to active tags and allows for the production of cheaper tags enabling tagging of a larger number of fish and of smaller fish. The lack of battery also allows for an extended lifetime (in principle unlimited life).

The caveat with PIT telemetry is the short detection range of the tags. Standard PIT tag range for a tagged trout may be as short as a few centimetres. Recent advances in technology and development of slightly larger PIT tags have enabled detection ranges of up to 1.3 m (Jes Dolby, personal communication). As a consequence of the short range, the use of PIT tags has been limited to simple recapture and identification purposes, or placement of antennas at narrow places where fish may pass (such as fish ladders at hydropower plants). The recent increase in range has made it possible also to study movement in smaller streams and rivers.

Two different PIT systems are used, which are the full-duplex system (FDX) and the half-duplex system (HDX). Both systems operate on the same frequency (134.2 KHz), but they differ in how the tags transmit and how the signals are received by the antenna. The FDX system receives and transmits simultaneously (hence, full-duplex) while the HDX system transmits, and then receives, so that half the time it sends and half the time it listens (hence, half-duplex). The FDX system may read up to 30 times per second, while the HDX system reads up to 14 times per second. The HDX principle of alternating between transmitting and receiving means HDX tags must have a capacitor to store the energy before transmission, giving greater output energy, but at the expense of a larger tag size. Full-duplex tags can be very small (8.5 × 2.1 mm) and can be implanted into very small trout, maybe as small as 45 mm. The antenna readers for FDX tags will have a shorter detection range, so tags must be closer to the reader antenna. FDX systems are typically used in restricted places, such as fish ladders, other fish passages and culverts. HDX tags are larger (typically 23 × 3.8 mm) and have been used in salmonids down to 80 mm in length. Recently, smaller tags (12 × 2.12 mm) have been introduced, enabling tagging of even smaller salmonids, however at the cost of a lower detection range than the 23 mm tags. An advantage of the HDX system is that antennas can be built to fit the purpose relatively simply, enabling researchers to design the antennas themselves. The larger range also means that they are better suited where a full stream width monitoring is desirable. An additional advantage is that HDX systems operate on 12–24 volts DC power, making them superior for running on batteries or solar power in remote areas.

PIT tags have been used in many studies of trout based on tagging and recapture of fish, without recording the fish between these events (e.g. Bohlin *et al.* 1996; Rifflart *et al.* 2006). PIT tags have also been successfully used with antennas installed at strategic sites for studying trout during downstream (Ibbotson *et al.* 2013; Winter *et al.* 2016) and upstream migration in rivers (Aarestrup *et al.* 2003; Wright *et al.* 2016), and for coupling morphology to survival in descending juveniles (del Villar-Guerra *et al.* in review), particularly in small streams or in weirs and fish passages where efficient antennas can be installed.

Radio Transmitters

Radio telemetry (Figures 17.4, 17.5 and 17.6) operates within the VHF band, with the majority of aquatic telemetry based on transmitters within the 30 MHz to 225 MHz range. As opposed to PIT tags, the transmitters are active and contain a battery, making them larger, heavier and shorter-lived compared to PIT tags. The transmitters elicit a signal at a certain frequency that can be detected by either a manual or an automatic receiver. The signal strength depends on the electrical power and the antenna used to emit the signal. The longer the antenna, the stronger is the signal. This means that most radio transmitters are produced with a trailing antenna to increase output. Antennas can be coiled into the tag, but this reduces the detection range. The lower frequencies have less attenuation and hence greater propagation through water than the higher frequencies. However, this comes at the cost of poorer transmitter and signal efficiency, and most important, increased size of the receiver antenna in order to have the same reception range. Large receiver antennas limit the use of these frequencies especially during mobile tracking and in remote areas. Therefore, most systems today are based on frequencies between 140 and 180 MHz.

Radio waves transmitted under water are reflected at angles less than 6 degrees when they hit the water surface, hence, only a limited amount of waves exit into the air. Once in the air, radio signals can travel for long distances without significant signal loss. The range can be in the order of kilometers once the signal has escaped water. Hence, the receiving antenna is often placed in the air and can be stationary or mounted on all kinds of vehicles depending on the study purpose and infrastructure in the study area. The signal is unaffected by acoustic noise and can penetrate through various physical obstacles, although the signal may interfere with other radio wave sources. The problem with competing interest in using the same radio frequencies has led many countries to reserve a certain bandwidth for scientific studies.

Transmitter size varies depending on purpose and longevity. The smallest commercial radio transmitter available today is 5 × 3 × 10 mm and weighs 0.26 g. Contrary to PIT technology, various sensors can be incorporated in radio transmitters, relaying information back to the observer on the physiology or environment of the fish. Many producers manufacture a range of radio transmitters capable of measuring and transmitting information such as temperature, pressure (depth), motion and muscle electromyogram (EMG) signals.

Figure 17.5 A sea trout tagged with an external radio transmitter, ready for release. Photo: Eva B. Thorstad.

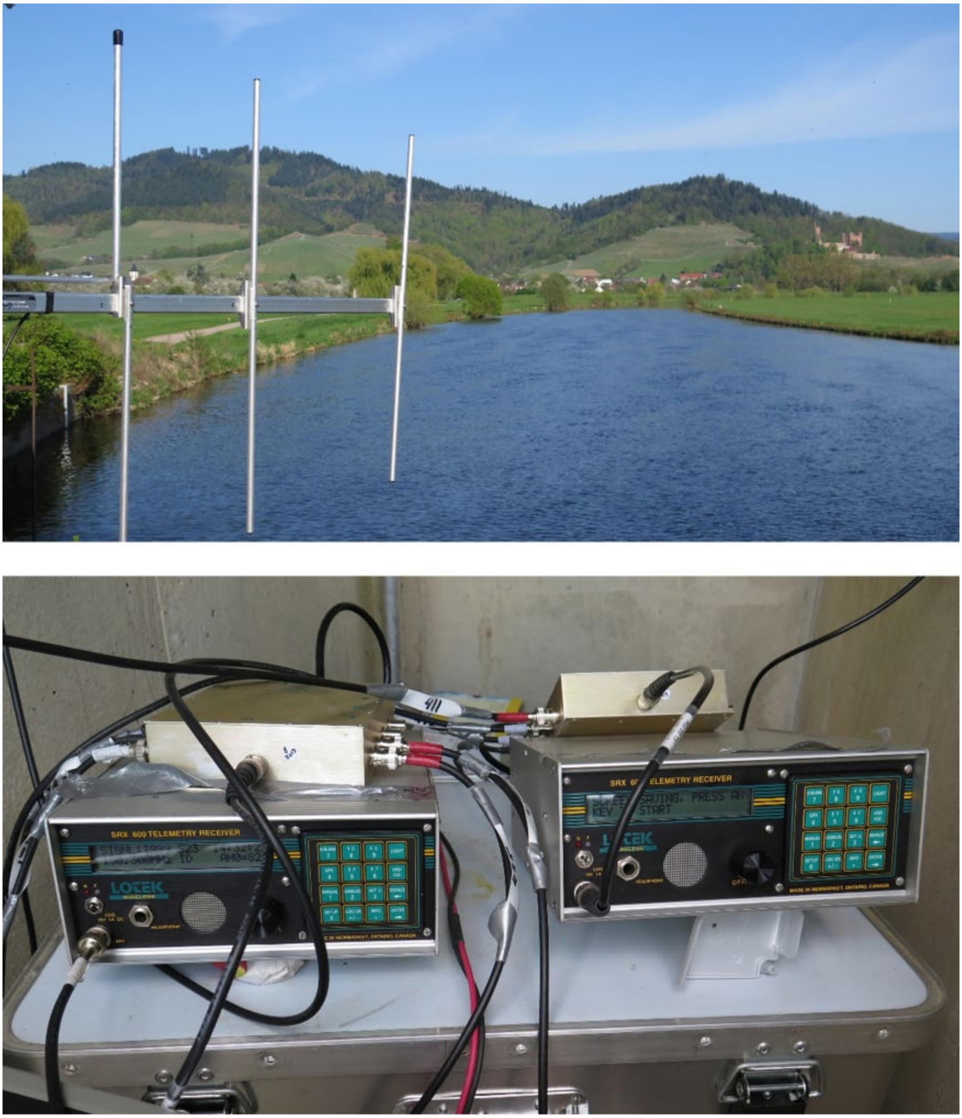

Figure 17.6 Automatic stationary data loggers with connections to multiple antennas (lower photo) and one of the antennas monitoring an area of the river (upper photo). Photos: Eva B. Thorstad.

A signal can be detected by manual tracking via a receiver, or by setting up automatic listening stations at strategic places. During manual tracking, the animal's position is often determined by cross bearing and for experienced users also by signal strength. The method is relatively inaccurate, but by moving closer and closer to the animal, it is often possible to physically observe (and potentially catch) the animal. In its simplest form, only a manual receiver is necessary to study movements of tagged fish. However, in many tracking studies, one or numerous automatic data logging stations are required. Some automatic listening stations also log signal strength, and multiple antennas with different ranges can be used to record the movement direction of the fish. For receiving the signal, a receiver antenna is needed. The same general principle as for the transmitter applies to the receiver; the larger the antenna, the larger the detection range. For automatic systems, a larger antenna may be preferable, while it may become unmanageable to handle a large antenna during manual tracking.

The major limitation with radio telemetry is that signal attenuation is relatively high in water and very much so at higher conductivity. In practical terms, this means that radio telemetry cannot be used in saline water, and also will be inefficient in deep water. Hence, the use of radio telemetry is basically limited to shallow freshwater, such as rivers, streams and shallow lakes.

Radio transmitters were first used on fish in 1960s (Lonsdale & Baxter 1968) and had an increased use during the 1970s. Today, the use of radio telemetry must be considered a standard method for studying fish movements and survival in the relevant habitats. The method has been used to study downstream migration of trout smolt (Jepsen *et al.* 1998; Aarestrup *et al.* 2002; Kraabol *et al.* 2008). The method has also been used to study upstream migration of adult trout (Aarestrup & Jepsen 1998; Östergren *et al.* 2011; Slavík *et al.* 2012; Finstad *et al.* 2005), often in relation to migration barriers and fish passages (Ovidio & Philippart 2002; Thorstad *et al.* 2014), and in studies of the post-spawning migration (Östergren & Rivinoja 2008). The studies have been instrumental in directly demonstrating the ultimate fate of the fish, for instance related to predation (Jepsen *et al.* 1998; Hyvärinen & Vehanen 2004). Advances in acoustic telemetry methods (see below) has resulted in increased use of acoustic telemetry instead of radio telemetry in many studies of trout and other species in freshwater habitats in the recent years.

Acoustic Transmitters

Acoustic telemetry (Figures 17.4 and 17.7) uses sound waves within the 10–500 kHz range to propagate signals, which is an entirely different technology than the technologies based on radio signals. This involves both advantages and disadvantages compared to the radio and PIT telemetry methods described above. Sound transmission is more effective, the denser the medium is. Consequently, sound propagates well in water, but

Figure 17.7 Acoustic receiver buoy in the sea (left photo) and the acoustic receiver attached to the rope under the buoy (right photo) Photos: Eva B. Thorstad.

has much shorter range in air. The propagation speed is considerably lower than for radio waves. Speed of sound waves in air is 332 m/s, and in water around 1500 m/s, because of the larger density of water.

As with radio signals, there is a trade-off in terms of frequency choice, because the higher the frequency, the shorter the transmission range. To generate the sound, a tag needs a transducer, which often comes in the form of a crystal. Electricity from the battery is used to vibrate the crystal to generate the sound wave. However, the frequency generated is inversely proportional to the size of the transducer, so the lower the frequency (which increases the range), the bigger the transmitter needs to be. Additionally, acoustic noise from the surrounding environment (e.g. wind and waves) increases at lower frequencies. Today, two main frequency areas are used. Many systems operate within the 69–76 kHz range, but recently, a number of systems operate within the 180-200 kHz range. A new system may even use 400 kHz signals, but higher frequency systems may perform best in freshwater.

Acoustic transmitters available today have a detection range from less than 100 m and up to 1 km or longer. The method can be used in both salt- and freshwater. However, it is sensitive to acoustic noise, physical blockage of the signal and bottom/side attenuation and deflections, limiting its use in shallow areas and also in meandering rivers. Furthermore, haloclines and thermoclines can also reduce the range. Significant challenges can also be foreseen close to hydropower turbines and in other noisy environments. A benefit with acoustic tags is that since the signal is generated by a transducer, no antenna is necessary.

As transmission in air is poor, a receiver needs to have a hydrophone placed in the water to receive signals from the acoustic transmitters. For manual tracking, a directional hydrophone and a boat is typically used to track the fish. Positions are determined by triangulation, or only by use of signal strength. Manual tracking of acoustic tags can be labour intensive, because often only one fish can be tracked at a time. Hence, most studies today use automatic listening stations placed at strategic positions.

Size of acoustic transmitters can be as small as 5 × 3 × 11 mm and 0.24 g, with some producers making transmitters in the 6–7 mm diameter range, which can readily be implanted in trout smolts. For salmon and trout smolts, some selection is needed because smolts smaller than 15 cm may have negative effects of tagging. A tag/body-mass ratio of up to 5% has been tested and may be acceptable for some fish, but a lower ratio is recommended (Jepsen *et al.* 2004). Lifetime (battery life) ranges from days in the smallest tags to 10+ years for large tags.

Compared to radio transmitters, acoustic transmitters and manual receivers are typically in the same price range. However, a number of producers have developed some rugged relatively cheap automatic data loggers, some of which are widely used in telemetry studies today. Various sensors have also been incorporated into acoustic transmitters, enabling transmission of information such as temperature, pressure (depth) and oxygen (Svendsen *et al.* 2006).

A special case of acoustic telemetry is the three-dimensional (3-D) approach. A number of systems today offer the possibility to get positions of a tagged fish in three dimensions. The systems are based on differences in signal arrival times at receiving stations at different distances from the fish. If the position of the receivers is known accurately, estimates based on the speed of sound in water can be used to generate a position of the transmitter (e. g. Baktoft *et al.* 2016). The technology is still relatively little used, but has great potential for detailed studies of fish movements.

The first acoustic equipment was developed in 1956 for examining salmon passage of dams in Columbia River, USA (Trefethen 1956; Trefethen *et al.* 1957). By 1967, acoustic transmitters were routinely used to investigate fish passages. Since then, the method has taken on tremendously (Hussey *et al.* 2015), to an extent where a global network approach to the method has been initiated (Ocean Tracking Network, http://oceantrackingnetwork.org/), also including studies of trout in this network (Eldøy *et al.* 2015; Flaten *et al.* 2016). The development in acoustic telemetry methods has particularly increased the knowledge on migration behaviour of trout at sea during the last ten to fifteen years (Middlemas *et al.* 2009; del Villar-Guerra *et al.* 2014; Aldvén *et al.* 2015; Aarestrup *et al.* 2014). However, acoustic transmitters have also been used increasingly in studies in freshwater habitats, both during the smolt migration (Moore *et al.* 1998; Serrano *et al.* 2009), spawning migration (Moore *et al.* 2012; Gauld *et al.* 2016) and post-spawning kelt migration (Bendall *et al.* 2005; Aarestrup *et al.* 2015).

Data Storage Tags (DST)

Data storage tags (DST, also referred to as archival tags) are essentially small data loggers measuring parameters and storing them for retrieval upon return of the tag (Figure 17.8). Hence, the fish must be recaptured, or the tag must be found, and returned to the researcher for download of the collected data. The tags contain a battery, various sensors and memory capacity. Many DSTs have a battery life lasting for years and may store large amounts of data. Different sensors have been incorporated into DSTs, including temperature, pressure (depth), light, salinity, pitch and roll and

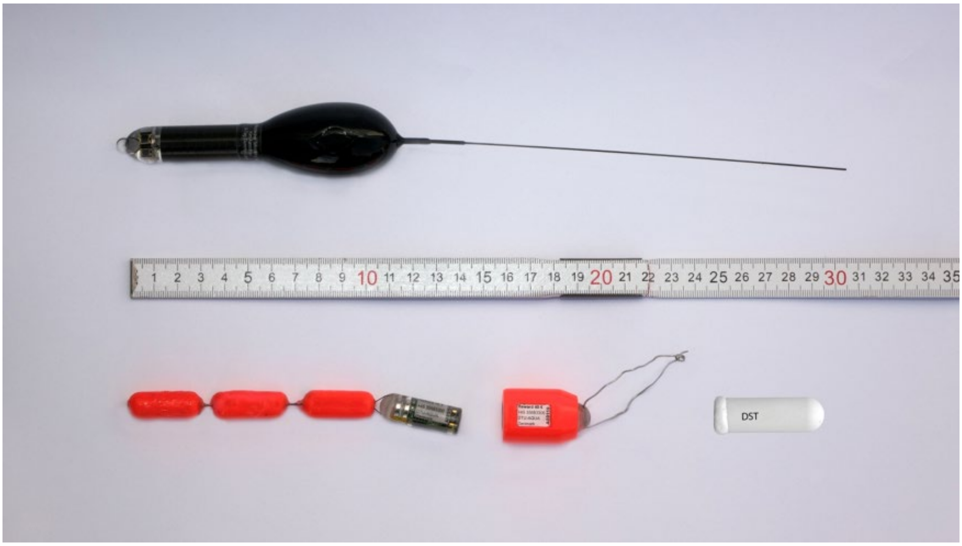

Figure 17.8 A selection of PSAT and DST tags, including a scale in cm. The upper black tag is a PSAT, while the three lower tags are DSTs, of which the left and middle tags have floats attached to make them buoyant. Photos: Jan Nielsen.

compass direction. Tag minimum size is dependent on the sensors used. The smallest temperature logger is 6 × 17.5 mm, weighing 1.3 g. The first deployment of DSTs on fish was the MK1 tag on plaice in the North Sea (Arnold *et al.* 1997). Early generation DSTs had a relatively limited memory, but data storage capacity has increased tremendously in later generation tags, enabling much higher resolution of the recorded data.

The fact that DSTs are expensive and must be recovered to retrieve the data may be the primary concern when using this technology. However, there is no need for expensive receiver equipment, and in some cases, it may be the only feasible technology available. For example, detailed information on the behaviour and habitat preferences of sea trout may only be acquired through this method in some marine environments. Some studies have increased tag recovery rates by using existing infrastructure like fish traps to recapture fish upon return to the stream. Recently, buoyant DSTs have been introduced, and may in many cases increase the recovery rate, because expelled tags drift ashore and can be found and returned instead of sinking to the bottom. This will also increase the knowledge as it enables return of data from dead fish. These data will potentially inform about predation events, including which predators that are responsible. They may then be used to compare behaviour between surviving and non-surviving fish (e.g. in relation to tagging effects).

DSTs have been relatively little used in trout, but a number of studies are ongoing and will likely provide important results in the coming years, both from the marine environments and lakes. DSTs were first used on trout in Iceland, where Sturlaugsson & Johannsson (1996) tagged a number of kelts in a river and later recaptured them. The DSTs logged temperature and pressure, and provided the first evidence of depth and temperature use by trout in the sea. The migration to and from the sea was revealed by the temperature record, because of a clear difference between river and sea temperature. The migration was generally nocturnal. Results showed residence times at sea from 33 to 93 days. Temperature experienced by the trout was generally 7–9 °C, with a few warmer recordings, suggested by the authors to be visits into the estuary. In the sea, the trout spent 91% of the time in the upper 7 m of the water column, but dives down to 26 m were observed. A closer examination was not possible due to the 4 h sampling rate of the tags.

A later study of marine behaviour of trout by use of DSTs was done by Rikardsen *et al.* (2007). The authors compared marine temperature and depth preferences of Arctic char *Salvelinus alpinus* and sea trout in the Alta Fjord in Northern Norway. The depth pattern of the trout was similar to the Icelandic trout, with 90% of the time spent at depths less than 3 m, but with dives down to 28 m. The mean temperature experienced by the trout at sea was 12.1 °C. Based on the temperature recordings, the authors suggested that trout preferred to stay in the warmer, inner parts of the fjord. By tagging the fish both internally and externally, reflecting the temperature in the body cavity of the fish and of the surrounding water, the authors demonstrated a short delay in changes of temperature by the internal compared to the external tags. Hence, whereas depth values are immediately changed, the internal temperature changes a bit slower than the water temperature experienced by the fish. This is an important consideration when interpreting temperature data from internally tagged trout. None of the above studies has reported depth and temperature experienced by trout migrating far from the tagging site, nor is there any information from late autumn, winter and early spring, since all fish were tagged in spring and recaptured within few months.

Jensen and Rikardsen (2012) captured adult trout in a river in Northern Norway in the autumn and double-tagged them with an internal temperature DST and an external salinity DST. The results showed that sea trout used the river, estuary and sea during winter, challenging the traditional view that sea trout in northern areas spend the entire winter in freshwater. Several individuals were observed to shift regularly between the different habitats during winter. The ambient temperature varied considerably among the river, estuary and sea. The salinity measurements were elegantly used to confirm the temperature data, and it was shown that DSTs based on temperature recordings alone can be used to monitor the habitat use of sea trout when alternating between the river, estuary and sea.

The studies referred to above demonstrate the applicability of DSTs in measuring environmental variables, which again can be used to make important inferences on the fish behaviour and habitat use. Furthermore, modelling can be also used to estimate geographic positions based on high-resolution recordings of depth and temperature, and coupling these with oceanic databases and models on temperature.

Pop-Up Satellite Tags (PSAT)

The most recent technology using electromagnetic signal propagation is satellite telemetry. Pop-up satellite tags (PSAT) record and store sensor data like light, pressure (depth) and temperature in the same way as the archival tags, but to be able to communicate this information and the geographic position to satellites, the tag antenna needs to be in air. PSATs are therefore equipped with a release mechanism and a float (Figure 17.8). At release from the fish, the tag floats to the surface and starts to transmit stored information and its present position to satellites. The frequencies used match the frequencies used on the low earth orbiting ARGOS satellites that receive the data.

PSATs are expensive and large, which limit the use to large-scale studies of large fishes, typically in marine areas. Still, the technology has a relatively wide application within marine mammal studies and larger marine fishes (Hussey *et al.* 2015). It has to our knowledge never been used on trout, but could be used with long-distance migrating trout in the sea and large lakes where access is difficult (e.g. in conflict zones) and provide detailed information on migration of trout, including validation of information gained from archival tags. However, only the largest individuals of trout (>2 kg) are large enough for tagging with these tags given the present size of available tags.

Evaluating the Effects of Handling and Tagging Fish

Before applying telemetry methods, a researcher has to ensure that the performance of tagged fish is representative of untagged conspecifics. There is little interest in learning about survival, behaviour, migration or spawning sites of tagged fish if they do not represent the untagged population. Yet, there is currently little documentation from field studies that tagged fish in general perform similarly to untagged individuals. Because fish live underwater, visual inspection is challenging. Furthermore, although we have some solid field-based evaluations of survival after tagging for lake-dwelling fishes such as pike, pikeperch and resident trout (Jepsen *et al.* 1999; Jepsen *et al.* 2001; Jepsen 2003; Jepsen *et al.* 2008), it is much more difficult to study tagging effects of migrating fishes (but see Aarestrup *et al.* 2002 for an exception), especially in marine environments. With both acoustic and radio technology, it is difficult to distinguish between fish mortality, tag loss and transmission failure (Corbett *et al.* 2012). Tracking of predators, having eaten the tagged fish, may be common (Thorstad *et al.* 2012), and is particularly a problem when the scientist is not aware that the fish is eaten and interprets the recorded behaviour as the behaviour of the tagged fish.

Most studies specifically designed to examine the effects of handling and tagging have been carried out in controlled settings such as laboratories, hatcheries and ponds (i.e. Donaldson *et al.* 2011; Corbett *et al.* 2012). Some species and life stages are particularly vulnerable to negative effects of confinement, and special consideration must be taken. For example, when wild fish are captured during their migration and confined to laboratories or semi-natural ponds, they may become stressed, resulting in high mortality for both treatment and reference groups (i.e. Donaldson *et al.* 2011; Corbett *et al.* 2012). Chinook salmon and Atlantic salmon are known to experience so-called frustrated smolt syndrome if they are held in captivity after they have adapted physiologically to enter seawater (e.g., Jepsen *et al.* 1998; Wargo-Rub *et al.* 2009). Such fish will display symptoms of stress and swim actively searching for a way to move downstream, and they are often susceptible to fungus infections and suffer high mortality. This may also be the case for trout smolts, but is to our knowledge not well studied.

Although a laboratory-based study may be the best (and in some cases the only) option for studying the effects of tagging in a particular situation, these types of studies can provide biased results. On the one hand, fish may perform better (e.g. exhibit higher survival and growth) in the laboratory compared to a natural setting, because they are being fed and are no longer subjected to the same metabolic stressors (e.g. swimming against currents, avoiding predators, or migrating large distances) as in their natural setting. In these cases, the effects of tagging may be underestimated, similar to that observed by Wargo Rub *et al.* (2009). On the other hand, fish in captivity may succumb to stress imposed from overcrowding, delayed migration, or poor water quality, which can lead to death, delayed growth, and secondary infection. To avoid these biases, more field-based tagging effect studies are needed to improve telemetry-tagging methods as well as to validate the results obtained from field studies where recapture is not possible. In addition, more studies are needed to identify the underlying causes for the observed effects. Here, we give a brief overview of the tag effects that have been observed to date in fish, with a focus on surgical implantation of tags. A thorough and recent review of the tag effects literature can be found in Cooke *et al.* (2011), and specifically for external tagging in Jepsen *et al.* (2015).

Fish Survival after Tagging and Transmitter Retention

Survival and transmitter retention (often evaluated together) are the most obvious indicators of tagging effects. Short-term survival and transmitter retention are easy to evaluate if fish are held for some time after tagging. If tagged fish die during this period, the handling and/or tagging methods were clearly not successful. On the other hand, short-term survival and tag retention do not ensure that the capture, handling and tagging did not impose any negative effects. Surgery related mortality as well as tag loss can occur days or even weeks post-tagging (Jepsen *et al.* 2008; Wargo-Rub *et al.* 2009; Corbett *et al.* 2012). Tag loss can occur passively if the incision opens up, or actively through expulsion through the body wall. Expulsion can take place long after the incision has healed. In some salmonid studies, up to 25% of study fish have been reported to expel the tags (e.g. Jepsen *et al.* 2008). The propensity to expel tags appears to be species specific and may also be temperature dependent and related to the ratio between tag size and fish body size. Tag expulsion does not appear to affect survival or the health of the fish. However, if tag loss is unknown, tagged fish released into the field will appear dead due to disappearance of the transmitter from the detection array or to the appearance of a sedentary transmitter. Survival and tag loss rates can be compared among tag types or one can turn to a related species to assess the relative effects of tagging (Matter & Sandford 2003; Keefer *et al.* 2004; Moser *et al.* 2007). However, O'Connor *et al.* (2009) tagged three fish species using the same method under similar conditions and documented that the propensity of tag expulsion varied significantly even between relatively similar species. More studies are needed to identify ideal shape, size, and coating material for transmitters, as well as to identify wound closure methods (including incision location, suture pattern, and closure materials) that will promote maximum healing with minimal long-term effects.

Growth and Swimming Performance of Tagged Fish

If fish with tags survive, do they also exhibit equivalent growth and swimming performance as untagged fish? Similar to long-term survival, most growth studies have been performed in laboratories. Important results are provided by field experiments where tagged fish are recaptured after a long period at liberty (e.g. Jepsen *et al.* 1999, 2000, 2008). Most of these studies show no, or a relatively limited, negative effect from tagging on growth. Swimming performance, buoyancy compensation, and the related abilities to avoid predation and exhibit normal social interactions (i.e., schooling, courtship) are of crucial importance. These factors have only been studied for a few species (Close *et al.* 2003; Moser *et al.* 2007). Generally, most internally tagged fish do not show decreased swimming performance, likely because tags used are often small compared to fish size. In some studies, large proportions of the tagged fish have been consumed by predators (Jepsen *et al.* 1998; Jepsen *et al.* 2006; Rieman *et al.* 1991; Koed *et al.* 2006). While these findings provide important information on predation levels, they have also fuelled speculation about the effect of handling and tagging on vulnerability to predation. A few studies have tried to address this issue, and have demonstrated that tagged fish are not necessarily easier prey than untagged fish (Jepsen *et al.* 2008; Anglea *et al.* 2004; Jepsen *et al.* 1998). Other studies have focused on the effect of handling and tagging on a fish's position in a social hierarchy (Connors *et al.* 2002; Swanberg & Geist 1997). When some species are kept in groups, a dominance pattern usually evolves and a change in the status of an individual fish can be linked to tagging effects. The weakness of this approach is that field studies are difficult to conduct. Thus, to our knowledge, only laboratory experiments have been reported (e.g. Swanberg & Geist 1997; Connors *et al.* 2002). Additionally, these types of studies are increasingly difficult to perform due to animal welfare constraints.

Physiology and Reproduction

Physiological effects of tagging have been examined for only a few species. Physiological features that have been assessed in relation to fish handling and tagging include the cortisol or stress response (e.g. Jepsen *et al.* 2001; Close *et al.* 2003; Mesa *et al.* 2003) and the fish's ability to heal (e.g. Mesa *et al.* 2011). Surgical implantation of a tag into the coelom can influence development and release of gametes. However, few studies have included reproductive performance as an indicator of tagging effects (Cooke *et al.* 2011). An effect by tagging on egg retention was found in steelhead trout (*Oncorhynchus mykiss*) (Berejikian *et al.* 2007), whereas no effect was observed in perch (Baras *et al.* 2000) and Pacific lamprey (Close *et al.* 2003). In cases when fish with surgically implanted tags are used to study spawning behaviour, it is of particular importance to know how the tag may affect the spawning physiology and behaviour. Advances in technology will provide new options for evaluating the effects of handling and tagging, such as the use of 3-D real time telemetry. In a lake, Baktoft *et al.* (2012) followed both predators and prey in real-time using a high resolution acoustic telemetry system, and they were able to use the results to analyse survival, general behaviour and predation (Baktoft *et al.* 2012). These methods also allow for detailed field tests of different tagging techniques and tagging effects.

Conclusion

Accurate knowledge on trout behaviour and survival is crucial for helping to build biologically realistic models and optimize future management on this important fish species. Because this is such a flexible species with variable behaviour, both among and within populations and geographic areas, it is especially difficult to generalize knowledge of behaviour patterns based on a few studies in a limited number of watersheds – or in the case of trout, sometimes only based on studies of other salmonid species. In a species like trout, attempts to generalize knowledge may sometimes hamper development of the knowledge base rather than developing understanding of the fundamental ecology of the species. One of the important keys to understand sea trout migrations may be to study and understand individual variation.

Telemetry is a rapidly growing technology used in fish research. The methods are used over a continuum of scales in freshwater and marine environments to address basic biology and a wide range of fisheries management issues. The diverse methods each have their advantages and disadvantages (Table 17.1). Telemetry can be the key to collect fundamental data related to field-based questions, with the principal advantages being multiple observations of the same individual and documentation of individual fate. Telemetry can provide behavioural data, which are fundamental for understanding aspects of fish life-cycles, and may be a pre-requisite for successful management of the species. Often, telemetry has revealed previously unknown behavioural characteristics and has changed general perceptions and even overturned dogmas within fisheries science, and will continue to do so.

Table 17.1 Different types of tags, technologies and specific information relating to important decision criteria for choice of method.

	PIT tags	**Radio transmitters**	**Acoustic transmitters**	**DST**	**PSAT**
Minimal fish size	45 mm	90–100 mm	90–100 mm	120–130 mm	5500 mm
Tag life time	Indefinitely	Weeks to several years	Weeks to 10 y +	Years	Up to 12 months
Freshwater/ Marine use	Both	Freshwater	Both	Both	Both
Range	Cm's	Several km	Up to 1500 m	NA (need recovery)	Several hundreds of km
Parameters recorded	None (just a code)	Temperature, pressure, motion, electromyogram activity	Temperature, pressure, motion, oxygen, acceleration	Temperature, pressure, oxygen, salinity, heart rate, acceleration, geomagnetic	Temperature, pressure, geomagnetic

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18

Sea Trout (*Salmo trutta*) in Galicia (NW Spain)

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Introduction

Brown trout (*Salmo trutta* L., 1758) is a polymorphic species exhibiting different migratory behaviours across rivers and populations. Populations may include juveniles that migrate to the sea, others showing less downstream movement and individuals who remain their entire lives in freshwater. The term '*partial migration*' is used to describe the phenomenon by which a population is divided into resident and anadromous individuals (Jonsson & Jonsson, 1993). In populations located in coastal areas with direct access to the sea, anadromous individuals migrate to the sea while residents spend their entire lives in fresh water (Jonsson, 1985; L'Abée-Lund *et al.*, 1989). Adult migrants and residents can successfully mate together (Jonsson, 1985; Pettersson *et al.*, 2001) and juveniles can live together being indistinguishable from ontogeny to smolt stage (Baglinière, 2000). Migrants reach maturity after a period of growth in the sea while residents mature in freshwaters often at a smaller size and younger age (Jonsson & Jonsson, 1993). Anadromy versus residency in fresh water is an example of phenotypic plasticity and is influenced by both genetic and environmental factors (Jonsson & Jonsson, 1993; Klemetsen *et al.*, 2003). Life strategies of brown trout constitute what is called a '*migration continuum*' by which the populations consist of individuals including those residing in their native rivers the entire life time (river residents), potamodromous individuals which migrate to areas further river downstream or lakes or reservoirs (Boel *et al.*, 2014) and anadromous individuals migrating to salt and marine water (Elliott, 1994; Klemetsen *et al.*, 2003; Cucherousset *et al.*, 2005).

Compared to Pacific (*Onchorhynchus* sp.) and Atlantic salmon (*Salmo salar*) few studies of sea trout have been conducted. Most of this knowledge has been compiled in three symposia (Le Cren, 1985; Harris & Milner, 2006 and the second International sea trout Symposium, Dundalk, Ireland in October 2015); four books on the biology and ecology of brown trout (Menzies, 1936; Frost & Brown, 1967; Baglinière & Maisse, 1991;

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

Elliott, 1994); a monograph on the ecology of salmon and brown trout (Jonsson & Jonsson, 2011), two monographs exclusively on sea trout (Nall, 1930; Fahy, 1978), a review on sea trout (Elliott *et al.*, 1992), a review of the life history of brown trout, Atlantic salmon and charr (Klemetsen *et al.*, 2003), and conclusions on the life history of sea trout (Cucherousset *et al.*, 2005). Mainly due to some international projects funded by the EU and the impetus of the ICES (International Council for the Exploration of the Sea), new interest and scientific information about the sea trout has been aroused. Finally, in spite of an overall lack of published studies, those on the sea trout populations of the Iberian Peninsula include Alvarez-Riera (1985); Lemaire (1991); Caballero & García de Leániz (1992); Toledo *et al.* (1993); Toledo (1996); Caballero (2002), Caballero *et al.* (2002), Caballero *et al.* (2006), Campos *et al.* (2007), Marco-Rius *et al.* (2012; 2013) and Caballero (2013).

In this study we review the distribution of sea trout in Spain and particularly in Galicia. We describe major life history traits of anadromous brown trout in the several Galician rivers with particular attention to migration, growth, reproduction and demographic characteristics.

Study Area, Material and Methods

Sea Trout Distribution in the Iberian Peninsula and Galicia

A Workshop (WKTRUTTA) organized by the ICES on the anadromous (sea-migratory) form of brown trout in 2013, resulted in a report on the status of the species throughout their natural distributional range including the Iberian Peninsula (ICES WK REPORT 2013). In order to get a more precise distribution in Spanish rivers, we contacted the authorities responsible for the management of fisheries and conservation of this species. This survey included 49 river basins of about 15 km or longer and concluded that sea trout are only absent in four rivers; in three rivers due to the poor water quality and in the fourth river due to the presence of an inpassable natural waterfall. The remaining 45 river basins represent an overall potential habitat of 3,000 km of river length of which nearly 1,200 km (40%) are presently accessible for this anadromous species (Figure 18.1; for Galicia see Figure 18.2). Lack of access to several rivers is caused mainly by the construction of hydroelectric power dams. Additionally in Spain, the sea trout is also present in many small coastal rivers under 15 km in length. More recently a new report on sea trout conducted by ICES in the WGDAM Group, has included sea trout distribution in Portugal (Almeida, P., pers. com.). In that report, Portuguese researchers from the Evora University concluded that the southern limit of sea trout is Mondego River in central Portugal.

Data Collection and Analysis

1 Fish Traps

Five facilities (Figure 18.3) allowed us to obtain the sea trout specimens and data for this study: one in the Landro catchment (Landrove, in the Landro River), two in the Ulla catchment (Ximonde, in the Ulla River and Liñares in the Liñares River, an Ulla's tributary); one in the Lérez catchment (Bora, in the Lérez River), and the last one in the Miño catchment (A Freixa, in the Tea River). Table 18.1 shows the number of sea

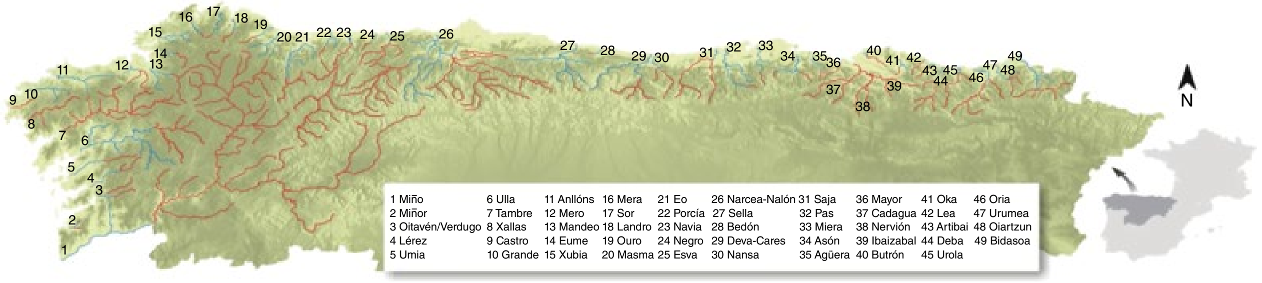

Figure 18.1 Map showing sea trout distribution in Spain, with the total length of the 45 Spanish major rivers that flow into the atlantic Ocean and to the Cantabrian Sea.

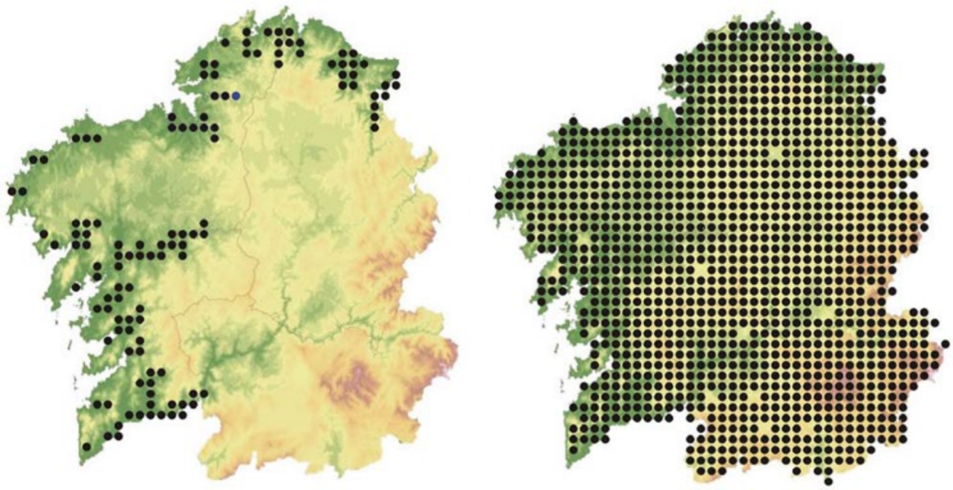

Figure 18.2 Distribution maps of sea trout (left) and brown trout (right) in Galicia. From Hervella & Caballero (1999).

trout adults and smolts caught at those five traps in different years. Data of 25,740 adults and 7,567 smolts are presented in this paper. Age of the sea trout was determined from scales for all traps, stages and years, with the only exception of the A Freixa trap. Three out of the five traps used in this study (Ximonde, Liñares and A Freixa) have downstream and upstream fish catching facilities, while the other two (Bora and Landrove) have only upstream catching facilities. Smolt data obtained from three fish traps (Ximonde, Liñares and A Freixa) are used in this work to describe the smolt migration including biometric and demographic characteristics and to compare the size of descending smolt with the sizes obtained by back-calculation of adults from the Official fishery.

Adult data obtained at the five traps, are used to describe the migration of adults and kelts (only in three traps) from and to salt water. This information was also used to compare adult growth between the studied populations. In the three traps where sea trout were tagged (Ximonde, Liñares and Bora), mark-recapture methods made it possible to describe migration and growth from the Ulla and Lérez populations.

In three (Ximonde, Liñares and Bora) of the five traps, sea trout, at least adults moving downstream or upstream, and a 20% of the smolts, were tagged as they made their way through. The first objective was to detect whether they return and were re-captured by a trap device, or whether or not the situation was identical with the initial capture. Floy tags allowed individual identification even when captured outside the traps, and also further information on the migration routes. Additionally, the use of individual tags allowed quantification of the growth between the initial tagging and recapture. The most used tagging method in this work, given its low price and high profitability was the panjet inoculation with Alcyan blue ink as described by Hart & Pitcher (1969). A baseline amount of scales were extracted from all individuals and the sea trout age determination from scale reading was carried out according to the findings of Richard & Baglinière (1990) and Elliott & Chambers (1996).

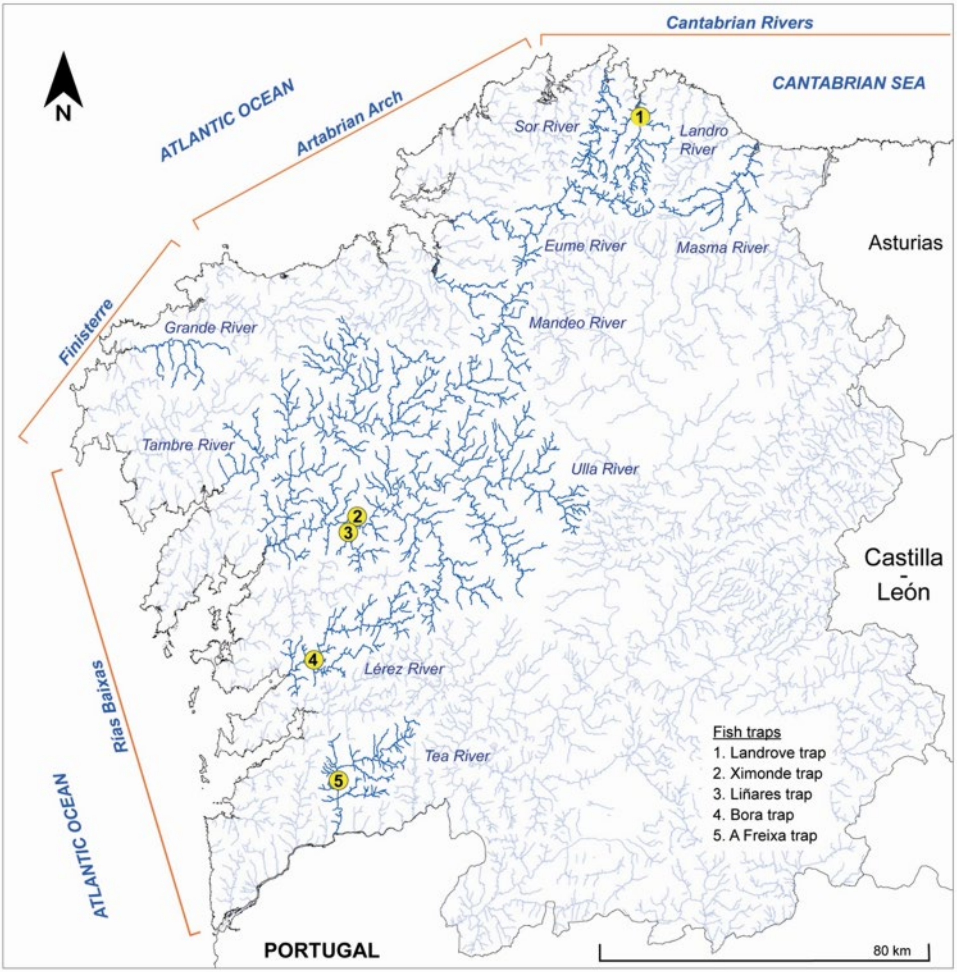

Figure 18.3 Location of the rivers which have been invented fish traps and included in this work.

Table 18.1 Fish traps and adult and smolt specimens of sea trout captured by time period.

	Bora Trap Lérez River 1999–2013	Ximonde Trap Ulla River 1993–2013	Liñares Trap Liñares River 1994–2004	A Freixa Trap Tea River 1996–2013	Landrove Trap Landro River 1996–1999	Total
Adults	3,265	5,356	178	16,533	408	25,740
Smolts	–	967	266	6,334	–	7,567

2 Official Sea Trout Fishery

Galician freshwater fishing law published in 1992, states that every angler who catches a sea trout or a salmon must register the fish. In Galicia, the sea trout register began in 1993, while this procedure had been in force for salmon since 1949 throughout Spain.

Table 18.2 Number of sea trout with age determined by scale reading (Age) in relation to the total of fish registered (Catch) at the Galician Official fishery from 1995 to 2002. (% = percentage of age determined specimens by river.)

	Eume		**Grande**		**Landro**		**Mandeo**		**Masma**		**Sor**		**Tambre**		**Ulla**		**Total**	
Year	**Age**	**Catch**	**Age**	**Catch**	**Age**	**Catch**	**Age**	**Catch**	**Age**	**Catch**	**Age**	**Catch**	**Age**	**Catch**	**Age**	**Catch**	**Age**	**Catch**
1995	474	720	15	120	23	23	243	222	19	19	78	354	254	456	53	57	1,159	1,971
1996	265	530	23	127	69	69	183	351	11	11	89	546	237	432	60	60	937	2,126
1997	269	549	19	52	96	101	253	402	29	30	39	527	101	379	56	57	862	2,097
1998	181	392	26	64	45	52	163	165	75	79	42	91	61	223	18	19	611	1,085
1999	250	486	12	124	36	41	165	218	34	42	35	90	234	437	121	124	887	1,562
2000	291	494	19	186	48	61	198	344	32	56	89	213	153	342	221	237	1,051	1,933
2001	327	646	33	158	87	103	287	391	18	23	167	643	212	450	203	232	1,334	2,646
2002	332	537	24	184	98	113	302	479	25	31	123	607	123	356	344	351	1,371	2,658
Total	2,389	4,354	171	1,015	502	563	1,794	2,572	243	291	662	3,071	1.375	3,075	1,076	1,137	8,212	16,078
%	54.87		16.85		89.17		69.75		83.51		21.56		44.72		94.64		51.08	

Data collected in accordance with this procedure include generally fork length (cm), weight (grams), name and origin of the angler, bait and place where the fish was caught and, in most rivers, a sample of scales was also taken.

Eight rivers containing enough data in all the time series (1995–2009) were included in this study: Masma, Landro and Sor in the Cantabrian Sea; Eume, Mandeo and Grande in the Artabrian Arch-Finisterre area (Atlantic Ocean); and Ulla and Tambre in the Rias Baixas (south of Galicia, Atlantic Ocean) (Figure 18.3). However, in order to correctly interpret the obtained data, it is important to take into account that the minimum legal size applied in Galicia for the sea trout was changed in the analysed time series (from 25 to 30 cm in 1996). This change has significantly affected the time series.

Table 18.2 shows the number of individuals caught in the Official fishery between 1995 and 2002, and the number and total percentage of individuals whose age was determined. Even though the proportion of sea trout ageing determination was low in the rivers Grande and Sor (16.85% and 21.56%, respectively) we decided to include both rivers in this study. For the rest of rivers, this proportion was significantly higher, from 44.72% to 94.64%. In short, scale reading allowed determining the age of 8212 specimens caught from 1995 to 2002 and extrapolation of these results to a total of 16,078 individuals caught in the Official fishery during the same years. We also used the data from fishery records to compare length and weight of the specimens caught until 2009, thus incrementing to 29,078 individuals used in this comparison.

Data obtained on adult sea trout from the Official fishery are used in this work to describe the characteristics (biometrics and demographics) of eight Galician populations; thus all comparisons between these eight populations come from the fishery data. Also the FW growth results come from the fishery records, although in this case only seven rivers could be compared. In this chapter we indicate the origin of the data used, i.e., Official fishery or Trap.

A total of 62,385 sea trout, including smolts (7,567) (Table 18.1) and adults (25,740) (Table 18.1) from five fish traps until 2013, plus 29,078 adults from the Official fishery catches between 1995 and 2009 (16,078 with the age determined between 1995 and 2002, Table 18.2; 1,562 fish from the fishery were used in back-calculation estimates, Table 18.3)

Table 18.3 Sea trout adults from seven Galician Rivers on which length at different age classes was backcalculated.

	Smolt age	**1**				**2**				**3**					
River	**Sea age**	**0+**	**1+**	**2+**	**Total**	**0+**	**1+**	**2+**	**Total**	**0+**	**1+**	**2+**	**3+**	**Total**	**Total**
Eume		–	–	–	–	83	169	32	284	64	50	5	5	124	408
Landro		–	–	–	–	20	33	2	55	21	23	7	–	51	106
Mandeo		–	–	–	–	40	191	34	265	44	63	3	–	110	375
Masma		–	–	–	–	23	34	8	65	4	8	–	–	12	77
Sor		–	–	–	–	4	14	4	22	19	26	6	–	51	73
Tambre		3	6	2	11	70	79	6	155	13	14	2	–	29	195
Ulla		7	1		8	45	223	8	276	14	29	1	–	44	328
Total		10	7	2	19	285	743	94	1,122	179	213	24	5	421	1,562

were used to carry out most of this work. *Back-calculation* is defined as estimating fish size at an earlier age or ages on the basis of corresponding measurements of fish size and the growth marks in calcified structures (e.g., scales, bones, otoliths, etc.; see Francis, 1990). This technique allowed us to estimate the fish size at its first year of life, at the second and so on. The back-calculation method used in this work is based upon the assumption of the body proportionality hypothesis (Francis, 1990), which assumes a constant deviation of each individual size through its life with respect to the population mean and use the regression parameters of the length over the scale radius. The proportional back-calculation methods, by contrast with those that only applied the regression as the predictive function, consider the individual variability of the measures.

We back-calculated the size at age of 1,562 adult sea trout individuals captured at the Official fishery in seven rivers (Table 18.3) to obtain data about their size the previous year in freshwater and saltwater. Nevertheless, the low number of scales obtained at the Grande River prevented the inclusion of this population. That is why eight Galician sea trout populations were compared but only seven were considered based on back calculated data.

Data obtained from each single fish at traps or fishery, after data collection and subsequent analysis in the laboratory were: date and trap device or fishing place, life stage, fork length (FL, mm), weight (W, g), condition factor (K, Fulton, 1911), freshwater (FW) or sea age, number of reproductions and first reproduction age.

The age notation used in this work follows Richard & Baglinière (1990). Sea trout age was noted with two numbers separated by a hyphen (e.g. 2-1 means two FW years and one year at sea). The first number refers to the smolt or FW age (1, 2, 3 or 4 years) and the second to the sea age. Frequently we note both smolt and sea age with a '+' sign because fish are usually caught before (in the sea) or after the winter annulus are formed (in FW). In the sea age notation we also frequently write 'SW' that means sea winter, for example 2+SW (two sea winters plus). The notation of age when adding back-calculated sizes in the Results Section does not include a '+' sign since the size is estimated by the end of the year, once the winter annulus is formed.

The following abbreviations will be used in this paper: Sea Winter = SW, Freshwater = FW, Fork Length = FL (in mm, to the nearest mm), and Weight = W (in g, to the nearest 0.1 g). Given the complexity of the sea trout life-cycle and for a better understanding of this study, the terminology of the life stages of the fish follows some of the criteria established by Allan & Ritter (1977) for salmonids but, adapted to the sea trout life-cycle. Nine categories were established:

1) **Alevin:** trout after hatching, first with yolk sac and then when it starts exogenous feeding, until it reaches the first summer of life.
2) **Parr:** brown trout juvenile from summer to smolt transformation.
3) **Pre-smolt:** brown trout juvenile that begins to show outward signs for their sea migration (silvery, loose of parr marks, white fins).
4) **Smolt:** juvenile with silver livery which begins its descent into the sea.
5) **Post-smolt or finnock:** sea trout returning to the river the smolting year, not necessarily to reproduce (sea age = 0+SW). Therefore, at the end of the smolt year can be mature or immature.
6) **Maiden sea trout:** has spent at least one season at sea (some months as finnocks or one or two sea winters) and return to the river to spawn for first time as 0+SW, 1+SW or 2+SW.

7) **Previous spawner:** when return to the river to spawn for at least a second time.
8) **Kelt:** sea trout that has been reproduced recently and has not yet begun a new period of growth.
9) **Resident trout:** trout remaining all their life in freshwater.

Additionally, we also follow a series of arithmetic values representing the so-called *key features* (Harris, 2006) of the age structure and reproductive history used to characterize sea trout populations:

- **Mean Smolt Age (MSA):** (Fahy, 1978) is the average number of years that juveniles spent in FW before migrating to sea as smolts. MSA = [% S1 + (% S2 · 2) + … + (% Sn · n)]/100. Where S1 = Smolt age class 1 FW year old, S2 = Smolt age class 2 FW years old, … Four FW age classes (1, 2, 3 & 4) have been detected in Galicia.
- **Mean Maiden Age (MMA):** The average number of years (winters) that post-smolts spent in the sea before returning to freshwater to spawn for the first time as a maiden fish.
- **Mean Spawning Frequency (MSF):** The average number of spawning marks detected on the scales of individual fish, which usually indicate that it has spawned on at least one previous occasion.
- **Mean Adult Age (MAA):** The average number of years (winters) as an adult after migrating to sea as a smolt (= MMA + MSF).
- **Mean Total Age (MTA):** Average age from birth to capture (= MSA + MAA).

For all captured salmonids, both alive in traps and dead individuals in the Official fishery, fork length (FL) and weight (W) were measured. Also, a silvery index was noted, both in adults and juveniles (0 = no silver, 1 = medium silver and 2 = very silver) in order to figure out the time spent in freshwater (adults) or when migration to the sea occurred (juveniles).

The mean values of the variables were compared among populations using analysis of variance (ANOVA) or the Student's *t*-test when only two groups are compared. When the assumption of normality was not met, the non-parametric test of Kruskal–Wallis (KW) was used. In both tests significance levels below 0.05 indicate that the means of the groups differ. All analyses were performed using the statistical software SPSS 18.

Combining both rivers with traps and those where Official fishery operates, we pooled ten rivers referred to in this paper; namely Eume, Grande, Landro, Lérez, Mandeo, Masma, Sor, Tambre, Tea and Ulla (the Liñares river is a tributary of the Ulla River) (Figure 18.3). Some hydro-morphological characteristics of those rivers previously reported from Río & Barja (1997) and Official data from Galician Water Agencies are shown in Table 18.4. Larger rivers (Ulla and Tambre) are located in the south of Galicia, while the shorter ones flow north into the Cantabrian Sea. River length varies from 40 Km (Landro) up to 133 Km (Ulla). Annual mean flow rate fluctuates between 8.8 m^3/s (Sor) and 140 m^3/s (Ulla); and the basin areas vary from 200 Km^2 (Sor) to almost 3000 Km^2 (Ulla). The mean effective accessibility for migratory fishes does not reach half the length of the main course for the ten rivers, ranging from almost 90% in Sor River to just 8% in Tambre River. All rivers were included within two degrees of latitude, from the Tea River located at 42 degrees north to the Sor River located at 43 degrees, 33 minutes north.

Other water parameters used in this chapter as water temperature and flow, were obtained from the Official Water Agencies for Galician Rivers (Aguas de Galicia and Confederación Hidrográfica del Miño-Sil). At the Ximonde Trap water temperature

Table 18.4 Major characteristics of the ten rivers included in this study.

	Catchment area (km^2)	River length (Km)	Flow (m^3/s)	Accessible length (Km)	% Accessibility	Latitude	Maximum altitude (m)	Sinuosity	Slope
Eume	470.20	80.00	19.10	11.70	14.65	43° 25’ 31”	880.0	1.76	1.1
Grande	282.90	42.10	8.30	9.00	21.38	43° 08’ 02’	567.0	1.70	0.9
Landro	269.60	39.60	7.10	17.30	43.69	43° 38’ 16”	875.0	1.50	2.6
Lérez	449.50	60.80	21.20	28.60	47.04	42° 26’ 05”	900.0	1.60	1.3
Mandeo	456.90	57.60	14.10	14.70	25.52	43° 17’ 10”	595.0	1.60	1.0
Masma	291.30	52.30	6.30	26.30	50.29	43° 34’ 06”	935.0	2.00	1.8
Sor	201.80	56.80	6.00	50.90	89.61	43° 41’ 50”	635.0	2.40	1.3
Tambre	1,530.00	124.50	54.10	10.90	7.84	42° 49’ 28”	733.0	1.80	0.4
Tea	411.00	50.00	17.50	35.60	71.20	42° 04’ 50”	940.0	1.51	1.1
Ulla	2,803.60	133.40	79,30	74.80	56.07	42° 40’ 41”	615.0	1.90	0.5
Mean	716.68	71.16	39,21	27.98	42.73	–	719.5	1.81	1.19

was measured with a data-logger Minilog type at 10 centimetres of water surface upstream and downstream the trap once every 2 minutes during the year. Photoperiod defined as the interval in a 24-hour period during which a fish is exposed to light, was obtained from the Galician Institute of Meteorology for different years and it was used to describe smolt migration in this work.

Results

Migrations

Smolt Migration

The collected data during the analysed time series in the Ulla catchment (from 1993 to 2005 at Ximonde and from 1994 to 2004 at Liñares traps), show that smolt sea trout migration takes place during the months of March, April and May, with no significant differences between traps (Figure 18.4). April was consistently the month with the highest activity within the Ulla River, both in traps and throughout all the years analysed, representing up to 70% of the catch. May, mainly during the first half of the month, was the second most active period with a mean of over 15%, although in some years catches came close to 40%. In March the catches were less important with only 10% of the total catch. Smolt migration in the Tea River from 2000 to 2005 was similar to the Ulla River and occurred between March and May with a greater movement of fish in April. Smolt migration in Tea only shows slight differences compared with the Ulla (Figure 18.5).

The relationship between smolt catches in the traps and three environmental variables (flow, water temperature and photoperiod) is described in Table 18.5. None of the three traps presented any statistical relationship between the number of smolts caught

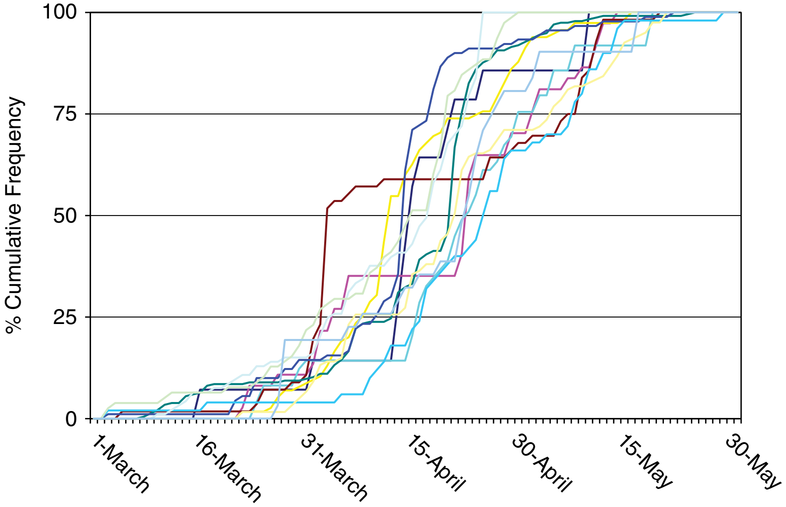

Figure 18.4 Cumulative frequency of annual ascend of sea trout smolt in the Ulla River (Data from Ximonde and Liñares traps, 1993–2005).

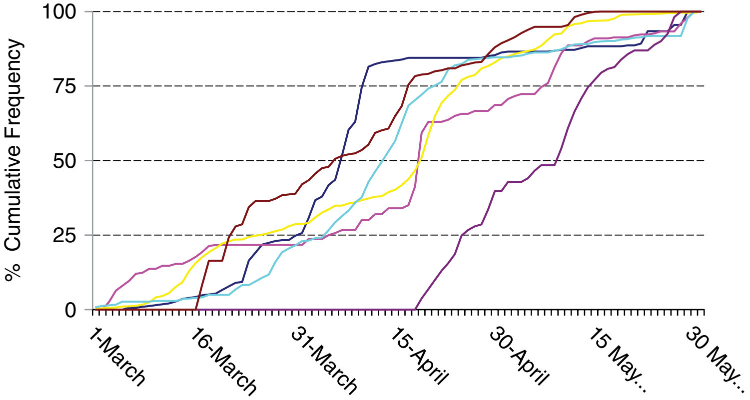

Figure 18.5 Cumulative frequency of annual ascend of sea trout smolt in the Tea River (Data from A Freixa trap, 2000–2005).

and the three environmental variables tested, although it seems that a greater movement of fishes occurs as flow increases. Migration starts when the photoperiod reaches 12 hours of light and is completed after a photoperiod of 13.5 hours. Regarding temperature, in general migration starts shortly before water reaches 12°C and finalizes close to 13°C, with some differences between the three rivers.

Movements at Sea

An overview of adult recaptures of tagged sea trout in Bora and Ximonde traps is presented in this section. Table 18.6 summarizes these practices: recaptures are divided into six categories: (A) specimens caught in the same trap of tagging in the same year of tagging, or one or two years later; and (B) the specimens obtained away from the tagging site, in the same river, in other rivers or at the sea. Figure 18.6 shows the location of recapture of sea trout adults originally tagged at Bora and Ximonde traps.

Between 1999 and 2005, a total of 1,731 adults and finnocks were tagged at Bora trap (Lérez River); between 2000 and 2006, 190 individuals were recaptured in Bora trap (11%) and 20 elsewhere (1.2%). Between 1995 and 2005 a total of 3,252 adults and finnocks were marked at the Ximonde trap (Ulla River); between 1996 and 2006, 159 individuals were recaptured in that same trap (4.9%), and 12 elsewhere (0.4%) A total of 32 tagged sea trout were recaptured outside Bora and Ximonde traps; and 21 recaptured outside the released river (other rivers or salt water) provide a picture of salt water migrations performed by sea trout in Galicia. From the post-smolts or adults tagged at Bora trap a total of 20 specimens were not recaptured at the trap (Figure 18.7 and Table 18.7). Nine of them were recaptured at the Lérez estuary, seven were reported by anglers from the Lérez catchment and four more were recaptured in other rivers. One of these 'distant' recaptures were located at the Tambre River, one was obtained at Ximonde trap and two more specimens were recaptured at the Cares River (in the border Asturias-Cantabria, more than 500 km away from Lérez River), one of them reported by an angler and the other one captured at a trap in autumn.

Regarding Ximonde trap (Figure 18.6), 12 sea trout specimens tagged at this trap (three smolts and nine post-smolts and adults) were not recaptured at the trap. One smolt was caught in the northern tip of the Ulla estuary and the other two in the

Table 18.5 Percentage of the cumulative frequency of smolt catch and three environmental variables [flow (m^3/s), Temperature = Temp (°C) and Photoperiod = Phot] at Ximonde (1993–2005), Liñares (1995–2004) and A Freixa (2000–2005) traps.

	25%				**50%**				**75%**			
Trap	**Date**	**Flow**	**Temp**	**Phot**	**Date**	**Flow**	**Temp**	**Phot**	**Date**	**Flow**	**Temp**	**Phot**
Ximonde	10 Apr	31.76	12.17	13.10	19 Apr	40.94	12.06	13.34	27 Apr	39.86	13.05	13.5
Liñares	2 Apr	–	11.97	12.58	14 Apr	–	11.83	13.23	21 Apr	–	11.97	13.46
A Freixa	29 Mar	4.53	11.82	12.37	18 Apr	3.82	11.67	13.30	26 Apr	3.78	12.72	13.64

Table 18.6 Summary of sea trout mark-recapture procedures at Bora and Ximonde traps. Individuals were tagged from 1999 to 2006 at Bora trap and from 1995 to 2006 at Ximonde trap. (Percentage of the total number of sea trout recaptured referred to the total individuals tagged in each trap.)

		Recaptures					
		(A) At the same trap			(B) Outside the trap		
Trap	Tagged specimens	Same year	1 year later	2 years later	Same river	Other river	At sea
Bora	1,731	25 (1.44%)	161 (9.30%)	4 (0.23%)	7 (0.40%)	4 (0.23%)	9 (0.52%)
Ximonde	3,252	81 (2.49%)	76 (2.34%)	2 (0.06%)	4 (0.12%)	3 (0.09%)	5 (0.15%)
Total	4,983	106 (2.12%)	216 (4.33%)	6 (0.12%)	11 (0.22%)	7 (0.14%)	14 (0.28%)

neighbouring estuary of the Tambre River. Five tagged post-smolts and adults were recaptured outside the Ulla River, in locations such as Aguiño (Ulla Estuary), Sanxenxo (Lérez Estuary), lower part of the Miño River, Anllons River and Tambre River; and finally four recaptures were obtained inside the Ulla River.

Return to the River (Upstream Migration)

A total of 16,069 ascending adult sea trout were caught in five traps located in rivers Ulla, Liñares, Lérez, Tea and Landro:

- Ximonde trap (Ulla River): 5098 specimens between 1993 and 2012.
- Liñares trap (Liñares River, Ulla basin): 178 specimens between 1994 and 2004.
- Bora trap (Lérez River): 3027 specimens between 1999 and 2012.
- A Freixa trap (Tea River, Miño basin): 7503 specimens between 1997 and 2012.
- Landrove trap (Landro River): 263 specimens between 1998 and 1999.

Catches are grouped into fortnights to evaluate the upstream run timing and, as it can be observed in Figure 18.7, there is great similarity in all three traps located on the main rivers, namely Ximonde (Ulla), Bora (Lérez) and Landrove (Landro); although at Landrove trap sea trout run starts earlier than in Rías Baixas Rivers. Sea trout starts to run in April and May, and 50% of the run is completed between June and July. A sharp decline of catches occurs normally in September, followed by a partial recovery in the upcoming months, from October to December. In fact, in Bora, Ximonde and Landrove, around 20% of annual sea trout catches are detected in the last three months of the year. However, the migration may continue into January the following year. In short, the most important upstream migration in these three rivers takes place by the end of spring and especially during much of the summer while autumnal migration, though important, has a minor impact.

Catches of adult sea trout obtained in the two tributaries considered for the study, Liñares and Tea, loosely mirrors the aforementioned main rivers. While there are great similarities in the upstream run of these two tributaries, sea trout movements at Liñares trap are greater in winter representing about 50% of the catches, followed by the slow

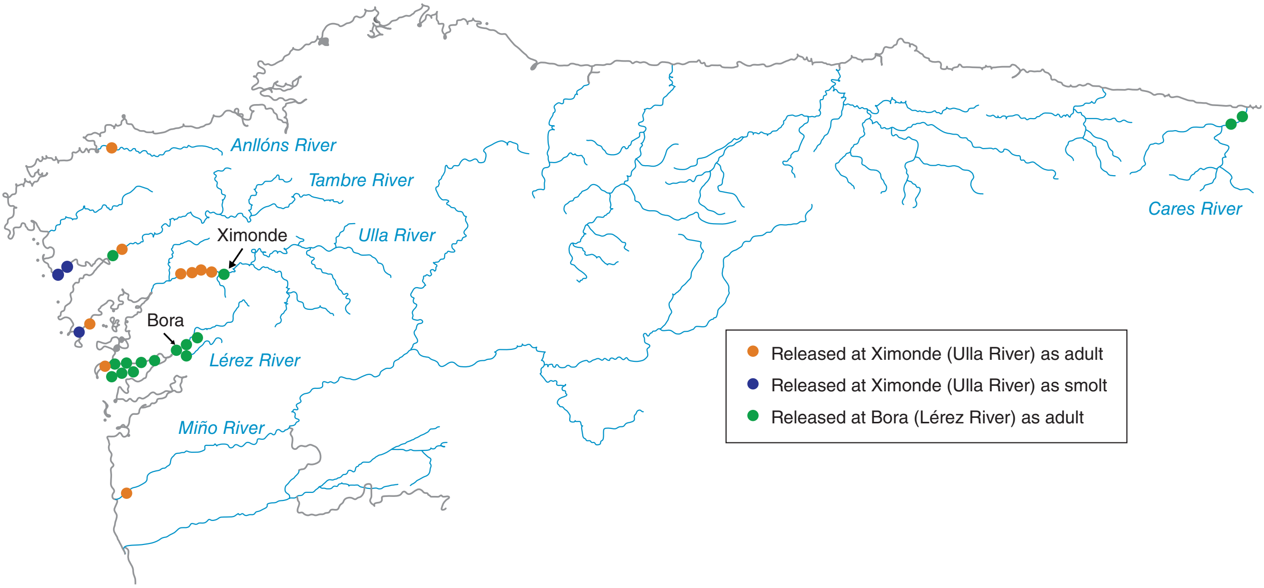

Figure 18.6 Location of recapture of sea trout adults originally tagged at Bora and Ximonde traps.

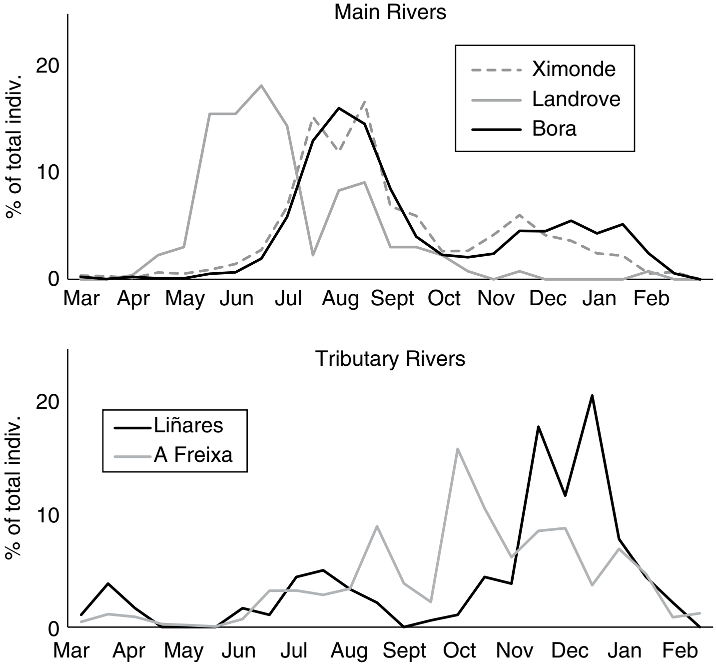

Figure 18.7 Ascending sea trout returning to the main Ulla, Lérez and Landro and tributary rivers (Liñares and Tea) based on recording in traps.

fall season with almost 30% and finally minor catches in summer (18%). In the Tea River, however, most of upstream movements occurs in fall (53%), followed by the summer (32%) and the winter (26%) periods.

Migration of the different age classes throughout the year in the rivers Ulla, Lérez and Landro (Figure 18.8) demonstrate the monthly changes in the MAA. At Ulla and Lérez rivers, the highest ages are detected at the beginning of migration (April–May), whereas July and August score the minimum values; even when a slight increase occurs in autumn, it falls clearly below spring levels. In the Landro River it varies somewhat, since values at the end of the year are very similar to those of spring; nevertheless, decline in the MAA is also detected in summer.

Kelt Return to the Sea

Once reproduction is completed, kelts commence downstream movements. Data from the traps of Ximonde, Liñares and A Freixa show that the migratory activity lasts from December to early June (Figure 18.9). Two distinct periods can be noted: a peak time in January and February followed by a slight decline which is followed by a recovery in the second fortnight of March, with an increased activity in April.

Growth

Freshwater Growth

FW age determination from sea trout smolt and adult scales, revealed 4 smolt age classes in Galicia (1+, 2+, 3+ and 4+) but the number of 1+ and 4+ smolts was very low

Table 18.7 Comparison between smolt size obtained by back-calculation and FL of smolts caught in the Ulla River traps between 1993 and 2001 in 2+ smolts (*Differ significantly when $p < 0.05$).

	FL (mm) in 2+ smolts						**Student's *t*-test**			
	Back-calculated			**Trap**						
Year	**N**	**Average**	**CI95%**	**n**	**Average**	**CI95%**	**Mean differences (mm)**	**Student's *t***	**df**	**Significance (p)**
1993	7	211.2	25.0	24	223.5	7.7	−12.4	−1.3	29	0.222
1994	36	224.8	13.8	28	207.0	6.1	17.8	2.3	48	0.025*
1995	41	218.7	11.7	72	206.6	3.2	12.1	2.0	46	0.058
1996	31	216.9	13.9	29	212.3	5.3	4.6	0.6	39	0.550
1997	27	219.4	12.0	7	207.7	10.2	11.6	0.9	32	0.356
1998	26	212.6	13.7	44	213.1	5.3	−0.5	−0.1	33	0.947
1999	21	215.4	13.5	214	213.0	2.1	2.4	0.3	21	0.738
2000	19	231.5	9.9	53	217.1	5.2	14.4	2.7	70	0.009*
2001	19	234.6	12.1	38	206.1	6.5	28.5	4.4	55	0.0004*
Total	227	220.7	4.6	509	212.1	1.5	8.6	3.5	273	0.001*

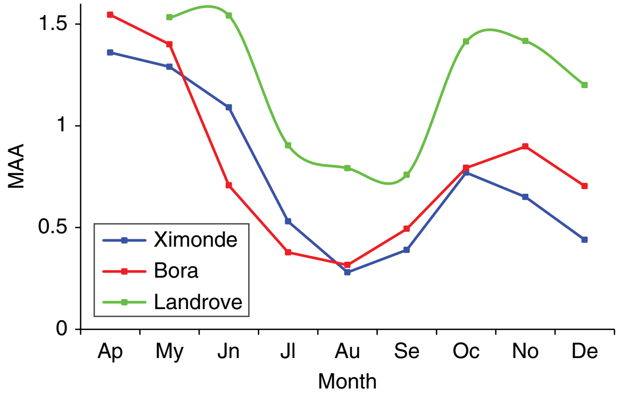

Figure 18.8 Seasonal change in the mean adult age (MMA, years) of the specimens captured at the rivers Ulla (Ximonde trap), Lérez (Bora trap) and Landro (Landrove trap).

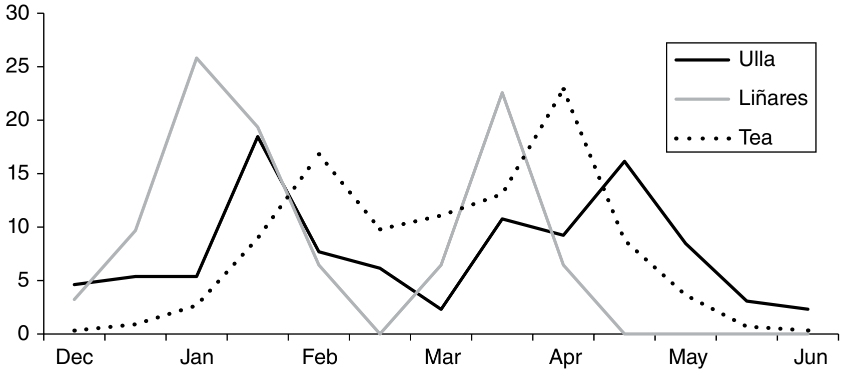

Figure 18.9 Downstream migration of sea trout kelt in the rivers Ulla, Liñares and Tea.

in the sample. For the total sample (Figure 18.10) in the first FW year (n = 1,562) lengths ranged from 4 to 17 cm, with a mean value of 8.7 cm (back-calculated mean FL for smolts: 1+ = 12 cm, 2+ = 9.3 cm and 3+ = 7 cm) and ranged between 5 and 11 cm for 87% of the individuals. In the second FW year (n = 1,543) lengths ranged between 9 and 29 cm, with a mean value of 18.5 cm (back-calculated mean FL for smolts: 2+ = 19.8 cm, 3+ = 15.3 cm) and ranged between 13 and 22 cm for 83% of the individuals. In the third FW year (n = 421) smolts achieved a mean size of 22.3 cm, with a length range between 13 and 30 cm and ranged between 18 and 25 cm for 81% of the sample.

When comparing the growth of smolts 2+ or 3+, differences were significant (student's *t*-test for the first FW year: t = 19,176 df = 937 $p < 0.001$; and for the second FW year: t = 10,595 df= 840 $p < 0.001$), showing that, in general, growth is stronger in rivers from southern Galicia (Rías Baixas), poor in the rivers up North (Cantabrian), and intermediate in the rivers from the Artabrian Arch and Finisterre.

Smolt size values obtained by back-calculation were validated by comparing them with FL values obtained from smolts captures within the Ulla River traps. Since analysed data suggest that smolt sizes can vary from year to year, only available data recovered from both methods were incorporated into this work: data from 1993 to 2001 (smolts captured at

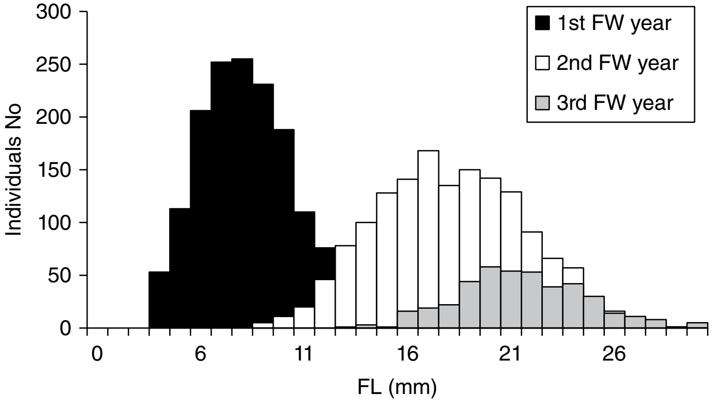

Figure 18.10 Length distribution of back-calculated sizes for three smolt age groups (n = 1,562 smolt sea trout).

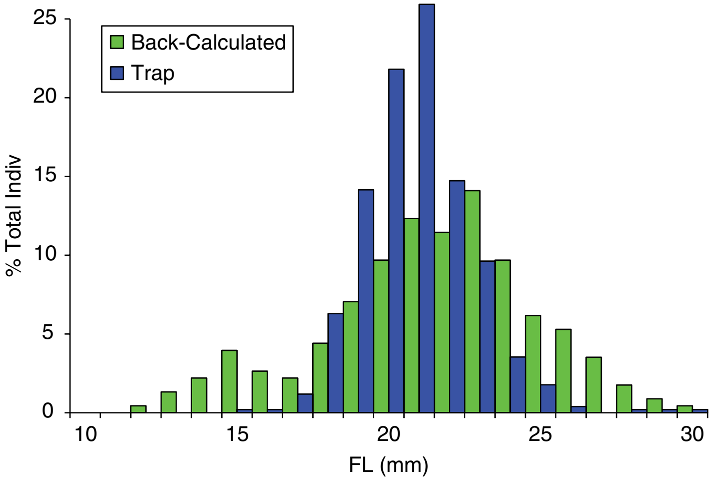

Figure 18.11 Distribution of back-calculated and empirical length of Ulla 2+ smolts. Empirical lengths were obtained from specimens captured in traps (Ximonde and Liñares) between 1993 and 2001 (FL = fork length).

Ximonde and Liñares traps) and sizes of smolt back-calculated on sea trout adults who had smoltified within those years. Since the proportion of smolt ages vary between the two groups of data, we chose age class of 2+ for comparison. Differences between the two methods are statistically significant (Table 18.7), being 8 mm larger for smolts obtained by back-calculation. However, the difference was only significant in three of the nine years. Moreover, as shown in the length frequency histogram of FL in smolts (Figure 18.11), FL distribution of smolts captured by traps tends to normality and with lower amplitude (range = 150-300 mm) than the back-calculated FL (range = 120–320 mm).

The compiled data suggest that the data obtained by back-calculation must be used cautiously. Nevertheless, we decided to include it in this work because it was one of the only way to obtain smolt sizes from multiple populations, and the differences were not always significant.

Marine Growth

Sea growth of sea trout populations in Galicia is analysed on the basis of two different methods: data analysis of adult sea trout recaptured in Bora and Ximonde traps and analysis of back-calculation data applied to adult sea trout obtained in the Official fishery from seven Galician rivers.

Regarding the first method, sea growth of the different age classes was compared (Figure 18.12) based on 216 specimens recaptured one year after been tagged in Bora (Lérez River, 161 *recaptures* in 7 years) and Ximonde traps (Ulla River, 76 recaptures in 11 years). Average size for each sea age class was considered, both at first capture and the recapture. Significant differences in size and weight were found between sea trout from both rivers: a positive difference of 5 cm length for the Ulla sea trout – on average – for all sea age classes, ranging from 4 cm in finnocks to 7.5 cm in 3+SW specimens. The weight differences reached a mean of 470 g more for Ulla sea trout, ranging from 160 g in finnocks to almost 1000 g more in 3+SW Ulla sea trout.

For the study of marine growth, measures on adult sea trout scales obtained at the Official fishery from seven Galician rivers were taken in consideration. Thus, data from 1,083 individuals were used: 963 specimens 1+SW to calculate the growth between the smolt stage and the first marine winter; and 120 specimens 2+SW to determine the sea growth between the first and the second marine winters (Table 18.8). In all cases there was no reproduction between these periods. For this parameter major differences were observed between both sea age classes (KW: $Chi^2 = 450.89$, df = 6, $p < 0.001$) as in the 1+SW (KW: $Chi^2 = 422.58$, df = 6, $p < 0.001$) and 2+SW (KW: $Chi^2 = 21.41$, df = 6, $p = 0.002$).

Significant differences in growth between the Galician populations were identified, both in the first sea year and the remaining years at sea. Growth in southern Galician populations (Rias Baixas) is clearly higher than in the northern populations.

Reproduction

Sex Ratio

The sex ratio (Male/Female) of sea trout captured in autumn and winter in the Ulla river between 1993 and 2012 was 1:2.3 (n = 1493), while in the Lérez, between 1999 and 2012, was 1:2.1 (n = 739). The differences between these sea trout populations were not statistically significant.

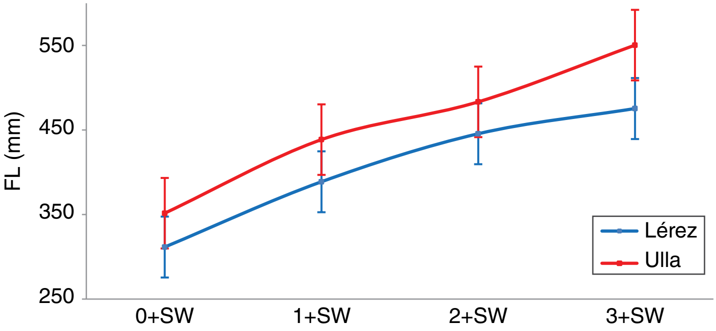

Figure 18.12 Marine growth of sea trout according to data obtained by recaptures in the rivers Lérez (Bora trap) and Ulla (Ximonde trap). Mean values ± 95% CI for each sea age class were used.

Table 18.8 Length increment (mm) between smolting and first sea winter for two Sea Age Classes (1+SW, 2+SW) in seven Galician sea trout populations.

	1+SW		**2+SW**		**Total**	
River	**N**	**Mean ± CI95%**	**n**	**Mean ± CI95%**	**n**	**Mean ± CI95%**
Eume	219	90.32 ± 3.87	37	85.10 ± 5.73	256	89.57 ± 3.42
Landro	56	101.07 ± 7.48	9	98.28 ± 18.17	65	100.68 ± 6.87
Mandeo	254	86.48 ± 2.97	37	81.22 ± 6.46	291	85.81 ± 2.72
Masma	42	91.73 ± 5.73	8	95.22 ± 10.33	50	92.28 ± 5.06
Sor	40	92.88 ± 5.48	10	68.19 ± 9.03	50	87.94 ± 5.45
Tambre	99	146.54 ± 7.58	10	107.82 ± 18.07	109	142.99 ± 7.37
Ulla	253	143.69 ± 4.41	9	96.34 ± 14.77	262	142.07 ± 4.41
Total	963	–	120	–	1083	–
Mean	–	109.90 ± 2.53	–	86.90 ± 3.98	–	107.35 ± 2.33

Significant differences were obtained when comparing the sex ratio factor for the three sea age classes with enough data to analyse (0+SW, 1+SW and 2+SW) within each population (KW Lérez $Chi^2 = 19.53$, df = 2, $p < 0.000$; KW Ulla $Chi^2 = 44.57$, df = 2, $p < 0.000$). Sex ratio at the Lérez River was 1:4 (0+SW), 1:2.05 (1+SW), and 1:1 (2+SW), while at the Ulla River sex ratio was 1:2.48 (0+SW), 1:3.45 (1+SW) and 1:2.51 (2+SW).

Mean Maiden Age (MMA)

From the sample of 16,078 sea trout obtained in the Galician Official fishery, scale reading showed a total of 3,720 repeat spawners. Three sea ages of first reproduction were detected (Table 18.9), showing that sea trout of these rivers can reproduce the first time as finnocks, 1+SW or 2+SW. Significant differences were found in the age of first reproduction among the eight populations studied (KW: $Chi^2 = 227.5$, df = 7, $p < 0.001$).

According to the detected age classes, reproduction of half of the sea trout included in the sample occurred as finnocks (0+SW) and a major percentage of the population reproduced as 1+SW (43.55%), while the sea trout which reproduced for the first time after spending two sea winters (2+SW) represented only a 6% of the total sample. Except in the rivers Sor and Mandeo, the main age of first reproduction were the finnocks (over 80% in the Ulla and almost 70% in the Grande), while in the Mandeo and Sor the main age class were the 1+SW. Data obtained indicates that the MMA ranged from a maximum of 1.7 years in the Sor River to a minimum of 1.14 years in the Ulla River (Table 18.9 and Figure 18.13).

Mean Spawning Frequency (MSF)

Regarding iteroparity or presence of multiple spawners, significant differences were observed among the eight populations studied from data obtained at the Official fishery (Table 18.10, Figure 18.14) (KW: $Chi^2 = 523.17$, df = 7, $p < 0.000$). The detected 3720 repeat spawners represented a 23% of the total sample (16,078 sea trout in eight rivers from 1995 to 2002), of which 84% had reproduced once, 15% (539 specimens) twice, 1.3% (47 specimens) three times, and only a 0.4% (15 specimens) had spawned in four seasons.

Table 18.9 Mean Maiden Age in sea trout populations from eight Galician rivers.

	0+SW		1+SW		2+SW		Total	
River	**N**	**%**	**n**	**%**	**n**	**%**	**n**	**Mean Maiden Age (years)**
Eume	556	58	348	37	48	5	952	1.47
Grande	121	69	46	26	9	5	176	1.36
Landro	84	52	73	45	5	3	162	1.51
Mandeo	252	39	356	55	37	6	645	1.67
Masma	45	53	38	44	2	2	85	1.49
Sor	426	40	545	51	101	9	1,072	1.70
Tambre	228	52	188	43	21	5	437	1.53
Ulla	165	86	26	14	–	–	191	1.14
Total	1,877	–	1,620	–	223	–	3,720	–
Mean	–	50	–	44	–	6	–	1.56

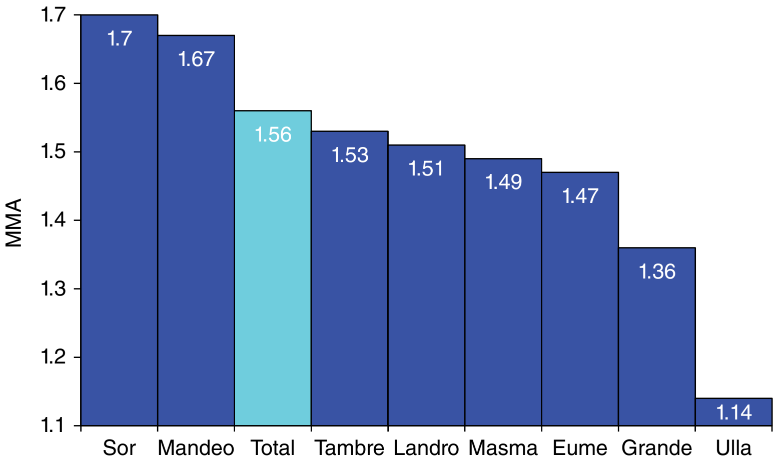

Figure 18.13 Mean Maiden Age (MMA) at first reproduction in eight Galician sea trout populations.

Biometrical and Demographical Characteristics of Galician Sea Trout Populations

Scalimetric age determination of 16,078 sea trout captured in the Official fishery from the eight surveyed rivers allowed us to obtain the number and proportion of sea trout assigned to different age classes, both fresh water and salt water, as well as the mean smolt age (MSA) and mean adult age (MAA). A total of four FW age classes (1+ to 4+) and 7 salt water ages (0+SW to 6+SW) were identified, and 19 out of the 28 possible combinations of FW-SW ages were also determined. The populations with greater diversity in age classes were detected within the rivers Eume, Sor, and Mandeo, allowing

Table 18.10 Mean Spawning Frequency (MSF) in the eight Galician rivers analysed.

	Frequency of reproduction											
	0		**1**		**2**		**3**		**4**		**Total**	
River	**N**	**%**	**n**	**%**	**n**	**%**	**N**	**%**	**n**	**%**	**n**	**MSF**
Eume	3,393	78.16	859	19.77	78	1.80	9	0.21	6	0.14	4,345	0.25
Grande	836	19.31	165	16.30	8	0.79	3	0.30	–		1,012	0.19
Landro	398	9.23	140	25.00	20	3.57	2	0.36	–		560	0.33
Mandeo	1,915	44.12	552	21.56	83	3.24	9	0.35	1	0.04	2,560	0.29
Masma	201	4.67	65	22.73	20	6.99	–		–		286	0.37
Sor	1,976	45.52	756	24.80	285	9.35	23	0.75	8	0.26	3,048	0.47
Tambre	2,637	60.69	394	12.82	43	1.40	–		–		3,074	0.16
Ulla	1,002	23.06	188	15.76	2	0.17	1	0.08	–		1,193	0.16
Total	12,358	–	3,119	–	539	–	47	–	15	–	16,078	–
Mean	–	76.96	–	19.40	–	3.35	–	0.29	–	0.09	–	0.27

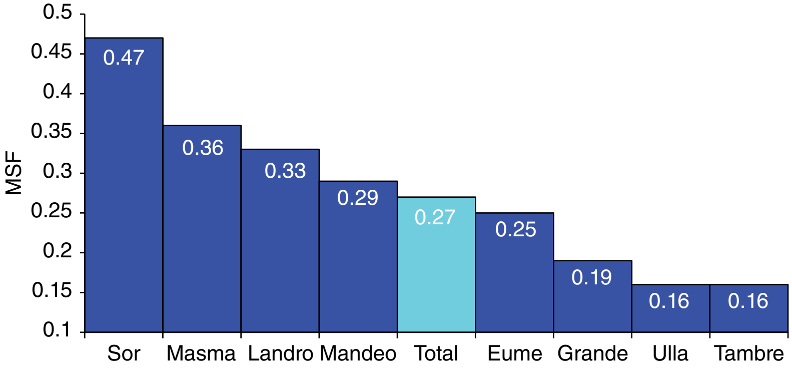

Figure 18.14 Mean Spawning Frequency (MSF) in the eight analysed sea trout populations.

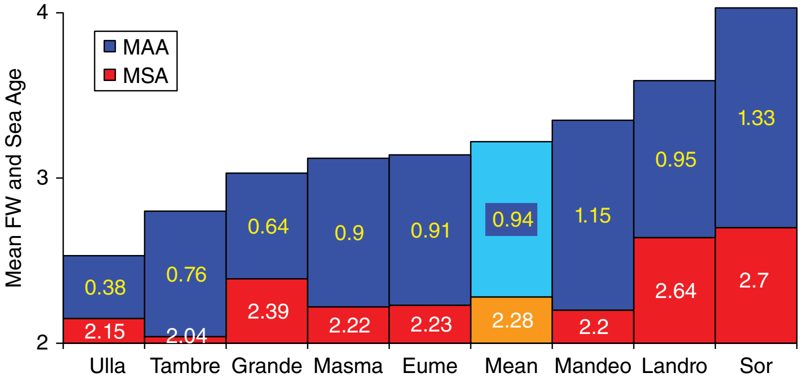

Figure 18.15 Mean total age (MTA = MSA + MAA) of sea trout in eight Galician populations.

for a total of 14 different age classes to be identified. Additionally, 13 age classes were detected within the Grande River, nine in Tambre River and eight in the rivers Masma and Ulla. The predominant age class was the 2-1 (located in the rivers Eume, Mandeo, and Masma) with 34% of the total sample, followed in importance by the 2-0 with 20% of the population (located in the rivers Grande, Tambre, and Ulla), and with 16% the 3-1 (within the rivers Sor and Landro). The classes 2-0, 2-1, 2-2, 3-0, and 3-1 accounted for 90% of the total sample. With respect to the total age (FW + sea), it varied from 1 to 8 years, the mean total age (MTA) of the eight populations studied (Figure 18.15) ranged from a minimum of 2.53 to 2.8 years (at Ulla and Tambre rivers, respectively) to a maximum of 3.59 to 4.03 years (within the Landro and Sor rivers, respectively).

The smolt age classes within seven Galician sea trout populations were compared using back-calculated sizes from the aforementioned 1,562 sea trout specimens (Table 18.11 and Figure 18.16). Differences comparing smolt size among rivers tested are significant for both age classes all together (KW: $Chi^2 = 141.25$, df = 6 $p < 0.001$) and for the 2 years (KW: $Chi^2 = 133.66$, df = 6 $p < 0.001$) and 3 years smolt classes (KW: $Chi^2 = 106.64$, df = 6 $p < 0.001$). The smolts recorded from the Ulla River are the largest, while those from the Cantabrian Rivers are smaller. The noticeably small sized smolts recovered from the Tambre River were striking.

Table 18.11 Back-calculated size (mm) of three smolt age classes from seven Galician rivers.

	1+		2+		3+		Total	
River	**N**	**Mean ± CI95%**	**n**	**Mean ± CI95%**	**n**	**Mean ± CI95%**	**N**	**Mean ± CI95%**
Eume	–	–	284	206.4 ± 3.1	124	233.3 ± 4.4	408	214.5 ± 2.8
Landro	–	–	55	201.3 ± 7.8	51	211.6 ± 7.6	106	206.3 ± 5.5
Mandeo	–	–	265	202.1 ± 3.5	110	223.0 ± 5.1	375	208.2 ± 3.1
Masma	–	–	65	218.12 ± 5.7	12	247.7 ± 10.01	77	222.8 ± 5.6
Sor	–	–	22	185.4 ± 10.0	51	194.4 ± 5.9	73	191.7 ± 5.2
Tambre	11	159.8 ± 13.4	155	193.0 ± 4.7	29	239.1 ± 9.4	195	198.0 ± 4.8
Ulla	8	144.7 ± 19.4	276	223.7 ± 4.2	44	247.2 ± 10.0	328	224.9 ± 4.1
Total	19	–	1,122	–	421	–	1,562	–
Mean	–	153.4 ± 11.45	–	207.8 ± 1.9	–	225.5 ± 2.9	–	211.9 ± 1.6

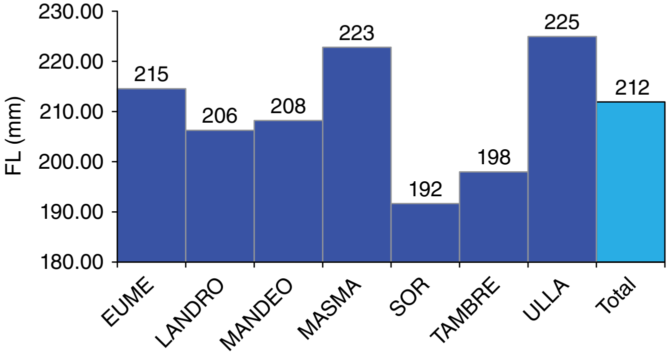

Figure 18.16 Mean size of sea trout smolts from seven Galician rivers.

Biometric data (length, weight and condition factor) from eight sea trout populations obtained in the Official fishery between 1995 and 2009 were analysed together and results are shown in Table 18.12 and Figure 18.17. After excluding 1300 specimens registered between 1995 and 1996 with a length range of 25-30 cm, an overall of 29,078 individuals were considered for this analysis.

Mean values obtained were: 587 g in weight, 364 mm in length and a mean condition factor (K) of 1.12. Differences between the eight rivers were significant for weight (KW: Chi^2 = 881.73, df = 7, p <0.001), length (KW: Chi^2 = 1,171, df = 7.49, p <0.001) and condition factor (KW: Chi^2 = 1,241.96, df = 7, p <0.001).

Mean size of sea trout samples taken after different periods at sea are also shown in this section (Table 18.13 and Figure 18.18). Among the 16,078 specimens whose age has been determined on the basis of scale reading, seven sea age classes were identified; but age class 6+SW was excluded from the table and figure due to only three individuals being detected with a mean size of 70 cm (2 in the Sor and 1 in the Mandeo Rivers). Data analysis showed significant differences in size among the rivers and for all age

Table 18.12 Mean values (± CI95%) of the biometric parameters obtained on the sea trout Official fishery between 1995 and 2009 from eight Galician rivers.

River	FL (mm)	Weight (g)	Condition factor (K)	N
Eume	352.3 ± 1.2	535.6 ± 7.5	1.122 ± 0.003	8,059
Grande	346.6 ± 2.1	516.2 ± 11.3	1.138 ± 0.005	2,302
Landro	367.9 ± 3.1	535.7 ± 16.2	1.024 ± 0.006	1,288
Mandeo	369.1 ± 1.5	599.6 ± 9.0	1.125 ± 0.004	4,040
Masma	369.2 ± 4.9	541.5 ± 24.4	1.049 ± 0.012	488
Sor	362.3 ± 1.8	572.7 ± 8.4	1.112 ± 0.003	5,789
Tambre	389.1 ± 1.9	718.2 ± 11.9	1.105 ± 0.004	4,928
Ulla	364.7 ± 2.2	606.8 ± 12.8	1.164 ± 0.006	2,184
Mean	364.3 ± 0.7	586.8 ± 40	1.117 ± 0.002	

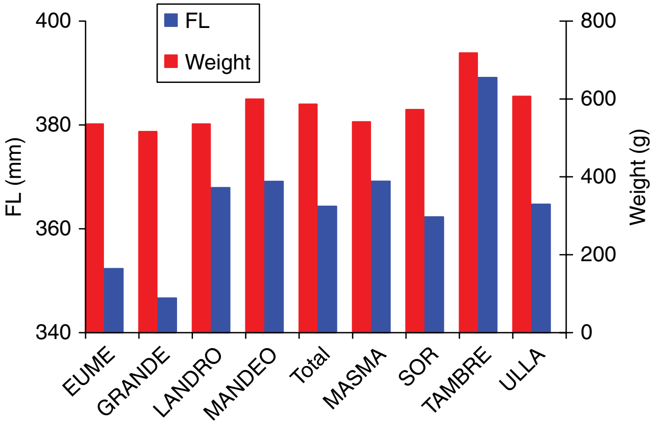

Figure 18.17 Mean values of weight and fork length (FL) from the eight surveyed sea trout populations. (Data from Official fishery between 1995 and 2009.)

classes (0+SW to 4+SW). Highest mean size values for each age class were registered in the two rivers located in the Rias Baixas area, while lower mean sizes were found in the Sor River (even when the longest-lived individuals were found in this river).

Discussion

Migration

According to Elliott *et al.* (1992), the sea trout smolt migration takes place in spring, primarily in April and May. In the Galician rivers, migration timing for smolts does not differ from those described for British, Irish and French rivers, while in Scandinavia the migration period continues until the beginning of June (Rasmussen, 1986; L'Abée-Lund & Vøllestad, Chapter 11, this volume).

Table 18.13 Mean size (mm) in different sea age classes of eight Galician sea trout populations.

	0+SW		1+SW		2+SW		3+SW		4+SW		5+SW	
River	**N**	**Mean ± CI95%**	**n**	**Mean ± CI95%**	**n**	**Mean ± CI95%**	**n**	**Mean ± CI95%**	**n**	**Mean ± CI95%**	**n**	**Mean ± CI95%**
Eume	1,142	312.5 ±0.9	2,556	356.3 ± 1.1	548	432.1 ±3.0	73	514.5 ±10.3	23	586.1 ±21.3	1	660.0
Grande	464	309.9 ±0.9	466	367.0 ±2.7	71	449.9 ±5.6	10	520.0 ±17.8	4	602.5 ±4.9	–	–
Landro	156	308.9 ±1.	299	362.4 ±3.3	90	431.1 ±7.8	17	473.9 ±20.5	1	550.0	–	–
Mandeo	306	309.4 ±1.4	1,671	356.3 ±1.2	499	420.5 ±2.3	71	490.6 ±8.1	14	537.1 ±19.9	–	–
Masma	96	317.3 ±3.7	139	371.8 ±4.8	40	422.3 ±7.6	11	470.0 ±10.9	2	550.0 ±19.6	–	–
Sor	348	303.0 ±0.8	1,623	346.1 ±1.0	866	405.9 ±1.8	163	468.5 ±4.8	32	549.1 ±10.2	11	631.8 ±19.6
Tambre	1,411	339.7 ±1.6	1,021	410.2 ±2.7	598	471.9 ±3.3	36	585.8 ±12.8	3	623.3 ±6.5	–	–
Ulla	777	333.9 ±1.7	381	398.6 ±4.3	34	473.5 ±11.4	1	600.0	–	–	–	–
Total	4,700	–	8,156	–	2,746	–	382	–	79	–	12	–
Mean	–	323.0 ±0.7	–	364.1 ±0.8	–	431.2 ±1.5	–	494.4 ±5.0	–	563.3 ±9.7	–	634.2 ±63.5
Test KW	Chi^2	1502.1		1846,2		981.0		151,1		24.7		
	Df	7		7		7		7		6		
	P	<0.001		<0,001		<0.001		<0.001		<0.001		

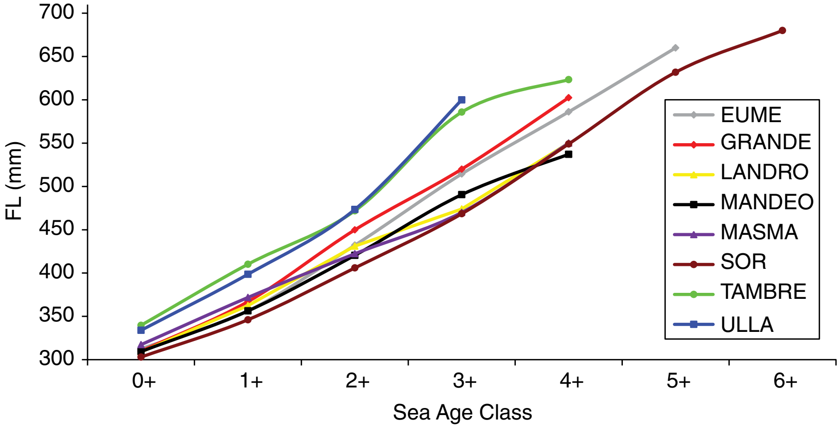

Figure 18.18 Variation of the mean size for every sea age class in eight Galician sea trout populations (FL = fork length).

Sea trout mark-recapture practices carried out at the traps located in Ximonde (Ulla River) and Bora (Lérez River) provided information on sea trout migration outside these rivers. Even though the number of recaptured specimens was relatively low (13 at Bora and 8 at Ximonde), these results allowed us to offer an image of sea trout movements from these two Iberian populations and to compare them with populations from elsewhere.

Data show that populations in southern Galicia behave alike other European populations when migrating to the sea: sea trout stay on areas close to their home river although sometimes scattered individuals may move over 200 km away (for instance, two specimens recaptured in Cares River >500 km away from Lérez River), but in no case far from the coast. The latter agrees with similar data reported from other regions such as Norway (Vardnes River, Berg & Berg, 1987a), Scotland (North Esk River, Pratten & Shearer, 1983a and b) or Normandy and Picardy (Euzenat *et al.*, 1991). Indeed, studies in Norwegian waters indicate that few sea trout move more than 70–80 km from their natal river and mostly remain in a range of 15 km or less (Berg & Berg, 1987a). In the British Isles and France, more limited studies based on mark-recapture indicate a restricted movement along the coast (Le Cren, 1985; Euzenat *et al.*, 1991), although the Norman sea trout were heading north, being recaptured even in Danish waters.

Regarding upstream migration, our data collected in five traps from three Galician main rivers (Ximonde at Ulla River, Bora at Lérez River and Landrove at Landro River) and two tributaries (Liñares at Liñares River and A Freixa at Tea River) suggest important differences regarding the entry of sea trout into each type of river. In the main rivers an initial start can be detected in April, followed by a peak in July and a cessation of activity in September. A migration re-start begins in autumn when the flow increases but in lower proportion than in the summer.

In marked contrast, most sea trout enter the tributaries later in the fall indicating that tributaries are mainly used when the breeding season approaches. These results are consistent with those reported elsewhere. Sea trout migrate back to small rivers to spawn and their migratory activity appears to be regulated by the water flow. For example, in the river Imsa (Norway) the amount of daily sea trout is correlated with the mean monthly flow in late summer and early fall (Jonsson & Jonsson, 2011).

Additionally, it has been also confirmed that in very small Norwegian rivers (<0.1 m^3/s) the entry of anadromous trout is delayed until the spawning time (Jonsson *et al.*, 2001).

Anadromous brown trout spawning occurs in late autumn or winter. Shortly after spawning, females leave the spawning grounds whereas males may remain longer and spawn with one or more additional females (Evans, 1994; Klemetsen *et al.*, 2003). Individuals that survive spawning are commonly referred to as kelts and migrate seaward soon after spawning or may overwinter and return to the sea in the following spring (Jonsson & Jonsson, 2002; Bendall *et al.*, 2005). Timing of kelts return to the sea from Ulla, Liñares and Tea Rivers is also similar to that observed in populations of Normandy-Picardy (Euzenat *et al.*, 1991), with two migration periods, one after spawning (December to February) and a second one in spring (March to early June). While in some Baltic populations sea trout kelts overwinter in the river until the migrating to the sea in May or June (Ostergren & Rivinoja, 2008).

Growth

Consistent differences were observed in the growth of smolts in freshwaters, although as shown in other studies in Galician rivers (Sanchez-Hernandez *et al.*, 2012) this is not exceptional since growth rates depend on the combination of factors such as water temperature (Elliot, 1994; Parra *et al.*, 2009), food intake (Elliot, 1994; Mambrini *et al.*, 2006), genetic factors (Jensen, 1985; McDowall, 1994), social interactions (Metcalfe, 1994; Lobón-Cerviá, 2007), latitude and altitude (Parra *et al.*, 2009) and the calcium content of the waters (Kennedy & Fitzmaurice, 1971). Current results are not always statistically significant and in some cases they even appear contradictory. However lower growth rates occur more frequently in Landro and Sor rivers and are therefore the only ones in which the main smolt age class was 3+. On the contrary, higher growth factor was detected in the Masma River probably due to high calcium content in this area. Freshwater growth rates at the Masma River were similar to those found in the Galician southern populations (Ulla and Tambre Rivers).

Significant differences in growth were observed when comparing smolt age classes. Smolts showed the highest growth rate after 1+ FW year with a mean of 13 cm length so they are able to smolt in one year when they reach a mean of 14.5 cm. However, 2+ year smolts average in their first year 10.4 cm and 20.8 in the second, reaching a mean size of 22 cm at the start of migration. Smolts 3+ grow up only to 8.6 cm in the first year, 17 cm in the second and 24 cm in the third migrating as smolts of nearly 25 cm length.

Comparison of the marine growth from smolt to 1+SW and from 1+SW to 2+SW, showed consistent differences between rivers from southern Galicia, Rias Baixas and others. Individuals from Tambre and Ulla rivers showed faster sea growth than those from the Cantabrian Arch and Finisterre regions (Eume and Mandeo) and also from those of the Cantabrian area (Masma, Landro and Sor). These differences could be explained by higher water productivity in southern estuaries (Prego *et al.*, 2013).

Figures of Ulla and Sor Rivers populations can be readily comparable to data from 13 European populations covering the entire range of the natural distributional area of sea trout (Alm, 1950; Went, 1962; Piggins, 1964; Potter, 1985; Elliot, 1985; Le Cren, 1985; Berg & Berg, 1987b; Fahy, 1978, 1985; Berg & Jonsson, 1990). Current results (Figure 18.19) show that the Galician populations may be included in the group of sea trout with '*poor growth*' relative to Asturians, British, Norwegian and Irish Atlantic populations whereas populations from Poland, Normandy and Irish Sea can be included

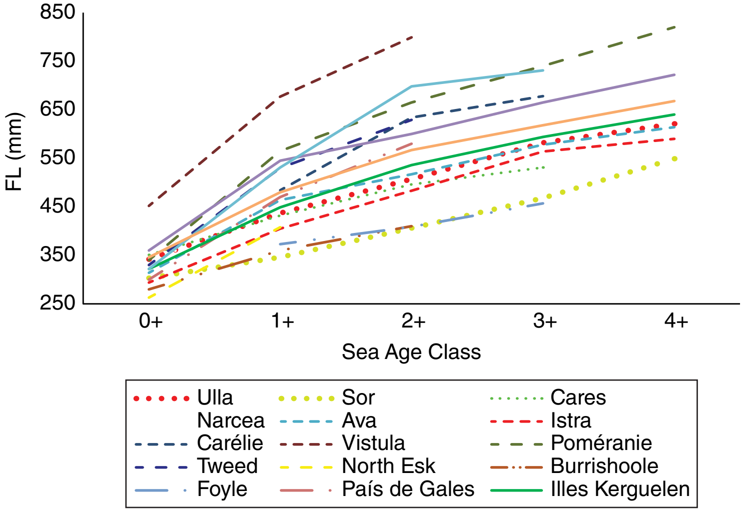

Figure 18.19 Sea growth compared among fifteen European sea trout populations (FL = fork length).

in a group with '*high growth*'. As for Sor River, sea growth is among the lowest of Europe and similar to the Irish rivers (Fahy, 1978), whereas the Ulla River shows a slightly higher growth but still remains below the average comparable to Norwegian populations (Alm, 1950; Berg & Berg, 1987b; Berg & Jonsson, 1990).

Reproduction

Sex ratio in sea trout from Ulla and Lérez Rivers systematically favour females by approximately one to two-factor, which is consistent with those found in other European populations (Alm, 1950; Jensen, 1968; Skrochowska, 1969; Harris, 1970; Campbell, 1977; Pemberton, 1976; Särdson & Fagerstroem, 1982; Pratten & Shearer, 1983a; Le Cren, 1985; Jonsson, 1985; Richard, 1986; Euzenat *et al.*, 1991). However, the sexual dimorphism in size observed in Lérez and Ulla where males are larger and older than females does not coincide with those reported for other populations. Thus, Jonsson & Jonsson (2006) stated that adult females are, on the average, older and larger but less heterogeneous (i.e. lower standard deviation) than male size. In contrast, females recorded in Lérez and Ulla tended to be smaller with a lower mean sea age. In addition, the standard deviation of size is larger in males suggesting that size is more heterogeneous among males.

In this study three sea age classes at sexual maturity have been identified (0+SW, 1+SW and 2+SW, Maiden Sea Age). Although some authors have described an age class over the 3+SW class in Norway (Jonsson & Jonsson, 2006) and Wales-England Rivers (Harris, 2006), this has not been the case in the rivers of our region. Comparing data among Galician populations, several significant differences were detected in terms of MMA of first reproduction. Individuals reproducing at 2+SW age represent a greater proportion than in northern rivers. It is possible that 2+SW class individuals were significantly more abundant for decades, but probably mortality factors (fishing, predation) related to the longer time spent in salt water, have contributed to its decline in a process similar to that observed in 3+SW specimens of the Galician and Cantabrian Atlantic salmon populations (García de Leaniz *et al*, 1992; Caballero, 2002).

The species of the genus *Salmo* are iteroparous although repeated reproduction is more common in trout than in Atlantic salmon (Jonsson & Jonsson, 2011). In a comprehensive study of 102 European populations of anadromous trout, it was found that the proportion of multiple spawners ranged in most cases between 20% and 70% (Jonsson & L'Abée-Lund, 1993). One of the reasons that may explain the higher frequency of previous spawners in sea trout is the length of the sea journey since the sea trout requires relatively less energy to be spent than Atlantic salmon. Generally, brown trout can spawn several times during their life (Jonsson, 1985; Elliott, 1994; Baglinière & Maisse, 1991) and in some populations the proportion of repeated spawners can be quite large (>50% according to L´Abée-Lund *et al.*, 1989). Thus, iteroparity is an important strategy for sustainability of sea trout populations and the life history trait allows individual genetic contribution to multiple generations and may also function as a safeguard against years when reproductive success is weak. Repeat spawners generally increase in size and fecundity between spawning events (Jonsson & Jonsson, 2002; Calles, 2005) which may be also important for population sustainability. In this study we found significant differences in the ratio of the eight sea trout populations studied. It was detected that populations located in the Cantabrian Rivers showed higher % of repeat spawners than in the southern, Rias Baixas regions, with 29–35% and 15%, respectively.

Demographics and Biometry

Age and size at smolt stage varied among individuals within the same population and among populations. In the same population, individuals with a slower growth tend to be older and larger when they migrate to the sea as smolts (Økland *et al.*, 1993), most likely due to different food consumption rates (Thorpe & Metcalfe, 1998). The limits for smolt age and size could be determined by the costs and benefits obtained going to the sea and are dependent on growth. While more energy is needed to grow rapidly, the size increment allows more fish to escape from predators. The metabolic rate for a juvenile trout with rapid growth is high, and they find energy constraints in freshwater at a smaller size relative to juveniles of slower growth from the same population (Forseth *et al.*, 1999; Gowan & Faush, 2002; Morinville & Rasmussen, 2003).

Thus, faster growing juveniles fit better as they move to richer habitats relative to lower growth individuals. Variation in smolt age within a population is likely to be mainly phenotypic while variation among populations may be largely inherited and not being accompanied by a change in size of smolts. Smolt size can be considered an adaptation to the conditions in the sea where water temperature, feeding opportunities and the presence of predators may act as selective forces. These variables are not experienced by fish before smoltification, therefore geographical variations in the smolt size appear to be influenced by local adaptation (Jonsson & Jonsson, 2006). Growth rate and mean smolt age in trout inversely increased with latitude in rivers of western European coast, but size is apparently not affected by latitude (Jonsson & L'Abée-Lund, 1993).

Overall, sea trout smolts are older than Atlantic salmon parr in the same river (Elliott *et al.*, 1992). In Ulla River, salmon smolts are on average one year younger than the sea trout smolts (Caballero *et al.*, 2002; Caballero, 2013). Changes in the mean smolt age (MSA) are related to the growth rate of juveniles, therefore a parr with a fastest growth smolt at a younger age than those with slower growth (Elliott *et al.*, 1992). The latitude of the river also influences MSA (Fahy, 1978; L'Abée-Lund *et al.*, 1989; Jonsson & L'Abée-Lund, 1993), because growth is related to water temperature and to the length of the growing season (Elliott, 1975). The sea trout MSA in Galician rivers (2.04 to 2.70 years) match exactly those expected from the latitudinal location. They are well below the ages described for rivers of northern Europe (Fahy, 1978; Richard, 1986; L'Abée-Lund *et al.*, 1989; Euzenat *et al.*, 1991); similar to those from Wales, England and Ireland (Fahy, 1978; Harris, 1970) and higher than those reported for northern France (Euzenat *et al.*, 1991) where most of the smolts are one-year old. The growth rate observed in the Galician parr during their first year of life (Figure 18.20) rarely allows them to reach the size to smolt at 1+ age (Caballero *et al.*, 2006).

However, significant differences were observed in the MSA of the eight studied populations. Rivers located in the Southern regions of Galicia showed MSA values ranging from 2.04 (Tambre River) to 2.15 years (Ulla River). However, those from rivers flowing to the Cantabrian Sea ranged from 2.7 to 2.64 years (Sor and Landro rivers, respectively), once again the Masma River being the only one not matching its geographical location, with an MSA of 2.22. Finally, intermediate values, between 2.2 to 2.39 years, were reached in the Artabrian Arch and Finisterre area.

Our demographical assessment of sea trout in eight Galician rivers emphasized the detection of four FW age classes (1–4 years), three sea age classes prior to the first reproduction and, due to iteroparity, a total of seven marine age classes (from finnocks or 0+SW to 6+SW). Galician sea trout are characterized by an MSA of 2.28 years and a MAA of 0.94 years meaning that class 2+ is the main smolt class (67%) followed by age class 3+ (31%), being sea age class 1+SW (51%) together with finnocks (29%) and 2+SW (17%) being the most abundant. This population structure differs little from the very few Iberian populations previously described from the Narcea and Sella rivers (Lemaire, 1991; Toledo *et al.*, 1993) and from English or Welsh populations (Harris, 2006).

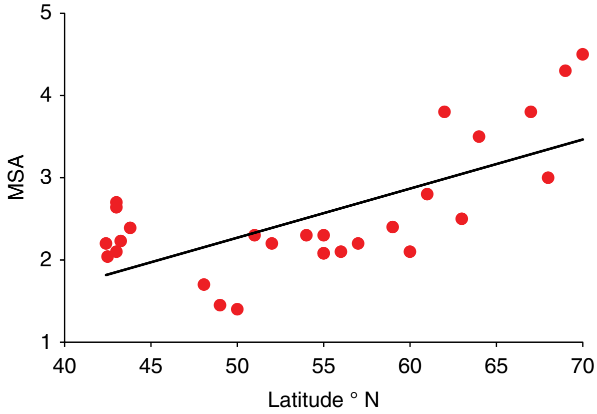

Figure 18.20 Relation between Mean smolt age (MSA) and latitude in European sea trout populations.

Of a total of 28 combinations of four freshwater and seven sea age classes found in Galician sea trout only 19 age classes were finally detected. Three rivers presented 14 classes, one river contained 13, a second river nine classes and two other rivers eight classes. Several (i.e., Harris, 2006) consider that a large diversity of age classes may indicate '*robustness*' or good condition of the population: a greater overlap between different age classes may enable faster recovery from catastrophic events. As an example the Dee River at the border between North Wales and England, can exemplify a robust population with 17 age classes reflecting a low exploitation rate (Harris, 2006; Shields *et al.*, 2006). According to this interpretation, sea trout populations from the rivers Eume, Sor and Mandeo seem to be the healthiest among the Galician populations, at least in the studied time series.

General Conclusions

Sea trout monitoring is costly and time consuming. However, long time series are essential to understand the complex biology of sea trout and other related species. This study using a rather larger database collected over a rather long time period (20 years) represents a good basis to provide insight into the freshwater and marine life stages of sea trout.

Significant differences among Galician sea trout populations were detected. Fish growth of the populations located further north was slower; both in freshwater and the sea. However, individuals appeared to live longer and reproduce more times in those areas. These results are remarkably similar to those observed in Norwegian studies conducted in rivers between 58° and 70°N (L'Abée-Lund *et al.*, 1989; Jonsson, 1991). Note however that in our study the latitude range was remarkably narrower (42° to 43°N).

Overall, differences among the Galician sea trout populations match the features expected from their geographical location, and they may be considered as adaptations to local environments. Consequently, such differences should be considered when conservation and management strategies are developed and implemented. Migration timing is a major part of phenotypic plasticity that conveys resilience to species, population complexes, and their fisheries (Eldøy *et al.*, 2015). Thus the sea trout migration calendar in all the life stages should also be taken into account when fishery conservation and management strategies are considered. The major aim of such implementations should be to preserve population traits and to establish a correct monitoring programme for the follow-up work on their development.

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19

Sea Trout (*Salmo trutta* L.) in Denmark

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Introduction

The brown trout is the most common salmonid species in Denmark (Figure 19.1), and occurs today in most streams and rivers with slopes exceeding 1‰, in lakes and the surrounding sea. The brown trout in Denmark is separated into three morphs: (a) none-migratory brown trout which live their whole life in streams and named baeck trout; (b) migratory lake-dwelling brown trout which spawn in the adjacent streams to lakes, smoltify and migrate to the lake, grow up there and later return as spawners to the same stream from where they came from, named lake trout and; (c) migratory brown trout which spawn in streams, smoltify and migrate to saltwater, grow up there and after a half to a couple of years migrate back to the same stream to spawn, named sea trout. In all stream and river systems the three morphs can spawn and grow-up as parr together. Most probably they are genetically more or less mixed together and they are considered as having three migratory strategies in order to optimize the population through survival, growth and spawning potential. The three morphs can easily be separated by their growth rate, size and external appearance. The differences in growth rates are, besides water temperatures, most probably because of different food items: invertebrates in baeck trout, invertebrates and different fish species (mostly cyprinids) in lake trout, and mostly different marine fish species in sea trout.

The other natural salmonid species in Denmark is the Atlantic salmon (*S. salar*) which occurred naturally in nine river systems in Jutland running to the North Sea and the Kattegat, and today is only spawning in four rivers going to the North Sea. During the last twenty years rehabilitation programs (habitat restoration and stocking salmon with first generation offspring from wild fish (F1 fish) in rivers draining into the North Sea). Wild Atlantic salmon occur together with brown trout, but if these two species compete is not fully known. However, unpublished results might indicate a reduction in numbers of brown trout in streams where salmon stock builds up, probably because a streams section can only carry a certain number of salmonids whether it is trout or salmon.

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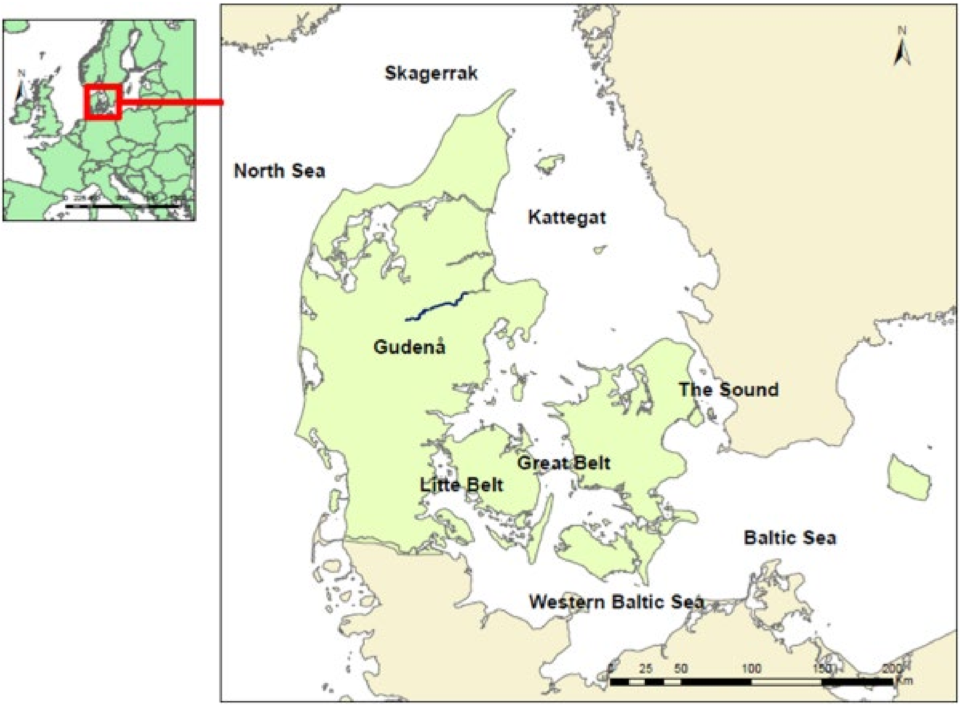

Figure 19.1 Map of Denmark showing the most important marine areas.

The grayling (*Thymallus thymallus*) occurs naturally in rivers to the North Sea, Jutland and is seriously threatened, mostly because of predation from the cormorant (*Phalacrocorax carbo*). Whitefish (*Coregonus lavaretus* and *C. albula*) occur in many lakes and estuaries throughout Denmark. The brook trout (*Salvelinus fontinalis*) introduced from North America more than hundred years ago occurs in a couple of cold-water streams in Jutland and rainbow trout (*Oncorhynchus mykiss*) escaped from hatcheries.

The brown trout has always been considered the most important species in the recreational fishery in freshwater, and with modern gear after World War II, the sport fishery has developed further along the Danish coastline. With habitat improvements and organized stocking activities during the last 30 years, the brown trout remains the most important salmonid species in freshwater and in the sea.

The largest sea trout caught in Denmark was 17.5 kg and about 120 cm in length. The fish was caught in 1935 by an angler in river Simested Aa, Jutland (Rasmussen, 2012).

This chapter describes:

1) The physical conditions, i.e. geology, climate, number of rivers and the sea around Denmark.
2) Environmental problems in freshwater.
3) Legislation.
4) Stock enhancement with fry, parr and smolts.
5) The biological characteristics of brown trout in fresh- and saltwater, research activities, freshwater phase and smolt production, marine phase and marine migration.

6) Examples of vital statistics from selected rivers (i.e. smolt age, sea age, spawning types and egg production and reproduction.
7) Finally, nominal catches of brown trout in fresh- and saltwater, including a simple catch model from number of smolts and mortalities in the sea are presented.

The Physical Conditions

Geology and Climate

Denmark (Figure 19.1) is a lowland area and formed by the Saale and Weichsel glacial periods. The highest elevation in Denmark is 171 m above sea level.

All rivers south to the Limfjord in western Jutland run to the North Sea through sandy and moraine deposits. The conductivity in these rivers is moderate and varies from 100 to 300 μS cm^{-1}. Drainage of areas with a pyrite content, and in some places lignite mining during the World War II, have made many streams acidic, with a high iron content and pH 3–6.5, especially during winter. This has adversely affected the spawning possibilities and restricted the distribution of salmonids (Geertz-Hansen & Rasmussen, 1994). In most streams with average width below 2–3 m and with proper slope, the brown trout is the dominating fish species often together with mostly sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*), but in many streams brown trout is the only fish species present.

The rivers in North and East Jutland drain into the Skagerrak, Kattegat and the Western Baltic Sea through moraine landscape. The conductivity in these rivers is above 300 μS cm^{-1}, and pH a little above 7. Brown trout is the dominating salmonid species in these rivers together with cyprinids, sticklebacks, pike (*Esox lucius*) and European eel (*Anguilla anguilla*). In most streams with average width below 2–3 m brown trout is the dominating fish species and in many streams, only together with sticklebacks.

The rivers on the islands Funen and Zealand and surrounding islands have outlet to the Kattegat and Western Baltic Sea through moraine landscape. The conductivity in these rivers is above 300 μS cm^{-1}, and pH above 7. Brown trout is the dominant species and often coexists with cyprinids, sticklebacks, pike and eel. In streams with average width below 2–3 m and with proper slope and river bed, brown trout is often the dominating species together with sticklebacks.

Bornholm is a small (588 km^2) rocky island (Cambrian, Mesozoic and Tertiary) with a thin layer of moraine. In most streams brown trout is the only fish species.

There are thousands of smaller lakes in Denmark; and the larger ones house lake-dwelling brown trout populations, which spawn in adjoining streams and rivers. Many of these brown trout grow up to sizes similar to sea trout.

The annual rainfall (Danish Meteorological Institute) in West and Middle Jutland is about 780–820 mm, in East and North Jutland about 690–720 mm, and Funen and Zealand get about 610–640 mm. Bornholm has a precipitation of on average of 610 mm. Generally, February is the driest month (about 40 mm precipitation) and November the wettest month with about 80 mm precipitation.

The average daily air temperature varies from approximate 0°C (night/day: –2.9/2.2°C) in January and February to about 15.7 (night/day: 11.3/20.0°C) in July and August, but temperature extremes of –31.2°C, and +36.4°C have been recorded. The annual average is slightly increasing to the present level which is 8.8°C (Danish Meteorological Institute).

The sea around the coastline (7,314 km) is shallow with many estuaries and fjords. The surface water in the inner waters comes mainly from the Baltic Sea (brackish). Overall currents through the Kattegat are towards north with brackish water. In the deeper parts of the Kattegat the main currents are running south from the North Sea and Skagerrak with lower water temperature and higher salinity. This means that temperature and salinity varies with depth and latitude.

The salinity around Bornholm is about 8–10‰; in the Kattegat the salinity is about 20–25‰, and in the Skagerrak and North Sea about 32–35‰. With the highly variable climate, ice cover along the coastline during winter varies between year and areas. In cold winters most fjords are ice-covered, and in severe winters ice may reach several kilometres out from the coastline.

The annual mean water run-off is about 10 L per second per km^2 area, but with variations from 22.2 (West Jutland) to 1.6 L per km^2 (Zealand) because of different precipitation and soil. The water flow in running waters is highest in winter and lowest between June and September. The mean maximum water temperature in summer is generally below 20°C. During cold winters water temperature can be slightly below zero, and sometimes anchor ice may be found in small gravelly and stony streams.

Number of Rivers

The total area of running waters in Denmark is estimated to about 15,000 ha and with 876 independent river systems (Berg & Rasmussen, 2012); from the very small streams with widths below 2 m, 1–2 km long and run-off area of few km^2, to the river Gudenaa with a total length of 160 km from spring to outlet in Randers Fjord and Kattegat and a runoff area of 3,200 km^2 and a mean annual water flow of 40 m^3 per second. The biggest river, Skjern Aa has a run-off area of 3,505 km^2 and a mean annual water flow of 50 m^3 per second to the North Sea.

Because there are no natural obstacles in Danish river systems (excluding a few streams on the rocky island Bornholm), it is assumed that after last the glacial period, nearly all river systems probably had brown trout populations which originated from immigrating brown trout from southerly populations and areas in Europe not glaciated at that time (Hansen *et al.*, 1993).

Environmental Problems

The present environmental problems can be summarized as follows: 62% of the area is agriculture area; nutrient content in rivers is high, resulting in the extensive production of water weeds. Most of the smaller and medium sized streams have at some stage been regulated and channellized, starting from the middle of the 1700s. Sand from cultivated fields and sand drifting downstream the river bed is a larger problem in most streams, especially in West Jutland. Water diversions by numerous weirs and dams at rainbow trout fish farms, old mills and small hydropower stations still create great problems for the freshwater fauna, especially the migratory species. Hansen *et al.* (2014) showed that genetic divergence of lake-dwelling brown trout in two Danish lakes in the Gudenaa river system reflects establishment of water mills and impassable weirs ca. 600–800 years ago rather than a natural genetic population structure. Research in the 1930s demonstrated that hydropower turbines were a major problem for down-migrating smolt, kelts and eel. In addition, smolts had high mortalities when passing weirs and lakes. The latter topic was taken up 70 years later; see section on Brown Trout Population Dynamics.

During the past three decades, restoration work in streams and rivers has been undertaken, and bypasses around existing weirs replacing traditional fishways have been established to secure free passage up- and downstream for all fish species. Very few streams are now polluted by wastewater. In streams with heavy sand loads, attempts to remove the sand by means of traps have been established in many streams but with limited success: traps are inexpensive to set up but expensive to maintain; but when maintained they work. Most streams are small and shallow with abundant growth of water weeds necessitating weed clearance, either with machines or with a scythe in small streams, to maintain the ability of the river to transport water from the surrounding agriculture areas. This weed clearance often results in a degradation of spawning and rearing habitat available for fish including brown trout. Many streams are shadowed by alder and other deciduous trees and overhanging vegetation. This shading clearly reduces river vegetation and the need for cutting water weeds, but on the other side reduces the number of hiding places for brown trout in water weeds and overhanging vegetation from banks.

Half the human population lives in Zealand and on this island as well as in some other urbanized areas the pumping of ground water for drinking water supply has lowered groundwater several meters. The dominating problem for brown trout in eastern part of Zealand is low water flow during summer and several known stocks have disappeared and can probably never be re-established.

Generally, the largest number of brown trout populations are found in Jutland, Funen, West/South Zealand and Bornholm.

Legislation and Management

Fishing rights to streams and lakes in Denmark belong to the owner of the adjoining land. The right to legally fish nearly all streams is privately owned.

The Fisheries Act empowers the Minister for Environment and Food to stipulate regulations governing inland and marine fisheries. The Act, together with associated regulations, specifies legal and illegal fishing gear, rights concerning the establishment of fish passage, minimum harvestable size, closed seasons, national and local advisory committees catch inspection and administration procedures, and penalties (Pedersen *et al.*, 2012).

The purpose of the regulations is to preserve and promote sustainable stocks of naturally-occurring fish species, for among other reasons, the opportunity for the public to go fishing. In particular, the regulations aim to ensure free passage of migratory fish between spawning grounds and feeding areas.

Gillnet fishing is therefore prohibited in streams, and fyke nets are not allowed in lakes until after 1st June, after the downstream migration of smolts has ended. However, very new results (Winter *et al.*, 2016, Rasmussen, 2016) have indicated that brown trout migrate downstream outside the legal smolt period (March–May) and this could have influence on the coming regulations and management. Moreover, fyke nets have to comply with certain mesh sizes and must include a device to prevent the trapping of otters, *Lutra lutra*, and to ensure that upstream-migrating adult salmonids are not caught (Koed & Dieperink, 1999). The regulations also specify protected zones at lake inlets/outlets and at the mouths of watercourses into the sea. Around the whole coast of Denmark gill nets can only be set at least 100 m or sometimes more from the coast line. In addition, smolts sluices have to be established at all dams and weirs at fish farms and operate annually from 1st March to 31st May, and gratings (6 and 10 mm) have to be established at all freshwater fish farm inlets and outlets, respectively. Many weirs have been removed, and if this is not possible, bypasses are established. Many old, poorly functioning traditional fish ladders are replaced with bypasses.

Recreational fishing (angling and amateur fishing) in Danish inland and marine waters requires a state permit and license fee. Anglers aged 18–65, other than the adjoining landowners in freshwater, have to pay a fee of (presently DKK 185 (EUR 25) annually) for rod and line fishing in both inland and marine waters. The license is valid for 12 months from the date of issue. In addition, anglers in inland waters have to obtain permission from the landowner, either individually or through membership of an angling association. Amateur fishermen using fixed gear such as gill nets, fyke nets and hooks in inland and saltwater are classified as amateur fishermen. The number of fishing gear used is restricted (i.e. three gill nets (a total length of 135 m), fyke nets and hook lines; a total of six gears. All amateur fishermen older than 12 years (other than the adjoining landowners in freshwater) have to pay a fee, presently DKK 300 (EUR 40). All amateur fishermen have to pay the fee for fishing in inland and marine waters. This license is valid within the calendar year. Caught fish (i.e. all fish species in freshwater and saltwater) from angling and amateur fishing is for personal use and is not legal to be sold.

The total annual revenue (2015) from anglers and amateur fishermen is about DKK 30 million (EUR 4 million). A web page (www.Fiskepleje.dk, in Danish and partly in English) was set up in 2002 and financed by the license fees. The site provides information on research activities, publications, fish biology in rivers, lakes and coastal areas, technical advice on restoration of streams. The prevailing stocking plans (see section on Stocking and Enhancement) for trout can also be found here. New results from research and other relevant issues are also published on the site. Newsletters are mailed to people who have signed up. The National Recreational License pays for the web page, and two consultants who give advice to anglers and amateur fishermen.

The license fees from anglers and amateur fishermen are also used for stock protection and enhancement activities such as stocking, river restoration and research projects, as well as for license administration, control and information activities. Anglers restore smaller streams paid by the fee in parallel with the larger restoration projects in Denmark in connection with the European Union Water Plans.

The Fisheries Act and associated Standing Orders are administered by the Ministry of Environment and Food, which also carries out surveillance activities such as spot checks to ensure that anglers and fishermen hold valid permits, use permitted methods, and do not catch undersized fish during closed season. Legal size for brown trout in freshwater is 30 cm and 40 cm in saltwater.

Commercial fisheries (not angling and amateur fishing) in Danish inland waters (mostly in lakes) are not subject to quotas. The Fisheries Act protects fish populations through the avoidance of overfishing. The rate of exploitation in commercial fisheries is regulated mainly through restrictions on permitted gear. In privately owned waters, it is incumbent on the owners to restrict fishing intensity but to respect minimum size and closed season. Recreational fisheries are not subject to quotas, but in several river systems the local anglers set up local quotas.

No up-to-date Official catch statistics for anglers and amateur fishermen are available for inland and marine fisheries as anglers, amateur fishermen and landowners are not required to report their catches. But many anglers club run their own statistics and recently a new catch journal (PC and smartphone) has been launched (www.fiskepleje.dk). Fishing locality, fishing hours, fish species and length/weight can be registered so that for example catch per unit effort can be calculated and used in management of the most important fish species.

Stocking and Enhancement

Basically nature should produce the resources needed for human exploitation. But, as described above, Danish streams and rivers have through time been very much destroyed through straightening, establishing of weirs and rough watercourse maintenance. Therefore, stocking of different fish species in fresh- and saltwater has been practised for many years in Denmark. This section describes the principles behind the stocking plans: (1) monitoring of streams by electrofishing and habitat description; (2) the biotope score for stocking different sizes of brown trout (i.e. fry and parr) and the calculation of number of smolt released as river mouth plantings (RMP); (3) the release of brown trout into saltwater, though these stockings have now been stopped because of straying and genetic reasons.

Freshwater

According to Danish law, stocking and moving inland and marine fish, including salmonids, requires permission of the authorities. Salmonids are stocked in numbers appropriate to the locality in question and according to a stocking plan that stipulates the number, size/age and location of stocking for the individual fish species, Larsen (1972); Rasmussen & Geertz-Hansen (1998). Salmonid species (actually other species as well) may only be released in an area if it can be demonstrated that the species is already present but in insufficient numbers, or that it has previously been present, but has now become extinct. This ‘principle of authenticity’ is the dominant guiding principle.

When fish are released, the genetic structure of the stock is inevitably disturbed (Hansen *et al.*, 1993; Hansen & Loeschcke, 1994). Each stocking location is evaluated taking this factor into account. The Ministry of Environment and Food and the Danish Technical University have drawn up guidelines (www.fiskepleje.dk) for catching and stripping wild fish for hatchery production of offspring for use in stocking.

The first stocking with brown trout fry in Denmark took place in 1858 (Rasmussen, 2012). In the following years, more or less uncoordinated releases with juveniles took place without regard to habitat quality, or fish requirements for depth and cover. In 1938, the first so-called modern stocking plan was introduced with release of fry during spring (up to two fry per 1 m^2) distributed in small streams with stream depths up to 10 cm (Otterstrøm, 1938). After introduction of electrofishing in Denmark in 1947 routine monitoring of a smaller number of trout streams took place and fry was released based on the monitoring results. Larsen (1955) studied population dynamics of trout in small streams (width <3 m) and realized that these small streams were used by sea trout and local brown trout for spawning, and that after a couple of years most of the parr migrated to sea as smolt. Due to his results, brown trout stocking plans now cover fry (fed for at least 3 weeks) and released in April at depths up to 10 cm; half-yearlings are released in September/October at depths 10–15 cm and one-year-old parr are released in spring at depths 15–25 cm. A stocking plan covers a whole river system from spring to outlet. Smolt (one-year- old and above 13½ cm) are released in weeks 15–17 in April, so that the time matches with silvering and temperature conditions in the sea. If stocked later in June, the smolts de-smoltify and stay in the river where they compete with the local brown trout (Danish Technical University, unpublished).

Since 2006, only first-generation offspring F1 from wild brown trout are used for all size categories and only released in rivers from where the parents came, or the offspring are stocked in some nearby rivers, where the brown trout are more or less genetically identical.

In total 876 individual river systems are monitored with a total of 7,480 monitoring stations all over Denmark, of which electrofishing (two or three pass sampling on a 50 m long section and wading) takes place on about 4,485 stations. The habitat conditions and water quality is only registered on the remaining 2,955 stations (see below). Every single river system in Denmark is monitored every seventh or eighth year in the period August to September. No fry are released in the monitored rivers during spring before monitoring in the same year. This allows estimation of the extent of wild spawning and wild fry density at the stations, and evaluating the outcome of earlier releases of fry and parr. Only streams with widths up to about 7–8 m are monitored (by wading), and very little is known of trout densities in larger rivers in Denmark. In a study comparing wild with domesticated brown trout in river Karup Aa in mid-Jutland (Pedersen *et al.*, 2006) electrofishing and monitoring of brown trout density was made on river stretches up to width of 15 m. Since 1997 the brown trout population from spawning brown trout coming from Lake Mossoe has been monitored each year on the upstream stretches of river Gudenaa with widths up to 20 m (Jan Nielsen, personal communication).

All monitored stations are described (length of electrofishing site, depth, width, water velocity, colour of water, bottom structure (i.e. soft, sand, gravel and stone), hiding places (bottom and stream banks), shade and vegetation cover. The station is evaluated for release of fry, half-year-old, or one-year-old trout according to a biotope scale from zero (not a trout locality) up to score five (highest quality).

Possible stockings are calculated from the biotope score and mean density of trout at the different biotope scores. For release of fry the highest number of fry released (score five) is 300 per 100 m^2, half-yearlings 75 per 100 m^2 and one-year-old parr 30 per 100 m^2. The number of fish released is adjusted according to the biotope score. For example, for fry biotope 2.5 the number of fry released is accordingly 150 fry per 100 m^2 if there are no wild fry. Wild fry and older parr present on the site are subtracted to calculate the number of fish released. But in recent years, stockings do not take place where a certain amount of wild spawning occurs, even though stocking could take place. From the total area of production (widths below about 7–8 m), it is expected that the original production of smolts was 7.5 smolts per 100 m^2. This number is a ‘rule of thumb’, and based on results from older research (Larsen, 1955 & 1972, Rasmussen, 1986b). The present production of smolts is calculated from total number of wild 0+ (as found during monitoring) plus released fry, ½- and one-year old fish, where released brown trout (i.e. fry, ½- and one-year old fish) are recalculated to smolt (see below). The difference between original and present smolt production gives the number of smolt released (river mouth plantings RMP) in spring.

The Danish Technical University performs the monitoring and the local anglers perform the releases after the guidelines set up by the Danish Technical University. In streams where stocking takes place, the local anglers collect wild sea trout (and salmon) for breeding every autumn in the main stems of the river systems. For genetic reasons at least 50 of each sex in each river system are caught and brought to a local hatchery, spawned and their offspring are grown up to the four stocking sizes as described. New spawners are caught every year. The National Rod License pays for the monitoring and release of trout and salmon.

Figure 19.2 shows the number of released fry, half- and one-yearling in the period 1987–2013 and the calculated number of resulting smolt. The number of smolt originating from stockings of fry and parr show a decreasing trend, from approximate 300,000 to approximate 100,000 smolts. The reason for this is the reduction in numbers of released fry and parr which in turn is due to increasing production of wild smolt, primarily because of habitat restoration and increased wild spawning.

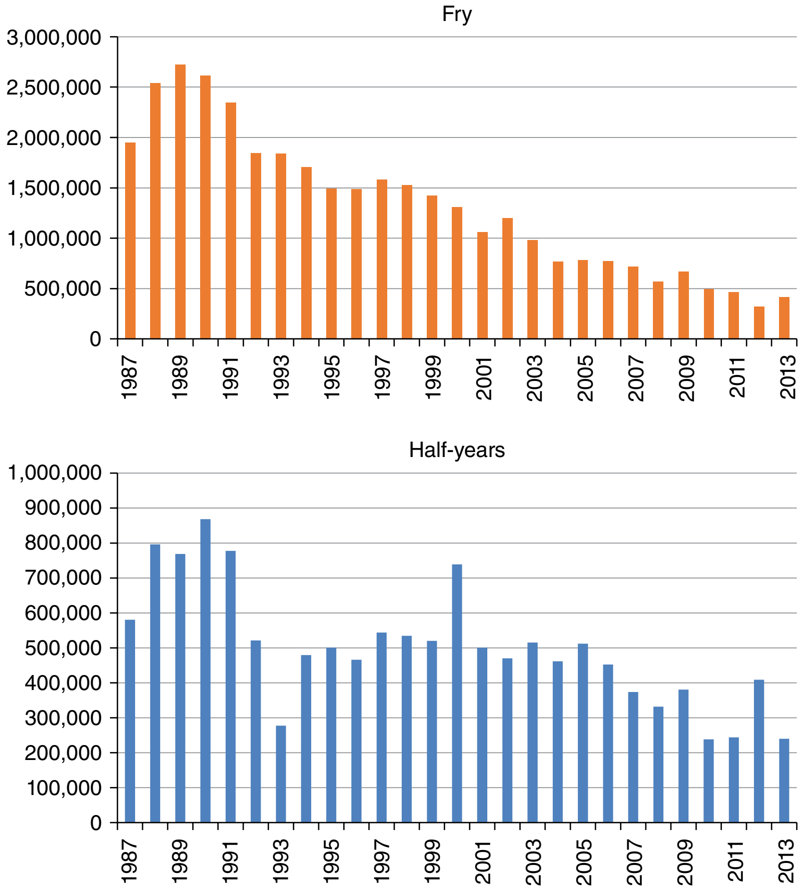

Figure 19.2 Releases of fry, half- and one-year-old brown trout in the period 1987–2013 and the calculated number of resulting smolt from the releases. These are calculated according to: 100 fry results in 2.5 smolts, 100 half-yearling 10 smolts and 100 one-year-old parr 25 smolts.

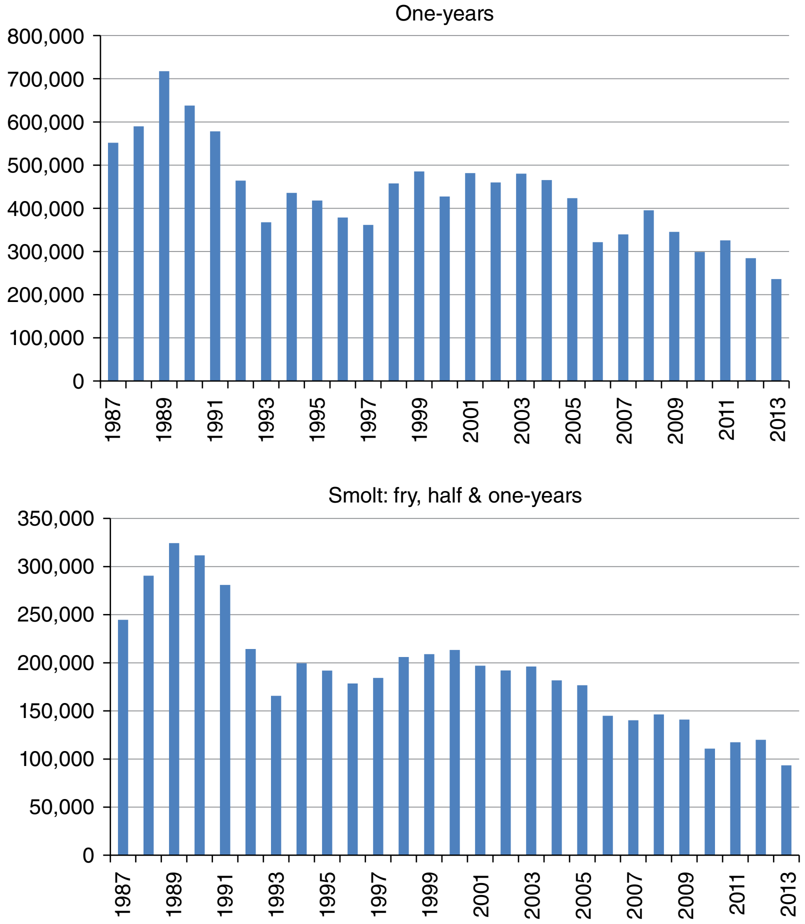

Figure 19.2 (Continued)

Table 19.1 shows the numbers of the total 876 independent rivers and stream systems in Denmark in different geographical areas. A little less than 50% of all streams evaluated in Denmark are not brown trout streams today, neither for wild brown trout or for stocking of fry and parr, but these streams are small and do not contribute much to the total stream area and total smolt production. Another quarter (220) of all streams evaluated are brown trout streams, but most have smaller amount of wild brown trout and the habitats are of such quality that supplementary stocking with fry, parr and smolts takes place. The remaining 27% of all streams are brown trout streams with only wild brown trout and no stocking takes place in these streams.

Table 19.1 also shows the total number of wild smolt calculated from the total number of wild 0+ during monitoring: in total approximately 1.1 million smolts. The number of stocked fry and parr according to the present management plans (period 2005–13) contribute with another approximately 120,000 smolts. But, as shown in Figure 19.2, the contribution from stocking of fry and parr in 2013 is approximately 100,000 smolts because of habitat improvement in the preceding period. So, wild smolt production has

Table 19.1 Number of streams and stocking of brown trout in different categories (fry, parr and smolt) and geographical parts of Denmark: Bornholm, Zealand with islands: Lolland, Falster and Moen (LFM islands), Funen, East Jutland with streams running to the Western Baltic Sea and Kattegat; North Jutland with stream running to the Skagerrak, Kattegat; West Jutland with stream to the North Sea. RMP: river mouth plantings with smolt. From the total number of wild 0+ brown trout and the total number of the different stocking categories the number of smolt is calculated.

	Bornholm	**Zealand**	**LFM islands**	**Funen**	**E Jutland**	**N Jutland**	**W Jutland**	**Total**	**%**
Not trout stream	20	103	76	22	81	115	66	417	47.6
Trout stream + stocking		15	12	13	33	70	11	220	25.1
Trout stream no stocking	26	25	15	26	101	46	0	239	27.3
Total	46	143	103	61	215	231	77	876	100.0
									smolt
0+ wild	393,664	455,251	44,427	1,003,399	2,231,024	2,123,145	626,349	6,877,259	1,086,724
Fry		23,600	41,100	18,900	153,100	207,700	153,750	598,150	14,954
Half-year-parr		66,825	0	13,400	23,400	95,550	116,050	315,225	31,523
One-year-parr		6,000	5,850	6,093	7,100	91,300	163,150	279,493	69,873
Smolt RMP		281,300	43,100	43,100	99,100	232,950	384,000	1,083,550	1,083,550
								Total smolt	2,286,623

increased accordingly and should appear in increasing numbers when all stocking plans are revised during the coming seven to eight years.

The municipalities on Funen finance the release of additional 450,000 smolts as river mouth planting to enhance tourism.

The total number of smolt from stocked F1: fry, half- and one-year and smolt and from calculated wild smolt is approximate 2.74 million smolts. But, from tagging results (Danish Technical University, non-published data based on catches and river returns) comparing wild smolt and reared F1 smolt it is estimated, that 1 wild smolt equals four stocked F1 smolt. Further studies are necessary to establish this.

In the period 1987–2003, brown trout a couple of cm below legal size of 30 cm were stocked in several bigger rivers in June after the smolt run. The idea was that they should adapt to the river conditions and after a short period grow up to catchable size. It can be considered as 'put and take' as a benefit for the anglers. Monitoring (Pedersen *et al.*, 2003; Aarestrup *et al.*, 2005) showed that the outcome was very limited, catches were low, mortality was high, and the fish simply disappeared. Due to economic considerations these stockings stopped. About 150,000 trout were annually released in this period.

The general view today is that stocking brown trout should gradually be reduced to zero and the original level of brown trout in rivers and smolt production to support recreational fishery should be achieved through habitat restoration and wild production of brown trout.

To fulfill the European Water Frame Directive in Danish streams, an index has been developed based only on brown trout using a total of five habitat indicators: width, depth, substrate, water current and shadow, Kristensen *et al.* (2014). The index shows the minimum expected number/density of brown trout in relation to a quantification of the five indicators and the index goes from one to ten, where index ten represents the highest habitat quality and the highest expected number of brown trout.

Saltwater

From 1987–2000, about 240,000 numbers of 19–25 cm brown trout were annually released into saltwater in many coastal areas in May, when sea water temperature was above 10°C. At this time brown trout of this size face no osmoregulatory problems when stocked directly from fresh to saltwater (Nielsen & Madsen 1999). Tagging results indicated good recapture rate but varying results, Glüsing & Rasmussen (1996), but the results also showed that because the fish had no homing to specific rivers, they strayed into many rivers. For genetic reasons these releases were stopped.

In the same period, experiments with delayed release of brown trout were made. Brown trout (18–25 cm) were released in net cages in saltwater in May, fed for one to two months, and then released (Pedersen & Rasmussen, 2000). Tagging data showed high recapture rates (higher compared to RMP brown trout smolt plantings), but because of straying and genetic concerns these releases with brown trout were stopped. In some years, the possibility of stocking the less costly hatchery raised rainbow trout directly into saltwater was discussed in order to benefit the recreational fishery. This species does not reproduce naturally in Denmark, probably because of a combination of domestication in hatcheries over nearly 120 years in Denmark, and competition in streams with wild brown trout (Rasmussen, 2012). Stocking results from tagged rainbow trout showed better catches in saltwater compared to stocked brown trout (Glüsing & Rasmussen, 1996), but because of the 'principle of authenticity' these stockings were stopped.

Brown Trout Population Dynamics

This section will describe the basic biology of brown trout in freshwater and in the sea in Denmark using a selection of old and new studies:

1) The freshwater phase includes the spawning of brown trout in autumn, recruitment of fry in spring and parr growth-up until most of the parr migrate as smolt to the sea.
2) Two examples of egg to smolt survival are presented.
3) Examples of estimating the number of smolt from trap catches and an estimation of the present smolt production from all Danish streams will be presented.
4) Present knowledge of brown trout in the sea will be presented and includes: migration, feeding, and immature sea trout's stay in rivers during winter.

Earlier Studies

In earlier Danish literature the brown trout was occasionally mentioned, often mixed together with descriptions of salmon, and there was very little understanding of its biology. Brown trout in streams, lakes and sea were described as different species, and the phenomenon of sea trout spawning in rivers, the parr growing up in rivers, and smolts migrating out from freshwater to sea to become sea trout, which subsequently migrated back to the same rivers from where they originated, was not fully understood.

Since the middle Ages there were several traps in the river Gudenaa catching sea trout and Atlantic salmon. The last trap Frisenvold, situated about 10 km upstream the outlet to the Randers Fjord, kept statistical catch data for sea trout and salmon from the period 1853 to 1918, and from 1898 up to 1918 all caught fish had length and weight recorded on a daily basis. These data combined with ageing from scales and fishing with hand nets (electrofishing was not known at that time) in the upstream smaller spawning streams made it possible to obtain a modern understanding of the dynamics of populations of brown trout and salmon (Johansen and Løfting, 1919). Their report describes that larger multi sea winter MSW (fish with at least 2 years in saltwater) sea trout enter the river in late winter/early spring well before spawning, whereas younger sea trout enter later or just before spawning, which takes place in the period November to the beginning of February. The spent fish leave freshwater in the period November to June. Interestingly, the results also recognized what was called silvering immature winter sea trout that came from the sea and fjord and stayed during winter in the lowermost reaches of the river Gudenaa. From scale readings (72 fish), the results showed that the sea trout had smoltified as one, two and three-year-old fish, and that first time spawners could be separated into four groups whose stay in the sea varied from a half year to four and a half years before spawning the first time. The study also includes results from some minor external tagging experiments with caught spawners in the river and young sea trout from the fjord. The sporadic recaptures were done in the river, the Randers Fjord and southwards to the Western Baltic Sea in Germany. Basically, all these different results are a full description of Danish sea trout.

Poulsen (1935) continued earlier research in river Gudenaa based on catch statistics in the river and the fjord, and scale-reading and back calculation from sea trout scales (287 fish). One-year-old smolt (average length 15.5 cm) contributed 19.5% of the smolt run; two-year-old smolt (average length 20.6 cm) contributed 78.7% and three-year-old smolt contributed 1.8% of the smolt run. These results were similar to earlier results (Johansen and Løfting, 1919). He also recognized that the average length of parr which migrate at a particular age is larger compared to parr of the same age which remain for an additional year, or years, in fresh water, but this difference in growth rate disappears more or less during the subsequent growth in the sea. When the smolts reach saltwater they stay close to the coast line during the first summer, but later they stay in deeper water. He also found that the smolts leaving the Randers Fjord and moving into the Kattegat mostly migrated in a southern direction in accordance with the earlier sporadic tagging results (Johansen and Løfting, 1919). The length increase of sea trout during the first growth season is 20 cm, after the second season 15 cm, the third season 10 cm, the fourth 12 cm and after the fifth and sixth season only 3 and 1 cm. Accordingly, a smolt with an average total length of 20 cm reaches a size of 81 cm after six growing seasons in the sea, and sizes up to 103.5 cm had been caught in the river Gudenaa, probably with a total age (freshwater + saltwater) of about ten years. Female growth was a little faster than male growth, but differences are small. Poulsen (1935) also analyzed the spawning migration to Randers Fjord and river Gudenaa for the different sea age classes. The trout with sea age of four and five growth seasons in the sea entered the fjord and river in April and May; sea trout with three years of growth in sea in June and September; and the youngest sea trout shortly before spawning in November and December. In the autumn and winter period immature, silvering trout were caught mostly in the brackish Randers Fjord, very few in the river Gudenaa. The registered catches in the fjord were highest in March with an average weight of approximately one kg per fish just before the spawning run started. In June and July very few trout were caught in the fjord and river, but average weights were 2.5 kg (sea trout in June) and 3.5 kg (sea trout in July), respectively. Later, until spawning, the catches in fjord and river increased considerably. Therefore, both catches and average size reflected the spawning run to the fjord and river with sea trout from the Kattegat.

The studies of Johansen & Løfting (1919) and Poulsen (1935) cover a period up to the 1930s, and more or less reflect the characteristics of Danish sea trout. Apart from new methods (e.g., electrofishing, electronic tagging and genetics), our basic understanding of brown trout biology in Denmark has not changed.

After 1935 and until the introduction of electrofishing (direct current DC) method in 1947 (Larsen, 1955) no further studies on the biology of brown trout took place in Denmark. The fish stocks were now analyzed in several small streams using electrofishing by wading. It was found that these streams mostly have brown trout, 3-spined stickleback and eel with brown trout (age 0+ to 3+) as the dominating species. It was concluded that these streams function as spawning areas for non-migratory brown trout and migratory sea trout, nursery areas for parr most of which smoltify during spring and leave in the period March to May as one to four-year-old smolt. In several streams, spawning runs were monitored by electrofishing in the 1950s and 1960s. Spawners were measured and aged, but very little was published. Larsen (1984, 1987, and 1991) collected available information, i.e. available electrofishing data, literature and fishery reports and interviewing local people with knowledge of local waterways (river systems with spawning brown trout populations, barriers, catches, run time, stock development) on most of the Danish trout streams in the period up to the 1960s.

Recent Studies

From the beginning of the 1970s new population dynamic studies began. Smaller streams were monitored continuously by electrofishing for different periods, either one time each year or at intervals of 1 to 2 months. This made it possible to determine the recruitment, growth and mortality, biological production, food consumption and ecological efficiency (i.e. growth/food) of trout. Trapping of smolts in river Gudenaa during smolt run started in the 1970s.

Christensen *et al.* (1993) gave an up-to-date review of knowledge of Danish sea trout at that time: the characteristics of brown trout streams, man-made changes of rivers and the reduction of wild brown trout spawning, reproduction and freshwater phase and population dynamics, marine phase, fisheries and management including stockings. Results in this paper have been used in this chapter to calculate percentage survival from egg to smolt, fishery yield per recruited smolt and mass loss because of reproduction.

Freshwater Phase of Young Brown Trout and Smolt Run

Spawning run of sea trout from saltwater takes place from spring and spawning of sea trout and local brown trout takes places in mainly in November–January; even in small baecks with sizes down to half to one meter wide. The kelts leave the streams and freshwater during winter and spring. The fry emerge from the gravel from mid-April to mid-May and establish the number of recruits of the cohort.

In the months after emergence, the fry stays close to the river bed (in small as well in larger streams) at low water currents hiding close to or within vegetation and overhanging vegetation. Later over the summer months when the parr are larger they spread to the entire river where substrate, depths and velocities are adequate (Søholm & Jensen, 2003).

Parr growth depends on water temperature and the density of trout (Mortensen *et al.*, 1988; Rasmussen, 1986a+b & 2016). The main prey is invertebrates, occasionally brown trout eggs during spawning time, smaller brown trout and other fish species (e.g. sticklebacks and rainbow trout), Rasmussen (1986a & 2016); Lousdal *et al.* (2002). Mortality is related to density of trout according to Mortensen (1977a+b+c); Rasmussen (1986b, 2016) and to the presence of predators: besides larger brown trout, pike (*Esox lucius*), Larsen (1966), burbot (*Lota lota*), Voldsgaard (1990), otter Taastrøm & Jacobsen (1999), mink (*Neovison vison*) and different fish-eating bird species predate on brown trout.

Biological production integrates recruitment, growth, and mortality. Danish trout streams are in general productive Mortensen (1977a+b+c+d, 1982, 1985a+b); Rasmussen (1986a+b, 2016) and the annual brown trout production varies from approximately 5 to 33 g wet weight per one m^2.

The smolts leave freshwater as one-year-old to five-year-old smolts, and are sized from approximately 10 to 30 cm in the period late March to early June, Nielsen (1985), Rasmussen (1986b+2016), Dieperink (1988), Nielsen (1996). Females constitute 70–75% of the smolts (Nielsen 1985; Rasmussen 1986b), and accordingly also the composition of sea trout later at the spawning runs. The sea trout males stay longer in the spawning streams compared to females (Danish Technical University, unpublished material).

During the smolt run, smolts in many streams have to pass weirs and lakes. Aarestrup & Koed (2003) showed smolt losses varying from 18 to 71% when trying to pass a weir. Losses may be because of trout penetrating grids erected at fish farm inlets, predation upstream the weir and delays, which may lead to de-smoltification. Jepsen *et al.* (1998) showed that approximately 90% of tagged smolts died because of predation, when passing a 12 km long shallow hydropower reservoir (Lake Tange) in river Gudenaa. Smaller shallow lakes have in recent years been established in rivers to get rid of nitrogen from agricultural areas; either placed directly in rivers where there were no lake before, or as restoration of earlier drained lakes. As a result the mortality may increase to 90% (Rasmussen & Koed 2005, www.fiskepleje.dk/Vandloeb/restaurering/vaadomraade/Soe-direkte-i-vandloeb-i-vaadomraade). The main cause of death was predation from fish (pike the most important species) and birds. Much effort has been spent to remedy the problems and to propose bypasses in the smolt period. Koed (2000) estimated that during the smolt run, accumulated pikeperch (*Stizostedion lucioperca*) below a hydropower plan (Lake Tange) consumed up to 95% of salmon and trout smolts in the river Gudenaa below the plan.

Egg to Smolt Survival; Two Estimations

It is of paramount importance to know the effects from destruction/rehabilitation of salmonid habitats and effects from fisheries on the number of spawners and stock sizes of fry, parr and smolts. Knowing the number of sea trout, the size distribution in sea age and the fecundity of a trout population makes it possible to model the relationship between total number of eggs spawned and the subsequent number of smolts. Two examples are described in the following.

Christensen *et al.* (1993) gives the numbers of spawners in 21 different streams in Denmark and from estimated mortalities the number of smolts can be calculated. From the fecundity relationship: Number of eggs = 0.0081 • length$^{3.0913}$, total length in cm, river Karup Aa (Pedersen *et al.*, 2006) we have the following (A.0+ means unknown smolt age spawning after half year in saltwater and so on):

Sea age	No. of females	Total length cm	No. of egg
A.0+	203	32.9	187,579
A.1+	200	43.7	428,952
A.2+	155	51.2	531,803
A.3+	74	60	406,412
A.4+	11	68	87,572
A.5+	4	72.5	38,510
Total			1,680,829
Total no. of smolt			5,226
No. of eggs per female			2,598
Survival egg to smolt%			0.31

In Brandstrup Baeck (Rasmussen 2016) we have a relationship between numbers of recruits in mid-April and number of 0+ in mid-November and from number of recruits to total number of smolt (aged one to four) of every year class. Based on the mean weight of 390 females collected during spawning run in several years, and a total estimate of females in 1984 (94 fish) and fecundity relationship (as above) we have the following:

Sea age	No. of females	Total mean length cm	Range cm	No. of egg
A.0+... A.7+	94	38.9	24–87	168,505
Total No. of fry mid-April				19,039
Total no. of 0+ November				8,439
Total no. of smolt				1,479
No. of egg per female				1,800
Survival egg to smolt%				0.88

The two results for calculated survival of eggs to smolts are more or less at the same level, taking into account that the materials and methods they are calculated from are different. So, as a 'rule of thumb' about 0.5% of brown trout eggs gives one smolt.

Wild Smolt Production

The original smolt production has been suggested to be 2.64 million annually (Rasmussen & Geertz-Hansen, 2001). In the 1960s the annual wild smolt production was estimated to approximate 0.2 million smolt (Christensen *et al.*, 1993). The present wild smolt production is estimated as 1.1 million (see above). This increase is the result of cessation of pollution, improvement of habitats, and regulation of sea fisheries. Estimation of the number of smolts from a single river can be based on: either (1) trap catches or (2) combining monitoring of densities of wild parr, stockings and survival rates. These two methods are compared in the following.

The presented smolt production from trap catches and smolt production from current monitoring in streams should not be directly compared. The estimates from trap catches include old estimates of smolt production in a time period when some of the river systems, especially in West Jutland, were in a worse habitat condition with less stockings and less wild smolt production compared to the situation today. In contrast the results from monitoring are based on streams with only wild fish and it is assumed that they represent the true present smolt production from Danish rivers. However, whether these represent the original wild smolt production before human interference is not known.

Smolt from Trap Catches

The wild smolt production from Danish streams and rivers is not known precisely apart from a few records based on captures of smolts in traps. As described earlier, the number of smolts resulting from stocked fry and parr has been calculated based on conversion ratios. Different local water authorities have monitored the smolt run in some rivers since 1995, but normally only in one single year. Table 19.2 shows smolt catches from trapping in different geographical areas and years in Denmark. From monitoring data, the spawning and growth-up areas in the same year with trap results have been calculated and from this the smolt yield in traps per 100 m^2 production areas is calculated. These trapping results are compared with the calculated smolt production in the same stream based on monitoring wild 0+ and releases of reared fish in the year with trap results using the conversion ratios. The two methods yield comparable

Table 19.2 Brown trout smolt catches in traps, and smolts per 100 m^2 spawning and growth up area and calculated smolt per 100 m^2 growth up area based on stocking plan. MSA mean smolt age, MSL mean smolt length. The column 'Stocking' shows where the smolt counting is in streams with either, a: stocking + wild or b: in systems with only wild trout. The results from the river systems marked with * are non-published data DTU.

River system	Area	Stocking	Year of study	Spawning and growth up area m^2	Trap number smolt	Trap 95% cl	Trap smolt per 100 m^2	Stocking plan smolt per 100 m^2	msa	msl cm	mode cm	smolt size range cm
Fladså	Zealand	None	2010	47,560	6,955	4,942–11,046	14.6	9.2	1.2	13–14	13½	10.0–22.5
Krobæk	Zealand	None	2012	14,700	5,984	n/a	40.7	16.7	1.6	13–14	12½	9.0–24.5
Elverdamså	Zealand	None	2010	24,450	2,721	1,907–3,673	11.1	17.3	1.2	13–14	13½	9.5–22.0
Herredsbæk	Zealand	None	2014	4,000	1,335	n/a	33.4	53.3	1.7	13–14	13½	9.0–20.0
Tuse å	Zealand	None	2008	40,600	5,873	3,642–9,995	14.5	2.8	1.1	17	17½	13.0–27.0
Halleby å	Zealand	Stocking	2000	136,640	2,397	1,720–3,074	1.8	1.6	n/a	n/a	n/a	n/a
Kornerup/ Langvad å	Zealand	Stocking	1997	83,650	2,190	1,632–3,200	2.6	2.0	1.1	16.1	17½	13.3–25.5
Tude å	Zealand	Stocking	2013	190,520	3,358	2,592–4,502	1.8	2.6	1.2	15	15½	11–25
Saltø å	Zealand	None	2011	87,420	23,811	4,845–42,776	27.2	3.3	n/a	n/a	14½	8.0–22.0
Bogense Bybæk	Funen	None	2014	8,640	300	190–418	3.5	8.9	2–3	15–18	15½	12–27
Stavids å	Funen	Stocking	1995	107,225	6,256	5,626–6,957	5.8	4.0	n/a	18.3	18½	11.5–30.5
Lindved å	Funen	Stocking	1995	38,850	880	581–1,399	2.3	3.9	n/a	19	17½	9.5–31
Odense å	Funen	Stocking	1995	224,900	653	308–1,507	0.3	3.6	n/a	18.7	n/a	12.0–30.5
Stokkebæk	Funen	None	1995	40,600	2,972	n/a	7.3	6.7	1.49	16.2	15½	10–29
Geels å	Funen	None	2012&2013	41,360	2,770	n/a	6.7	7.3	n/a	n/a	n/a	n/a
Bygholm å	E Jutland	Stocking	1992	150,100	6,708	n/a	4.5	2.3	1.72	16.3	14½	9.5–28.5
Tved å/Ribe å	E Jutland	Stocking	1987	219,180	2,651	2,084–3,755	1.2	1.8	1.85	17.2	16½	12.5–32.0

Kolding å*	E Jutland	None	2006	236,710	43,898	34,463–53,333	18.5	7.0	n/a	n/a	n/a	n/a
Gudenå/Up	E Jutland	Stocking	1993	188,260	1,187	n/a	0.6	2.6	2	18.3	17½	12–25.5
Gudenå/Lilleå*	E Jutland	Stocking	2008&2009	302,220	28,500	n/a	9.4	4.2	n/a	n/a	n/a	n/a
Villestrup å*	E Jutland	None	2008&2009	89,510	4,760	n/a	5.3	13.7	n/a	n/a	n/a	n/a
Århus å/Århus å	E Jutland	Stocking	2004	52,050	1,449	685–3,344	2.8	5.9	n/a	15.3	15½	8.0–26.5
Århus å/Lyngbygårdså	E Jutland	Stocking	2004	130,300	11,830	9.892–14,140	9.1	5.6	n/a	13.6	13½	8–26
Karup å	N Jutland	Stocking	1997–99	194,559	23,645	n/a	12.2	6.8	1.8-2.2	n/a	n/a	n/a
Skjern å	W Jutland	Stocking	2000	882,580	8,530	6,081–10,979	1.0	1.1	n/a	n/a	n/a	n/a
Skjern å	W Jutland	Stocking	2002	882,580	7,072	4,630–9.514	0.8	1.1	n/a	14.6	14½	7.5–24.5
Skjern å	W Jutland	Stocking	2005	882,580	7,927	5,573–10,283	0.9	1.1	n/a	n/a	n/a	n/a
Varde å	W Jutland	Stocking	1994	691,870	8,221	6,403–11,619	1.2	1.7	n/a	n/a	12½	9–27
Sneum å	W Jutland	Stocking	1995	341,810	4,848	4,348–5,477	1.4	1.9	n/a	n/a	15½	11–29
Kongeå	W Jutland	Stocking	1994	203,270	866	789–961	0.4	2.2	n/a	n/a	17½	11–29
Ribe å	W Jutland	Stocking	1994	985,320	25,946	23,750–28,590	2.6	2.1	n/a	n/a	17½	10–30
Brøns å	W Jutland	Stocking	1996	92,460	370	281–631	0.4	3.4	n/a	n/a	15½	13–28
Brede å	W Jutland	Stocking	1996	354,750	2,110	1,710–2,752	0.6	2.0	n/a	n/a	15½	10–28
Vidå	W Jutland	Stocking	1995	387,150	5,354	3,956–8,277	1.4	3.3	n/a	n/a	16½	10–29

numbers of smolt (P ~0.5), although the stocking plans on average estimate about 15% less smolt compared to the trap data.

The trap data are mostly for only one year of study, and therefore do not take into account that wild recruitment normally varies from year to year. In addition, the estimates from traps have high confidence limits, which indicate uncertainty around the actual estimate. In contrast, the stocking plan stipulates the exact number of fish released every year. But the calculation of smolt (from released and wild brown trout) is also based on the number of wild 0+ in the year when monitoring took place, and this number of wild 0+ is also based on varying recruitment from year to year. As mentioned earlier each river system is only monitored with intervals of seven or eight years, so the number of wild 0+ is also based on expected varying recruitment. Therefore, both trapping results and results from monitoring plus stocking of fry, half-year and one-year brown trout in the same stream will vary from year to year, and the two methods should not be expected to give the same results, but at least to be at the same level of smolts. Apart from these considerations the results show that the smolt sizes range from about 10–30 cm with a mode of about 12.5 to 18.5 cm irrespective of geographical area. Very few smolts were aged, but the mean smolt age MSA vary from one to two year-old smolt. The smolt production per 100 m^2 from traps and stocking plans varied from about 1.1 to 2.0 in West Jutland, from 5.4 to 6.4 in North and East Jutland, from 4.3 to 5.7 in Funen and from 12.1 to 16.4 smolts per 100 m^2 in Zealand.

Smolt from Monitoring in Streams

As described above, 876 river systems are monitored with intervals of seven or eight years. A total of 239 systems in all geographical areas in Denmark (calculated in 2014) have only wild trout and no releases take place in these streams. The production area in total m^2 and total number of wild 0+ during monitoring is calculated, and the wild smolt production per 100 m^2 can then be calculated. As described in the preceding paragraph, the main problem using monitoring results of 0+ to calculate smolt production is that the wild recruitment is expected to vary from year to year and therefore also the number of smolt coming from each river system. However, given a larger number of river systems in each geographical area and within an eight-year period and calculating the smolt production from each river system based on the mean number of wild 0+ it is expected that this mean represents the geographical level of smolt production. This method contrasts with the results from trap catches as described above.

The mean numbers of 0+ in all river systems covering all geographical areas in August–September vary from 40 to 94 per 100 m^2; the lowest densities are found in West Jutland with sandy areas and they are highest in North and East Jutland and Zealand with fertile moraine.

It is assumed that small streams through time have been more vulnerable to habitat degradation and are more vulnerable to varying recruitment from year to year (e.g. cold winter, dry summer, high water flow at swim-up time). Accordingly, all streams with a calculated annual smolt production below 500 individuals (a total of 111) have been excluded from the analysis. Streams and rivers with a higher calculated annual smolt production exceeding 500 smolts (a total of 128) are considered more stable from year to year and probably better reflect the mean annual smolt production per area.

The stocking plans stipulate that 10% of the number of wild 0+ trout equals the number of smolt from this number of 0+ parr. This percentage has been used in stocking plans for at least 30 years, and is based on earlier survival data of brown trout populations and assumptions about how many smolt a year class produces after fixed two years from recruitment as two-year-old smolt. But the essential is that the figure of 10% has never been verified from trap catches. Later results in two streams in Jutland (Rasmussen 2016), where the accurate total smolt production (trap catches) from accurate monitoring data of recruitment and number of 0+ in September–November show, that the percentage figure depends on density of 0+: high percentage at low density and low percentage at high density. Combining the results from all years the mean number of smolt (one to four-years old) can be calculated from the number of 0+ using a mean figure of about 16% of number of 0+.

The smolt production in a river system basically depends on recruitment, density of parr, mortality, growth rate and food production. So, the 16% from two streams (Rasmussen, 2016) in mid-Jutland cannot be expected to cover all rivers in Denmark. This is especially because (see above) the densities of 0+ vary between geographical areas in Denmark, and why different percentages might be expected: i.e. low density in West Jutland compared to high density in moraine areas in East Denmark. The age distribution of smolt also influences the percentage figure because of natural mortality through years: streams with a low mean smolt age (MSA) are expected to have a higher percentage figure compared to streams with a higher MSA given the same number of 0+. The smolts on Zealand are dominated by one to two-year-old smolt (see Table 19.2), so it could be expected that in these more fertile areas the percentage is higher.

Nevertheless, using the figure of 16% (Table 19.3) shows the wild smolt production and smolt production per 100 m^2 productive area (i.e. spawning and growth-up habitats for fry and parr) in different geographical areas of Denmark.

The production of wild smolt in 2014 in the moraine areas (Zealand, Funen and part of Jutland) with high conductivity and nutrients varies from 12 to 15 smolts per 100 m^2, whereas the smolt production in West Jutland with sandy areas is only approximately six smolts per 100 m^2. Table 19.3 gives the present calculated smolt production rate. It is difficult to assess if the numbers represent the original smolt production before the interference of man or if the current smolt production is larger than the original, due to a general increase in nutrients. As described in section on Stocking and Enhancement, very little is known about brown trout presence and densities on river stretches with widths above 7–8 m. Therefore, wild smolt production in the larger rivers in Jutland is likely higher than calculated here in Table 19.3.

Because of a possible autumn migration of parr (Rasmussen 2016; Winter *et al.* 2016) the true brown trout smolt production from Danish river might be higher.

Marine Phase of Sea Trout

It is of paramount importance to known what happens with the wild smolt, post-smolt (i.e. the stage in saltwater until first winter) and sea trout life stages in the coastal area around Denmark. This knowledge started with the results of recaptures in saltwater from a small number of tagged brown trout in river Gudenaa, Johansen & Løfting (1919) and Poulsen (1935). Thousands of domesticated brown trout smolt have been tagged and released in many coastal areas around Denmark, but it is not expected that these

Table 19.3 Wild brown trout smolt production in different geographical areas of Denmark. Only river systems with a calculated annual smolt production above 500 individuals have been included. Abbreviations: LFM islands: Lolland, Falster and Møn.

	Bornholm	**Zealand**	**LFM islands**	**Funen**	**E Jutland**	**N Jutland**	**W Jutland**	**Total**
Number of streams	26	9	2	14	46	24	7	128
Productive Area m^2	N/A	181,320	14,940	282,440	1,103,645	762,040	1,321,910	3,666,295
Number of smolt	62,206	21,330	2,217	33,110	137,317	98,751	83,860	438,790
Number per 100 m^2	N/A	11.8	14.8	11.7	12.4	13.0	6.3	12.0
Median	N/A	11.1	5.7	10.8	17.5	18.2	5.7	15.2

recaptures (Kristiansen & Rasmussen, 1993) of brown trout represent the behaviour of wild brown trout, for example migration in saltwater. Survival in saltwater might also be lower for domesticated brown trout compared to wild brown trout.

When salmonid smolts reach fjords and the shallow coastlines they are subject to predation from several bird species (cormorants and sea gulls), especially if caught in pound nets Dieperink (1994), Dieperink *et al.* (2001) and Dieperink *et al.* (2002), Koed (2006), Baktoft & Koed (2008). To avoid this, legislation states that the upper line of pound nets must be below the water surface during the smolt run in spring to allow smolts to escape the pound nets. In many fjords with commercial and recreational fishery for herring (*Clupea harengus*) and whitefish, many smolts and adult sea trout are caught in gill nets and pound nets. Restrictions on such fisheries have been implemented in many areas.

Migration in Sea

Thousands of domesticated smolts (one-year and two-year-olds from about 15 to 25 cm) have been tagged with Carlin tags and released at the lowermost parts of several rivers e.g. Kristiansen & Rasmussen (1993); Pedersen & Rasmussen (1997 & 2004). Most of the sea trout were caught within 100–200 km from releasing points, but many trout migrated several hundreds of km away and there was much straying to other rivers. Most of the sea trout migrated in a southerly direction towards less saline waters (southern Kattegat and the Baltic Sea), but some fish migrated east and northerly to the Swedish and Norwegian coast in the Skagerrak and from here out to the Atlantic Sea and some brown trout migrated up to about 1,400 km, probably led by the upper northerly surface current. It is assumed that because they are of domesticated origin, their migration routes probably do not represent the migration routes of wild sea trout. Pedersen *et al.* (2006) tagged wild smolt, reared F1 and domesticated smolt and wild sea trout in river Karup Aa. This river goes to the Limfjord in Jutland with in/outlets to the North Sea and the Kattegat, respectively. The migration of the domesticated brown trout was more random and the domesticated sea trout stayed in the fjord, whereas the wild fish migrated eastward out of the fjord to the Kattegat, towards and into the southwestern part of the Baltic Sea (one recapture about 1,100 km away at the Swedish island Gotland in the middle part of the Baltic Sea). They also found that sea trout of wild origin did not stray to other rivers.

These results were confirmed by Carlin tagged reared F1 wild smolt from the river Kolding Aa strain and Carlin tagged wild sea trout kelts of the same strain caught in the river. River Kolding Aa goes to the Kattegat south of the shallow strait Little Belt (Figures 19.1 & 19.3) which has a strong, but varying northern surface current from the Baltic Sea.

A total of 9,000 F1 smolts (reared F1 offspring from adults collected in the river Kolding Aa) were Carlin tagged. 3.46% were recaptured in freshwater (mostly river Kolding Aa and some in nearby rivers. 1.38% of the tagged smolts were recaptured in saltwater as sea trout; the last fish recaptured 3.6 years after release.

A total of 4,935 wild sea trout kelts were Carlin tagged. 3.34% were recaptured in freshwater (mostly river Kolding Aa and some in three nearby rivers. 12.02% of the tagged sea trout were recaptured in saltwater; the last fish recaptured 4.5 years after release. Most of the recaptures (Figure 19.3) were made in the southern direction from the river outlet and to the southern part of Little Belt and western part of the Baltic Sea.

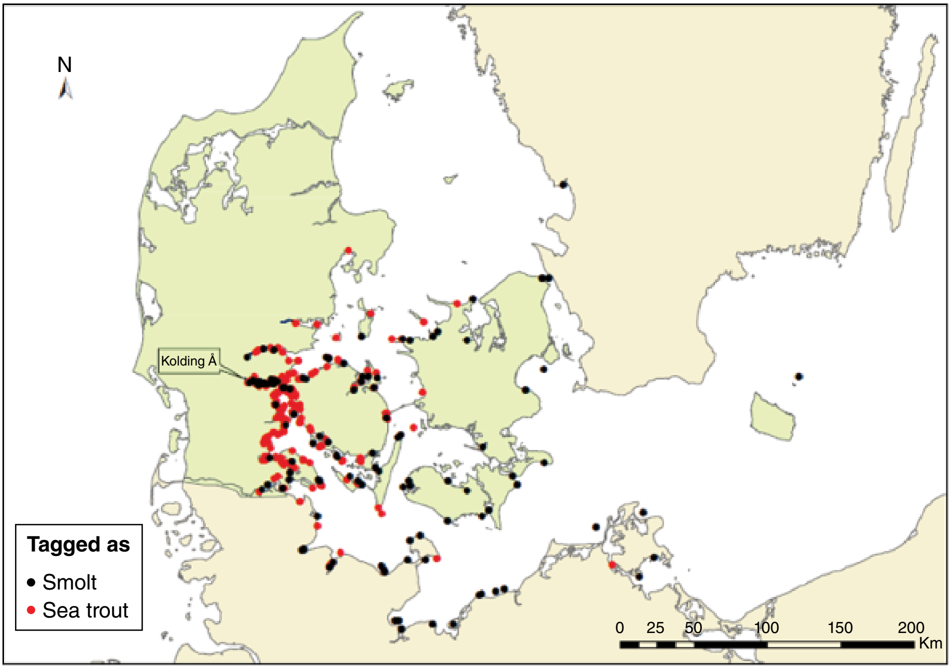

Figure 19.3 Recaptures of Carlin tagged smolts and sea trout in river Kolding Aa.

Though the recaptures of sea trout from smolts in saltwater are low compared to tagged sea trout, the results show that after release the smolts migrate around in saltwater to a much higher extent than sea trout that prefer to stay in the neighbourhood. The share of sea trout that migrate much longer distances away from the southern parts is higher for smolt. External tagging only shows the position where the fish is caught and does not tell the true migration route, so the results should be taken with reservations when discussing the migration of sea trout in freshwater and saltwater. The results also show that more that 95% of the tagged smolt and sea trout home back to their home river and the rest stray to nearby rivers.

These results from river Kolding Aa with wild F1 smolt and wild sea trout confirm the earlier results of Johansen and Løfting (1919); Poulsen (1935); Kristiansen & Rasmussen (1993) and Pedersen *et al.* (2006), that sea trout from Eastern Jutland probably migrate southwards to the lesser saline Baltic Sea; but much more has to be done in this topic. Very little is known of the migration routes of sea trout from rivers with outlets to the Skagerrak and the North Sea. Using Passive Integrated Transponder (PIT-tags) and acoustic tags on smolts in river Villestrup Aa (Mariager Fjord with outlet into the Kattegat), it was demonstrated (del Villar-Guerra *et al.*, 2014) that a little over 50% left the fjord and migrated to the Kattegat, while the rest stayed in the Mariager Fjord. This suggests, together with the other mentioned tagging results, that partial migration in saltwater is a common phenomenon in sea trout in Denmark. This was also confirmed in freshwater with smolts migrating from small streams to Lake Hald (river Gudenaa system); some smolts stayed in the lake and others migrated further downstream to the Kattegat (Boel, 2012). Research using Data Store Tag (DST-tags) and tagging wild kelts is presently ongoing to obtain a more precise knowledge of migration route of wild trout.

Feeding at Sea

Stomach contents from caught, stocked domesticated smolts suggest that the food consumption in general reflects the prey species composition of the localities. Among the food items of sea trout from North Sea (Ringkoebing Fjord), clupeids of all species were found in most stomachs and in largest quantity, followed by smelt (*Osmerus eperlanus*). The most significant food items for sea trout from Southern Kattegat (Isefjord) included in the order mentioned: clupeids, gadoids, stickleback (*Gasterosteus aculeatus*), Gobidae and *Crangon* species (Danish Technical University, unpublished). Sea trout (domesticated and wild) from the Limfjord (Pedersen *et al.*, 1995; Ebert, 1996), consumed mostly crustacea and insects during their first months as post-smolts; fish contributed less than 50% of the consumed biomass. Later, during the first year at sea, about 75% of the consumed biomass was stickleback, Gobidae species, and clupeids. In the following years mostly different marine fish species were eaten, but rarely eel and cod (*Gadus morhua*).

Immature Sea Trout Migrating into Freshwater

In the Northern Kattegat, Limfjord and North Sea immature sea trout migrate back from saltwater and overwinter in freshwater. This has been known by anglers for many years and these immature fish are heavily fished. This has been the subject of two studies, Jensen (1988); Koed & Thomsen (2005) and Thomsen *et al.* (2007). Johansen & Løfting (1919) made the same observations. The extent of migration to freshwater depends on how severe the winter is.

A total of 417 immature wild sea trout (range 26–70 cm) from river Ribe Aa going to the North Sea were aged and had their stomach contents analysed (Jensen, 1988). Of these 417 individuals about 47% of the fish were female and 53% were male with smolt ages similar to the mature sea trout in Ribe Aa and sea ages one (78%), two (20%) and three (2%). Fish stomachs varied from nearly empty to completely full, and the food items were different insects, crustaceans, molluscs, trout eggs and a single frog. The immature trout left the river in the period March and April with increasing water temperature.

Laboratory experiments and analysis of Na^+/K^+-ATPase showed, Koed & Thomsen (2005), Thomsen *et al.* (2007) reduced osmoregulatory capacity of sea trout from river Ribe Aa (North Sea) and River Grenaa (Kattegat) at low water temperature and high salinity. It is concluded that overwintering in freshwater is partly driven by compromised osmoregulatory physiology, but because not all fish in the two populations overwinter in freshwater but stay during the winter in the sea, the phenomenon may also reflect diverging life strategies.

Vital Statistics of Brown Trout

The preceding section describes in broad terms the biology of brown trout in fresh- and saltwater, based on different reports and publications. Smolt ages, sea ages and spawning types (most often based on scales collection from sea trout and scale readings) are all important life characteristics of Danish sea trout and ultimately determine growth rates and spawning/egg capacity.

In the next section, sea trout data from river Gudenaa are used to show (1) the distribution of the sea trout smolt ages for female and male; (2) to calculate egg capacity for different spawning types; (3) the egg capacity is calculated for the different spawning/sea age types independent of smolt age. Smolt age and spawning type are therefore two predictors for egg capacity, and most possibly the population genetics adapts from these two predictors to produce the highest number of eggs at spawning.

In the following two sections sea trout data from river Gudenaa and from Christensen *et al.* (1993) covering 21 different streams in Denmark are used to show the mean sizes of female and males vs. sea age and spawning types respectively.

In the third section the mass loss of sea trout in connection to spawning and influence on growth rate is presented.

Smolt, Sea Age and Spawning Types

Sea trout were collected (electrofishing) in the main stem of the river Gudenaa and in several tributaries below the hydro power station at Lake Tange. The river and the brown trout population here are assumed to be representative for a larger river system in East Jutland. The fish were measured (total length), weighed and scales were sampled and aged, i.e. smolt age, sea age, sea age at first spawning and subsequent spawning. TYPE I denotes a trout spawning first time after one summer in sea, TYPE II after 1½ years in sea, TYPE III and IV and V fish spawning after 2½, 3½ and 4½ years in sea, respectively, see terminology in Frier (1994). Each female with specific smolt age and spawning type might further contribute to the total amount of egg in the subsequent spawning. The percentage egg contributions calculated for either smolt age or spawning type are therefore calculated (see egg/length relationship in section on Egg to smolt survival; two estimates)) for the accumulated egg contributions for each smolt age or spawning type, respectively. A total number of 1,123 females (71%) and 450 males (29%) were aged. Smolt age could not be determined for 86 females and 32 males.

The first box shows the distribution of smolt ages for females and males, respectively, and the percentage contribution of eggs from the five female smolt age groups. Sea trout with each smolt age is followed in the subsequent sea age years and number of eggs calculated from first spawning to last spawning. The sex composition between female and male smolt is 0.71: 0.29 which is in accordance with Nielsen (1985), Rasmussen (1986b) and the general knowledge from other river systems, e.g. Dieperink (1988), Nielsen (1996). The results show that two and three-year-old smolt dominate the smolt run in this river for both females and males, followed by one-year-old smolt, and that four and five-year-old smolt are rather rare in number. MSA for female is 2.1 years and for male 2.0 years. Two and three-year smolt contribute most to the total egg production.

Gudenå	**Female**		**Egg**	**Male**	
Smolt Age	**No.**	**%**	**%**	**No.**	**%**
One	75	7.2	8.9	42	10.1
Two	798	77	74.9	327	78.6
Three	161	15.5	15.9	46	11.1
Four	2	0.2	0.2	1	0.2
Five	1	0.1	0.1		
Total	1037			416	

The second box shows the distribution of spawning types and means lengths at first spawning for females and males and the percentage contribution of eggs during spawning from the five female spawning types (i.e. TYPE I to TYPE V) calculated from the accumulated contribution of egg; i.e. from first to last spawning. About 28% of female and 59% of males spawn first time, TYPE I after a half year in saltwater at length about 33 cm, and because the growth of females after spawning is reduced (see section on Reproduction loss) their total egg contribution is only 8.5% of the total sea trout population. Type I spawners are small fish at first spawning; their survival is low after spawning which is why their total egg contribution is low. The dominating spawning type (i.e. total egg contribution) for females is TYPE III (41.3% in number), and with a much larger length/mass at first spawning this spawning type contributes 52.1% of the total egg production. Very few females and males spawn at first time as TYPE IV and TYPE V in water and because of total mortality in the years from smolt to first spawning, their total number is only 9.2%, and because their survival after first spawning is very low, these big trout contribute only 21.8% of the total egg contribution for the population.

		Female		**Egg**	**Male**	
Gudenå	**Sea Age**	**%**	**Length cm**	**%**	**%**	**Length cm**
Type I	one	27.9	33.4	8.5	59.1	33.1
TYPE II	two	21.6	46.5	17.6	11.3	43.8
TYPE III	three	41.3	54.0	52.1	21.6	54.5
TYPE IV	four	8.6	65.9	19.7	6.5	69.2
TYPE V	five	0.6	76.8	2.1	1.4	82.1

The two boxes show that using smolt age and spawning types as predictors for the optimal sea trout egg production in river Gudenaa, a combination of females with a smolt age two and three and spawning types as TYPE II to TYPE IV, gives the highest egg contribution and therefore, recruitment of fry to the population; the rest of the smolt ages and spawning types contribute less to recruitment. Probably this combination of smolt age, spawning type and subsequent survival is a population specific genetic adaption to optimize stock size.

Spawning Type, Smolt and Sea Age and Growth

In the material from river Gudenaa a total of 1,449 sea trout (female + males) could be separated on smolt age, the five spawning types and repeat spawners, and of these a total of 1,206 sea trout were first spawners. The difference (243 fish) was repeat spawners.

Table 19.4 shows the number of fish and mean length and size ranges at first and subsequent spawning for the different spawning types, distributed smolt ages and sea ages. Females and males are combined because there were no differences in mean size;

Table 19.4 Number and spawning type of sea trout in river Gudenaa distributed on smolt age and sea age, and TYPE I spawn after half year in saltwater and TYPE V after four and a half year in saltwater. 1.0+ means a one-year-old smolt sea trout spawning as a one-year-old smolt after half year in saltwater, and 1.G+ means a one-year-old smolt repeat spawner, and so on. The percentage distribution of the five spawning types for all sea ages within each spawning type and at first spawning.

	Female + Male				
	Smolt & Sea age	**No.**	**Length cm**	**Min cm**	**Max cm**
TYPE I	1.0+	17	30.9	28.2	35.4
TYPE I	1.G+	3	50.7	40.7	60.8
TYPE I	2.0+	391	33.2	24.8	40.9
TYPE I	2.G+	28	44.6	33.4	55.8
TYPE I	2.GG+	8	54.1	47.8	63.8
TYPE I	2.GGG+	3	57.4	53.3	63.8
TYPE I	2.GGGG+		NA	NA	NA
TYPE I	2.GGGGG+	1	78.8	NA	NA
TYPE I	3.0+	60	35.4	28.6	44.3
TYPE I	3.G+	10	45.5	40.4	49.4
TYPE I	3.GG+	1	60.3	NA	NA
TYPE I	3.GGG+	1	65.8	NA	NA
TYPE I	4.0+	1	47.3	NA	NA
TYPE I	4.G+	1	46.8	NA	NA
TYPE II	1.1+	16	40.1	31.4	51.8
TYPE II	1.1G+	4	50.4	44.8	57.3
TYPE II	1.1GG+	2	59.1	50.9	67.3
TYPE II	1.1GGG+	1	71.3	NA	NA
TYPE II	1.1GGGG+		NA	NA	NA
TYPE II	1.1GGGGG+	1	62.3	NA	NA
TYPE II	2.1+	148	45.6	29.9	68.7
TYPE II	2.1G+	27	56.2	42.3	74.0
TYPE II	2.1GG+	14	66.3	47.3	75.3
TYPE II	2.1GGG+	5	70.5	58.3	82.3

Table 19.4 (Continued)

	Female + Male				
	Smolt & Sea age	No.	Length cm	Min cm	Max cm
TYPE II	3.1+	36	50.1	37.8	63.3
TYPE II	3.1G+	11	54.7	46.3	71.7
TYPE II	3.1GG+	2	59.8	57.3	62.3
TYPE II	4.1+	1	61.3	NA	NA
TYPE III	1.2+	36	50.1	42.8	59.3
TYPE III	1.2G+	8	60.5	50.3	69.3
TYPE III	1.2GG+	1	75.3	NA	NA
TYPE III	2.2+	334	54.1	40.3	70.4
TYPE III	2.2G+	61	64.1	47.8	78.3
TYPE III	2.2GG+	11	74.3	61.3	86.3
TYPE III	2.2GGG+	2	75.8	74.3	77.3
TYPE III	2.2GGGG+	1	77.3	NA	NA
TYPE III	3.2+	58	57.9	47.3	78.3
TYPE III	3.2G+	14	63.3	55.3	76.3
TYPE IV	1.3+	21	61.4	47.3	72.3
TYPE IV	1.3G+	2	82.8	77.3	88.3
TYPE IV	1.3GG+	1	72.3	NA	NA
TYPE IV	1.3GGG+	1	77.3	NA	NA
TYPE IV	2.3+	64	67.7	51.3	87.3
TYPE IV	2.3G+	9	70.7	61.8	84.3
TYPE IV	2.3GG+	4	89.8	87.3	93.3
TYPE IV	2.3GGG+	2	83.8	80.3	87.3
TYPE IV	3.3+	12	70.8	58.8	80.3
TYPE IV	3.3G+	2	83.3	79.3	87.3
TYPE V	1.4+	3	74.1	68.3	79.3
TYPE V	2.4+	8	80.8	75.3	84.3
TYPE V	3.4+	1	84.3	NA	NA

(Continued)

Table 19.4 (Continued)

		All sea age		1th spawning
		%		%
TYPE I	525	36.2	469	38.9
TYPE II	268	18.5	200	16.6
TYPE III	526	36.3	428	35.5
TYPE IV	118	8.1	97	8.0
TYPE V	12	0.8	12	1.0
Total number	1449	100.0	1206	100.0

see next paragraph. For example, a 2.0+ fish means a two-year-old smolt spawning first time after one summer in sea (TYPE I); a 2.GGG+ fish means a two-year-old smolt spawning first time after one summer in sea (TYPE I), and then repeating spawning in the following three years and the fish is on its fourth spawning run. Also a 2.4+ fish means a two-year-old smolt first time after four and a half-year at sea (TYPE V), and so on.

Testing mean size of sea trout at first spawning for the different spawning types (for example size of TYPE I for different smolt ages: 1.0+, 2.0+ and 3.0+ or TYPE II for different smolt ages: 1.1+, 2.1+ and 3.1+ and so on against each other) were significantly different. This is probably because of difference in smolt size regardless spawning type. Testing mean size at first spawning within the different smolt ages of females and males (for example size of female 2.1+ against male 2.1+) were not significant. Assuming the same growth rate in the sea between the two sexes, this means that the size of females and males at a certain smolt age is probably the same. The importance of smolt age and spawning type on growth is evident from Table 19.4. For example, TYPE II (i.e. one and a half year in sea at first spawning) and smolt age one, has a mean length of 40.1 cm, whereas TYPE II and smolt age three has a mean length of 50.1 cm at first spawning and so on. The ranges of mean sizes at first spawning for the different spawning types vary from 30.9 cm (1.0+, range 28.2 cm–35.4 cm) to 84.3 cm (3.4+, one individual). For all spawning types, the growth rates decrease in the years following spawning because of reproduction loss; see section on Reproduction loss. So, the question: how fast do the sea trout grow in river Gudenaa is difficult to answer, because growth depends on smolt age and spawning type. The question is how specific these results in river Gudenaa are compared to other rivers in Denmark.

To answer this, data from river Gudenaa is compared with the data from Christensen *et al.* (1993) (data from 21 streams around in Denmark), where smolt age and spawning type is not known; only sea age is known. In the following box the data from river Gudenaa has been distributed on sea age regardless of smolt age and spawning type, and compared with Christensen *et al.* (1993). The results are more or less in accordance with each other and with Jensen (1988) and differences probably reflect sampling and local differences in growth and mortality.

Table 19.5 Catch model parameters for sea trout (Christensen *et al.* 1993). A.0+. A.5+ denotes unknown smolt age groups contributing to the fishery after half year in saltwater and up to five and a half years. A total of six year classes contribute with a total of 5,226 smolts.

				Mean	Mean				Mean	Mean		
	No.	Length	weight	G	weight	M	Z	F	No.	Biomass	Fishery	Fishery
		cm	g		g					g	g	No.
Smolt	871	12.5	20									
				2.8865	117	0.2045						
A.0+	773	31.8	357									
A.1 (15. March)	738	31.8	357			0.1409						
				0.7092	520	0.1244						
A.1+>= 40 cm (15 June)	715	40	726									
				0.2307	817	0.1070	0.4764	0.3694	569	464,440	171,564	210
A.1+	444	43.1	914									
				0.5384	1,211	0.0938	0.5390	0.4452	343	415,792	185,106	153
A.2+	259	51.3	1,567									
				0.5505	2,089	0.0782	0.9319	0.8536	168	351,996	300,475	144
A.3+	102	61.3	2,717									
				0.4366	3,407	0.0665	1.6805	1.6141	49	168,249	271,567	80
A.4+	19	70.6	4,204									
				0.0821	4,382	0.0611	1.5581	1.4970	10	42,182	63,148	14
A.5+	4	72.5	4,564									
Total											991,860	601
										Smolt No.	5,226	
										Fishery g	991,860	
										Fishery/smolt g	189.8	
										Mean weight kg	1,651	
										No. smolt per sea trout	8.6972	

River Gudenå				**Christensen *et al.* (1993)**		
	Female			**Female**		
Sea age	**No.**	**%**	**Length cm**	**No.**	**%**	**Length cm**
One	261	23.2	33.7	203	31.4	32.9
Two	213	19.0	46.3	200	30.9	43.7
Three	422	37.6	54.2	155	24.0	51.2
Four	180	16.0	64.7	74	11.4	60
Five	35	3.1	74.7	11	1.7	68
Six	8	0.7	82.5	4	0.6	72.5
Seven	3	0.3	81.6			
Nine	1	0.1	85.3			
Total	1,123			647		
	Male			**Male**		
Sea age	**No.**	**%**	**Length cm**	**No.**	**%**	**Length cm**
One	248	55.1	33.1	571	59.8	30.7
Two	53	11.8	44.3	244	25.5	42.4
Three	84	18.7	55.2	104	10.9	51.3
Four	43	9.6	65.7	28	2.9	62.5
Five	18	4.0	75.3	8	0.8	73.1
Six	4	0.9	78.5			
Total	450			955		

Reproduction Loss

Reproduction loss is a broad terminology and includes the effects on the individual reduction of weight/mass because of spawning migration, stop of feeding in fresh and saltwater, and loss of gametes. Tagging results from domesticated sea trout (Pedersen & Rasmussen, 2000) and analysis of scales from wild sea trout in the Limfjord (Frier, 1994) indicate that immature sea trout grow about 20 cm from mid-March to mid-November; this means an eight month growth period with a monthly length increase of approximately 2.5 cm. Setting up a simple linear growth model, and using the data from Christensen *et al.* (1993) and river Gudenaa and calibrate the model against observed age/mass data for all spawning types, indicates a spawning loss of about 40%. There were no statistical differences between the two sexes, and the results are close to Frier (1994). This clearly illustrates why growth rate decrease and length increase stops sharply after first spawning, because the spent trout and in general repeat spawner fish species have to recover mass before length increase can start again (From & Rasmussen 1989).

Fishery

The most important salmonid species for recreational fishing (anglers) are brown trout in rivers and lakes, sea trout in rivers and saltwater, Atlantic salmon in rivers and saltwater and grayling in rivers (Rasmussen & Geertz-Hansen, 2001; Rasmussen *et al.*, 2002). Amateur fishermen mostly fish in saltwater and besides salmonids they mostly go for marine species, such as different species of flatfish (flounder, plaice and turbot), eel, whitefish and cod (*Gadus morhua*). Catches of brown trout and other fish species from anglers and amateur fishermen are not registered and not allowed to be sold; they are only for private use. Each caught sea trout in the recreational fishery creates a social value of about DKK 4,300 (EUR 570) (http://mfvm.dk/nyheder/nyhed/nyhed/foedevareminister-booster-baeredygtigt-lystfiskeri-1).

Nominal Catches

A survey in 2010 (Sparrevohn *et al.* 2011) estimated that the annual recreational fishery (anglers and amateur fishermen) for brown trout caught total: 81 tonnes in freshwater and 482 tonnes in saltwater. The anglers caught 75 tonnes in freshwater and 365 tonnes in saltwater. Amateur fishermen caught 6 tonnes in freshwater and 117 tonnes in saltwater. With a mean weight of 1.651 kg per caught trout (op. cit.), a total of about 341,000 trout have been caught in fresh and saltwater. As mentioned earlier there are at present no records of effort, so catch per unit effort cannot be calculated. We estimate 2.97 million smolts (see section on Catch Model and Total Fishery) would be needed to produce this number of trout. The calculated number of smolt (wild and released) today from Danish rivers is about 2.74 million smolts (see section on Stocking and enhancement – freshwater). The survey must be taken with reservation, because sea trout from Denmark, Germany and Sweden migrate around in the Western Baltic and Kattegat, and trout from other areas may be caught along the Danish coast and vice versa. A new project has been started where anglers throughout Denmark collect tissue samples from caught sea trout to be genetically analysed and compared with genetic data from rivers in and outside Denmark. This is expected to give reliable information on sea trout migration in this greater region and tell which river systems contribute to the catches. However, the preliminary catch results show that sea trout are heavily fished upon, which is also demonstrated by the high annual instantaneous fishing mortality F, varying between 0.48 to 1.68 (see section on Catch model and Total Fishery).

Catches of sea trout from the Danish commercial fishery and landed in Danish harbours are registered (http://naturerhverv.dk). Mean catches of sea trout from 2001–2014 were as follows for the following marine waters: the North Sea: 403 kg; Skagerrak: 134 kg; Kattegat: 710 kg and from the Baltic Sea: 25 tonnes. The relatively high catches of sea trout in the Baltic are because sea trout have been caught as a by-catch in the Danish salmon fishery. The brown trout caught in this fishery are probably from many rivers in the Baltic Sea area, most likely Denmark, Sweden, Germany and Poland. The commercial catches of sea trout are decreasing; in 2001, they totalled about 61 tonnes and in 2014 about 25 tonnes.

Catch Model and Total Fishery

Several tagging results with reared domesticated trout have showed that about 10 tagged smolts give about one kg caught fish (Nielsen & Rasmussen, 1982). The results should be interpreted with reservation because tagging (external Carlin tags) are presumed to increase mortality and because tag reporting rate is limited. Amateur fishermen especially do not report back because they believe that the results will be used for regulation of the fishery and not for their benefit. Some experiments (Pedersen *et al.* 1995) in the Limfjord and the Roskilde Fjord showed that a higher recapture prize (five times the normal prize) increased the reporting rate and a raising factor (1.65, op. cit.) is necessary to get more reliable catch rates from tagging results.

We used electrofishing data from 21 river systems throughout Denmark (Christensen *et al.* 1993) during spawning run of wild sea trout to set up (Table 19.5) a more reliable model for estimating fishery catch (sport, recreational and commercial). The fish (a total of 1,602 electrofished sea trout) were sexed and aged from scales and distributed in sea age.

The basic idea with the model is, from known numbers of sea trout distributed to several sea age classes (scale reading), to calculate total mortality Z (i.e. $\log_e N(i+1)/N(i)$, where N(i) is number of fish in year i and N(i+1) is number of fish the year after). From natural mortality M the total number of smolts recruited to the fishery can be calculated. As the fishery does not discriminate between smolt ages, sex and spawning types all the samples have been pooled. From sea age distribution the total mortality Z can be calculated (see above) for sea age groups above legal size limit of 40 cm. The natural mortality M is unknown from the samples, but can be calculated as a function of weight (Ursin, 1967; Lorenzen, 1996), because it is reasonably that smaller fish have a higher natural mortality than a bigger fish. This model to describe natural mortality was used by Rasmussen (2016) in a small stream. Because $Z = M + F$, M and F can be calculated. One objection is that an eventual spawning mortality is not known, therefore F could be biased and the calculated fishery too high. The smolt run in the calculation takes place in mid-April and the smolt are recruited to the fishery mid-June 14 months later when they reach a mean length of 40 cm. Here after they are exposed to the fishery and F is calculated as Z–M. Mean number and mean weight (calculated from observed length) is calculated from the observed numbers and weights of the succeeding age groups of sea trout from the assumption, that mean number and mean weight within a period (i.e. a year) can be described by integrated exponential function.

Table 19.5 shows the calculated mean weights, mean numbers and fishery from an estimated number of 871 smolts recruited to the fishery. Because there are six year classes in the spawning run, the total number of smolt contributing to the annual fishery is 5,226 smolts. The fishery yield per smolt is about 190 g with a mean weight of the sea trout of 1.65 kg per fish, and about nine smolts equals one caught sea trout. Including the approximate (i.e. wild + released) smolt production (i.e. 2.74 million) the total fishery is approximate 520 tonnes, which is close to the survey (i.e. 563 tonnes) in 2010 (Sparrevohn *et al.*, 2011). The results are more or less in accordance with the raised recapture data (Nielsen & Rasmussen, 1982), but it is of paramount importance to test and eventually incorporate spawning mortality in the model.

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Section 5

Brown Trout as a Global Invader

20

Brown Trout as an Invader: A Synthesis of Problems and Perspectives in North America

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Introduction

Brown trout are one of the most pervasive and successful invaders in North America, negatively impacting native fishes and ecosystems not only through predation and competition, but also by acting as vectors of exotic parasites. They do, however, represent a paradox as they are extremely popular sport fish (Figure 20.1), and they often thrive in novel, man-made ecosystems (e.g., dam tailwaters, reservoirs). Nonetheless, due to pervasive negative impacts, brown trout have recently been the focus of numerous removal programs, policy changes, and overall efforts to shift angler focus back to native trout. In this chapter, we synthesize the type and extent of invasive brown trout impacts on native ecosystems and their native fishes. We also discuss their paradoxical popularity as river and lake sport fish as well as their role in novel tailwater and reservoir ecosystems. Lastly, we discuss future management and the factors both limiting and facilitating their success, including the role of climate change. Our chapter is focused on the Intermountain West (IMW) of the USA, a geographic and geological region of the Western United States located between the Rocky Mountains on the east and the Cascade Range and Sierra Nevada Range on the west (Stewart *et al.* 2002). However, Utah is in many cases representative of surrounding states (from a brown trout perspective), and we have direct access to data and expert opinion in the state and a long history of detailed study. Thus, many of our examples are from within Utah but are generally applicable beyond (e.g., Logan River; Figure 20.2).

Many sources of information suggest that brown trout have been introduced and/or established in most areas of the world capable of supporting them (McIntosh *et al.* 2011). In the early 1900s, brown trout embryos from cultured European populations were stocked into the United States including in the IMW by the predecessor of the now United States Fish and Wildlife Service (Mather 1889; Courtney *et al.* 1984). These stocking efforts were very successful, in part because the IMW has ample high latitude areas, which are nearly ideal for brown trout, but also because of continued

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Figure 20.1 Brown trout photo taken in the Logan River, Utah, USA by Michael Ebinger showing spots.

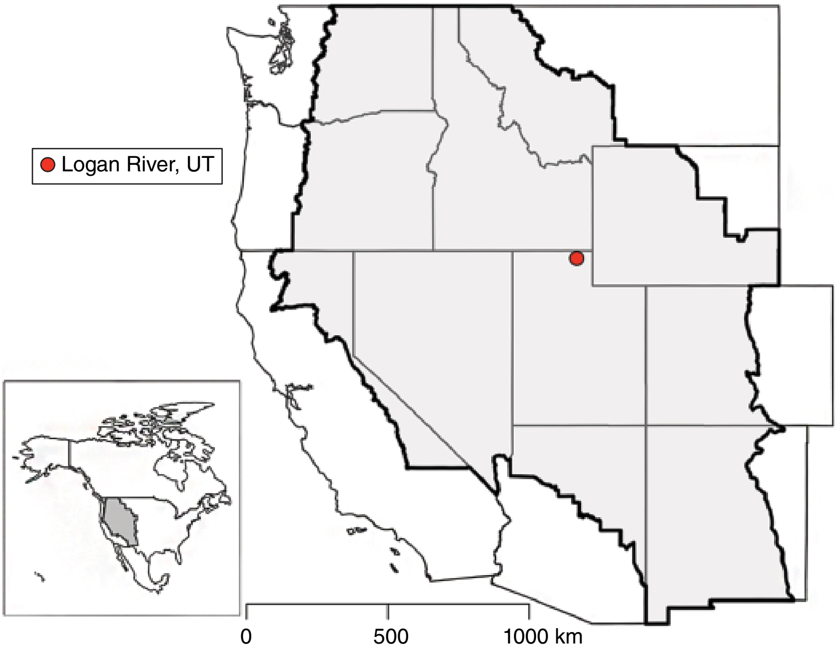

Figure 20.2 Map of the Intermountain West, USA, shown as an inset of North America. North America map reproduced with permission from Michigan State University Map Library, Data Source: ESRI. The red circle denotes the Logan River, Utah, an area of extensive and long-term studies on exotic brown trout referred to frequently in the text.

propagule pressure (i.e., repeated stockings; discussed further below). From the 1960s to the present, brown trout ranges have expanded as viable reproducing populations increased and stocking efforts continued. Now, brown trout are found in all eight of the IMW states (Montana, Idaho, Wyoming, Utah, Nevada, Colorado, New Mexico, and Arizona), and in many places, their densities greatly surpass those observed in their native range (McIntosh *et al.* 2011). In the Logan River, Utah, for example, densities of exotic brown trout reach almost two fish/m^2 (Budy *et al.* 2008), whereas in their native range, recorded densities average only 0.4 fish/m^2 (Budy *et al.* 2013). Exotic brown trout are widespread and abundant because they are vagile (capable of dispersal) and have a large fundamental niche (described in detail in McIntosh *et al.* 2011 and other chapters in this volume). However, in the IMW they thrive not only in nearly all types of natural aquatic ecosystems such as ponds, lakes, streams, and larger rivers (e.g., Budy *et al.* 2013), but also in novel and disturbed ecosystems in which natives may struggle to establish, such as reservoirs and tailwaters below dams (e.g., Dibble *et al.* 2015).

Brown Trout as Invaders: Negative Impacts on Aquatic Communities

Brown trout have been included in the top 30 worst invasive species on the globe due to their overwhelming success as invaders and the plethora of negative impacts they have had on invaded ecosystems (reviewed in McIntosh *et al.* 2011; International Union for the Conservation of Nature). Similar to places like New Zealand, aquatic ecosystems in the IMW may be highly sensitive to the negative impacts of brown trout due to naturally low native species diversity and lack of competitive ability of many natives developed over long geologic isolation (Griffith 1988; Dunham *et al.* 2002). Small stream size and isolation can also contribute to this sensitivity (Shemai *et al.* 2007). McIntosh *et al.* (2011) summarized the 'mounting evidence' of the negative impacts of exotic brown trout into three general categories: (1) distributional evidence suggesting historical displacement; (2) observational or experimental studies assessing mechanisms of impact; and (3) temporal data sets documenting decline following invasion.

Distributional Patterns

We have all three types of evidence of negative impacts of brown trout in the IMW. First, native cutthroat trout (*Oncorhynchus clarkii*) did not persist in many places in the West after brown trout were stocked (reviewed in Fausch 1988; Benke 1992). Although this evidence is purely temporal (e.g., category 3 above) and distributional (e.g., category 1 above), the evidence strongly suggests that brown trout displace native fishes largely via the well-documented mechanisms of predatory and competitive interactions. Strong allopatric patterns of native cutthroat trout and exotic brown trout are common in the IMW and are often longitudinal along elevational gradients of montane rivers (Vincent and Miller 1969; de la Hoz Franco and Budy 2005; McHugh and Budy 2005). For instance, native trout are often found at high densities in upper elevation reaches while exotic brown trout (and often exotic rainbow trout, *Oncorhynchus mykiss*) dominate lower elevation reaches. The mid-elevation reaches often hold both species, but at very low densities. In most of these rivers, cutthroat trout historically occupied the entire river, however, distributional evidence indicates exotic trout, often brown trout, have displaced these natives (Fausch 1988; Budy *et al.* 2007).

This type of allopatric pattern of species distribution can be the result of either contemporary competition, the ghost of competition past, and/or environmental constraints that co-vary with elevation (Fasuch *et al.* 1994; McHugh and Budy 2005). The former are discussed below under 'Competition'. As an example of the latter, brown trout in the Poudre River, Colorado, were found to be restricted to elevations of less than 2,680 m, a boundary the authors assumed was based on thermal tolerance (i.e., above this elevation, stream temperatures were too cold; Vincent and Miller 1969; but see Saunders and Budy, in prep). Fausch (1989) similarly demonstrated that standing stocks of brown trout decreased with elevation in Colorado streams. In the Logan River, Utah, brown trout densities decrease with increasing diel temperature fluctuations, which are generally greater at higher elevations in this system (de la Hoz Franco and Budy 2005). Some observational and model-based evidence suggests that summer temperatures, stream scour and its influence on spawning gravel availability, and the presence of anchor ice all limit the upper distribution of brown trout in the Logan River, Utah (Meredith 2012; Meredith *et al.*, 2016). Bozek and Hubert (1992) were similarly able to predict the absence of brown trout with 94% accuracy based on elevation, gradient, and wetted width measurements in streams of Wyoming. Nonetheless, while some environmental factors may limit the expansion of brown trout into upper elevation reaches, brown trout are superior competitors to native trout, as has been firmly demonstrated experimentally (e.g., category 2 above). This competitive advantage explains why brown trout dominate the lower portion of many rivers and displace native trout.

Competition

Although strong anecdotal and observational evidence since the beginning of brown trout introductions have suggested that brown trout were superior competitors to native trout, the first experimental evidence did not emerge until the late 1990s (e.g., evidence category 2). In aquaria experiments in Montana with age-1 trout, Wang and White (1994) demonstrated that exotic brown trout were involved in more inter-specific agonistic events in sympatry with native greenback cutthroat trout (*O. clarkii stomias*). A more recent set of small scale enclosure experiments revealed that exotic brown trout reduced the growth and condition of native trout in several locations along elevational gradients (McHugh and Budy 2005). At the same time, likely because they are competing for space and dominating the preferred territories, brown trout were unaffected by the presence of native trout, and were more affected by intraspecific competition among brown trout (McHugh and Budy 2005). Somewhat surprisingly, competition in these enclosures was not mediated by temperature. In fact, when experimental brown trout were reared at cold, steep gradient, high elevation locations where they rarely occur, their growth rates were even higher than at low elevation sites, where they commonly establish. Notably however, all reaches of the Logan River, Utah, are within the suitable temperature range for brown trout and native trout; elsewhere, brown trout have a competitive advantage over native trout when habitat degradation has increased stream temperature to a range still suitable for exotic brown trout, yet too warm for native trout (Closs and Lake 1996; Keleher and Rahel 1996; McHuch and Budy 2005; Fausch *et al.* 2009).

In larger reach-scale experiments, brown trout similarly reduced the growth, altered the diet, and suppressed the movement of native trout (McHugh and Budy 2006). Based on a variety of other observations (e.g., Saunders and Budy, in prep), and because many brown trout streams flow over a limestone base and are extremely productive (e.g., Logan River; Almodóvar *et al.* 2006), we believe the likely mechanism is interference competition, i.e., competition for space, not food. Shemai *et al.* (2007) similarly observed that exotic brown trout were superior competitors to native Rio Grande cutthroat trout (*O. clarkii virginalis*) in stream enclosure experiments in New Mexico and concluded that elevated aggression by brown trout altered foraging behavior of native trout. Collectively these experimental studies, while not an exhaustive list, demonstrate that exotic brown trout out-compete native trout in the IMW and that the mechanism appears to be aggressive behavior and competition for space.

Predation

Negative impacts on native fishes due to novel predator-prey interactions with exotic brown trout are relatively straightforward and also well-documented based on observational and experimental studies. Based on observational studies in the Logan River, Utah, brown trout tend to have similar diet preferences as native trout, but ingest larger prey, including fishes (McHugh *et al.* 2006). Indeed, isotopic nitrogen signatures indicate brown trout occupy a higher trophic position than their native counterparts. In small-scale experimental studies aimed at understanding inter-specific interactions, predation of adult brown trout on adult native trout accounted for 20% of observed mortalities (Saunders and Budy, in prep). Further, in observational studies in the Logan River, Utah, up to 33% of brown trout diets were composed of native sculpin (*Cottus* sp.), while native trout consumed almost none (Meredith *et al.* 2014). Bioenergetics simulations based on these diet proportions indicates an adult brown trout consumes up to 34 native sculpins a year. Given brown trout densities of more than 1 per m^2, these rates of predation almost surely have negative effects that ramify through the fish community and likely have counterparts in similar systems (Budy *et al.* 2008). Furthermore, based on an international comparison spanning five countries, fluvial brown trout demonstrate a much greater degree of piscivory in their exotic habitat and reach substantially larger sizes and older ages, relative to their native habitat, further enhancing their predatory ability (Figure 20.3; Budy *et al.* 2013). Larger body size also typically infers superior competitive ability among fishes and can exacerbate other community-level impacts including interspecific competition discussed above (Fausch 1984; Rasmussen *et al.* 2011; Louhi *et al.* 2014).

The negative effects of predatory brown trout on native fish communities are not unique to the IMW and have been documented for eight families of native fish and numerous species across many countries and continents (reviewed in McIntosh *et al.* 2011). Further, although we do not have direct evidence of brown trout egg predation on native trout eggs in the IMW, brown trout have been observed eating native eggs elsewhere (Greeley 1932; Aymes *et al.* 2010). In addition, our observations of slightly higher nitrogen isotopic signatures (^{15}N) in brown trout in the Logan River, Utah, could indicate egg or larval predation (McHugh *et al.* 2006), and we have directly observed brown trout eating eggs of other fishes (e.g., kokanee salmon, *Oncorhynchus nerka*) in Utah. Egg predation by exotic brown trout could exacerbate the other known negative impacts on native fishes.

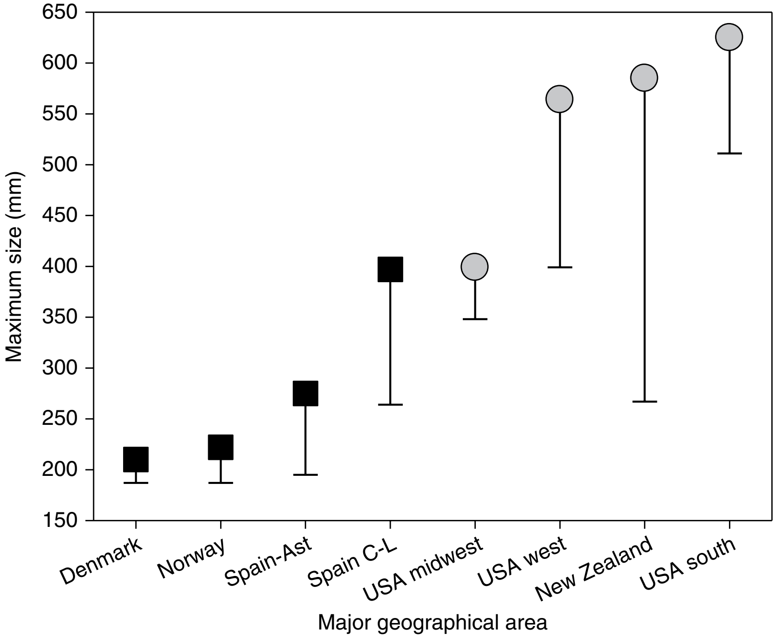

Figure 20.3 Reproduced with permission from the authors (Budy *et al.* 2013). Maximum body size (downward error bar represents range) attained by brown trout in different major geographical areas. Black squares are native habitat, and grey circles are exotic habitat.

Other, Indirect, and Synergistic Impacts

In addition to competitive and predatory impacts, there are other potential impacts of exotic brown trout on native fishes related to natural history and demography. For example, in contrast to most native fishes in the IMW, which spawn in the spring, brown trout are autumn spawners ('spring' here refers to when the weather becomes warmer and leaves and plants start to grow again). This reproductive timing may give exotic brown trout an advantage over native fishes or alternatively may leave brown trout maladapted to expand further under current climatic regimes. Because they spawn in the autumn and emerge during the early spring, age-0 brown trout will have a strong size advantage over native trout in the summer, a critical time period for growth ('summer' here refers to the warmest time of year and typically the period of greatest trout growth; Fausch 1998). This size advantage could intensify competitive interactions, particularly aggressive behavior and competition for space (e.g., Keeley 2001), thus giving brown trout a likely advantage.

Alternatively, brown trout may have a reproductive strategy maladapted to many mountain streams (Fausch 1988; Moyle and Light 1996; Fausch *et al.* 2001). Autumn spawning at high elevation in mountain streams can expose embryos and hatchlings to very cold water temperatures (which may delay in development), high spring snow melt floods (which scour and displace eggs), and anchor ice formation (which limits spawning success). For example, Reiser and Wesche (1979) experimentally demonstrated that intra-gravel ice limits brown trout egg survival in streams exposed to harsh winter conditions on the Laramie plains, even though the spawning habitat was suitable and the eggs were buried at 15–18 cm. At a broader scale, in the Logan River, Utah, anchor ice was in the top performing models exploring the abiotic and propagule pressure covariates that best explained brown trout redd density along an elevational gradient (Meredith 2012; Meredith *et al.* 2016). In contrast, however, brown trout eggs reared in incubation boxes and placed along the elevational gradient of the Logan River, Utah, demonstrated that harsher over-winter conditions did not preclude hatching success; ≥ 36% of eggs successfully hatched at high elevation sites, although survival was higher at low elevations (Wood and Budy 2009). In addition, most climate warming predictions for this region include warmer winters and wetter springs, conditions that could facilitate higher reproductive success of brown trout in high elevation areas. In contrast to elsewhere, however, in the IMW neither hybridization of native trout with exotic brown trout nor egg superimposition (e.g., Essington *et al.* 1998) represent native fish conservation issues associated with brown trout. They are autumn spawners and so temporally segregated, and they cannot hybridize with native trout (but see McIntosh *et al.* 2011).

In combination with the direct impacts that brown trout have on native fishes through inter-specific interactions, there are other potential impacts that are less direct. First, they serve as vectors of disease. Brown trout carry the exotic European parasite, *Myxobolus cerebralis (Mc)*, which causes whirling disease; however, they are much less vulnerable to the impact of the disease than *Oncorhynchus* species (i.e., native trout; Baldwin *et al.* 2000). Furthermore, stressed fish are more susceptible to disease (Wedemyer *et al.* 1970; Fagerlund *et al.* 1995), as may be the case with native trout stressed by competitive interactions with exotic trout, a potentially important negative synergy (Rassmusen *et al.* 2010; Houde *et al.* 2015). In addition, brown trout are less sensitive to degraded habitat compared to most *Oncorhynchus* species (McIntosh *et al.*, 2011), and *Mc* secondary hosts prefer degraded habitat. Thus native fishes may have a further disadvantage in degraded habitat; exotic brown trout will have the competitive advantage, and the concentration of *Mc* parasites may be high. This is another complex synergy that could exacerbate the impacts of brown trout on native fishes (Wilson 2000; Hansen and Budy 2011). While we are aware of these potential synergies, it is likely that brown trout have other complex and unknown negative impacts on other aspects of aquatic ecosystems that may impact and trickle through multiple trophic levels (e.g., New Zealand; Townsend and Simmon 2006). For example, exotic brown trout have caused strong cascading effects on mayflies down to algae in New Zealand streams and also appear to alter primary and secondary production (Huryn 1988; McIntosh and Townsend 1996).

Paradoxical Popularity

Despite these well-documented and more recently accepted negative impacts of exotic brown trout, they remain extremely popular as sport fish and are still actively managed fisheries in many systems in the IMW. The history of brown trout stocking in Utah provides a good example of the extent and consistency of these stocking efforts as reported by the state fisheries management agency, Utah Division of Wildlife Resources (Figure 20.4). Stocking efforts were greatest and the most extensive from 1940 to 1950 and included most water bodies that were accessible (including by plane) and likely to

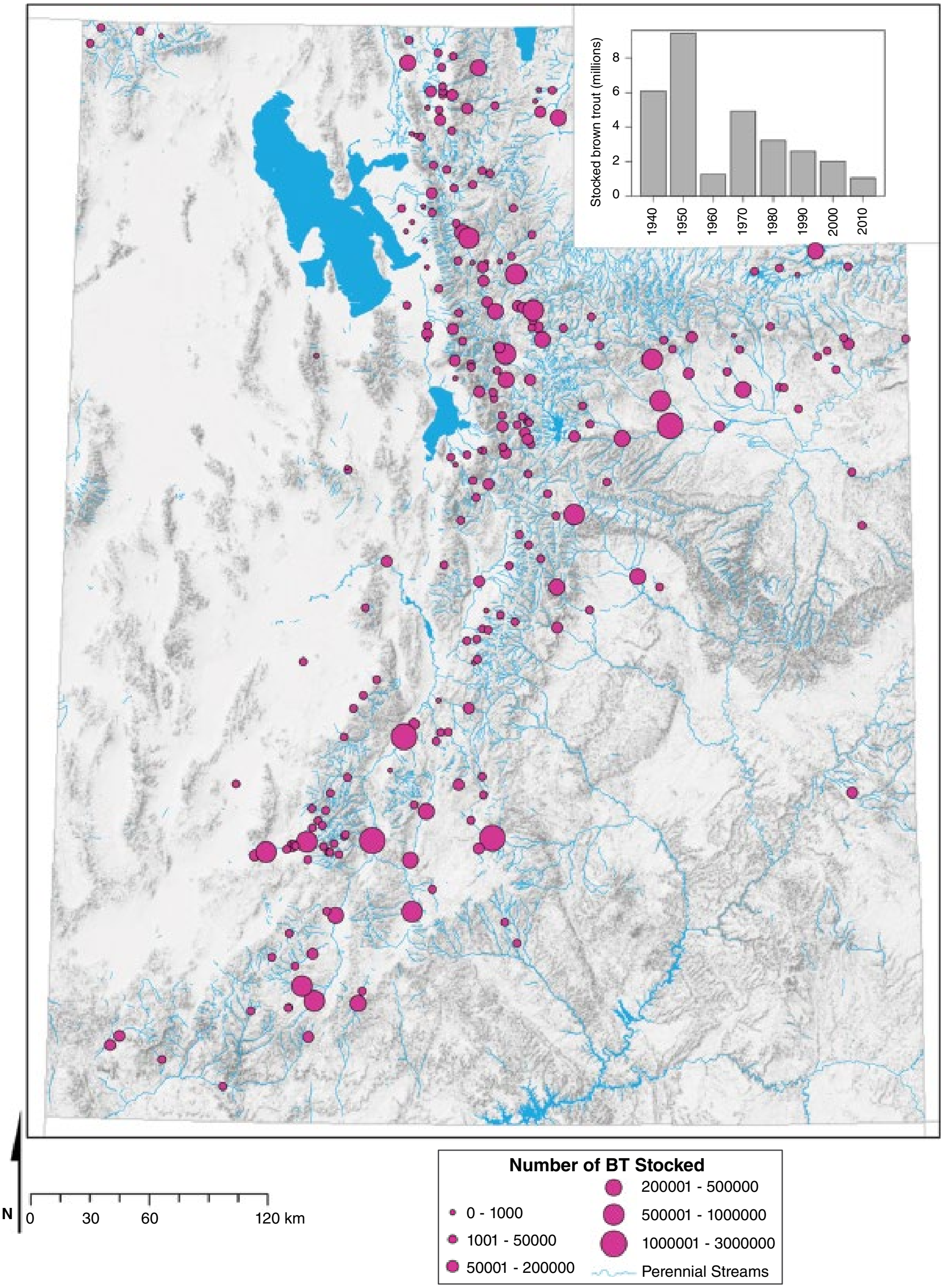

Figure 20.4 Map showing the intensity and spatial distribution of records of individual brown trout stocking efforts throughout the state of Utah for time periods 1940–2010. The upper right insert bar graph represents the millions of brown trout stocked (y axis) by decade (x axis) over this time period.

support brown trout statewide. After an odd drop in the 1960s these stocking efforts continued at relatively high levels from 1970 to 1990, but then began to substantially decline after 2000. In fact, over the last ten years, there have been only approximately 50 brown trout stocking events in Utah, and similar trends are noted anecdotally in other western states. A noteworthy point, however, is that many stocking events were unrecorded and/or unofficial (i.e., private parties stocking), suggesting our records represent a likely significant underestimate of stocking effort both temporally and spatially. Nonetheless, this intensive and extensive stocking effort clearly contributed to the expansion and establishment of exotic brown trout in the IMW via continued propagule pressure (MacCrimmon and Marshall 1968).

Brown trout prosper in many natural and managed ecosystems, with the state trophy brown trout recorded in reservoirs in Idaho, Wyoming, and Utah, in lakes in Arizona, Montana, and Nevada, and even in ponds in Colorado (Table 20.1). These state trophy records, and other non-recorded, big brown trout catches represent impressive fish, but anglers also enjoy catching more modest-sized brown trout as well (Figure 20.5). The state records, while impressive, cannot however compete with the world trophy record, ironically also an exotic brown trout captured in a canal in New Zealand that was 140% bigger than any USA – IMW state trophy records.

Brown trout anglers in the IMW have varied opinions but do point out several motivations for targeting this exotic species including: (1) the belief that they are the most challenging of the trout species to catch; (2) they are often found in streams that are of marginal quality for other native trout; and (3) they are often the biggest fish in a stream, and anglers like big fish. A comparison of brown trout populations in catch-and-release and harvest (i.e., take) sections of a river demonstrated that the catch-and-release section held brown trout and rainbow trout, with rainbow trout comprising approximately 60% of the population relative to only 20% in the more heavily fished

Table 20.1 Official state trophy catches of exotic brown trout shown by U.S. state, location, year caught, and size (weight [kg] and length [m]). The worldwide recorded record is also shown for an exotic brown trout caught in New Zealand. Data are taken from: https://www.landbigfish.com/staterecords/ and https://www.igfa.org/.

State in USA	Location	Year	Weight (kg)	Length (m)
Arizona	Reservation Lake	1999	10.4	0.91
Colorado	Roaring Judy Ponds	1988	13.8	0.92
Idaho	Ashton Reservoir	2007	12.4	0.93
Montana	Wade Lake	1966	13.2	NA
Nevada	Cave Lake	1984	12.4	0.84
New Mexico	Chama River	1946	9.2	0.88
Utah	Flaming Gorge Reservoir	1977	15.3	1.02
Wyoming	Anvil Draw, Flaming Gorge Reservoir	1982	11.7	0.87
WORLD				
New Zealand	Oahu Canal	2013	19.1	NA

Figure 20.5 Happy anglers showing off their brown trout caches. In the top panel, Paul Thompson, avid angler and fish biologist holds a 0.71 m brown trout caught in the Weber River, northern Utah. In the bottom, Kiera Saltern holds a more modest and commonly-caught size brown trout captured in Porcupine Reservoir, also in northern Utah.

downstream reach (Anderson and Nehring 1984). In other words, many more brown trout survived in the heavily fished section potentially providing support to the argument they are more challenging to catch. With regard to their presence in streams of marginal habitat, across streams, brown trout account for more of the caught fish (as compared to rainbow trout) as temperature increases (see also ‘novel habits’ below; McMichael and Kaya 1991). And because they are difficult to catch, from a state management perspective, in some cases it is easier to maintain a brown trout fishery since it is difficult to overfish. Alternatively, in other cases, the difficulty of anglers catching (and keeping) brown trout may lead to higher densities of smaller-sized brown trout than desired (e.g., Blacksmith Fork River, Utah; Jenkins *et al.* 1999). Nonetheless, the difficulty of catching brown trout and the declining desire to keep them once caught may mean managers do not have to rely as heavily on expensive stocking efforts that are not always successful, a perspective driving the trout management in the state of Wyoming, for example (Wiley *et al.* 1993).

The popularity of brown trout is also exemplified by their status with Trout Unlimited, the largest and certainly most prominent cold-water fishery conservation association in the USA with more than 150,000 members including lawyers, policy experts, and scientists (http://www.tu.org). Accordingly, brown trout are featured frequently in their magazine 'Trout Magazine', they publish videos of anglers catching 'monster browns', tips for catching brown trout, and support restoration efforts that enhance brown trout angling opportunities. In fact, as in New Zealand (Chapter 22, this volume), in Utah, some anglers refer to brown trout as 'native browns' and are clearly unaware they are exotic or invasive (Budy and others, personal observation). Trout Unlimited, however, has more recently acknowledged the paradox of which they are part, as they simultaneously promote and enhance brown trout fisheries in some places while acknowledging they have a negative effect on native trout in other places (Williams *et al.* 2015).

In addition to general sport fish popularity, brown trout may play a special role as one of the more dominant and successful sport fish in novel, managed, and artificial riverine ecosystems including reservoirs and tailwaters behind dams. Reservoirs differ from the natural riverine environment in that they are low or no velocity, often warmer and stratified, and behave in general more like a lentic environment. Food sources and energetic pathways differ accordingly. Conversely, tailwaters in the IMW are often hypolimnetic release and thus very cold relative to the natural riverine system and can also be extremely variable in terms of flow due to hydro-peaking management at the dam (e.g., Dibble *et al.* 2015). Consequently, these novel riverine systems differ significantly from the natural and historical river ecosystem and thus may not be hospitable to native western fishes and trout, which have, in general relatively narrow fundamental niches (e.g., Benke 1992). Exotic brown trout have been stocked and maintained in these novel and highly-managed ecosystems, and in many cases they thrive and reproduce naturally due to their plasticity (e.g., Dibble *et al.* 2015).

In order to qualitatively document the quality of brown trout fisheries in reservoirs and tailwaters, we solicited experts throughout the IMW to participate in a survey where they were asked to rank the quality of brown trout fisheries. Specifically, we included reservoirs, tailwaters, and adjacent reaches immediately upstream of the reservoir (0–5 miles upstream) and downstream of the tailwater, below the physical effects of the dam. Respondents were asked to consider the given system or systems they are most familiar with relative to the average quality of all brown trout fisheries they manage, study, or work on within the IMW. Quality was qualitatively defined as 'a metric based on size-structure, body condition, density, and angler satisfaction.' Experts included avid anglers, guides, state and tribal government resource managers and biologists (hereafter, resource managers), and members of Trout Unlimited (TU; TU 'members' identified themselves as 'Public Lands Coordinator', 'Chairman of State TU Council', 'Backcountry Coordinator', 'Project Manager', or 'Western Agriculture and Water Policy Counsel').

A total of 79 unique respondent-system observations were collected. Of those, 25 were repeat system observations for a given system. We only report the opinion of one respondent per system. The process of choosing which respondent was based on the following criteria: resource managers were selected over any other group; finally, if multiple resource managers responded, we selected the manager with the most years of experience. Finally, if a respondent answered 'I do not know' for any reach, the entire response was excluded; this final step eliminated three systems from our final results. Our selection criteria reduced the dataset to opinions from one angler, one member of Trout Unlimited, two fishing guides, one member of a tribal government, and 19 resource managers, resulting in a total of 51 systems from eight states.

Brown trout fisheries in tailwaters were ranked as 'Excellent' or 'Above average' for 55% of systems and ranked 'Poor' in only 8% of ranked systems (Figure 20.6). The downstream reach, upstream research, and the reservoir were ranked as 'Excellent' or 'Above average' for 24%, 22%, and 18% of systems, respectively, and received the rank of 'Poor' in 8%, 6%, and 12%, respectively. Brown trout fisheries were absent from the upstream reach, the reservoir, or the downstream reach in 31%, 33%, and 10% of systems, respectively. The waters adjacent to the tailwater were also ranked relative to the tailwater in each system. The survey indicated that the brown trout fisheries in tailwaters were ranked as the best reach in 69% of systems and were the best or second best in 96% of systems (Figure 20.7). The tailwater fishery was *never* ranked as the worst reach in a given system. Collectively, our expert opinion survey indicated that tailwaters are unique habitats that often support superior brown trout fisheries relative to adjacent lotic reaches and reservoirs. Indeed, our findings indicate that brown trout tailwater fisheries are very often among the best brown trout fisheries in the IMW.

Management in the Future

Despite their popularity as sport fish and given the widespread impacts brown trout have had on native fish communities, management and angler perspectives towards exotic brown appear to be shifting in the IMW. With support from the state government and most anglers, Saunders *et al.* (2014) completed a two-year experimental mechanical removal of brown trout in a tributary of the Logan River, Utah. Ten years prior to this, such an effort would have had no support. The mechanical removal of more than 15,000 brown trout resulted in a strong recruitment pulse of small fish, demonstrating that prior to the removal, adult fish suppressed recruitment through some sort of density-dependent effect (i.e., reduced survival or increased emigration). These results suggest that mechanical removal is not a viable management strategy for reducing brown trout abundance, and rather, eradication requires extensive and repeated chemical treatment (Finlayson *et al.* 2005; Meyer *et al.* 2006). In related work, we hypothesized that biotic resistance (Elton 1958), in this case expressed as high densities of native cutthroat trout, is the mechanism limiting the expansion and establishment of brown trout into the upper headwaters of IMW streams (Saunders and Budy, in prep). We demonstrated experimentally that while brown trout are unaffected by increasing densities of native cutthroat trout, cutthroat trout performance increases with increasing densities of conspecifics. We theorize, once cutthroat trout densities are high enough, it may be difficult for brown trout to expand and become established. These results are promising for native fish management, as they indicate that it may be sufficient to shift the balance of dominance back to native fish, rather than try to eliminate every unwanted brown trout. In addition, the use of beavers (*Castor canadensis*) for passive stream restoration is increasing

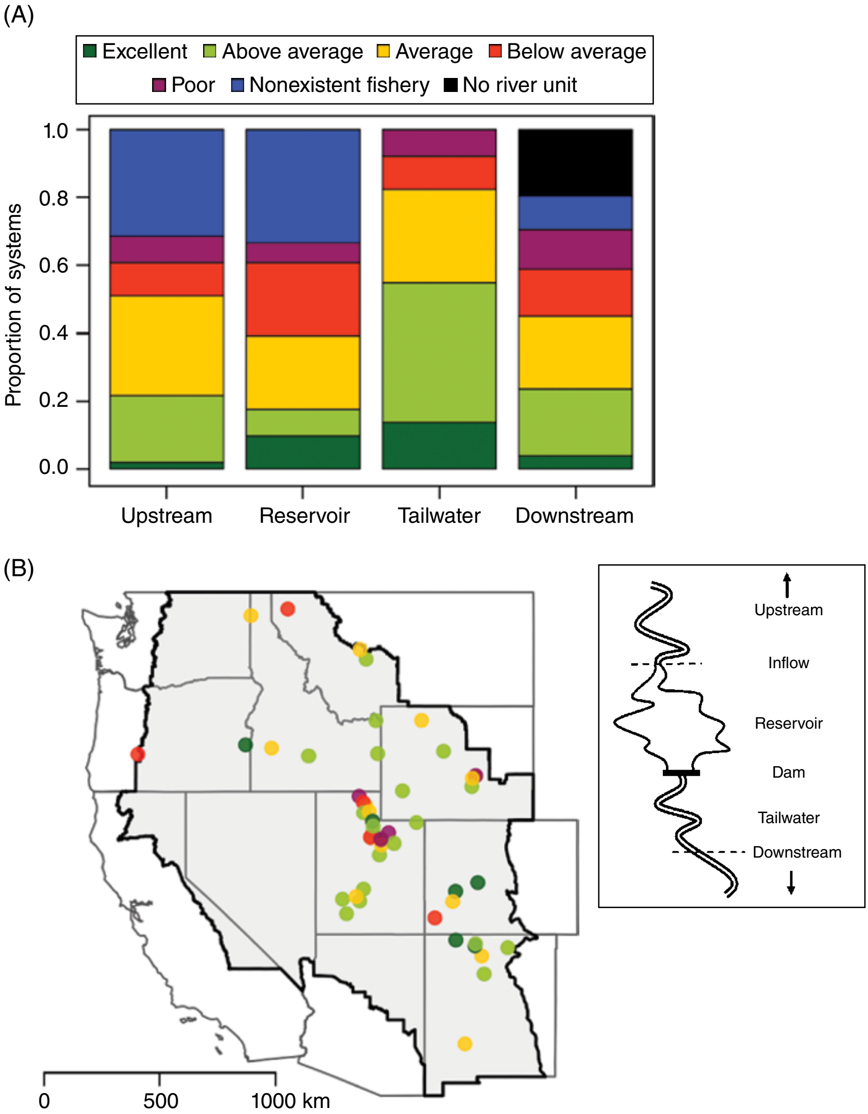

Figure 20.6 (A) The quality of brown trout fisheries in various river reaches (upstream of the reservoir, the reservoir, the tailwater, and downstream of the effects of the tailwater) relative to other brown trout fisheries as classified by expert opinion survey respondents, and (B) the spatial location and quality of tailwater fisheries (n = 50) shown with the Intermountain West boundary. The color in (B) corresponds to the tailwater bar in (A).

dramatically in popularity and application across the IMW (Pollock *et al.* 2015). While movement of native cutthroat trout is not impeded by beaver dams, exotic brown trout have difficulties passing through dams (Lokteff *et al.* 2013). This difference in passage ability past beaver dams could favor native trout as beaver dam densities increase in the future.

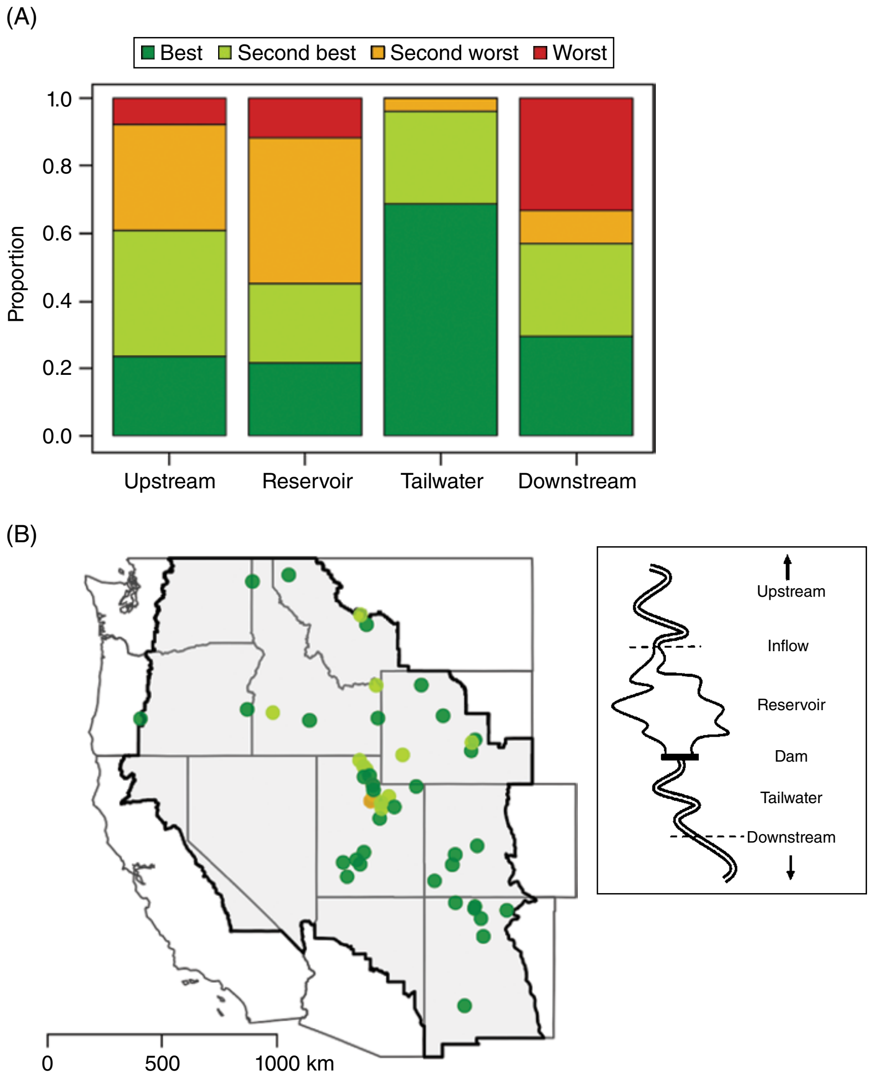

Figure 20.7 The system-specific (n = 50) rank of each river unit evaluated by survey respondents. (A) the proportion of systems in which the river unit-specific brown trout fishery was ranked or tied as the best, second best, second worst, or worst. (B) the spatial location and ranking of each tailwater fishery (n = 50); shown with the Intermountain West boundary. The color in (B) corresponds to the tailwater bar in (A).

The Utah Division of Wildlife Resources has also been monopolizing on natural large-scale wildfire as a reset for native trout streams (Hepworth and Whalen, personal communication). After the fire, they remove the few remaining exotic brown trout and restock the streams with native trout. In this case, the fire helps with public support, as they are not killing very many brown trout themselves. After native trout are re-established, anglers will likely be largely satisfied. In the IMW, more than 80% of anglers do not have a preference for brown trout over other trout, as long as they can fish in a beautiful mountain stream and catch trout (Budy *et al.* 2003; Nadolski and Penne 2013). Similarly, in a recent statewide 'Attitudinal Survey' about angling in Utah, survey respondents ranked exotic brown trout and native cutthroat trout about equally in terms of their preference of species they are interested in catching (Krannich 2011). This general angler attitude opens doors for brown trout removal and native trout conservation in the future (Saunders *et al.* 2014; Saunders *et al.* in prep). However, the great majority of stream anglers in the IMW are also catch-and-release fishermen, which suggests increasing or lifting bag limit regulations would have little utility in reducing brown trout numbers unless this change was also accompanied by an extensive outreach effort to educate anglers.

In contrast to promising changes in perspective about exotic brown trout, predictions of future climate change favor the expansion of brown trout. Although variable and a difficult region within which to make climate predictions, most predictions of the future climate on the IMW are for warmer winters, less snow, and more precipitation as rainfall (Kunkel *et al.* 2013; Cook *et al.* 2015). Less snow pack equates to smaller spring floods and less scour, and there is some evidence that scour may limit reproductive success and early survival of exotic brown trout in the upper portions of mountain streams (Jensen and Johnson 1999; Wood and Budy 2009). In addition, in the Logan River, Utah, we are observing less anchor ice, a factor that may also partially limit brown trout spawning success in the upper portion of mountain rivers (Meredith 2012; Meredith *et al.* 2016).

Finally, the IMW has increased in average annual temperatures by almost 3 °C (Kunkel *et al.* 2013). Although we have not observed evidence of temperature-mediated competition in previous experiments, those experiments were not completed at temperatures near the thermal limits of native trout (McHugh and Budy 2005). Brown trout have a broader thermal niche than most native trout in the IMW (McIntosh *et al.* 2011), they have strong potential to adapt to changing temperature regimes (Jensen *et al.* 2008), and they exhibit flexibility in spawn time and migratory behavior (Valiente *et al.* 2010). Collectively these characteristics could mean that warmer streams could give exotic brown trout an even greater competitive advantage over native trout in the future. The future of exotic brown trout in the IMW will depend on the nexus of public sentiment and policy, the effectiveness of eradication efforts, and the effect of climate change on both the native fishes and exotic brown trout. Regardless, brown trout are pervasive and have a broad distribution through the IMW – these factors will likely ensure that local populations of this species will persist into the future in-spite of public sentiment/policy, eradication efforts, and changing climate change.

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21

The Introduction of Brown Trout to New Zealand and their Impact on Native Fish Communities

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The Introduction of Brown Trout to New Zealand

Early European settlers lamented that New Zealand's many rivers and lakes were 'destitute of fish' and 'profitless to the sportsman' (Spackman, 1892); an observation that resulted from most native New Zealand species being small-bodied and cryptic, and hence, of little value from a recreational fisheries perspective. Although the indigenous Maori people had subsisted on native eels, lamprey, grayling, galaxiid whitebait, and smelt for many centuries (Sherrin, 1886), European colonists wanted salmonids, which were, and still are, highly prized for recreational fishing. Acclimatisation societies invested massive efforts in introducing a range of salmonids from the mid to late 1800s onwards (see Wilson, 1879). Early attempts to transport live fish and ova from the northern hemisphere by ship were met with failure. Transport times were too long, and the housing facilities inadequate, to ensure the fish survived the journey across the equator, where salmonids had to survive temperatures often approaching 30 °C (Dorsey & Closs, 2012). However, persistence paid off, and live salmonid ova were successfully transported on ice from Europe to Tasmania, Australia, in 1864 (Wilson, 1879). Following this success, millions of salmonid eggs were shipped from Europe and North America to hatchery facilities in the Southern Hemisphere.

In New Zealand, attempts were made to introduce a wide range of salmonids including Atlantic salmon *Salmo salar*, Chinook (Quinnat) salmon *Oncorhynchus tshawytscha*, rainbow trout *Oncorhynchus mykiss*, sockeye salmon *Oncorhynchus nerka*, brook char *Salvelinus fontinalis*, and mackinaw *Salvelinus namaycush*. These introductions were met with varying degrees of success, some species establishing and spreading quickly, while others simply disappeared once liberated or linger on as very small, often declining populations (McDowall, 1990). By far the most successful introduction was brown trout *Salmo trutta*.

Brown trout were first introduced to the South Island of New Zealand from a batch of juveniles shipped over from Tasmania in 1867 (Spackman, 1892). Shipments continued into the 1880s, and various hatcheries established across the country acted as bases for

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intensive stocking efforts of most habitats deemed suitable by acclimatisation societies. By 1921, an estimated 60 million brown trout had been released in New Zealand waters (McDowall, 1990), and further introductions have occurred even into the 21st century (McIntosh *et al.*, 2010). Brown trout have now established self-sustaining populations in all large rivers on the South Island and most North Island systems (Figure 21.1). Only in the far north of the North Island, where summer temperatures are too high, and on the east coast of the North Island, where there is a lack of suitable spawning gravels, have brown trout failed to establish a secure stronghold (McDowall, 1990). On the South Island brown trout are near ubiquitous in most freshwater systems (McDowall, 2006; Figure 21.1), except where large waterfalls or other barriers have prevented their colonisation (Townsend & Crowl, 1991).

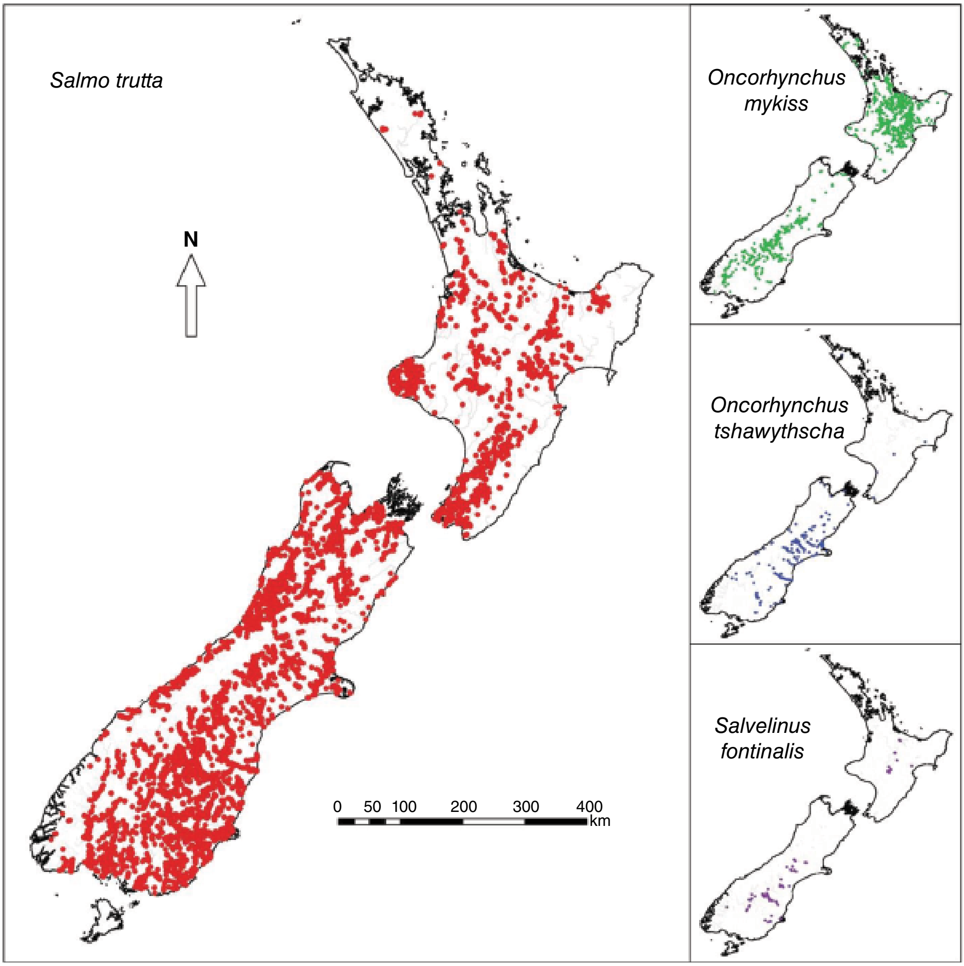

Figure 21.1 The distribution of *Salmo trutta*, *Oncorhynchus mykiss*, *Oncorhynchus tshawythscha* and *Salvelinus fontinalis* in New Zealand. (Data obtained from New Zealand Freshwater Fish Database; NZFFD, 2014.)

Brown trout have colonised habitats ranging from the Clutha River, which has a mean annual discharge of over 600 $m^3 s^{-1}$, to small intermittent creeks less than 0.5 m wide. Unconnected catchments were quickly colonised by sea-run brown trout moving around the coast (McDowall, 1990), and they have even been introduced (by the now defunct Wildlife Service!) to small inaccessible lakes in remote areas like the West Coast and Fiordland (McIntosh *et al.*, 2010). Their colonisation has been so complete that brown trout are now the most widespread and often the most abundant fish species (including both native and introduced) in the lakes, streams and rivers of New Zealand.

This phenomenal colonisation success of brown trout contrasts starkly with the comparative failures of efforts to introduce many other salmonid species. Despite a staggering effort involving the release of over 2.5 million individuals, Atlantic salmon never secured a strong foothold in New Zealand (Wilson, 1879; Dorsey & Closs, 2012), and the single extant population is now thought to be dwindling towards extirpation (NIWA, 2015a). New Zealand systems appear unsuitable for Atlantic salmon and no return migrations from the sea were ever confirmed (McDowall, 1990). The exact reasons for this failure are unknown, but likely owe to a complex life history involving an obligate pelagic stage. Similar relative failures occurred for Mackinaw and Sockeye salmon with both species having only very restricted distributions (McDowall, 1990). There are self-maintaining populations of Brook char in some areas of the country but this species has a fragmented distribution, limited to high altitude headwater streams (McDowall, 1990; Figure 21.1), with few individuals exceeding 20 cm (Dorsey, 2013). Runs of Chinook salmon have established in the some of the large braided rivers on the eastern side of the South Island (Figure 21.1) and are highly valued as sports fish, but numbers have never reached expectations. Apart from brown trout, rainbow trout is the only other salmonid species that has established widely in New Zealand. Rainbow trout have a fairly large range in some areas of the North Island and have established populations in many of the larger systems in the South Island (McDowall, 1990; Figure 21.1). However, only brown trout seem to have the life history flexibility to dominate across most freshwater systems in New Zealand (Budy *et al.*, 2013).

Brown trout can survive across a wide range of water temperatures, from 0 to 25 °C, although the limits for egg development are more constrained (0–15 °C; Elliot, 1994). This broad temperature tolerance means that most New Zealand systems are suitable for brown trout. They can utilise spawning gravels ranging from 30-100 mm (depending on female size; Raleigh *et al.*, 1986), meaning that a high proportion of New Zealand's largely gravel substrate rivers and streams are suitable for reproduction. The majority of New Zealand watercourses are swift flowing systems draining montane areas, and are thus highly saturated with oxygen, providing adequate aeration for eggs. Most systems also support abundant macroinvertebrate communities, providing suitable food for all size classes of brown trout (Townsend, 1996). At least historically, most systems also supported high densities of small-bodied native fish (Spackman, 1892), the various life stages of which provide perfect foraging for brown trout of all size classes (McIntosh, 2000). Historical reports show that some native fishes were so abundant that early settlers used them as fertiliser for their crops (Walrond, 2012), indicating how dense populations must have been and what an abundant food source they may have provided. Also, the relative lack of competitors or predators (except longfin eels *Anguilla dieffenbachii* and shag *Phalacrocorax* sp.), compared to native

Europe, provided brown trout the opportunity to colonise watercourses almost unimpeded (McDowall, 1968). However, many of the other salmonid species introduced have similar habitat and food requirements to brown trout, and the receiving environment seems, at least superficially, suitable to most salmonid species. So what characteristics have allowed brown trout to successfully spread and establish in such a wide range of habitats in New Zealand?

Brown trout exhibit an exceptional degree of life history plasticity which facilitates their colonisation of a wide range of habitats (Budy *et al.*, 2013). Their facultative migratory behaviour allows them to adapt to, and dominate in, a wide variety of freshwater systems. Small streams are generally populated by small (<30 cm) resident brown trout, whereas sea migratory trout in larger coastal rivers can often reach large sizes (>50 cm; P. Jones, pers. obs). Even in small streams, brown trout are substantially larger than most native species, enabling competitive dominance (Townsend, 1996). Their capacity to grow to large sizes also makes them less vulnerable to predators (Townsend, 1996). Large brown trout are predatory on small fishes and are aggressive competitors for space and food (McDowall, 1990; Crowl *et al.*, 1992). They can also be prolific spawners, commonly producing up to 1000 eggs per kilo body weight (McDowall, 1990; Townsend, 1996). Brown trout can also disperse across large distances, including through marine environments (McDowall, 1990), and have the ability to jump over barriers up to almost 2 m high (Ovidio *et al.*, 2007). This combination of traits, in addition to the expansive liberation program implemented by acclimatisation societies, allowed brown trout to quickly establish a near ubiquitous distribution in all almost suitable watercourses in New Zealand (MacCrimmon & Marshall, 1968; McDowall, 1990).

Given an abundance of suitable habitat, an absence of competitors, few predators, and an abundant food supply (in the form of abundant native fish and invertebrate communities), brown trout experienced very high growth rates when first introduced. In the late 1800s trout commonly experienced growth rates of 1.5–2 lbs (0.7–0.9 kg) a year, in some locations reaching 3.5 lb (1.6 kg) per annum (Spackman, 1882). The capture of individuals of over 10 lb (4.5 kg) was an everyday occurrence, and there are reports of some specimens reaching up to 34 lb (15.4 kg) in weight (Spackman, 1882). Recreational fishermen on the east coast of the South Island reported catches of 100 lb of trout in a single day (Spackman, 1882). The phenomenal growth rates and sizes observed in these early years were probably due, in part, to the abundance of small native forage fish. For example, Spackman (1882) reports catching an 11 lb brown trout with 85 native fishes in its stomach. Although the size range and numbers of trout have declined since (likely in substantial part due to reduced food supplies), New Zealand still supports a brown trout fishery of world renown. Trout are still abundant in most rivers and lakes, and trophy fish upwards of 10 lb (4.5 kg) are still regularly caught (Fish & Game, 2015).

The brown trout fishery is of high recreational and cultural importance. Some 6% of New Zealanders participate in freshwater fishing, the mainstay of which is the brown trout fishery (Atkinson & Joy, 2012). Indeed, brown trout have become such an integral part of New Zealand culture that many New Zealanders are unaware that they are introduced at all; incorrectly thinking they are a native species (P. Jones, pers. obs.). Brown trout fishing is an important component of New Zealand's tourism industry, attracting fishermen worldwide, and contributing substantial economic benefits to many rural areas (Atkinson & Joy, 2012). However, the colonisation of New Zealand systems by brown trout has also resulted in substantial impacts on freshwater communities, most severely on the native fishes.

New Zealand's Native Freshwater Fish Community

Despite having been described as 'depauperate' by some biologists (e.g. McIntosh & Townsend, 1995; Ling *et al.*, 2001; McDowall, 2010), New Zealand's native freshwater fish community is now represented by 54 taxa (Goodman *et al.*, 2013). Relative to land area, this actually represents comparable species diversity to temperate regions of Australia, North America, and Europe (Burkhead, 2012). Many taxa are of ancient Gondwanan origin (McDowall, 2010), and 87% of species are endemic to New Zealand (Goodman *et al.*, 2013). The community includes representatives from nine families but is dominated by Galaxiidae and Eleotridae.

Apart from the catadromous eels (Anguillidae) and lamprey (Geotriidae), and three families that are largely marine (Mugilidae, Pleuronectidae, Triptigenidae), all species are amphidromous or directly descended from amphidromous ancestors. Amphidromy is a life cycle where fish spend the majority of their adult lives in fluvial freshwater habitats but maintain a marine (or lentic) pelagic larval rearing period (McDowall, 2007), a strategy which allows the early life stages access to abundant food resources during this critical early life stage (Closs *et al.*, 2013). The amphidromous members of the native fauna tend to be relatively widespread within New Zealand (Leathwick *et al.*, 2008) as this lifecycle promotes dispersal between river catchments (McDowall, 2007). However, many species of Galaxiidae (and some Eleotridae) have abandoned amphidromy, completing their entire lifecycles in fluvial habitats. These non-migratory species tend to be more range restricted, often confined to single catchments, the edges of their distributions generally determined by catchment boundaries (McDowall, 2010). The non-migratory members of the fish community represent the highest diversity, the complex New Zealand landscape having promoted relatively rapid speciation (McDowall, 2010).

The majority of native New Zealand fish are small-bodied benthic macroinvertebrate feeders (McDowall, 1990). Most Galaxiidae rarely reach sizes greater than 120 mm, excepting some of the amphidromous species, the largest of which, *Galaxias argenteus*, can reach 340 mm (Jellyman *et al.*, 2013a). The majority of eleotrids do not exceed 100 mm (McDowall, 1990). Only the lamprey and eels attain any great size, the largest of which, *Anguilla dieffenbachia*, can reach lengths of over 1.5 m and can weigh up to 15 kg (33 lb; Jellyman *et al.*, 2013a).

The unique ichthyofauna of New Zealand has suffered, and still is suffering, widespread decline. One species is extinct (*Prototroctes oxyrhynchus*), 74% are considered either 'threatened' or 'at risk', five species meet the highest threat classification levels: 'Nationally Critical' and 'Nationally Endangered', and the conservation status of many taxa has deteriorated within the last decade (Hitchmough *et al.*, 2007; Allibone *et al.*, 2010; Goodman *et al.*, 2013). Even those species not imminently threatened with extinction have suffered widespread range reductions over the last 150 years (Allibone *et al.*, 2010). Multiple factors are responsible for the continuing decline of the native fish community in New Zealand, but the two main stressors are habitat loss and degradation due to land use intensification (Hanchet, 1990; Allibone *et al.*, 2010), and negative pressures from invasive salmonids (Goodman *et al.*, 2013), principally brown trout (McDowall, 2006).

Impact of Brown Trout on Native New Zealand Fish

Perhaps the strongest evidence of the impact of brown trout has been their often non-overlapping distributions with native fish species. Unfortunately, data on the historic distributions of native species (prior to the introduction of brown trout) are scarce (Allen, 1961), and what information exists is largely anecdotal (Townsend, 1996). Hence, while the often allopatric distributions of native species and trout are compelling, these patterns do not definitively establish cause and effect. Indeed, in the view of many early New Zealand biologists, the evidence of exclusion was largely circumstantial. For example, in response to claims that trout were having detrimental effects on native species, Allen (1961) commented that 'sentiment has played an undue part in the formation of some of the opinions expressed'. Allen (1961) concluded that 'the introduction of Salmonidae has probably not led to any great change in the fauna of New Zealand waters'. However, since then, intensive research has built up a substantial body of evidence demonstrating the severe and widespread impact of brown trout on indigenous species.

McDowall (1968) was amongst the first to highlight the plight of New Zealand's native freshwater fishes in the face of competition and predation by invasive salmonids. This study cited studies of native fisheries catch rates showing that populations of *Galaxias maculatus*, a relatively widespread migratory species, had been in decline since the approximate time that brown trout were introduced. McDowall (1968) also observed that the abundance of non-migratory galaxiids (e.g. *G. divergens*, *G. vulgaris* and *G. paucispondylus*) was substantially higher where brown trout were absent, and suggested that the native fauna had low competitive ability because they had evolved in isolation and were therefore vulnerable to continental species with higher competitive ability. He also argued that New Zealand fauna lacked escape mechanisms, because they had evolved in the near absence of predators, making them highly vulnerable to predation. McDowall (1968) argued that native fishes needed protection from trout in order to persist. However, the severity of the impact appears to vary across the native fish community.

There is little evidence of trout having any major impact on the larger-bodied eels (Anguillidae) and lamprey (Geotriidae), except perhaps for some limited competitive interactions for food with eels (Cadwallader, 1975). However, human intervention for the benefit of trout resulted in mass culls of these large native fish in many areas. Due to a perception that longfin eels (*Anguilla dieffenbachia*) were predating heavily on trout, acclimatisation societies encouraged extermination campaigns to remove these 'public vermin', even offering bounties for dead eels over 10 lb (PCE, 2013). Acclimatisation societies placed slogans like 'Every angler should make war on eels' on fishing licences. In 1933, one ranger stated, 'Where infestation is bad it is possible to wade up a stream beheading the eels in one's stride' (PCE, 2013). The result of these campaigns was that hundreds of thousands of eels were destroyed (PCE, 2013). This practice was only discontinued when evidence emerged suggesting that eel predation could actually increase the size range of brown trout populations (PCE, 2013).

Localised declines in the abundance of amphidromous species have been associated with the presence of brown trout (Taylor, 1988; Minns, 1990; Allibone & McIntosh, 1999). In particular, amphidromous galaxiids (e.g. *G. maculatus*, *G. brevipinnis* and *G. faciatus*) can suffer heavy predation by brown trout as they migrate back upstream from the coast during juvenile 'whitebait' stage, and these impacts have been associated reduced abundances and range reductions in many areas (McDowall & Eldon, 1980; Main *et al.*, 1985; Minns, 1990; McDowall, 2006; Allibone *et al.*, 2010). There are also indications that the presence of brown trout can change the foraging behaviour and habitat use of some migratory galaxiids (Hayes, 1996; Glova, 2003), although evidence of this is not consistent (Bonnett & McIntosh, 2004). The impacts of trout on other members of the amphidromous community such as Eleotridae, Cheimarrichthyidae and Retropinnidae have not been so well examined, although they regularly appear in gut contents of brown trout (Allibone & McIntosh, 1999; M. Warburton, pers. comm.; P. Jones, pers. obs.). However, while amphidromous members of the native fish fauna have been extirpated in some locations (Taylor, 1988), in general their populations show substantial resilience to brown trout predation (McDowall, 2006; McIntosh *et al.*, 2010). Most species' ranges overlap with brown trout, and have often remained abundant in areas inhabited by brown trout for over 100 years (Rowe, 1993; McDowall, 2006; McIntosh *et al.*, 2010). McDowall (2006) suggested that this resilience may owe to the prolific spawning habits exhibited by amphidromous species. Because the larvae of amphidromous species rear in productive pelagic habitats (relative to fluvial systems), the adults are able to maintain high fecundity, by reducing egg (and larvae) size (Closs *et al.*, 2013). It is probable that this high fecundity plays a strong role in the population resilience of these migratory species to brown trout predation (Jones, 2014; Jones & Closs, in press).

The group of fish most affected by brown trout pressure are the non-migratory galaxiids, especially members of the most speciose group, the *Galaxias vulgaris* complex (McDowall, 2006; Allibone *et al.*, 2010; McIntosh *et al.*, 2010). This complex was originally thought to be a single variable species, *Galaxias vulgaris sensu lato* (McDowall, 1990), but morphological variation across ecoregions of the South Island prompted further investigation. Intensive morphometric and genetic analysis revealed the existence of a cryptic species complex made up of at least ten genetically distinct lineages (e.g. Allibone *et al.*, 1996; McDowall & Wallis, 1996; Waters *et al.*, 2010), six of which have been formally recognised as species (McDowall, 2000). All lineages (henceforth referred to as species) are endemic to the South Island, where they have largely allopatric distributions (McDowall, 2010). They are predominantly found in small to moderate-sized streams (1st to 3rd order), but are also found in larger rivers in some areas (McDowall, 1990). Adults are small-bodied, rarely larger than 120 mm (Jellyman *et al.*, 2013a; Jones *et al.*, 2014) and are generally sedentary, rarely moving more than 200 m within their adult home ranges (Cadwallader, 1976). All species complete their entire lifecycles in fluvial freshwater habitats (McDowall, 1990; Jones *et al.*, 2014).

The first quantitative analysis of trout and non-migratory galaxiid distribution patterns showed that brown trout presence was associated with the absence of non-migratory galaxiids (Minns, 1990). However, there was a widely held opinion that habitat degradation related to land use change was the predominant cause of native fish decline (Main, 1988; Hayes *et al.*, 1989; Hanchet, 1990), and critics claimed that evidence of brown trout's impact was circumstantial (e.g. Allen, 1961). To address this uncertainty, an influential paper by Townsend & Crowl (1991) used a broad-scale electrofishing survey, sampling across several different land uses, to evaluate the impact of trout on non-migratory galaxiids (*Galaxias vulgaris sensu lato*). They observed almost completely non-overlapping distributions of trout and galaxiids (Figure 21.2) and found that, while forestry and agricultural pressures were associated with lower densities of fishes, the presence of galaxiids was best explained by the absence of trout, with galaxiids generally existing only where large waterfalls had prevented colonisation by trout. Townsend and Crowl (1991) concluded predation by trout was likely to be the principal driver of the widespread decline and population fragmentation of galaxiids.

Trout predate on all size classes of non-migratory galaxiid (i.e. there is no upper size refugia; McIntosh, 2000), but juvenile and larval galaxiids are especially vulnerable to predation, even by small trout (<80 mm; Glova, 1990; Jellyman & McIntosh, 2008; 2010). It is likely that the most intense period of predatory interactions occurred in the past, before galaxiid populations were fragmented, but contemporary predation continues to occur in areas where trout and galaxiids are sympatric (Figure 21.3). Predation by trout is likely to have been the major driver of the fragmentation and decline of non-migratory galaxiids (Townsend & Crowl, 1991; McDowall, 2006; McIntosh *et al.*, 2010), but competition may also be important. Brown trout are voracious invertebrate feeders and are capable of consuming the entire invertebrate production of streams (Huryn, 1998). Thus, they compete for food resources with galaxiids which are primarily benthic macroinvertebrate feeders (Cadwallader, 1975; Glova *et al.*, 1992; Glova & Sagar, 1993). In addition, brown trout also compete aggressively for space, and are known to spatially exclude galaxiids and displace them from prime feeding habitat (McIntosh *et al.*, 1992).

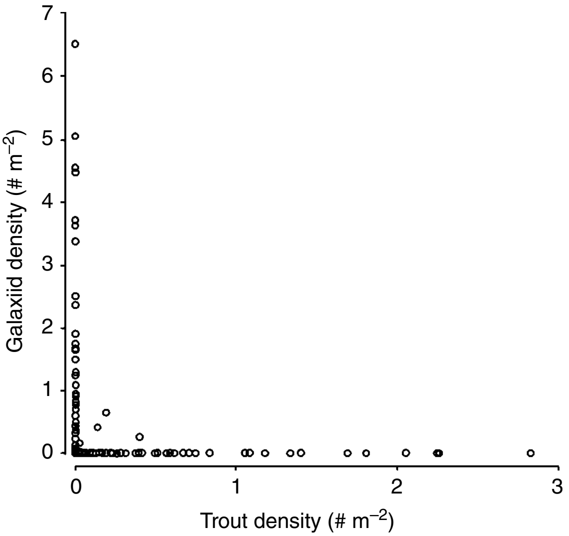

Figure 21.2 Relationship between trout and galaxiid (*Galaxias vulgaris sensu lato*) densities in the Taieri River catchment, New Zealand. (Adapted from Townsend & Crowl, 1991.)

Figure 21.3 A brown trout caught in a South Island stream with six juvenile-adult *G. anomalus* in its stomach. (Photo credit: D. Jack.) Scale bar: approx. 10 cm.

Severity of Impact Differs with Habitat

While the evidence that the introduction of trout has contributed to the fragmentation and decline of non-migratory galaxiids is almost irrefutable (McDowall, 2006), the severity of their impact appears to differ depending on the morphology of stream and river channels. For example, galaxiid–trout co-existence is often found in the unstable shifting braided rivers of Canterbury (e.g. Glova & Sagar, 1993; Woodford & McIntosh, 2010), whereas galaxiids are typically extirpated in the simple single-channel systems found in many areas of Otago (e.g. Townsend & Crowl, 1991; Allibone, 1999). It is thought that the complex habitat found in braided systems may provide refugia for galaxiids, thereby reducing the intensity of interactions with trout (Townsend & Crowl, 1991; Glova *et al.*, 1992). Galaxiids are known to change their foraging behaviour and reduce their trophic niche breadth to avoid predation and aggressive behaviour by trout (McIntosh *et al.*, 1994; McHugh *et al.*, 2012). For instance, by occupying small side braids and utilising benthic feeding positions, galaxiids can in some instances persist in trout-invaded reaches, provided trout densities are not too high. However, by inhabiting inferior habitats and changing foraging behaviour (McIntosh *et al.*, 1994; McHugh *et al.*, 2012), it is likely that galaxiid growth is reduced. Similar to the effect of habitat complexity, the intensity of galaxiid–trout interactions can vary with stream size. Predatory and competitive interactions are more acute in small streams whereas larger systems provide more spatial refugia for galaxiids (Woodford & McIntosh, 2010; 2011).

Galaxiid–trout interactions can also be strongly mediated by local flow regimes. Many areas of central and eastern New Zealand regularly experience high temperatures and low rainfall in the summer months (NIWA, 2015b). The resultant low flows are often exacerbated by widespread water abstraction for irrigation (Allibone, 2000). Low flow conditions can switch the competitive balance from trout to favour galaxiids (Leprieur *et al.*, 2006), because they are considerably more tolerant of warm temperatures (McDowall, 1990) and are able to burrow into interstitial spaces to avoid desiccation during short-term extreme low flow events (Dunn & O'Brien, 2006). Interestingly, stream reaches exposed to regular low-flow disturbance can provide refugia for non-migratory galaxiids, as trout are often absent or substantially reduced in number in these habitats (Leprieur *et al.*, 2006). This finding has been interpreted to mean low flows are 'good' for galaxiids by many interested parties, which is an inaccurate and over-simplistic interpretation of the situation. Outdated legislation relating to old gold mining water abstraction rights effectively means that farmers can take 100% of the surface flow in some South Island streams. Extreme low flows can cause catastrophic mortality of galaxiid populations and have detrimental effects on wider stream ecology (Allibone, 2000; Shelley, 2012). Hence, while low flow disturbance can to some extent benefit galaxiids through negative effects on trout numbers and distributions, excessive water abstraction can add further stress on already depleted and endangered populations.

Disturbance associated with floods and substrate instability can also play an important role in influencing the outcome of galaxiid–trout interactions. Large areas of New Zealand experience regular heavy rainfall events and many river systems are inherently flashy in nature, sometimes experiencing large-scale bed movement (Crow *et al.*, 2013; Jellyman *et al.*, 2013b). Small-bodied galaxiids are resilient to these disturbances, whereas introduced trout populations are vulnerable to high flow events (Woodford & McIntosh, 2010; Jellyman *et al.*, 2013b). Therefore, in areas frequently disturbed by high flows, trout densities are often lower, and such reaches often support denser populations of galaxiids. However, trout are able to quickly recolonise these areas (Davey & Kelly, 2007), so such disturbance generally only offers galaxiid populations a transient respite from the negative effects of trout.

Source–Sink Metapopulation Dynamics

Since the Townsend & Crowl (1991) study, many examples of apparent trout–galaxiid coexistence have been reported in the literature (e.g. Glova *et al.*, 1992; McIntosh *et al.*, 1992; Leprieur *et al.*, 2006; Davey & Kelly, 2007), and there are records indicating that they may co-occur over large areas of South Island riverscapes (NZFFD, 2014). This pattern suggests that the co-existence of trout and non-migratory galaxiids often involves some subtle and more complex outcomes than complete exclusion. From the mid-2000s onwards, a number of studies have examined the mechanisms determining whether coexistence or exclusion occurs.

The importance of the abundance and movements of the early life stages is gaining increasing recognition as being a key mechanism driving galaxiid population dynamics (Jellyman & McIntosh, 2008, 2010; Woodford & McIntosh, 2010; Jones & Closs, 2015a). The presence of trout has been related to reduced larval galaxiid abundance, often resulting in zero recruitment in reaches inhabited by high densities of trout (Jellyman & McIntosh, 2008; Woodford & McIntosh, 2010; Figure 21.4). This relationship is likely to be due to a combination of competition and predation on adult galaxiids before spawning, and direct predation on larval galaxiids (Jellyman & McIntosh, 2008; Woodford & McIntosh, 2010). The lack of recruitment in heavily trout-invaded reaches

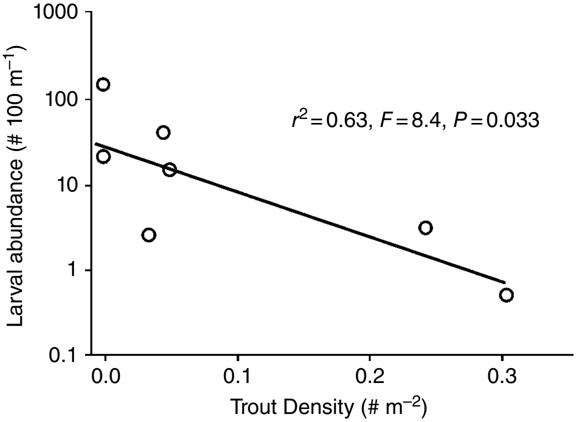

Figure 21.4 Relationship between abundance of *Galaxias vulgaris sensu stricto* larvae and trout density. (Adapted from Jellyman & McIntosh, 2008.)

suggests they exist as 'sink' populations, supported by immigration from upstream trout-free 'source' populations (normally above large waterfalls which exclude trout) where there is positive net recruitment (Woodford & McIntosh, 2010). Hence, the persistence of galaxiid populations in trout-invaded reaches appears to be dependent upon the presence of upstream trout-free 'source' populations and their location within the riverscape (Woodford & McIntosh, 2011). This source-sink metapopulation system potentially supports the co-existence of non-migratory galaxiids with trout in many South Island riverscapes (Woodford & McIntosh, 2010; 2011).

Woodford & McIntosh (2010) did not explicitly test the mechanisms driving immigration into 'sink' habitats, but suggested that the movement of the early life stages are likely to be important. This is highly probable as adult non-migratory galaxiids are sedentary, generally moving less than 200 m in their home ranges (Cadwallader, 1976; P. Ravenscroft, unpubl. data; P. Jones; pers. obs.), whereas the larvae are potentially highly mobile, especially when they are newly hatched because their poor swimming ability makes them prone to dispersal in stream currents (Jellyman & McIntosh, 2010).

Upon hatching larvae of *G. vulgaris sensu stricto* are unable to resist current speeds higher than 10 cm s^{-1} (Jellyman & McIntosh, 2010), and are carried downstream in currents until they are able to settle in slow-moving backwaters where they form pelagic feeding congregations (Jellyman & McIntosh, 2008). Trout-free 'source' populations of *G. vulgaris sensu stricto* produce large numbers of potential larval recruits (Jellyman & McIntosh, 2008, 2010; Woodford & McIntosh, 2010), and their small, poorly swimming larvae have the potential to disperse downstream over large distances (Jellyman & McIntosh, 2010), a pattern also observed in a very similar species in Australia (Dexter *et al.*, 2013). Hence, it is thought that larval dispersal is the mechanism driving source sink metapopulation dynamics, and enabling galaxiid–trout coexistence in certain rivers.

The Role of Life History in Mediating Galaxiid/Trout Interactions

Until recently, it was assumed that other species in the *Galaxias vulgaris* complex followed similar metapopulation dynamics to those seen in *Galaxias vulgaris sensu stricto*. There were reports of non-overlapping galaxiid–trout distributions in some areas of the country (Townsend & Crowl, 1991; Allibone, 1999), which contrasted strongly with reports of widespread coexistence in other catchments (e.g. McIntosh, 2000; Davey & Kelly, 2007; Woodford & McIntosh, 2010), but these inconsistencies were put down to the mediating effect of habitat and local densities of trout rather than any galaxiid-species specific response to trout pressures. However, recent research has highlighted the importance of interspecific differences in life history traits in mediating galaxiid–trout interactions.

A number of landscape-scale gradients are now known to exist in the basic life history characteristics of non-migratory galaxiids (Closs *et al.*, 2013; Jones *et al.*, 2014). Differences in productivity and disturbance regimes between the various habitats occupied by each species are associated with substantial differences in reproductive traits such as fecundity, egg size, gonadosomatic index (GSI), and size/age at the onset of maturity (Closs *et al.*, 2013; Jones *et al.*, 2014). These trait differences vary approximately along altitudinal upstream/downstream gradients and with local microclimatic conditions (Jones *et al.*, 2014). Species associated with high altitude, small cold headwater creeks have larger egg sizes, lower fecundities, mature later and commit less of their body weight to reproduction than those associated with larger, warmer and less-shaded lower catchment systems (Jones *et al.*, 2014; Figure 21.5). It is thought that the local food availability, especially the abundance of small prey items for the larval fish, drive galaxiids to differentially provision eggs (Closs *et al.*, 2013; Jones *et al.*, 2014).

In food-scarce environments (i.e. headwater streams) female galaxiids allocate more resources to the individual egg (and offspring), but this leads to trade-offs with a suite of other traits such as fecundity (Figure 21.6), minimum size at maturity and reproductive effort. Hence, headwater species have size-relative fecundities averaging around three times lower, contribute up to 10 % less of their body weights to reproduction, and probably mature at least one or two years later than lower catchment species (Jones *et al.*, 2016). The interspecific life history variation observed closely represents a fast-slow life history gradient (Pianka, 1970), i.e. fast life histories in lower catchment systems, slow life histories in headwater streams. These life history gradients also vary with upstream-downstream gradients in disturbance (Jones *et al.*, 2014). Species exhibiting fast life histories are found in areas where piscivorous fish (both native and introduced) are common, and in streams subject to high flow disturbance (regular droughts). In contrast, the slow life history headwater species are found in streams with stable flows and generally an absence of predatory fishes.

The interspecific life history differences observed in the *Galaxias vulgaris* complex are known to have consequences for population dynamics in the various species (Jones & Closs, 2015a). Populations of species with fast life history traits (high fecundity, high reproductive effort, early maturation) produce large numbers of potential recruits, larval abundance being 6–9 times higher in reaches occupied by headwater species compared to slow life history species (low fecundity, low reproductive effort and late maturation) (Figure 21.6; Jones & Closs, 2015a). Differences in early life history traits (larval size and swimming ability at hatch) are also thought to drive interspecific differences in the scale of larval dispersal. Larvae of the larger-egged headwater species hatch on average up to 40% larger (8–9 mm compared to 5–7 mm) and with better swimming ability, compared to lower catchment species (Jones & Closs, 2014). Catchment-scale surveys of larval distributions indicate the larvae of lower catchment

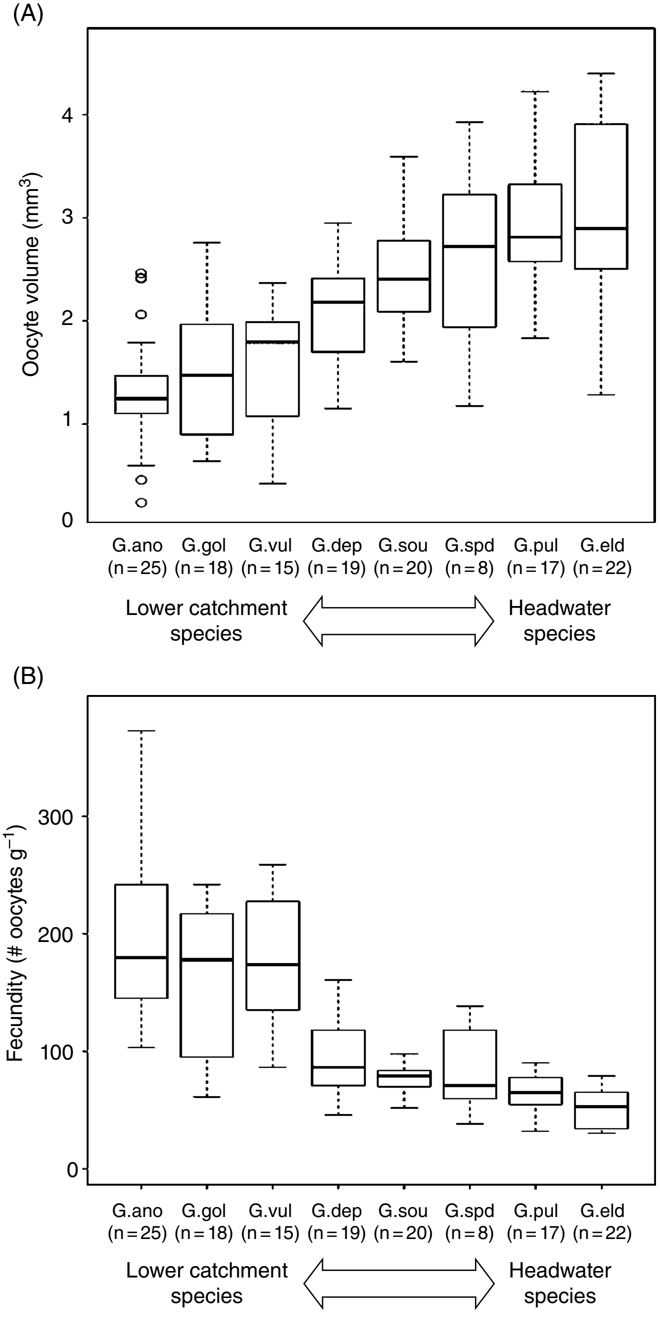

Figure 21.5 Interspecific differences in (A) oocyte size, and (B) fecundity, in the *G. vulgaris* complex (adapted from Jones *et al.*, 2014). G.ano = *G. anomalus*, G.gol = *G. gollumoides*, G.vul = *G. vulgaris sensu stricto*, G.dep = *G. depressiceps*, G.sou = *G.* 'southern sp.', G.spd = *G.* sp. D, G.pul = *G. pullus* and G.eld = *G. eldoni*.

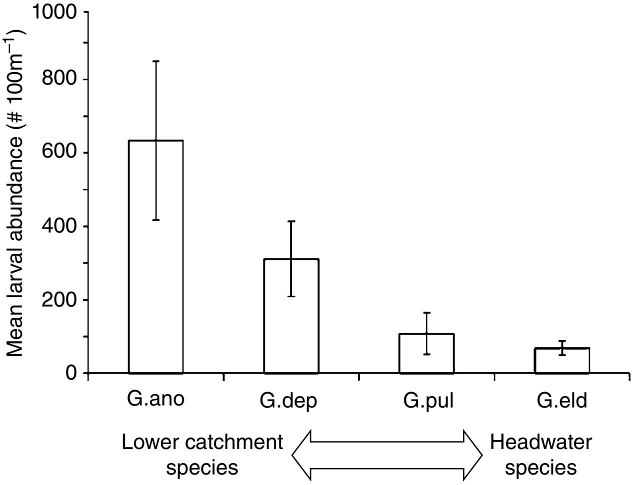

Figure 21.6 Differences in larval abundance immediately following peak hatching in stream reaches support populations of *G. anomalus* (fast life history), *G. depressiceps* (intermediate life history), and *G. pullus* and *G. eldoni* (slow life histories). For statistics see Jones & Closs (2015b).

species disperse widely downstream from adult populations (up to over 12 km), probably because their small size and limited swimming ability makes them highly susceptible to passive drift in stream currents (see Jones & Closs, 2014). In contrast, the larger better-swimming larvae of the headwater species (Jones & Closs, 2014) never dispersed more than 300 m downstream of adults, and were consistently scarce or absent even immediately downstream of likely spawning areas (see Jones & Closs, 2015a). Hence, the mechanism necessary to support a source-sink metapopulation system (i.e. large numbers of dispersal larvae; Woodford & McIntosh, 2010) is present in the fast life history lower catchment species, but effectively absent in the slow life history headwater species. This has major implications for how these species with contrasting life histories interact with trout.

Spatial analysis suggests that species-specific interactions with salmonids (mainly brown trout) differ with respect to the life histories of various non-migratory galaxiid species (Jones & Closs, 2015b; Figure 21.7). Fast life history species exhibit extensive overlap with salmonids, co-occurring with trout in over 50% of reaches where they are found, and often long distances downstream from the nearest trout-free source populations (Jones & Closs, 2015b). In almost complete contrast, slow life history species co-occur with salmonids in less than 6% of sites in which they occur, and are usually absent even short distances downstream from the nearest trout-free populations (Jones and Closs, 2015b). An explanatory model of galaxiid–trout distributions identified that species' life history strategies were the dominant factor influencing whether galaxiids co-occurred or were excluded by salmonids, even while controlling for the possible confounding effects of habitat (see Jones and Closs, 2015b). The best explanation for this is that differences in population dynamics associated with species life history strategies play a strong role in determining how non-migratory galaxiids spatially interact with salmonids (Jones & Closs, 2015a, b).

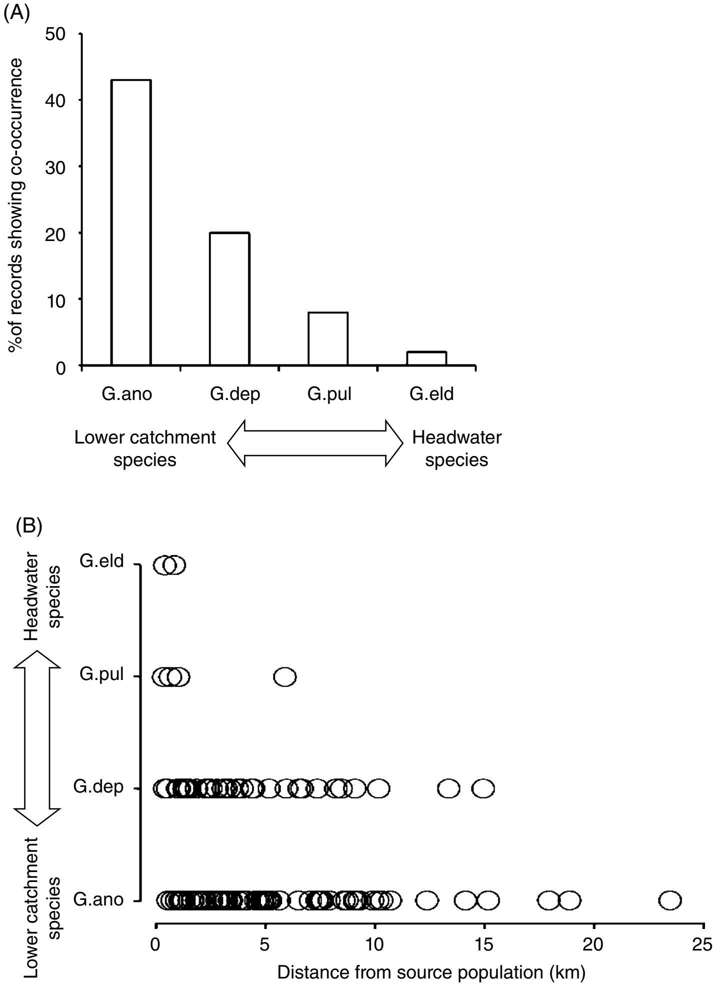

Figure 21.7 Interspecific differences in: (A) percentage of records showing 'co-occurrence'; and (B) distance of co-occurrence reaches from nearest source ('galaxiids only') population, for G. ano = *G. anomalus* (fast life history), G. dep = *G. depressiceps* (intermediate life history, G. pul = *G. pullus* (slow life history), G. eld = *G. eldoni* (slow life history). (Adapted from Jones & Closs, 2015b.)

The high reproductive output of fast life history species and dispersive nature of their larvae means they are likely to follow a source-sink metapopulation system, similar to *Galaxias vulgaris sensu stricto* (Woodford & McIntosh, 2010), another fast life history species (Figure 21.6; Jones *et al.*, 2014). Large numbers of larvae passively drifting down the system results in immigration from upstream source populations to downstream sink populations in trout-invaded reaches (Figure 21.8; Jones & Closs, 2015a). There is some evidence from these and closely related species that the dispersers which survive to the juvenile stage can migrate back upstream once they are large enough to negotiate currents (Figure 21.8; Cadwallader, 1976; Green, 2008; Jones & Closs,

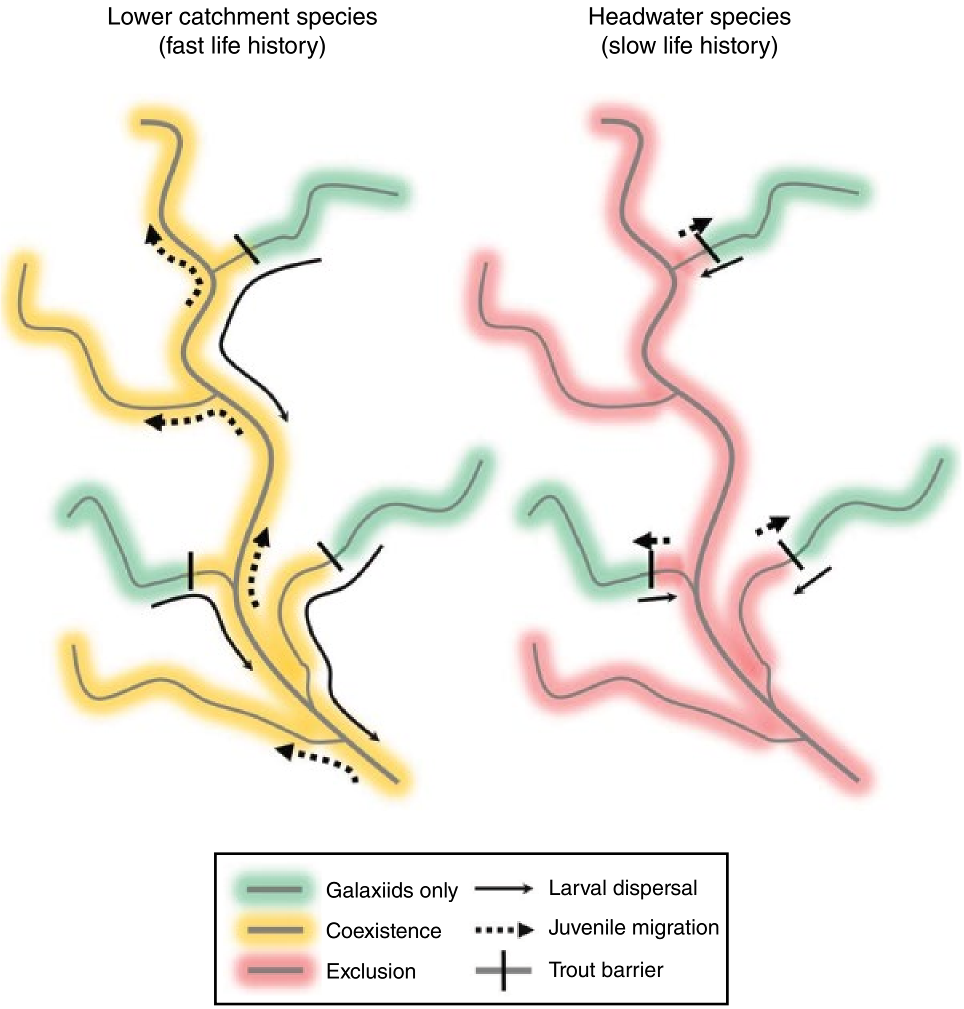

Figure 21.8 Hypothetical models of how populations of fast and slow life histories are likely to spatially interact with trout populations. (Adapted from Jones & Closs, 2015a.)

2015a). This dynamic population structure is likely to facilitate varying degrees of coexistence in these fast life history species, allowing these species to overlap widely with trout, and to some extent providing them with some resilience to negative pressures from trout. However, slow life history species produce small numbers of potential larval recruits and their large better-swimming larvae show minimal dispersal (Figure 21.8). Hence, the mechanism necessary for maintaining a source-sink metapopulation system is effectively missing in these species, meaning they are more prone to being excluded by trout and to form isolated and fragmented population structures. As a consequence of their slow life histories, these species are likely to be much more vulnerable to exclusion by trout.

Changing Perspectives, Conflicting Interests and Technical Challenges: Galaxiid Conservation and Trout Fisheries Management in New Zealand

As summarised in the proceeding sections of this chapter, a substantial research effort has led to a paradigm shift in perceptions of galaxiid–trout interactions in New Zealand. Initial warnings of the negative impact of trout on the native fish fauna were originally viewed with scepticism, and perhaps even denial, by many New Zealanders (see McDowall, 2006). Subsequent research, however, has provided compelling evidence that the introduction of brown trout has led to the widespread decline and population fragmentation of native fishes, especially the non-migratory Galaxiidae. Early surveys indicated predation by trout led to complete exclusion of non-migratory galaxiids, and that the latter only occurred in refugia upstream of large waterfalls that had prevented trout incursion (e.g. Townsend & Crowl, 1991). This led to the formation of a widely held 'stable state' viewpoint, i.e. because brown trout had been present in most catchments for over 100 years, it was assumed that the damage had been done, and that trout no longer threatened extant galaxiid populations (e.g. Department of Conservation, 1993). However, these opinions were later deemed as misguided, as trout colonisation of New Zealand is an ongoing process with further incursions occurring within the last decade (P. Ravenscroft, pers. comm.; P. Jones, pers. obs.). Also, many galaxiid populations are in contact with trout populations, where trout cause more subtle demographic responses rather than complete exclusion (e.g. Woodford & McIntosh, 2010).

The more contemporary perspective of galaxiid–trout interactions, therefore, is one of a much more complex situation, mediated strongly by factors such as habitat type, disturbance regimes, land use, and galaxiid life history. Hence, the outcomes of trout–galaxiid interactions are far less easy to predict than once thought, and trout can cause large scale fluctuations in galaxiid population abundance and distributions (McIntosh *et al.*, 2010). Far from being 'stable', trout interactions with galaxiids have the potential to cause further decline to galaxiid populations, which have become even more vulnerable due to their highly fragmented state and other negative pressures associated with land use intensification (Allibone *et al.*, 2010). Therefore, non-migratory galaxiids require urgent conservation action to ensure the long-term survival of these unique endemic species.

A number of mitigation methods are available to conservation managers to control trout and to expand and protect galaxiid populations in New Zealand. The reinforcement of existing waterfalls and installation of artificial barriers such as weirs have been successful in limiting trout incursion, but a lack of resources has meant that these approaches have not been used widely. Also, many New Zealand streams are unstable braided streams where installing effective barriers is technically very challenging. The recent success of piscicides (rotenone) in New Zealand to remove trout demonstrates its usefulness as a control technique (Pham *et al.*, 2013). However, current legislation severely restricts its use in New Zealand (P. Ravenscroft, pers. comm.). Another challenge is that galaxiids and trout co-occur in many reaches where the use of piscicides would risk impacting non-target galaxiids. Selective electrofishing has been used to effectively remove trout from some reaches, but the intensive nature of this approach severely limits its utility over larger areas. There is potential to control brown trout distribution via exploiting their lower tolerance to warm temperatures and low flows compared to galaxiids (Closs & Lake, 1996; Leprieur *et al.*, 2006). Artificially reducing stream flow could be used to tip the competitive balance in favour of galaxiids and exclude trout from target reaches. However, low flows also negatively impact galaxiid populations (Allibone, 2000), as well as macroinvertebrate communities (Shelley, 2012), so small scale trials would be needed before any widespread implementation. Given the scale of the impact of salmonids in New Zealand, more research needs to be directed at developing effective brown trout control and galaxiid restoration techniques. If galaxiid populations are not given sufficient protection and reserves are not established, there is a high risk that incremental decline will lead to the eventual extinction of many galaxiid populations and ultimately species, especially the most range-restricted (McDowall, 2006).

The need to conserve native galaxiids conflicts with the promotion of trout fishing values. The primary remit of Fish & Game New Zealand, the agency charged with the management of the New Zealand trout fishery (and the successor to the acclimatisation societies), is to 'maintain and enhance sport fish (salmonids) and their habitats' (Fish & Game, 2015). While Fish & Game make substantial contributions to the promotion of water quality standards and campaign for best practice land management (Fish & Game, 2015), current practice continues to prioritise introduced trout to the detriment of native fishes. Trout are still actively stocked in some areas of the country where populations are not self-sustaining, and fisheries managers are generally unwilling to support trout removal even from small streams due to a perception that they act as important spawning areas for fisheries lower in the catchment (McIntosh *et al.*, 2010). However, there is little evidence that these very small streams are significant exporters of recruits to larger rivers, and in many streams the majority of individuals are small resident trout of little recreational value (McDowall, 2006). Another issue is the deliberate and illegal release of brown trout in upland watercourses not yet colonised by trout (McDowall, 1990; 2004).

These clandestine releases have the potential to be extremely detrimental, especially in systems where galaxiid presence relies on upstream 'source' populations (Woodford & McIntosh, 2010), and where headland creeks represent the only remaining extant galaxiid populations (Townsend & Crowl, 1991; Jones & Closs, 2015b). The responsibility for conserving galaxiid biodiversity lies with the New Zealand Department of Conservation (Department of Conservation, 2015), which has recently suffered extensive funding cuts, and is constrained by a lack of effective legislation. Ironically, the only native New Zealand fish unequivocally covered by protective legislation went extinct at least 80 years ago, whereas trout and salmon are specifically protected under New Zealand law (see McDowall, 2006). This imbalance between the prioritisation of recreational trout fisheries and conservation of native species is contributing to the widespread decline of non-migratory galaxiids.

Despite these challenges, the promotion of galaxiid conservation and recreational trout fisheries do not necessarily have to be at odds with one another. If more trout-free galaxiid populations could be established, they have the potential to be highly productive (at least in fast life history species), supplying downstream reaches with dispersing recruits (Jellyman & McIntosh, 2008), and thereby substantially increasing their range in trout-invaded reaches (Woodford & McIntosh, 2010; Jones & Closs, 2015a,

Figure 21.8). The removal of trout from many of these small streams is likely to have little impact on recreational fisheries value, as most only support very small resident trout. Dispersing galaxiids from trout-free source populations could even act as an important food resource to trout, potentially increasing growth rates and therefore perhaps leading to increases in the numbers of large trout of recreational value. Hence, if effective control methods were developed, this could be a rare example of a win–win situation, whereby conservation goals could be met, while enhancing the fisheries value of an introduced recreational sports fish.

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22

The Effects of Brown Trout on the Trophic Webs of New Zealand Streams

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Introduction

The impacts of introduced fish on natural communities have been documented in freshwater ecosystems worldwide (Miller *et al.*, 1989; Harrison & Stiassny, 2004). In New Zealand, the most widespread and common introduced fish is brown trout (*Salmo trutta*). These fish were first released into South Island waters in 1867 and were subsequently liberated in streams, rivers and lakes throughout much of the country. The releases proved so successful that brown trout have been called 'the jewel in the crown' of New Zealand's Fish and Game organisation (McDowall, 1994). Superb brown and rainbow trout (*Oncorhynchus mykiss*) fisheries now exist throughout New Zealand, giving the country international renown as a trout angling destination. However, the more widely spread brown trout has likely caused the greatest change to both native communities and instream processes. Whilst brown trout populations and their impacts have been studied in countries throughout the world, the present understanding of brown trout impacts at multiple levels of ecological organisation (i.e. individual, population, community and ecosystem level) is arguably the most complete for New Zealand streams. Here we review this state of knowledge by firstly examining how physical factors affect brown trout in New Zealand, secondly reviewing brown trout impacts at each level of ecological organisation, and thirdly detailing how their effects can vary with spatial scale. With a much greater emphasis now placed on protecting native biodiversity, we conclude by discussing some of the management issues associated with balancing a highly-valued sports fishery alongside an increasingly-threatened native fish fauna.

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

Physical Factors Controlling Brown Trout Populations and Distribution

Stream flow has long been known to be a key driver of fish community structure (e.g. Nikolski, 1933) and flow regime alongside the other instream properties it influences (bed stability, habitat availability, water velocity, depth, clarity, etc.) can have a major effect on trout populations. When examining flow effects on brown trout in New Zealand waterways it is important to recognise that these flow regimes are globally distinctive (Poff *et al.*, 2006). Compared to waterways on large continents, flow regimes of New Zealand rivers show minimal seasonality because large rainfall events and resultant floods can occur during any month of the year (Jowett & Biggs, 2009). This has important implications for brown trout populations because the timing of their life cycle is relatively well-defined (i.e. they spawn in late autumn-early winter in New Zealand streams; McDowall, 1984) and these flow-driven disturbances likely mediate interactions between brown trout and other parts of the trophic web of New Zealand streams.

Compared to the native freshwater fauna that have evolved in New Zealand's unpredictable and flood-prone rivers, brown trout have only had c. 150 years to adapt to such conditions. To persist in these flood-prone systems, the native fauna has developed a number of mechanisms/strategies: benthic invertebrates have poorly synchronised life histories (Winterbourn *et al.*, 1981), non-diadromous bullies (e.g. upland bully, *Gobiomorphus breviceps*) can have multiple broods (up to eight) throughout spring and summer and diadromous galaxiids utilise floods to rapidly disperse their larvae out to sea during winter (McDowall, 1990). Although brown trout do have quite a large amount of habitat flexibility (McIntosh *et al.*, 2012), they have not developed any such life-history strategies in the time they have been present in New Zealand. Their early winter spawning results in trout fry emerging in early spring, which means brown trout fry can maximise growth potential over the spring and summer (McDowall, 2006). However, early winter spawning can also leave alevins and fry exposed to some of the harshest flow conditions which generally occur during winter and early spring.

Flood timing is critical for brown trout survival because even moderate floods (e.g. of a four-year return period) are capable of impairing recruitment if they occur during the late incubation and early fry stages (August to November; Hayes, 1995). Given the unpredictable timing of floods in New Zealand, winter spawning by brown trout may not be any riskier than the strategy of non-diadromous *Galaxias* spp., which spawn during spring when high rainfall and melt water from snow often combine to create large spring floods. Whilst a moderate flood event in December (austral summer) could be catastrophic for small, non-diadromous *Galaxias* fry, floods at this time may only have a minor effect on trout fry abundance (Hayes, 1995; Jellyman & McIntosh, 2010). Another major advantage of early winter spawning for brown trout is that by the time native fish fry (e.g. non-diadromous *Galaxias*) are hatching out and settling into stream backwater habitat, brown trout have a large size advantage and are already large enough to prey on them (Jellyman & McIntosh, 2010; Figure 22.1); the impacts of this are discussed in a later section.

Most fish species are susceptible to extreme flood events, but fish-tagging research on native fish and brown trout suggests that fish extirpation/mortality as a result of extreme floods is likely to be more severe on adult brown trout compared to native fish species (Young *et al.*, 2010; McEwan & Joy, 2013). Radiotelemetry work has shown that

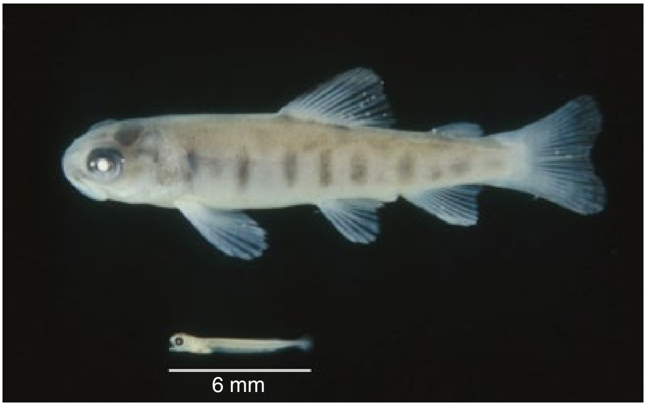

Figure 22.1 Comparison of the body size of a typical brown trout fry (top) and non-migratory galaxiid fry (bottom) in early summer from rivers in Otago, very soon after the galaxiid had hatched. For reference the galaxiid fry is about 6 mm long.

extreme floods (i.e. 50-year return period) can result in 60–70% mortality of adult brown trout (Young *et al.*, 2010). Earlier research on the effects of a major flood on brown trout across multiple rivers (return periods varied from 19 to >100 years) found that flood impacts varied with trout size; the abundance of small fish (10–20 cm) were reduced by 90–100%, medium fish (20–40 cm) by 62–87% and large fish (>40 cm) by 26–57% (Jowett & Richardson, 1989).

Whilst brown trout, particularly larger trout, can tolerate major floods, fish species native to New Zealand conditions are thought to be less affected by floods than trout and McIntosh (2000) considered that exotic fish were less ‘well-adapted to disturbance regimes’ than native fish. Trout recovery to floods has been examined in recent years and juvenile brown trout populations appear to have remarkable flood resilience in some catchments. The same extreme flood that devastated adult trout in the research of Young *et al.* (2010) similarly reduced the density (66%) and biomass (73%) of 0+ juvenile brown trout (Hayes *et al.*, 2010). However, the cohort was able to respond with compensatory survival such that 1+ fish from the cohort were of comparable density and biomass to other years (Hayes *et al.*, 2010). Thus, whilst brown trout may not have evolved the same resistance to floods as native fish species, they may be able to compensate with high population resilience to large flood events.

Research from rivers prone to low flows or drying suggests that brown trout are also more susceptible to the stresses associated with receding flow than are native fish (Leprieur *et al.*, 2006). Periods of low or no flow, which can reduce streams to a series of isolated pools, generally results in streams with high water temperatures and low dissolved oxygen conditions which native fish species, through mechanisms such as subcutaneous respiration (Phillips, 1926) and burrowing behaviour (Hartman, 1990), generally tolerate better than salmonids (Closs & Lake, 1996). Although in rivers where low flows are not associated with large increases in mean water temperature or declines in dissolved oxygen, then sustained low flows (e.g. up to 50 days) may have no adverse effect on 0+ juvenile brown trout (Hayes *et al.*, 2010). An investigation of sustained loss of surface flow in the Selwyn River in Canterbury revealed that some brown trout as well as Canterbury galaxias (*Galaxias vulgaris*) and upland bullies migrated to upstream flow refugia as the drying front moved upstream (Davey & Kelly, 2007). The brown trout were surprisingly resilient in this study, being able to recolonise recently rewetted reaches as fast as some native fish. Nevertheless, even brief episodes of drying (flow permanence 89%) considerably changed the riverine fish fauna, with only native Canterbury galaxias, the most resilient fish, being able to consistently persist at this level of flow loss (Davey & Kelly, 2007).

Flow regime and the availability of physical habitat are among the main abiotic factors influencing local brown trout abundance in New Zealand waters (the important role of biotic interactions is discussed in later sections). At a national scale, these factors play a lesser role in determining brown trout distribution, which is primarily influenced by water temperature (McDowall, 1984; Jowett, 1992). McDowall (1984) postulated that water temperature probably regulates the whole migratory behaviour of brown trout because pre-spawning upstream migrations and spawning timing are both likely to be related to the search for rivers with sufficiently cool waters. In New Zealand, brown trout distribution is limited by minimum annual water temperature (Jowett, 1990) because trout are absent, or at very low abundance, in many waterways in the upper North Island where winter water temperatures are generally greater than 10 °C (Jowett, 1992; Figure 22.2). Moreover, summer water temperatures in New Zealand's northern waters also regularly exceed 19 °C, the temperature at which adult brown trout generally stop feeding (Elliott, 1994).

At the regional scale, brown trout distribution and abundance are likely limited by the availability of suitable spawning rivers. Brown trout abundance is negatively correlated with the percentage of sand and volcanic ash on the river bed (Jowett, 1992), presumably because such bed materials are not suitable for trout spawning. Therefore, brown trout abundance, and thus the impact of brown trout, is likely to be markedly lower in many streams along the east coast of the North Island where this bed material results in a lack of spawning waters (Figure 22.2). Although parts of New Zealand may differ in their suitability for brown trout, the main physical factors (e.g. flow stability, cool water temperatures) that influence trout populations are not particularly different from those in other parts of the world where this species has successfully invaded (McIntosh *et al.*, 2012).

The Impact of Brown Trout at Different Levels of Ecological Organisation

Research examining the effects of an introduced species at multiple levels of ecological organisation is rare (Simon & Townsend, 2003; Townsend, 2003). The example of introduced brown trout in New Zealand fresh waters is a notable exception and numerous researchers, particularly over the last 25 years, have identified a plethora of brown trout related effects in stream habitats. Below we detail research where brown trout effects have been identified at the individual, population, community and ecosystem level in these streams.

The Effect of Brown Trout at the Individual Level

One of the most influential impacts of brown trout invasion on aquatic communities in New Zealand has been the change in the risk of predation experienced by the rest of the aquatic community. This change has created far-reaching effects on the behaviour and life history of fish and invertebrates, and it underpins effects at other ecological

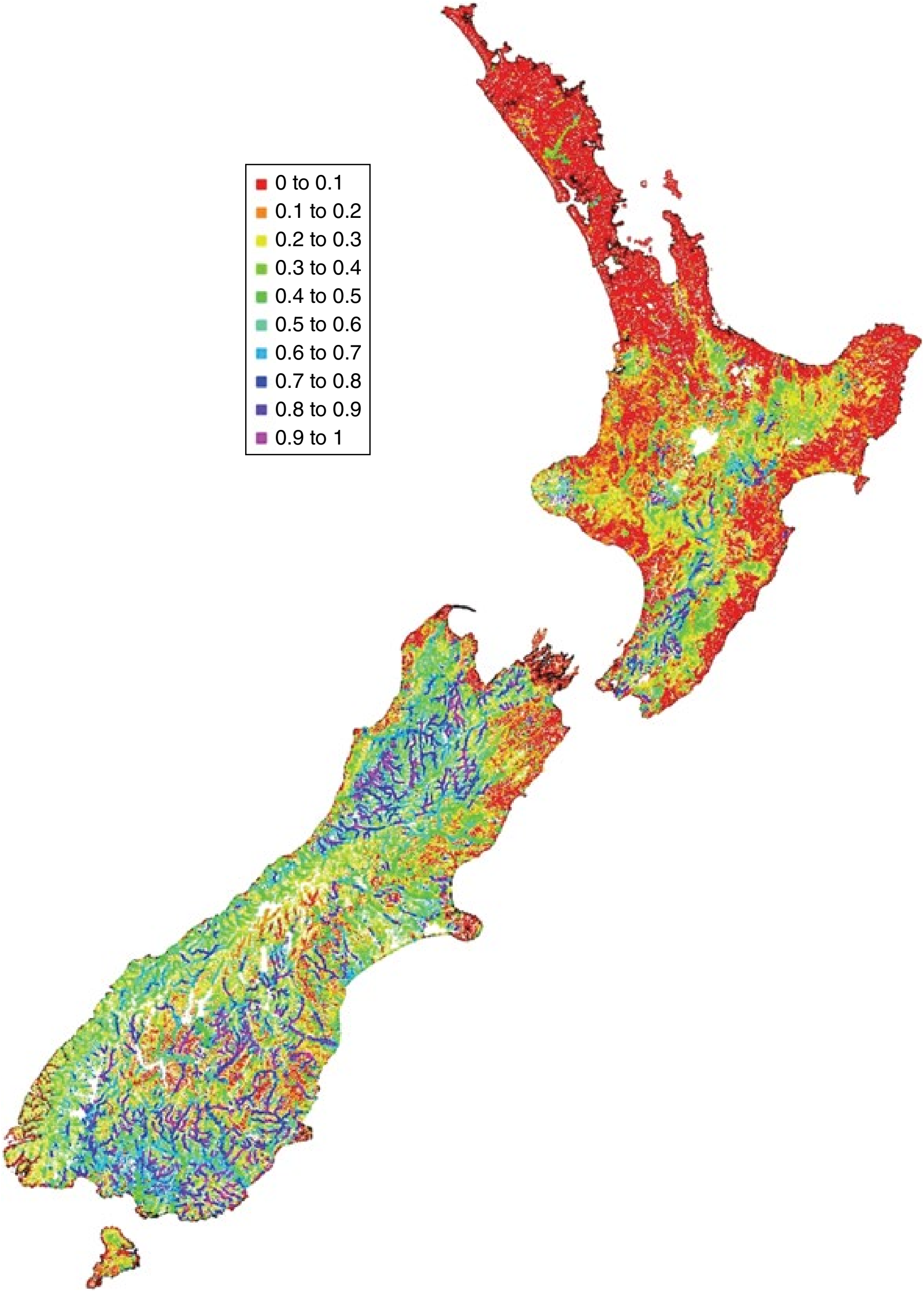

Figure 22.2 Predicted probability of brown trout occurrence of from electric fishing data collected in river reaches around New Zealand. The model uses presence/absence data from approximately 30,000 freshwater fish records to determine the probability of capturing brown trout in a river reach based on a suite of spatial, environmental and hydrological variables that represent that particular river reach. Red-coloured segments indicate there is <10% chance of capturing a brown trout whereas magenta segments indicate there is >90% chance of capturing brown trout. Prediction map generated by S.K. Crow, NIWA.

levels described below. Essentially, the introduction of trout brought a new kind of predator to New Zealand waterways. Various native fish probably had some day-active drift-feeding components to their foraging behaviour prior to trout introduction (e.g. giant kōkopu, *Galaxias argenteus*; Hansen & Closs, 2005), but none posed as big a day-time threat as brown trout due to the trout's high visual sensitivity and reaction distance. Thus, comparisons between the foraging of non-diadromous *Galaxias* which inhabited upland Otago streams prior to brown trout introduction and that of brown trout revealed a very big change; brown trout present a more day-biased pattern of foraging activity and a much higher predation risk compared to the native galaxiids (McIntosh & Townsend, 1995a). In contrast to brown trout, most native fish are either mainly nocturnal or more benthic in their mode of foraging (McIntosh, 2000a), which generally means that brown trout are more effective predators, consuming more prey in equivalent situations than native predatory fish (e.g. Nilsson *et al.*, 2006; Jellyman & McIntosh, in review).

The major consequence of this shift in both the timing and magnitude of predation risk has been an enhanced disposition for nocturnal behaviour in the at-risk inhabitants of streams where brown trout are present. In a stream channel experiment, *Nesameletus* mayflies sourced from Otago brown trout streams had more strictly nocturnal patterns of foraging and movement behaviour in comparison to *Nesameletus* from streams with only galaxiids present (McIntosh & Townsend, 1994). In multiple tributary streams of the Taieri River system in Otago, the foraging patterns of *Deleatidium* mayflies were also more nocturnal than those in equivalent streams with only non-diadromous *Galaxias* present (McIntosh & Townsend, 1995b).

These patterns of trout-induced invertebrate behaviour are likely to be widespread and general. A study of 16 Canterbury High Country streams, for example, revealed highly nocturnal patterns of invertebrate drift and suppressed drift magnitudes in streams with mostly brown trout, whereas in streams with native fish only or no fish either drift magnitudes were higher and/or day-night periodicity was reduced (Drinnan, 2000) (Figure 22.3). These patterns of behaviour also concur with those found elsewhere around the world whereby increasing risk of predation by drift-feeding diurnally-active salmonids has led to increasingly nocturnal behaviour in vulnerable stream invertebrates, especially mayflies (Flecker, 1992; Douglas *et al.*, 1994; McIntosh *et al.*, 2002).

Importantly, these patterns of trout-induced behavioural change also have consequences for other trophic levels, with the restrictions on daytime activity due to the presence of trout causing reduced grazing of algae in New Zealand streams (Flecker & Townsend, 1994; McIntosh & Townsend, 1996; McIntosh, 2000a). Moreover, effects are not restricted to grazing invertebrates; the daytime activity of predatory stoneflies like *Stenoperla* is reduced in the presence of brown trout (McIntosh, 1994). It had been proposed that large detritivorous invertebrates like the leaf-shredding caddisfly *Zelandopsyche ingens* might be less vulnerable to predatory fish like brown trout because they may be protected amongst the detritus that constitutes stream leaf packs. That is not the case, however. *Zelandopsyche ingens* are highly vulnerable to brown trout, and in fact build much more substantial cases in the presence of brown trout (McIntosh *et al.*, 2005).

Another likely individual-level consequence of trout influences on invertebrate prey is altered body size distribution associated with life history changes to growth and development. The presence of predatory salmonids can bring about large alterations in

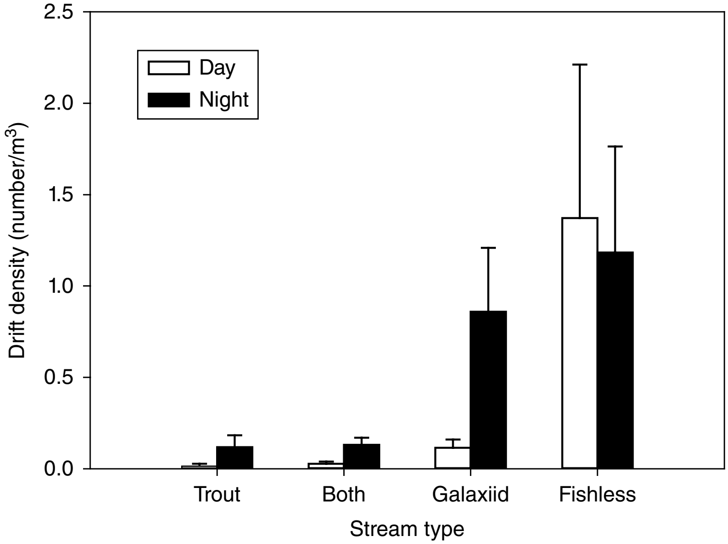

Figure 22.3 Drift density (mean + SE) during the day and night of *Deleatidium* spp. mayflies in streams (n = 4 in each category) of the upper Waimakariri River catchment differing in the presence and absence of either predatory trout (mostly brown trout) or native Canterbury galaxias (*Galaxias vulgaris*). Other characteristics of the streams were not significantly different. From Drinnan (2000).

prey body size through a range of mechanisms (e.g. Peckarsky *et al.*, 2008), and while this sort of influence has not been fully investigated in New Zealand, there is evidence such effects are likely to be important. A suite of invertebrate taxa from different orders, including *Archichauliodes* (Megaloptera), *Aphrophila* (Diptera), *Zealandoperla* (Plecoptera), *Polyplectropus* (Trichoptera) and *Nesameletus* (Ephemeroptera), had generally smaller body sizes in streams containing brown trout compared to similar neighbouring streams containing only non-diadromous *Galaxias* (Huryn, 1998; Townsend & Thompson, 2007). Drift-feeding salmonids are size-selective foragers and preferentially select larger individuals and taxa, and the smaller prey body sizes observed in the presence of brown trout are consistent with a range of international studies reporting adaptive body size alterations, sometimes caused by life history switches (e.g. Peckarsky *et al.*, 2001), in response to salmonid predation risk.

Alterations to prey behaviour and life history caused by predators are sometimes associated with subsequent nonconsumptive effects (i.e. effects caused by ‘fear’ rather than actual predation) on fitness (e.g. Peckarsky *et al.*, 2008). Only one rather surprising example of this has been investigated, in association with the brown trout predation on *Z. ingens* caddisflies. Brown trout, when present, greatly suppress *Z. ingens* abundance, and this releases the few remaining *Z. ingens* individuals from intraspecific competition, allowing them to grow much faster and to subsequently attain a much greater size than larvae developing in fishless streams (Greig & McIntosh, 2008). The effect on the fitness of these few remaining individuals is not insubstantial; a 33% increase in fecundity. Nevertheless, this is not enough to offset the 71% reduction in abundance due to trout, and the net effect is an estimated 54% reduction in subsequent caddisfly eggs produced (Greig & McIntosh, 2008).

Figure 22.4 Schooling kōaro (*Galaxias brevipinnis*) in a troutless lake in the South Island of New Zealand. Such phenomena are very rarely observed in lakes containing brown trout.

The effects of brown trout introductions on the behaviour and life history of native fishes have received rather less attention than these influences on invertebrates. This is probably attributable to the paucity of co-occurrence between brown trout and many native fish, making comparisons of native fish behaviour and life history in the presence and absence of brown trout difficult (but see Jones *et al.*, chapter, this book). Nevertheless, there is good evidence indicating considerable influence by brown trout on native fish individuals. Firstly, anecdotal observations of habitats lacking trout reveal native fish behaviours which are not observed in habitats where trout are present. For example, pelagic schools of juvenile kōaro (*Galaxias brevipinnis*) can be observed in the few trout-free lakes remaining (Figure 22.4) and were commonly recorded by early explorers (McDowall, 1990) prior to trout introduction, whereas these have never been reported in lakes where there are trout present. Similarly, Hayes (1996) reported observing surface-feeding kōaro in the pools of a trout-free stream, whereas kōaro are typically exclusively nocturnal in streams with trout (Glova & Sagar, 1989).

Experimental comparisons of native fish behaviour indicate brown trout tend to be dominant over native fish. Cadwallader was the first to address this issue in a series of field and laboratory studies (e.g. Cadwallader, 1975). McIntosh *et al.* (1992) observed that a non-diadromous Otago galaxiid was forced to occupy sub-optimal habitats with lower water velocity when brown trout were present. Finally, Edge *et al.* (1993) conducted a series of laboratory observations of the behaviour of three Otago non-diadromous *Galaxias* species, sourced from trout-free streams, in the presence of small brown trout. Considerable variation in behavioural responses was observed, but all galaxiids fed less frequently in the presence of brown trout compared to when trout were absent. Considerable work was done by Glova and colleagues (e.g. Glova *et al.*, 1992) in multiple studies to assess the effects of brown trout in various assemblages on native fish feeding and diet, but these comparisons were complicated by the lack of trout-free controls.

Building on this breadth of work describing the individual consequences of brown trout presence on invertebrate and fish behaviour, McDowall (2003) proposed there was a feedback loop whereby: 'native fish may be less able to obtain food owing to changes in their own behaviour, insect behaviour, and insect abundance, all of which are induced by trout predation (p. 229)'. Some of the components of this feedback loop have been demonstrated, as discussed above and in the population section below (i.e. changes in native fish activity, and changes in insect prey abundance, activity and life history), but the extent to which those behaviour-induced influences have affected native fish fitness and ultimately abundance or distribution still remains largely unknown. Mostly it has been the direct effects of brown trout predation on native fish that have been investigated rather than the combination proposed by McDowall in his 2003 paper.

Population Level Impacts of Brown Trout

Brown trout have had a number of direct and indirect impacts on the distribution and abundance of native fish. Many of the most identifiable impacts have been at the population level, and have occurred through predatory impacts on invertebrates and native fish, and via competitive displacement of native fishes in the numerous catchments where trout and native fish distributions overlap.

Impacts on Invertebrate Populations Due to Brown Trout Predation

Aquatic invertebrates are the primary food resource for the majority of native fish species in New Zealand streams but the widespread introduction of brown trout has altered invertebrate behaviour (McIntosh & Townsend, 1994), abundance (Jowett, 1992), size structure (Townsend & Thompson, 2007) and in some streams, secondary production (Allen, 1951; Huryn, 1996). As a drift-feeding fish, brown trout require more prey resources per unit time than benthic feeding fishes (i.e. most native species) because drift feeding is energetically 'expensive'. Consequently, brown trout would be expected to have a strong association with their invertebrate prey. Jowett (1992) found that the variable which explained the most variation in trout abundance at 89 sites in large rivers throughout New Zealand was total invertebrate biomass. Recent research has shown that brown trout can also have considerable effects on invertebrate density and biomass in small streams (Flecker & Townsend, 1994; Huryn, 1998). Whether or not the trout-induced impacts on invertebrate populations observed in smaller streams – where the trout population is 'stunted' (i.e. brown trout do not grow larger than 250 mm) – also occur in bigger rivers with large trout (sensu those surveyed by Jowett, 1992) has not yet been researched in New Zealand.

There are clearly severe impacts of brown trout on benthic invertebrate populations in some New Zealand streams (McIntosh, 2002), but the impact trout exert is likely to be context-dependent (Jellyman *et al*., 2013). In physically benign streams (e.g. stable bed substrate, low flow variability and low flood frequency), brown trout can achieve high biomass but their predation efficiency can be reduced through various prey defences (see previous section for examples) (Figure 22.5). The biomass of morphologically-defended (i.e. protective case) invertebrates is highest in benign streams, but unlike in other parts of the world where these invertebrates may grow large enough to escape fish predation (Wootton *et al*., 1996), this does not appear to occur in New Zealand because brown trout can consume even the largest cased caddisflies (McIntosh *et al*., 2005). As streams become more physically disturbed, the biomass of morphologically-defended invertebrates declines and the relative proportion of undefended prey in the invertebrate

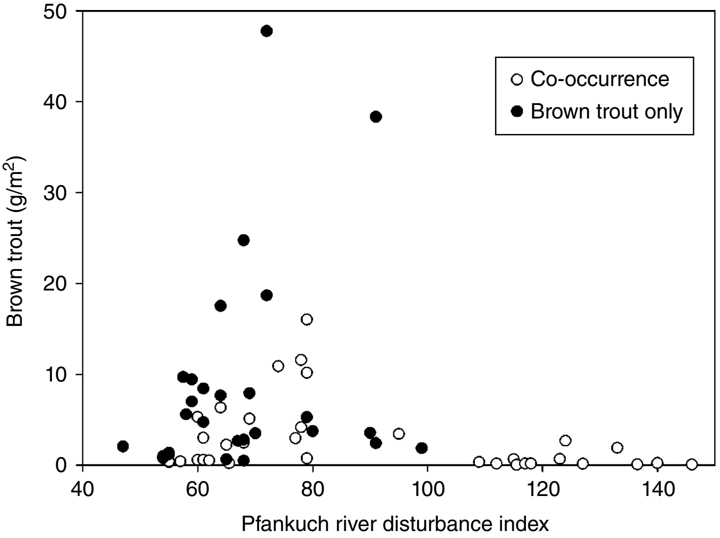

Figure 22.5 Variation in brown trout biomass across a gradient of flooding-related river disturbance (measured by the Pfankuch river disturbance index). Brown trout achieve particularly high biomass at moderately disturbed sites, and are often able to exclude/eliminate galaxiids from such sites. As sites become highly disturbed, brown trout biomass decreases and they no longer completely exclude galaxiids. The range of the Pfankuch river disturbance index is 38–152; small numbers indicate the waterway is stable whereas a larger number signifies the waterway is physically unstable/highly disturbed (see Jellyman *et al.*, 2013 for further details). Data from electrofishing sites in Canterbury, New Zealand from 1998–2009.

community increases (Jellyman & McIntosh, in review). Brown trout biomass seems to peak in streams which are moderately disturbed (Figure 22.5) which may be linked to: (1) an increase in the relative proportion of their preferred undefended prey; (2) an increase in the mean size of their preferred prey once undefended prey have less competition from defended taxa; or (3) increasing drift propensity as rivers start to become more disturbed (Jellyman & McIntosh, in review). A decline in the biomass and size of eels, the largest native predatory fish, as rivers become increasingly affected by disturbance may also contribute to higher brown trout biomass at moderately disturbed sites (Jellyman *et al.*, 2014, Figure 22.5).

Compared to streams, the effect of brown trout on benthic invertebrates in lakes has received almost no attention. Anecdotal evidence suggests that trout introductions are likely responsible for declines in the abundance of two large-bodied freshwater invertebrates (crayfish, ‘koura,’ *Paranephrops planifrons* and crabs, *Halicarcinus lacustris*) from North Island lakes, although quantitative data are not available (McDowall, 1990). To date, there has only been one study that has comprehensively examined the impact of trout on lake benthic communities (Wissinger *et al.*, 2006). In contrast to streams, the study found few impacts on benthic community composition or biomass in lakes with and without trout (Wissinger *et al.*, 2006). Wissinger *et al.* (2006) suggested that extensive vegetation, benthic invertebrate traits and a tendency towards piscivory over benthivory by large trout in high clarity lakes might explain why trout exert weak predation pressure on the benthic invertebrate community in these habitats.

Predatory Impacts of Brown Trout on Different Native Fish Life Stages

The impact of brown trout on native fish species varies with life stage, as does the mechanism by which brown trout affects these fishes. For larval and juvenile native fish, predation is the major threat posed by brown trout, but for adult native fish it can be either predation or competition, or as is often the case, a combination of both. The larvae of diadromous species are either already at sea or are quickly washed out to sea when they are very small (<10 mm) so predatory impacts of brown trout are on the returning juvenile and adult life stages. Non-diadromous species spend their entire lifecycle in fresh water so all life stages can potentially be exposed to brown trout predation.

Diadromous fishes from the families Galaxiidae (galaxiids) and Retropinnidae (smelt) can be heavily preyed upon when they enter fresh water by large, anadromous and estuarine-living brown trout as these trout attempt to recover condition following the previous winter's spawning (McDowall, 1990). Although all juvenile diadromous species are at high risk of predation when re-entering fresh water, the risk to galaxiids and smelt fishes is much higher because at this life stage they are typically shoaling, pelagic fish. Galaxiids and smelt are also larger prey (45–60 mm long, but commonly 50–55 mm) for brown trout compared to other diadromous species re-entering fresh water such as bullies (*Gobiomorphus* spp.) (15–20 mm) and torrentfish (*Cheimarrichthys* sp.) (25–35 mm) (McDowall, 1990). The predation risk to juvenile (and adult) native fish from brown trout may be greatest around the southern coasts of New Zealand where lower temperatures may result in a higher proportion of anadromous brown trout (McDowall & Eldon, 1980; McDowall, 2006). The heaviest losses due to predation by brown trout are probably inflicted upon īnanga (*G. maculatus*) because it is the most abundant pelagic fish that re-enters fresh water each year (McDowall, 1990). Because īnanga does not penetrate far inland, their distribution overlaps with that of anadromous and estuarine-living brown trout across the majority of its range. Whilst large brown trout may heavily prey on juvenile and adult īnanga (which typically grow to 100–120 mm long), Bonnett & McIntosh (2004) found no identifiable impacts of juvenile brown trout (65–115 mm) on īnanga (51–100 mm) in a stream mesocosm. Moreover, high rates of density-dependent mortality later in the life cycle of īnanga may mean that mortality of the juvenile migratory stages, such as that due to trout predation and harvesting, are only compensatory because their populations are generally not recruitment-limited and conditions in adult habitat generally limit population abundance. In comparison, because brown trout are widespread, predation on juvenile kōaro is likely to be particularly intense and may be more influential on adult numbers because this species can penetrate up to several hundred kilometres inland and brown trout are likely to be present along much of their migration route (Allibone & McIntosh, 1999). Influences of brown trout predation on the juvenile stages of the other New Zealand diadromous galaxiids may fall somewhere in between these two extremes, but remain largely unstudied.

The other large, juvenile fishes immigrating into fresh water are glass eels (*Anguilla* spp.), but they are smaller (0.2 g) than *Galaxias* spp. juveniles (0.4 g) and may not be as actively targeted by brown trout. Glass eels can form estuarine shoals which are known to be consumed by adult brown trout (Kennedy & Fitzmaurice, 1971), although this impact has never been quantified in New Zealand. Because elvers live in river gravels, the risk of brown trout predation to this eel life stage is likely to be much lower, except around migration barriers where brown trout may congregate and consume elvers as they try to negotiate structures such as dams (Jellyman, 1977). Moreover, as noted in a later section, eels eventually grow to a size where the threat of predation can become reversed, so the influences on population dynamics may be quite different.

For non-diadromous native fish (and landlocked galaxiid, smelt and bully species), the threat of brown trout predation exists as soon as the larvae hatch from eggs. As described above, the winter spawning of adult brown trout gives their YOY offspring a major size advantage over native fish which start to hatch from spring onwards (Figure 22.1). Whilst non-diadromous bullies are a major food source for brown trout, particularly in lakes (McDowall, 1990), the impact of trout on bully populations has not been measured; research into brown trout impacts on non-diadromous native fish has been largely focused on stream-dwelling galaxiid fishes. In streams where brown trout are abundant, larval settlement and survival of native fish can be impacted through a negative feedback loop. Brown trout initially limit the abundance of native fish, resulting in fewer spawners, and then trout consume the larvae that are produced, translating into rapid declines of native fish populations over time (Jellyman & McIntosh, 2008; 2010). An experiment assessing brown trout predation of non-diadromous *Galaxias* fry found fry losses were over four times higher with brown trout present with 85% of fry lost in 48 hours (Jellyman & McIntosh, 2010). Beyond juveniles, the density of non-diadromous *Galaxias* adults is also much lower in streams containing brown trout (McIntosh *et al.*, 1994; Jellyman & McIntosh, 2010). Field surveys and experiments have shown that there is no size refuge for non-diadromous galaxiids from predation by large trout (>150 mm long) – all sizes of galaxiids can be consumed (McIntosh, 2000b).

Effects on Native Fish Species Distributions

Because brown trout are widely distributed throughout New Zealand, they have the potential to impact almost all species in the native fish fauna. Native fish from the families Galaxiidae and Retropinnidae make up the majority of species in the native fauna, and in an analysis of the effects of salmonids on these fish families, McDowall (2006) cited brown trout as a serious threat for 79% of the species. Moreover, this percentage is likely to have increased as more species from these families have recently received a threatened fish ranking (see Goodman *et al.*, 2014). The impact of brown trout on native fish has been severe but their full impact will never be known due to the near-total lack of native fish data prior to brown trout introduction and spread. Our understanding of brown trout impacts is therefore largely informed by limited historical accounts of native fisheries in certain areas of New Zealand (McDowall, 1990; 2006) and through contemporary studies examining the presence/absence of native fish in either trout-invaded catchments (Townsend & Crowl, 1991; Woodford & McIntosh, 2010) or across abiotic gradients of trout invasion (McIntosh 2000b; Leprieur *et al.*, 2006). Studies of brown trout impacts on native fish distributions in New Zealand have focused on riverine influences and their effects on native fish communities in lakes have received less attention.

The New Zealand fish fauna lacks specialist lentic fish species, so brown (and rainbow) trout have successfully filled this vacant niche in many catchments. Although brown trout are primarily regarded as a riverine fish (McDowall, 1990), the creation of dam reservoirs in many parts of New Zealand has undoubtedly facilitated the introduction, establishment and proliferation of brown trout because they are able to use these artificial lakes as a 'stepping-stone' for their continued spread (Allibone, 1999; Jellyman & Harding, 2012). Because the outlets of many of New Zealand's large lakes have also been dammed for hydro-electric power generation, the impact of brown trout on native fish may have been exacerbated due to eels frequently being prevented from accessing habitats above dams potentially, thereby allowing juvenile brown trout to proliferate in the absence of predation pressure (discussed further below). In lakes where brown trout compete with *Galaxias* fishes, brown trout are the dominant species and *Galaxias* fishes are displaced (Allibone, 1999). The clearest example of this is from New Zealand's largest lake, Lake Taupo, where stocks of juvenile kōaro had long provided a valued food supply for local Māori communities living around the lake shores (McDowall, 1990). The introduction of brown trout to the lake in 1886 rapidly led to a huge population of large trout which fed on the vast shoals of juvenile kōaro (Phillipps, 1924); in the early 1900s trout had become so abundant that it was suggested that 2000–3000 tonnes could be taken out of the lake every year without any harm being done to trout stocks (Fletcher, 1919; McDowall, 2006). However, native kōaro 'underwent very substantial decline in abundance' due to trout predation to such an extent that the trout were starving because their primary food resource was so depleted (McDowall, 2006). Kōaro stocks in Lake Taupo have never recovered, most likely because of the heavy lake predation and also competition between trout and adult kōaro in the tributaries (Kusabs & Swales, 1991). The decline in food availability for trout has been alleviated by introducing indigenous common smelt (*Retropinna retropinna*) into the lake, which is now the major source of food for the current trout population (McDowall, 2006).

While the impact of brown trout in New Zealand lakes has been substantial, the greatest impact of brown trout has been in streams. Brown trout have been linked to the extinction of New Zealand grayling (*Prototroctes oxyrhynchus*), the only species in the freshwater fish fauna to have disappeared since European settlement (McDowall, 1990). However, like many native fish declines, the grayling extinction also occurred at a time of rapid land-use change in New Zealand, so declines in habitat quality may have also been involved. Nevertheless, many contemporary studies have been able to separate these influences, and brown trout have mutually exclusive distributions with many native *Galaxias* species (McDowall, 1990; Townsend & Crowl, 1991).

Prior to the study of Townsend & Crowl (1991) it was argued that reductions in native fish abundance and distribution were primarily a result of land-use change and not brown trout invasions. By examining fish distribution patterns in Otago catchments with differing land uses, the negative effect of brown trout on native fish was disentangled from the influence of land use. The presence of waterfalls at least 3 m high downstream of a sampling site was the best predictor of *Galaxias* occurrence because waterfalls prevented brown trout from penetrating into upstream habitats, where galaxiids were present, whereas below the waterfalls galaxiids were repeatedly absent (Townsend & Crowl, 1991).

The presence of brown trout, however, does not necessarily mean that galaxiids will be extirpated. As rivers become increasingly disturbed, brown trout co-occurrences with galaxiids increases (Figure 22.5). As previously mentioned, it appears native fish such as galaxiids may be better adapted than brown trout to flood-prone conditions, because co-occurrence is most common under such conditions. Nevertheless, these conditions may be far from optimal for native species because they are known to utilise different habitats and flow conditions when trout are absent (Townsend, 1996; Chadderton & Allibone, 2000; McIntosh, 2000b). For non-migratory *Galaxias* species

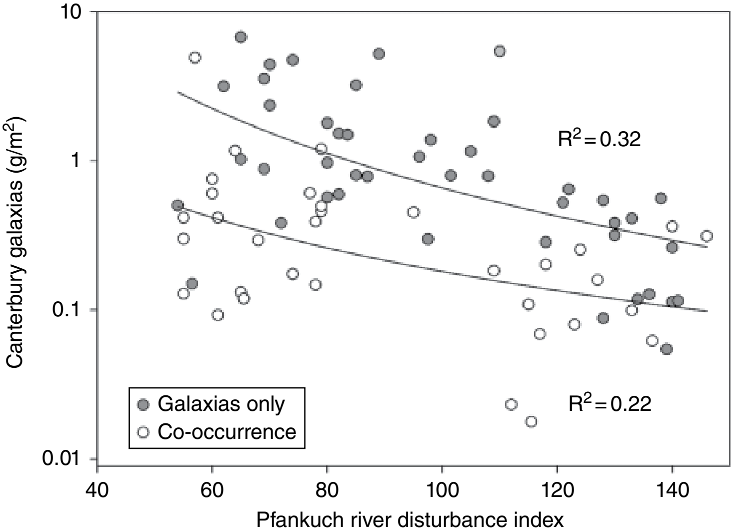

Figure 22.6 Variation in Canterbury galaxias biomass across a gradient of river disturbance at sites with (white) and without (grey) trout. It is evident that co-occurrence with trout has an impact on Canterbury galaxias biomass across the disturbance gradient. Data from sites electrofished in Canterbury 1998–2009.

in particular, the presence of brown trout is likely to have an impact on abundance across the disturbance gradient (i.e. from physically benign to highly disturbed waterways) because *Galaxias* biomass is consistently higher in streams when trout are absent, regardless of disturbance (Figure 22.6).

One of the main reasons that brown trout impacts on non-migratory *Galaxias* species seems to be so much higher than for other native species (e.g. non-migratory bullies) is that brown trout and non-migratory *Galaxias* have similar habitat and food requirements (Cadwallader, 1975; McHugh *et al.*, 2012). Stable-isotope analysis suggests that galaxiids occupy the same trophic position as trout in food webs, regardless of trout presence or absence. Some galaxiid species may be able to make subtle changes in behaviour (e.g. prey choices or use a narrower resource set) to facilitate long-term co-occurrence (Glova & Sagar, 1991; 1993; McHugh *et al.*, 2012), and whether or not native species can exhibit some niche flexibility in the presence of brown trout may be a critical factor in determining to what extent their catchment, regional and national distributions are affected by brown trout.

Interactions Between Brown Trout and Larger Native Fish Species

As previously noted, the predatory impacts of brown trout on the New Zealand native fish fauna are widespread and well-documented (McDowall, 2006; McIntosh *et al.*, 2010). However, not all native fishes are able to be eaten by brown trout. The largest native fishes are the shortfin and longfin eel, and these fish regularly grow to 1000 mm and 1200 mm, respectively (Jellyman, 1995). Trout regularly co-occur with eels but juvenile brown trout are often found in the stomach contents of eels (Jellyman, 1996).

Predation on trout, primarily juveniles, by eels meant that early trout-fishery managers considered eels as a serious threat to the sports fishery, thereby prompting an intensive campaign of eel destruction in some parts of New Zealand (McDowall, 1994). Whether eel predation actually affected a trout population was examined in a multi-year experiment (1959–1964) where more than 2,700 eels were removed from a spring-fed stream in which a fish trap had been installed (Burnet, 1968). With almost all eels removed, the brown trout population increased on average by 250% (some study reaches had a tenfold increase), primarily due to increases in juvenile trout. Consistent with Allen (1951), who showed that increasing trout abundance negatively impacted trout growth, trout growth rates also halved following eel removal in the Burnet study (i.e. time needed to reach 280 mm increased from two to four years). Moreover, the increase in juvenile trout abundance also reduced condition of larger trout (Burnet, 1968). Thus, ironically, it appears that predation by eels can facilitate a trout fishery of greater value by suppressing juvenile trout abundance and indirectly enhancing growth of larger adult trout.

With the notable exception of eels, brown trout are typically larger than New Zealand's native fish species because most galaxiids, smelt and bullies are smaller than 125 mm in length. However, native kōkopu species commonly grow to over 200 mm and the largest of the three species, giant kōkopu, regularly grows to 300–400 mm (McDowall, 1990). In a study examining the distribution of brown trout and giant kōkopu in small streams, distinct longitudinal separation of the two species occurred (David *et al.*, 2002). The authors suggested that large giant kōkopu, which can be piscivorous and territorial, were capable of excluding similar-sized (and smaller) brown trout at a local scale. Goodman (2002) reported shortjaw kōkopu (*Galaxias postvectis*), another galaxiid that can reach relatively large sizes, co-occurred at local scales with brown trout, but were more likely to be absent when trout abundance was high. Overall, whilst limited overlap in the spatial distribution of brown trout and some kōkopu species may occur at a local scale, brown trout still likely pose a serious threat to all kōkopu species (McDowall, 2006).

Community-Wide Effects of Brown Trout

In addition to influencing the behaviour and demography of New Zealand's native fish and invertebrates through mechanisms like competition and predation, brown trout have effects on whole aquatic communities that are also noteworthy. Here we consider two components of community-level impacts of brown trout: effects on community structure (food-web structure and community composition) and effects on community processes.

Community structure can be characterized in many ways, but metrics describing food-web architecture offer useful insight by integrating feeding relationships that underpin energy and nutrient flows. In a broad sense, the introduction of brown trout can affect the structure of stream food webs in one of three ways, trout may (1) replace existing top predators (i.e. substitution/replacement); (2) increase the richness of the existing predator community (i.e. net species gain); or (3) add a new trophic level (Eby *et al.*, 2006). Past work suggests that brown trout have primarily altered the trophic structure of riverine food webs in New Zealand in the first two ways. Evidence of food-web substitution is ubiquitous, indicated by the presence of trout and absence of galaxiids at sites that are otherwise suitable for the latter (reviewed in McIntosh *et al.*, 2010) and the similar trophic positioning of the two taxa (McHugh *et al.*, 2012). These observations suggest that high-level food-web summary statistics will not vary in the presence or absence of trout. Although not collected expressly for addressing brown trout research questions, data compiled from several published New Zealand stream food-web studies (Townsend *et al.*, 1998; Thompson & Townsend, 2005, McHugh *et al.*, 2010; 2015) suggest that this is in fact the case (Figure 22.7). The height (food-chain

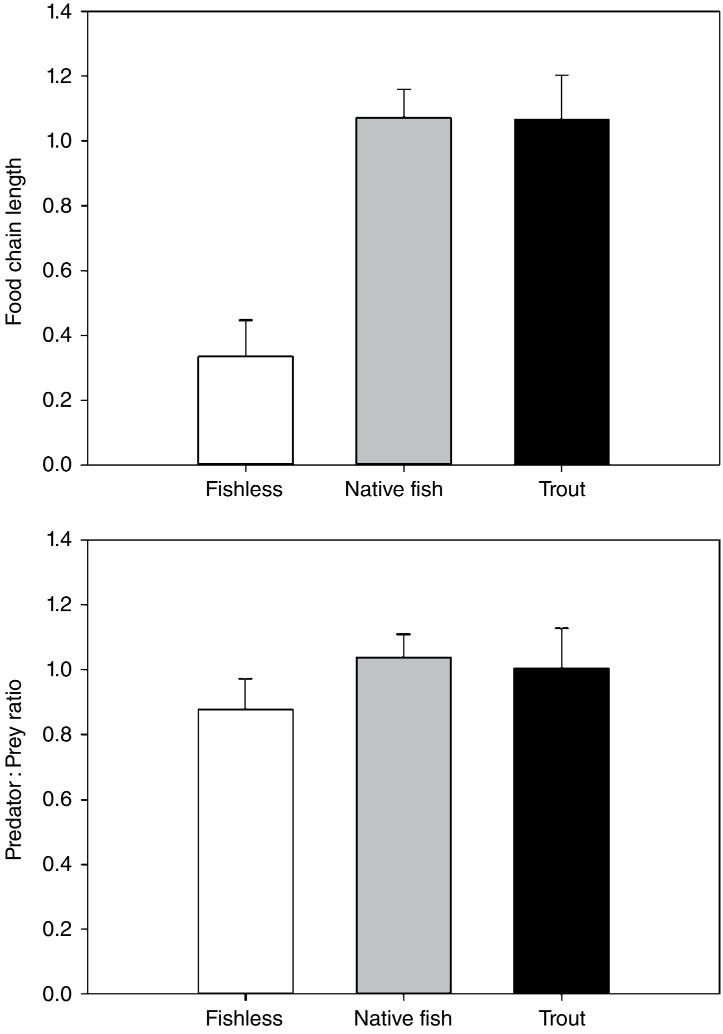

Figure 22.7 Food chain length (top) and predator:prey richness ratio (bottom) in streams without fish (n = 7), with native fish only (n = 20), and with trout present (n = 19). Values are means + 1 SD and were standardized to within-study/method minimum (food-chain length, standardized FCL = yij – min(yij)) and mean (predator:prey ratios, standardized ratio = yij/mean(yij)) values to facilitate comparisons across studies using different laboratory methods. Data are from Thompson & Townsend (2005) and McHugh *et al.* (2010, 2015).

length) and shape of food webs (predator:prey richness ratios) is essentially the same in fish-inhabited streams with and without trout. Thus, barring cases involving fishless streams, where trout introductions would lengthen food chains, the effect of trout on coarsely resolved food-web attributes is all but indiscernible.

Despite a generally modest effect on the structure of food webs, a different story emerges when the strength, not just the presence, of food-web interactions is considered. In particular, brown trout can have top–down effects that are sufficiently pervasive to propagate across trophic levels. Owing to their ability to consume nearly all invertebrate production within a stream (Allen, 1951) and/or alter the foraging behaviour of grazing mayflies (McIntosh & Townsend, 1995b), the presence of brown trout translates into reduced herbivory by mayflies, and in turn, greater algal biomass than is observed in the presence of native fishes (Flecker & Townsend, 1994; McIntosh & Townsend, 1996). Indeed, the case of brown trout and New Zealand streams is considered to be one of the better-documented examples of a top–down trophic cascade in modern ecology (Eby *et al.*, 2006). This strong top–down control is also related to changes in ecosystem-level processes, which we discuss in the following section. For more detailed reviews of this subject, see Townsend (2003), Simon & Townsend (2003), and McDowall (2003) and references therein.

One of the main drivers of community-level impacts of brown trout is likely to be changes in the size structure of the invertebrate community (Townsend & Thompson, 2007). Body size distributions are thought to be a 'super driver' of food-web structure (Cohen *et al.*, 2003) because they drive predator–prey interactions. In a fishless stream in Britain the arrival of trout dramatically altered invertebrate size structure, with flow on effects for food-web structure and ecosystem function (Layer *et al.*, 2011). The lack of similar dramatic effects of trout invasion on food-web structure in New Zealand is likely explained by small trout occupying a similar trophic role to small-bodied native fish (Townsend & Thompson, 2007).

In contrast to streams, relatively little is known about how the structure of lacustrine communities has (or has not) been affected by brown trout, despite their long-standing (>100 year) presence in many New Zealand lakes. Available evidence from New Zealand lakes and temperate lakes with related Gondwanan taxa elsewhere (i.e. Tasmania, Patagonia) suggests that brown trout can alter lake food webs/communities; however, the presence and magnitude of impact appears to be highly variable. For example, the effect of brown trout on lake-dwelling benthic invertebrates, as noted above, is indiscernible in some lakes (Wissinger *et al.*, 2006) whereas native fish (Stuart-Smith *et al.*, 2007) and/or zooplankton communities (Jeppeson *et al.*, 2000; Reissig *et al.*, 2006) show a clear response in others. At the level of whole-lake food webs, effects are similarly variable. By causing their native galaxiid prey to forage at lower trophic levels, for example, brown trout have effectively eaten their way to shorter food chains in some Patagonian lakes (Correa *et al.*, 2012; Elgueta *et al.*, 2013). In contrast, clear segregation of trout and galaxiid niches was seen in a food-web study of a different and considerably larger/deeper Patagonian lake (Juncos *et al.*, 2015). In other systems, trout may have eliminated native top predators but continue to play a similar ecological role (Eby *et al.*, 2006).

Beyond descriptive food-web studies, a recent manipulative 'experiment' provides practical insight on the potential severity of brown trout effects at the community level. Duggan *et al.* (2015) tracked the response of the Lake Karori (North Island, New

Zealand) zooplankton and phytoplankton communities following the experimental removal of brown trout from the lake and catchment. Following removal, there was a general decrease in the abundance of large-bodied zooplankton, an increase in rotifers, and a concomitant shift in the phytoplankton community, all of which was concurrent with the timing of larval galaxiid recruitment. Thus, the removal of top predators (i.e. brown trout) from Lake Karori appears to have caused community change at multiple trophic levels. Taken together, these results suggest many lakes may have been quite different prior to the introduction of trout and underscore the need to understand how lake conditions (e.g. size/depth, temperature, morphometry, etc.) lead to stronger/weaker trout impacts.

Ecosystem-Level Alterations Due to Brown Trout

The influence of brown trout on ecosystem processes has received far less attention than the effects of trout at lower ecological levels, and studies are restricted to streams. While few in number, several studies provide clear examples of how brown trout have altered energy flux, nutrient dynamics and decomposition. The energetic role of brown trout was first examined in New Zealand by Allen (1951), who famously showed that brown trout feeding was so effective that there was a mismatch between the amount of prey that could be maintained and the biomass of the brown trout population (later termed 'Allen's paradox'; Huryn, 1996). This essentially meant that there seemed to be insufficient food to support the observed trout biomass. A later study showed that the production budget for brown trout only balanced when terrestrial prey, hyporheic invertebrates and trout cannabilism were included (Huryn, 1996; 1998). If brown trout could consume all the available benthic invertebrate production then clearly trout had the potential to have a major impact on invertebrate communities (Tillyard, 1920; McDowall, 2006). In contrast, native *Galaxias* fishes were consuming only a modest proportion (~18%) of benthic invertebrate production (Huryn, 1998). These findings further highlight how remarkable it is that the simple measures of food-web trophic structure, like food chain length, described above are very similar.

The trophic cascade induced by brown trout results in higher algal biomass that presumably should result in higher rates of primary production and altered energy balance at higher trophic levels. Huryn (1998) examined this issue by contrasting highly detailed production-demand budgets for a stream with native fish and a stream with brown trout. He found rates of net primary production up to six times higher in the trout stream. Differences in algal productivity were variable over the year, with greatest differences in late summer and most similar rates in winter. Only a small portion (21%) of the algal production in the trout stream was consumed by invertebrates while essentially all algal production was consumed by invertebrates in the stream with native *Galaxias*. Somewhat surprisingly, rates of secondary production by primary consumers in the two streams were virtually identical. It appears that in streams with native fish, primary and secondary production are tightly connected with top–down and bottom–up constraints balanced. The addition of trout decouples these processes by exerting substantial top–down control. Indeed, energy demand by trout was nearly ten times higher than that of native fish. Biggs *et al.* (2000) quantified rates of primary production and community respiration on substrates from pairs of trout and *Galaxias* streams with chamber respirometers. While algal biomass tended to be higher in trout streams, rates of primary production and respiration were similar between stream types. Metabolism estimates were highly variable in that study, likely reflecting the difficulty in accurately quantifying system metabolism with the chamber method. In that same study, nutrient diffusing substrates were used to examine nutrient limitation of biofilms. All streams were nitrogen limited and the presence of trout did not enhance bottom–up limitation by alleviating grazing by herbivores.

The consequences of trout-induced trophic cascades for nutrient dynamics have been explored in more detail through the use of stable isotope tracer additions. Simon *et al.* (2004) conducted long term $^{15}NH_4^+$ additions to a trout and *Galaxias* stream to quantify whole-stream nitrogen demand and nitrogen uptake through the food web. Given trout can increase algal biomass it might be expected that they would boost demand for nitrogen. Somewhat surprisingly there was no difference in demand for ammonium, although nitrate demand was somewhat higher in the trout stream (Simon *et al.*, 2005). While there was no large difference in total demand for nitrogen, analysis of nitrogen uptake into the food web showed a major reorganisation of where nitrogen was cycling. Most of the nitrogen uptake and retention occurred in riffles where biofilms were much more active, and this is where the effect of trout was manifested. In the trout stream, most nitrogen was routed through algal biofilms in riffles whereas in the *Galaxias* stream, uptake was more evenly distributed across primary uptake compartments (algal films, coarse and fine organic matter) in riffles and pools. This rerouting of nitrogen cycling appears to have been due to suppression of grazers, especially *Deleatidium* mayflies, in riffles. In the trout stream those grazers accounted for less than half as much nitrogen uptake as in the *Galaxias* stream. Analysis of natural abundances of carbon and nitrogen isotopes confirmed that *Deleatidium* had shifted their diets from algal biofilms to other foods. It appears that the trout-induced changes at the individual, population and community levels change where, and through whom, nutrients were cycling.

The potential for trout to induce cascading effects on decomposition have also been examined in New Zealand streams. Greig & McIntosh (2006) used experimental mesocosms to parse out the potential effects of trout on leaf decomposition through lethal and non-lethal effects on leaf shredding invertebrates. They found that trout suppress leaf decomposition rates by reducing the abundance of the leaf-shredding caddisfly *Zelandopsyche ingens*. These animals were insensitive to trout chemical cues indicating that non-lethal effects of trout did not influence shredders and their potential to decompose leaves. This is an interesting contrast to the cascading effects on algae where grazer abundance and behaviour responses to trout are both important. Subsequent comparisons of real streams with trout to streams with no fish confirmed the suppression effect of trout on leaf decomposition. The effect was again mediated through *Zelandopsyche*, which were present in fishless streams and all but absent in streams with trout. This type of top–down control of detrital pathways is rarely seen in other contexts. It appears that the strong effect of trout on the large, vulnerable shredder *Zelandopsyche*, combined with the absence of other effective shredders that could be resistant to trout, results in the clear trophic cascade affecting the 'brown' (i.e. detrital) food web. Thus, the clear cascading effect of trout on decomposition may be a unique consequence of low diversity of shredding invertebrates in New Zealand streams.

Spatial Extent of Brown Trout Effects

Judging from the volume of literature detailing the impacts of non-native brown trout in New Zealand, one might assume that a story of 'trout introduction = native system decline' is unilaterally true. Yet, it has become increasingly apparent in recent years that the presence and/or extent of impact by brown trout within invaded systems can vary considerably across space and time and as a result of physical (e.g. flood disturbance; McIntosh, 2000b) and spatial (e.g. source-sink dynamics; Woodford & McIntosh, 2010) processes. This suggests that to fully understand and manage the undesired consequences of brown trout invasions, a landscape-level and non-equilibrium view of riverine fish assemblages is needed and, further, that patterns must be considered at multiple scales.

Overall, brown trout have a very widespread distribution in the South and North Islands of New Zealand, although they are absent from most offshore islands, including Stewart Island. Given almost 150 years of human-assisted dispersal, they are very likely to now be present in all accessible potential habitat, and some inaccessible habitat where they have been transported above barriers. In some areas, however, invasions are still ongoing, such as cases in Otago and Canterbury where brown trout are known to have accessed previously trout-free reaches in the last ten years. For example, brown trout were first recorded in the upper reaches of Coach Stream in the headwaters of the Waimakariri River during 2008 after being absent from electrofishing surveys during the previous eleven years. These fish, which traversed a previously inaccessible road culvert, have subsequently eliminated Canterbury galaxias from the invaded reach (Jellyman & McIntosh, unpublished data).

More broadly, the extent of brown trout distribution can vary markedly at the subcatchment, whole catchment, regional and national scale. For example, 85% (30.1 out of 35.2 km surveyed) of fish inhabited river length in two headwater branches of the Waimakariri River (Woodford & McIntosh, 2013; although this estimate is for brown and rainbow trout combined). In contrast over the whole of the North and South Islands, based on the modelling approaches of Crow *et al.* (2013) and taking into account the distributional influences mentioned above, current model estimates indicate brown trout are present in around 38% of modelled river segments where at least one fish is present (S.K. Crow, pers. comm.). Combining all salmonid species, that figure increases to 42%. In general, across these river networks, brown trout have the largest spatial coverage after longfin eels, and in terms of non-diadromous fish, brown trout have roughly the same spatial coverage as all remaining non-diadromous species combined (S.K. Crow, pers. comm.). Thus, brown trout are very widespread indeed, so the impacts described above are likely to have had a pervasive influence on the trophic webs of New Zealand rivers.

Brown trout's ubiquitous distribution, combined with the existence of localized native-fish refugia (e.g. above waterfalls [Woodford & McIntosh, 2013] or upstream of drying segments [Leprieur *et al.*, 2006]) sets the stage for source-sink metapopulation dynamics at the catchment scale (Woodford & McIntosh, 2010; 2013). Two trout-invaded South Island catchments (the Broken and Porter rivers) provide excellent case examples of this phenomenon. In both systems, small trout-free tributaries 'leak' *Galaxias* larvae to mainstem habitats where trout predation (primarily) and habitat instability otherwise limit local reproductive success (Woodford & McIntosh, 2010). Woodford *et al.* (2011) also showed that *Galaxias* persistence in sink environments depends on where one is located within the river network. Such landscape-scale processes undoubtedly explain some of the localized cases of trout–galaxiid 'co-existence' that researchers have sought to explain with reach-scale variables and without deference to catchment context (e.g. McIntosh, 2000b; McHugh *et al.*, 2012). Further, these insights illustrate that network configuration, geomorphology, and hydrology can interact to moderate the response of native fish populations to trout invasions. Other work is also revealing that life history differences among galaxiids also affect the potential formation of these metapopulation dynamics (see Jones & Closs, Chapter 21, this volume).

Beyond space, there is a significant component of temporal variability in the impact of brown trout in New Zealand. A characteristically variable climate, combined with the negative influence of extreme hydrological events – both low-flow minima and floods – on brown trout populations (Leprieur *et al.*, 2006; McIntosh *et al.*, 2010; Holmes *et al.*, 2014), means that abundance in many catchments is in a constant state of flux and far below what it might be under stable flow conditions (McIntosh *et al.*, 2010; Jellyman *et al.*, 2013). In such systems, trout are either too few or too small to eliminate the native fauna which are typified by life histories that are well suited to the very dynamic environment (McIntosh, 2000b). This suggests that trout, too, may comprise source-sink metapopulations in some of New Zealand's braided river landscapes, given the juxtaposition of stable spring streams (sources) and constantly shifting alluvial channels (Gray & Harding, 2007). Importantly, strong hydrologic forcing of brown trout population dynamics means that changes to hydrology, e.g. due to the development of hydropower dams or irrigation schemes, may tip the balance in favour of brown trout in cases where intact native communities occur. Thus, facilitation of further trout influences on native fish could be an unintended consequence of further impoundment of New Zealand rivers (Jellyman & Harding 2012).

Conclusions

Understanding of the effects brown trout on the trophic webs of New Zealand streams has come a long way since Colin Townsend and Todd Crowl stimulated interest in the effects of brown trout introductions in New Zealand by launching their study in streams of the Taieri River catchment in Otago in the late 1980s (Townsend & Crowl, 1991). There have been investigations ranging across the whole range of ecological scales, including some textbook classics (e.g. Flecker & Townsend, 1994). Thus, it is safe to say that we now know a great deal about how brown trout have influenced New Zealand streams. Although fundamental measures of trophic structure, such as food chain length, have not altered, almost everything else about New Zealand streams has been affected by the introduction of brown trout. The identity and distribution of fish species has been changed, the behaviour and habitats used by fish and invertebrates have been altered, the abundance and community composition of invertebrates and fish have been affected, and the flow of energy amongst food-web compartments and overall productivity of ecosystems have been modified. Thus, the impacts of brown trout introductions on the trophic webs of New Zealand streams have been substantial and far-reaching.

Studies in other parts of the world where brown trout have been introduced are also revealing influences of brown trout on stream trophic webs, especially native fish populations (see McIntosh *et al.*, 2012 for a summary). For example, effects of brown trout on *Galaxias* populations have been detected throughout the range of the Galaxiidae family (i.e. Argentina, Australia, Chile and South Africa), underpinning McDowall's (2006) warning of the 'crying shame' that trout-related impacts had caused galaxiid fishes to be amongst the world's most endangered. Moreover, in some places understanding of effects of brown trout on freshwater trophic webs is more advanced than in New Zealand (e.g. the knowledge of brown trout influences on Patagonian lakes cited above).

Widespread international examination of controls on the type and extent of brown-trout influences on trophic webs is likely to be particularly fruitful because it could reveal information important for fisheries management. For example, flow regimes in New Zealand are often unpredictable and flashy and this appears to play a key role in mediating interactions involving brown trout and galaxiids. As flows are now modified in many rivers (e.g. abstraction, hydro-electric dams), understanding how different aspects of the flow regime alter brown-trout impacts could reveal useful information for management. Furthermore, the effects of invaders such as brown trout are likely to interact with other global change drivers like climate-warming, which will alter water temperature (e.g. Boddy & McIntosh, 2017), so an expanded context for understanding impacts of brown trout may be required for managing their impacts in the future.

Managing brown trout in places where they also provide an immensely valued fishery (e.g. New Zealand; Deans *et al.*, 2016) greatly depends on the available technology and social context (see McIntosh *et al.*, 2012 for a review of current technology). In New Zealand we feel there is now a much greater awareness of the influence of trout on freshwater ecosystems, at least among sports fishery managers, if not anglers. However, whether there is a need to manage those influences, and how that might be done is still debated. For example, the removal of trout using rotenone from a lake associated with a large terrestrial restoration project where all non-native terrestrial mammals had already been eradicated (Zealandia sanctuary in Wellington) was controversial and met some opposition. For example, one politician said, 'To poison a lake and all of its tributaries in order to kill some introduced trout, which most people see as a positive recreational resource, just because they are an exotic species is just crazy' (Peter Dunn, press release, 27 October 2010). Despite the opposition, the New Zealand Department of Conservation and Zealandia proceeded with the eradication which has now successfully restored one species of native fish, banded kōkopu (*Galaxias fasciatus*), to the sanctuaries upper waterways (Pham *et al.*, 2013).

These issues are also greatly complicated by the widespread declines in freshwater ecosystem quality which have taken place in New Zealand due to rapid agricultural intensification and urbanisation. Angling advocates have generally been at the forefront of efforts to maintain water quality, and have been justifiably quick to point out the positive effects of their efforts (Deans *et al.*, 2016). Nevertheless, farmers, city-dwellers and anglers must all accept responsibility and deal with all the problems they have created. As part of that, anglers need to accept that the brown trout-based sports fishing resources, which are highly valued and woven into the fabric of New Zealand life, have had significant deleterious effects on native biodiversity.

In their 2010 review of the impacts of trout on galaxiid fishes in New Zealand, McIntosh and co-workers called for increased restoration efforts to address impacts of trout on native fish and the seriously endangered galaxiid fauna. In recent years, restoration efforts have slowly increased, with projects like that at Zealandia, as well as others involving the installation of barriers to ensure the upstream trout-free reaches are maintained. These efforts will not address the more insidious effects associated with trout being virtually everywhere and having changed the whole trophic ecology of New Zealand streams. However, in many ways that is the new reality in New Zealand, and there are probably more important targets for conservation efforts such as protecting the many elements of unique New Zealand freshwater biodiversity threatened by ongoing trout invasion, and offsetting and mitigating the ongoing effects of land-use intensification. The perilous situation facing many galaxiid populations in New Zealand, the urgent need for action, and a good part of the remedy, is summed up in a recent comment by New Zealand Department of Conservation ranger, Pete Ravenscroft (press release, 11 June 2014): 'In the last 13 years, 20 percent of Otago's populations of rare [native] fish have been lost and 60 percent of Clutha flathead [galaxias] populations have gone. These losses are alarming. There's room for everyone – galaxias, trout and landowners – if we can work together on a solution'.

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23

Brown Trout in Argentina: History, Interactions and Perspectives

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Patagonia Argentina and its Ichthyofauna

Patagonia is a broad territory located on the southern tip of the American Continent, which is shared between the republics of Chile and Argentina (Figure 23.1). Due to its great latitudinal range and surface area, and the composition of the landscape, Patagonia is a highly variable territory. In general, the argentine part could be separated into two major ecological units: (a) at the west, the Andes Mountains, whose height decreases towards the south; and (b) the Patagonian Plateau (*Meseta*), located eastern, which slopes gently toward the sea. The region shows pronounced environmental gradients, with greater rainfall to the west and lower temperatures to the south. The mountain range area was shaped by glacial action, and has therefore a considerable number of large deep oligotrophic lakes, and rivers and streams with torrential flows, most of them of nivo-glacial regime. There are some great basins that drain into the Atlantic Ocean and others into the Pacific from large rivers like Negro, Chubut and Gallegos in the first case, and Manso and Futaleufú in the latter. The Meseta is crossed by some of these rivers, but its hydrography is less developed, with meandering courses, which are also dependent on rainfall in the mountainous area, or lakes whose basins are endorrheic or even arrheic.

Little is known of the limnological features in general and of the native fish communities in particular before the introduction of salmonids to the country in 1904. The chronicles of explorers and visitors to the region in the second half of the XIX century often refer to the native fish fauna, some of which were used as food (Moyano 1887, Moreno 1879, Musters 1871). Thus, it is difficult to evaluate the effects that such introductions had. Aquatic environments without salmonids are scarce, but they are currently being studied to determine the characteristics of the native fish communities before the introduction of this.

The native fish fauna of the Patagonian Ictiogeographic Province is relatively poor and is represented by specimens of the families Percichthyidae, Atherinopsidae,

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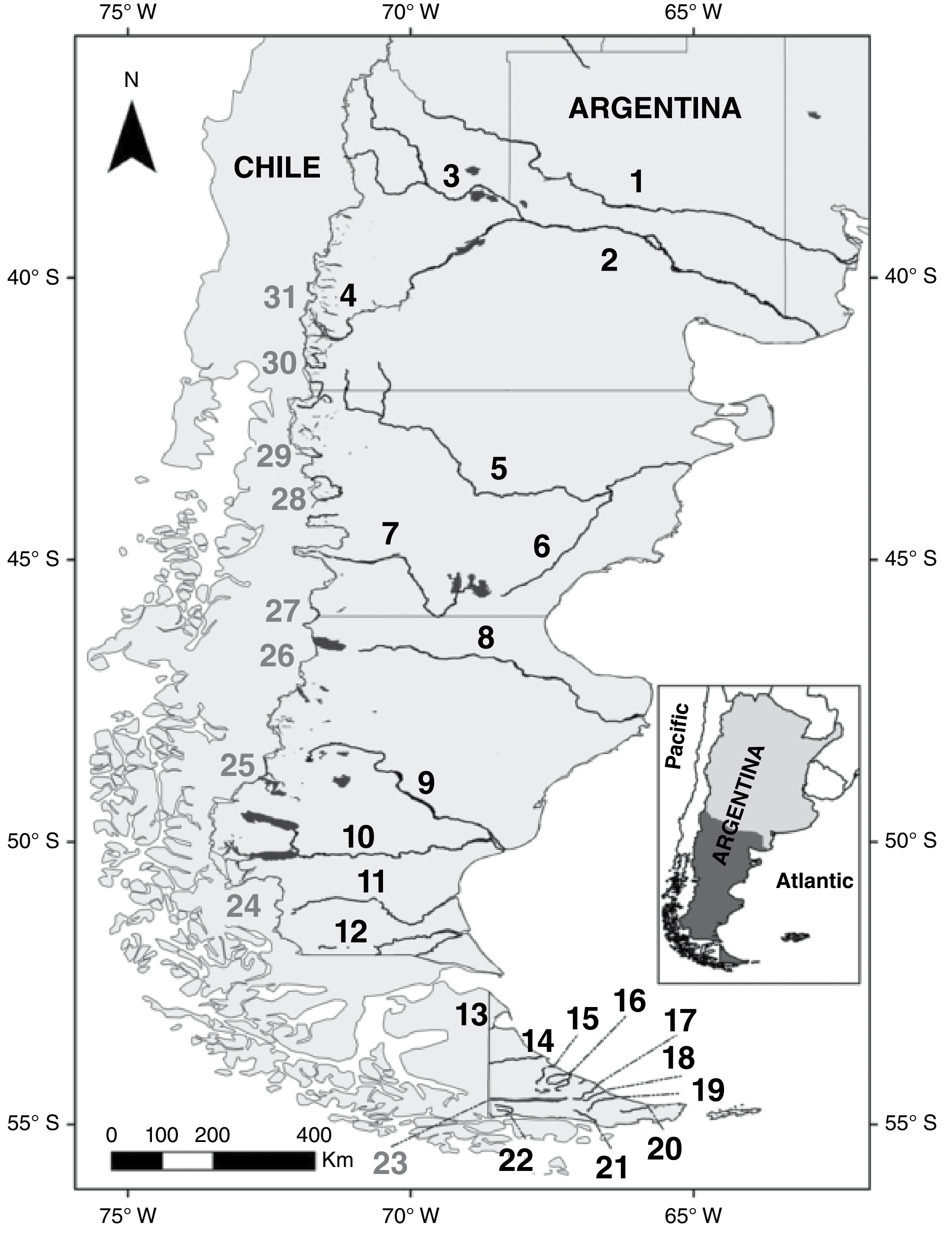

Figure 23.1 Major drainage watersheds in Continental Patagonia Argentina and Tierra del Fuego.

Galaxiidae and Siluridae. Also, exotic species such as salmonids and cyprinids are present, in addition to species introduced from neighbouring Paranoplatense and Cuyana Ictiogeographic Provinces. (Lopez & Miquelarena 2005). Finally, some marine species use rivers and estuaries to feed or spawn. At present, there are more than 30 species in the region (Pascual *et al.* 2007), as shown in Table 23.1.

Table 23.1 Fish species list for the Patagonian inland waters. MA: Marine; EX: Exotic; PP: Paranoplatense Ictiogeographic Province; CU: Cuyana Ictiogeographic Province; PA: Patagonian Ictiogeographic Province. *: Endemic Species.

Order	Family	Species	Origin	Common name
Petromyzontiformes	***Petromyzontidae***	*Geotria australis* G ray 1851	MA	Lamprey
		Mordacia lapicida Gray 1851	MA	Lamprey
Cypriniformes	***Cyprinidae***	*Cyprinus carpio* Linnaeus 1758	*EX*	European carp
Characiformes	***Characidae***	*Astyanax eigenmanniorum* Cope 1894	*PP*	Mojarrita
		Cheirodon interruptus Jenyns 1842	*PP*	Mojarrita
		Gymnocharacinus bergii Steindachner 1903*	*PA*	Mojarra Desnuda
		Oligosarcus jenynsii Gunther 1864	*PP*	Dientudo
Siluriformes	***Diplomystidae***	*Diplomystes cuyanus* Ringuelet 1965	CU	Velvet catfish
		D. mesembrinus Ringuelet 1982	PA	Velvet catfish
		D. viedmensis MacDonagh 1931	PA	Velvet catfish
	Callichthyidae	*Corydoras paleatus* Jenyns 1842	PP	Tachuela
	Trichomycteridae	*Hatcheria macraei* Girard 1855	PA	Torrent catfish
		Trichomycterus areolatus Valenciennes 1840	CU	Torrent catfish
Osmeriformes	***Galaxiidae***	*Aplochiton marinus* Eigenmann 1928	PA	Peladilla
		A. taeniatus Jenyns 1842	PA	Peladilla
		A. zebra Jenyns 1842	PA	Peladilla
		Galaxias maculatus Jenyns 1842	PA	Small puyen
		G. platei Steindachner 1898	PA	Big puyen

(Continued)

Table 23.1 (Continued)

Order	Family	Species	Origin	Common name
Salmoniformes	***Salmonidae***	*Salvelinus fontinalis* Mitchill 1814	EX	Brook trout
		S. namaycush Walbaum 1792	EX	Lake trout
		Salmo salar Linnaeus 1758	EX	Landlocked salmon
		S. trutta Linnaeus 1758	EX	Brown trout
		Oncorhynchus masou Brevoort 1856	EX	Cherry salmon
		O. mykiss Walbaum 1792	EX	Rainbow trout
		O. kisutch Walbaum 1792	EX	Coho salmon
		O. tshawytscha Walbaum 1792	EX	Chinook salmon, King
Atheriniformes	***Atherinopsidae***	*Odontesthes hatcheri* Eigenmann 1909	PA	Patagonic silverside
		O. bonariensis Valenciennes 1835	PP	Silverside
		O. argentinensis Valenciennes 1835	MA	Marine silverside
Cyprinodontiformes	***Poeciliidae***	*Cnesterodon decemmaculatus* Jenyns 1842	PP	Madrecita
	Anablepidae	*Jenynsia multidentata* Jenyns 1842	PP	Madrecita
Mugiliformes	***Mugilidae***	*Mugil liza* Valenciennes 1836	MA	Mullet
Pleuronectiformes	***Paralichthydae***	*Paralichthys brasiliensis* Ranzani 1842	MA	Flounder
Perciformes	***Percichthyidae***	*Percichthys trucha* Valenciennes 1833	PA	Perch
	Nototheniidae	*Eleginops maclovinus* (Cuvier 1830)	MA	Snook
	Cichlidae	*Crenicichla scottii* Eigenmann 1907	PP	Chanchita

Introduction of Salmonids in Argentina

In 1904, salmonids were introduced in the Argentinean part of Patagonia. To the present, 14 species of fish, 10 of the Salmonidae family and four of families Atherinopsidae, Cyprinidae, Characidae, and Callichthydae were stocked. Among the salmonids, most of introduced species are eight established self-sustaining populations, except the attempts with *Coregonus* sp. and *Oncorhynchus nerka*, which apparently they have not succeeded in the region (Macchi & Vigliano 2014). Thus, the continental fish fauna of Patagonia is composed of 36 species of which 19 have been transplanted from neighbouring ictiogeographic regions or introduced from other continents (Table 23.1).

The main objectives of the introductions were to increase the diversity and abundance of fish fauna and the development of fisheries with species of high economic and sporting value (Valette 1924). In relation to these objectives, the Ministry of Agriculture, Livestock and Fisheries of Argentina created two aquaculture centers in the region: Nahuel Huapi salmonid hatchery (which operated from 1904 to 1931), installed on the Limay river, responsible of the stocking of the different species in northern Patagonia, and Santa Cruz river hatchery (which operated between 1904 and 1915), responsible for the introduction of fishes in southern Patagonia (Marini, 1936). In 1932, the Nahuel Huapi salmonid hatchery was relocated a few kilometres away in the Gutierrez river basin, and renamed as Bariloche Fish Farming Center, becoming the only federal establishment responsible for the collection, breeding and distribution of salmonids in the country until its closure in 1994. The usual practice was release small-sized fish in the water bodies or courses and to obtain gametes from feral fish in those environments through the practice of ranching in streams and rivers used by fish during their reproductive movements. Wild fish are also kept in nurseries for spawning in the breeding season. Macchi *et al.* (2008) and Macchi & Vigliano (2014) made a detailed analysis of the history of the introduction and dispersion of salmonids between 1904 and 2011. They found that the most important factors in the successful establishment and the current distribution of salmonids were management policies, availability of funds for stocking, watershed accessibility, environmental characteristics and the dispersive capacity of each species.

Brown Trout

The first record of brown trout in Argentina dates from 1906, when 6,000 embryonated eggs from North Wales were received in the Santa Cruz hatchery. These fish were released into the Gallegos river basin, but the success of this introduction is unknown (Valette 1924). The second introduction was made in 1931 with eggs from Germany, possibly from the Elba River (Valiente *et al.* 2007), which were obtained in Chile and translated to the Northern Patagonia. In that year, a large number of fish were introduced in different water bodies in the Limay and Manso river basins and in the Lácar lake. Between 1935 and 1937 the specie was introduced by a settler in the Isla Grande de Tierra del Fuego (Bruno Videla 1978, Casalinuovo *et al.* 2002). In 1941 a new import of eggs from Chile were stocked in several Patagonian watersheds.

In the late 1940s brown trout began to be abundant in water bodies of Northern Patagonia and the first mature adults and eggs were obtained from the field (Macchi & Vigliano 2014). The stocks obtained were dispersed artificially to almost all Patagonian basins (Table 23.2). The species had also been introduced in water bodies of Cuyo and

Table 23.2 Presence and introductions of brown trout by basins and sub basins of Argentine Patagonia. In the Pacific basins, only the introductions from the Continental Argentine territory are recorded. ID numbers correspond to Figure 23.1.

Drainage	Basin	ID	Sub Basin	Stocked	Presence
Atlantic	Colorado	1		Yes	No
	Negro	2		Yes	Yes
	Neuquén	3		Yes	Yes
	Limay	4		Yes	Yes
	Chubut	5		Yes	Yes
	Chico	6		No	No
	Senguerr	7		Yes	No
	Deseado	8		No	No
	Chico	9		No	No
	Santa Cruz	10		Yes	Yes
	Coyle	11		Yes	Yes
	Gallegos	12		Yes	Yes
	San Martin	13		Yes	Yes
	Grande	14		Yes	Yes
	Fuego	15		Yes	Yes
	Ewan	16		Yes	Yes
	San Pablo	17		Yes	Yes
	Láinez	18		Yes	Yes
	Irigoyen	19		Yes	Yes
	Moat	21		Yes	Yes
	Olivia	22		Yes	Yes
Pacific	Valdivia	31	Lácar	Yes	Yes
	Puelo	30	Puelo	Yes	Yes
			Manso	Yes	Yes
	Futaleufú	29	Futaleufú	Yes	Yes
	Palena	28	Corcovado	No	Yes
			Pico	No	Yes
	Simpson	27	Simpson	No	Yes
	Baker	26	Buenos Aires	Yes	Yes
	Pascua	25	San Martín	No	Yes
	Vizcacha	24	Vizcacha	Yes	Yes
	Fagnano	23		Yes	Yes

Central regions of Argentina. It should be noted that the presence of brown trout and other salmonids in some Pacific basins is due to stocking or aquaculture escapes in Chilean waters.

As a result of introductions, regular stocking and natural dispersion, brown trout is now established in most of lakes and rivers of the Patagonia Argentina (Figure 23.1, Table 23.2), showing a significant capacity to adapt to different types of ecosystems. Due to its adaptive life history traits (Valiente *et al.* 2010), brown trout is one of the most widely distributed species in Patagonia, together with rainbow trout (Pascual *et al.* 2002). It has also been established in other areas outside Patagonia such as the Provinces of Córdoba (Las Cañitas river), Mendoza (Mendoza and Grande rivers, Potrerillos dam) and San Juan (Castaño, Jáchal, Los Patos and San Juan rivers).

Biology and Ecology

Most of the research conducted in Argentina on the biology and ecology of the species has been carried out in the Andean Northern Patagonia and in the rivers and lakes of Tierra del Fuego, so the results presented in this chapter considers particularly environments in these sites. The studies include spatial and temporal distribution, movements and migration, growth, mortality, reproductive aspects, trophic relationships, interaction with native species and fisheries management. The sampling methodologies have included gillnets stratified by depth, coastal trawling in lakes, electrofishing and casting nets in streams, and lure fishing in rivers, streams and lakes.

The relative importance of brown trout in fish communities is variable and is strongly influenced by the presence of other fish species therein (Habit *et al.* 2015). An extensive study that analyzed summer and autumn gill net survey catches in four large basins: Limay (7 lakes), Manso (7 lakes) Futalafquen (3 lakes) and Fagnano (5 lakes) (Vigliano *et al.* 1999) demonstrated that brown trout has a greater presence in environments where the perch, *Percichthys trucha* – a native piscivorous species – was not present, such as lakes of Fagnano and Manso basins (Figure 23.2). These results are consistent

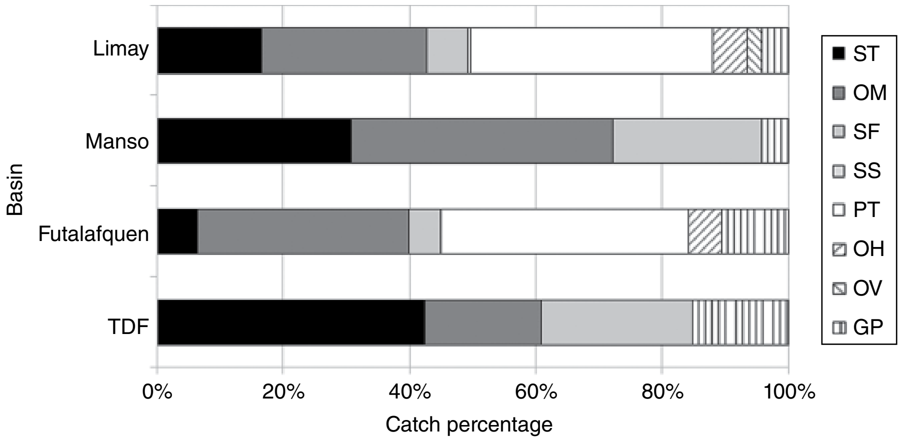

Figure 23.2 Specific composition on the natural and artificial lakes in Patagonia. References: ST: *Salmo trutta*, OM: *Oncorhynchus mykiss*, SF: *Salvelinus fontinalis*, SS: *Salmo salar*, PT: *Percichthys trucha*, OH: *Odonthestes hatcheri*, OV: *Olivaichthys viedmensis*, GP: *Galaxias platei*. Lakes ordered in N-S axis.

with those found by Habit *et al.* (2015), who state that the perch acts as a top predator and thus regulates the trout population. Regarding the other two species of salmonids, rainbow and brook trout with whom brown trout never coexisted in its original distribution ranges, a relatively complex community structure is established, which shows differential spatial distributions that probably avoid or reduce competition for resources (Juncos *et al.* 2014). If the relative importance of brown trout in lakes of different basins is observed, this species is ranked third in the presence of perch and is the second most abundant species in the absence of perch, behind the rainbow trout. Only the lakes of the Fagnano basin show a clear dominance of brown trout over other salmonids and species of native fish. Abiotic conditions (such as climate regime, physical and chemical variables) are often very important to explain the success of invasive species (Moyle & Narchetti 2006). In fact, Fausch (2008) postulated that the success of the invasion of rainbow trout in basins of the eastern United States is founded on the fact that water regimes of new environments are similar to those of the basins where this species is native. So, it is possible that abiotic conditions of water bodies of Lake Fagnano basin could be, for brown trout, similar to the conditions of their native environments, thus explaining the dominance of the species.

The species shows preference in its spatial distribution in the lakes studied, being captured both in epibenthic and pelagic zones. The highest abundances were observed during the summer up to 30 m deep in the benthic layers, although brown trout were also found up to 50 m. The pelagic zone was less used by fish in general, but individuals of brown trout were recorded up to 30 m deep. This pattern is observed in three of the basins considered, with different specific compositions (Figure 23.3). Possible reasons for this differential distribution relate to trophic movements and/or reduced competition for food resources, as suggested by Rechencq *et al.* (2011, 2014). These authors describe the distribution and movements of fish daily in Andean lakes, and studied the diel variations in the movement of plankton, larvae of big puyen, *Galaxias platei*, small puyen, *G. maculatus* and adult fish that move following the plankton to feed them. Furthermore, it has been found that in general, fish with larger maximum sizes in

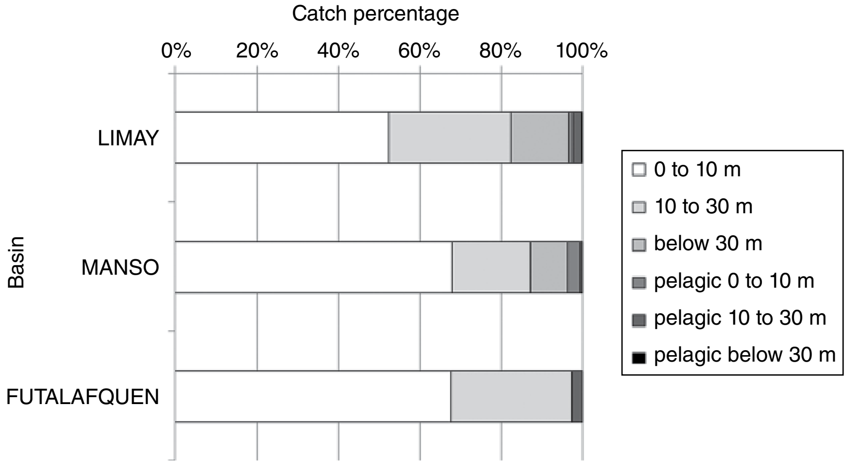

Figure 23.3 Deep strata distribution of *Salmo trutta* by basin in three Patagonian basins.

assemblages are brown trout, which can be related to the piscivorous habits of the species and the role of top predator, consuming fish and decapods, prey of high energetic value or large sizes, which appear to be related to higher rates of growth (Macchi *et al.* 1999, Ciancio & Pascual 2006).

Systematic studies of anadromous brown trout behavior in marine migrations have not yet begun. It is presumed that, as in the rest of the world (Jonsson & Jonsson 2011), their movements are coastal and close to river mouths. That presumption is strengthened by the observation that catches only occur in coastal gillnets and there are no records of catches by fishing boats farther away from the coast (Casalinuovo *et al.* 2012), as is the case with chinook salmon (Ciancio pers. comm.) In the Grande river of Tierra del Fuego, upstream migrations into freshwater after the marine feeding phase occur all year round and involve large numbers of migrants, 55,000 to 85,000 fish depending on the year (O'Neal *et al.* 2007, Klaich *et al.* 2012), although two peaks are recorded around mid-January and mid-February or March (O'Neal *et al.* 2007, Giese 2011). This migration is associated with the tidal cycle (Figure 23.4), and total catches are related to maximum tidal amplitudes of the estuary in the first kilometres of the river (Giese 2011). The relationship between catches and tides was also verified near Irigoyen river in the marine coastal area where catches in gillnets were related to high tides (Casalinuovo *et al.* 2012). Finally, the entry of fish from the sea is structured by age since younger individuals arrives later (Giese 2011).

Studies on the movement of fish using hydroacoustic (Niklitschek *et al.* 2012) and radio telemetry in Rio Grande (Casalinuovo 2013) demonstrated that the use of the river is not homogeneous. A Didson type echo sounder was used in the first case, at three sites: the first near the estuary (28 km from the mouth to the sea), the second on the Chilean–Argentine border (km 88 from the mouth to the sea), and the third in the confluence of the Grande and Blanco rivers (146 km from the mouth to the sea), in Chile. The study revealed that 22% of the fish reached the border and only 16% reached the confluence of the two rivers. These differences became more pronounced for trophy-sized fish (over 650 mm). Meanwhile, 50 sea run brown trout were captured and radiomarked near to the estuary (km 25 from the mouth to the sea) and followed by

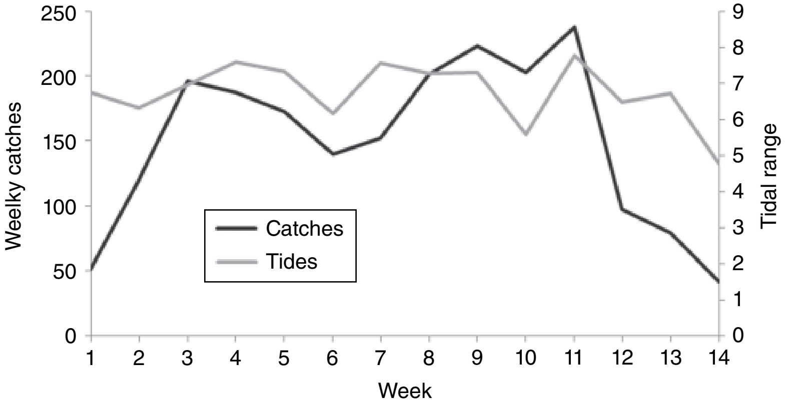

Figure 23.4 Weekly average number of daily catches and maximum tide amplitude per week versus time (according to Giese, 2011).

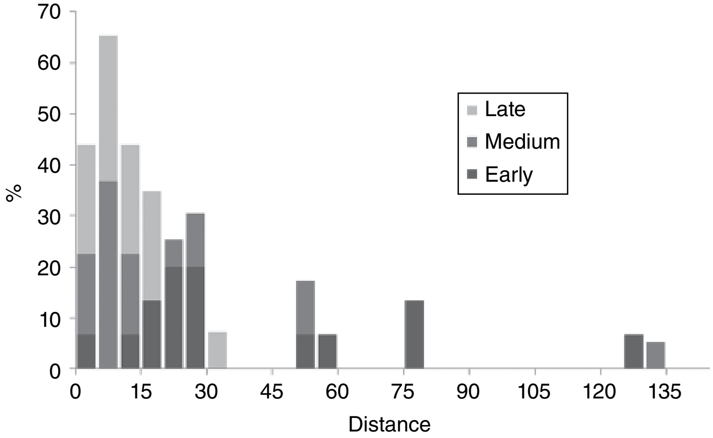

Figure 23.5 Settlement distances from the river mouth expressed as a percentage for the anadromous brown trout in Grande river. Early: fish caught in January; Medium: fish captured in February; Late: Fish caught in April.

land and air for a year. Most of them settled in the first kilometres of the river, with a strong tendency to settle in only one place for their entire stay in fresh water. The same study showed that fish entering the river early (January and February) established throughout the system, whereas those entering later (April) were located closer to the estuary (Figure 23.5).

Life Strategies

Life strategies include early history in breeding sites, age of first sexual maturity, and the preference of residence sites for feeding periods. The great adaptability of brown trout is seen in the Patagonian aquatic environments through a wide variety of strategies involving populations living exclusively in freshwater and anadromous stocks. In a typical life cycle, individuals of brown trout hatch in rivers or streams where they live from a few months to several years and migrate later to higher flow rivers, lakes, reservoirs or in some cases the sea, where they generally live until they reach sexual maturity. Then they begin to take part in the massive spawning migrations, repeating these movements between feeding and breeding areas throughout the life of the fish. Some proportions of a population have been recorded to remain in the birthplace. These resident forms show particular population characteristics that reflect the environmental conditions in which they live (Lippolt 2004). A special case are immature anadromous fish that return from the sea to rivers of Tierra del Fuego in order to overwinter (Pascual *et al.* 2007, Casalinuovo *et al.* 2002, Casalinuovo *et al.* 2014).

Early Life Histories

The time spent by juveniles in their breeding sites before they move to larger environments varies among regions, but these traits are generally defined by the characteristics of habitat, mainly the flow water speed, substrate type, coverage for shelter and food availability. The most common situation in the life cycles of freshwater environments is that after a period of up to three years, fish move to lakes or large rivers to begin their adult stage. This movement pattern is common in most of the basins analyzed. Research carried out in 22 tributary streams of Nahuel Huapi lake (Limay river basin), concluded that the brown trout prefer pool type habitats with moderate currents, thus segregating from other salmonid species that prefer areas with higher speeds currents (Lallement, in press). The prevalent age groups of brown trout are 2 and 3-year-old fish, with some individuals of 4 years old. Showing a clearly different strategy, rainbow trout mostly live a year in their breeding sites, with a minor presence of 2-year-old fish and occasionally older individuals are present (Juárez, pers. comm.). This greater permanence of brown trout in the streams would explain the scarcity of juveniles in catches in lakes with gillnets. In the mountain rivers and streams of Neuquén province, the age at which the fish leave their breeding environments is strongly related to the seasonality of water flow (Sakai 1994). This author found that the most common age groups were 1+ and 2+ age groups, with minor presence of older fish in a set of streams with different hydrological regimes.

In the case of trout with anadromous behaviour, there are detailed descriptions of the biology and ecology of the species for the Ewan river (Casalinuovo *et al.* 2002), the Grande river, (Luizón 2009, O'Neal & Stanford, 2011) and the Gallegos river (Amaya Santi & Pascual 2006 a, b, c, Casalinuovo *et al.* 2014). In all known cases, there are partial migratory populations, (i.e. a fraction of individuals remain all their lives in freshwater while the others migrate to the sea to feeding). In the latter case, juveniles generally have a residence period in freshwater for 2 years, but varying between 1 and 5 (Casalinuovo *et al.* 2002, Luizón 2009, Casalinuovo *et al.* 2014). Brown trout smoltify and move downstream to the sea, presumably with spring flooding. It would appear that at least some of these fish, still sexually immature, return to the river at the end of the next summer to overwinter, as indicated by captures of small silvery fish in the commercial fishing operations of the Grande River, the most studied of Tierra del Fuego (Casalinuovo & Castro 2014). During the first years of life, juveniles appear to associate with environments that offer food and shelter outside the mainstream, such as side braids and channels. They later migrate into the mainstream as age and size increase (O'Neal *et al.* 2007, Casalinuovo *et al.* in prep.). Table 23.3 summarizes the results in the environments considered.

Sexual Maturation and Spawning

The age of first sexual maturity may differ between populations, but it generally comes after at least one year of growth in lakes or sea. A fraction of the fish can remain in their birth streams and become sexually mature without leaving (Lippolt 2004, Suárez, pers. comm.). In general, the age of first sexual maturity occurs in the third year of life, although sexually mature fish can be found in the second through to the sixth year of life, as illustrated in Table 23.4 (AIC 2000, 2012, 2014, CEAN 1997, 2010, Pascual & Amaya 2006, Kuroda 2015).

The spawning season varies by region and is associated with decreasing photoperiod and temperature, generally coincident with flooding, usually from May to September. In a study of fish assemblages in the Limay River, important differences in species composition, relative importance and age composition between the reproductive and non-reproductive periods of rainbow and brown trout were observed

Table 23.3 Residence time of juveniles in their birth places before migrating to feeding grounds. *: Anadromous individuals.

		Age class (%)						
River	Flow (m^3/sec)	I	II	III	IV	V	VI	VII
San Pedro	<1	73.50	24.50	2.00	–	–	–	–
Pino Huacho	<1	20.00	60.00	20.00	–	–	–	–
Traful	47	100.00	–	–	–	–	–	–
Caleufú	48	28.10	53.10	14.10	4.70	–	–	–
Collón Cura	203	40.00	45.50	7.25	7.25	–	–	–
Chimehuín	100	70.54	17.86	3.57	3.57	3.57	–	0.89
Limay	720	80.00	20.00	–	–	–	–	–
Grande *	45	–	48.72	47.44	3.84		–	–
Irigoyen *	7	–	18.92	59.46	18.92	2.70	–	–
Menéndez *	5	–	54.35	42.39	3.26	–	–	–
Ewan Sur *	2	–	54.35	42.39	3.26	–	–	–
Gallegos *	15	5.00	60.00	20.00	15.00	–	–	–

Table 23.4 Percentage of first sexual maturity for brown trout of different environments of Patagonia. *: Anadromous individuals.

	Age class (%)				
River	II	III	IV	V	VI
San Pedro	4.08	55.10	38.80	2.02	–
Pino Huacho	–	–	40.00	60.00	–
Traful	70.00	30.00	–	–	–
Calefú	3.45	58.65	37.90	–	–
Collón Cura	–	88.90	11.10	–	–
Chimehuín	2.70	48.65	40.54	5.41	2.70
Limay	–	37.50	50.00	12.50	–
Gallegos*	–	8.20	54.10	34.43	3.27

(Rechencq 2003). Brown trout remains in the river all year round, although their relative abundance and average size is larger in the reproductive months. Bigger fish living in lentic environments (Nahuel Huapi and Traful lakes and Alicura reservoir, in this case), move into rivers to spawn and then return to their feeding sites. Age composition in reproductive and non-reproductive periods also differs. In the first case the prevalent fish groups correspond to 5 and 6 years old, while in summer, the prevalent age groups are 3 and 4 years old. This is corroborated by the analysis of seven rivers from the north of Neuquén, where the quality of fishing, measured as average and maximum sizes, tends to increase on dates close to the reproductive season, which has been interpreted as being associated with a massive influx of older fish from adjacent lakes (Casalinuovo 2012). This is even more evident in the rivers with anadromous stocks, where the age composition and the sizes increase dramatically when fish move upstream in the spawning season after a marine feeding period (Casalinuovo *et al.* 2002, Luizón 2009).

Growth

Concerning growth and age structure, the populations studied in Patagonia generally include between 5 and 12 age classes (García Asorey 2001, Rechencq 2003, Luizón 2009, Casalinuovo *et al.* 2002, Casalinuovo 2011, Casalinuovo *et al.* 2014, Giese 2011, Del Valle 1999). Growth follows the model of von Bertalanffy (1938) in most of the populations studied. Figure 23.6 shows brown trout growth in a variety of both lotic and lentic aquatic environments. The highest growth of anadromous specimens compared to residents of both lakes and rivers becomes evident.

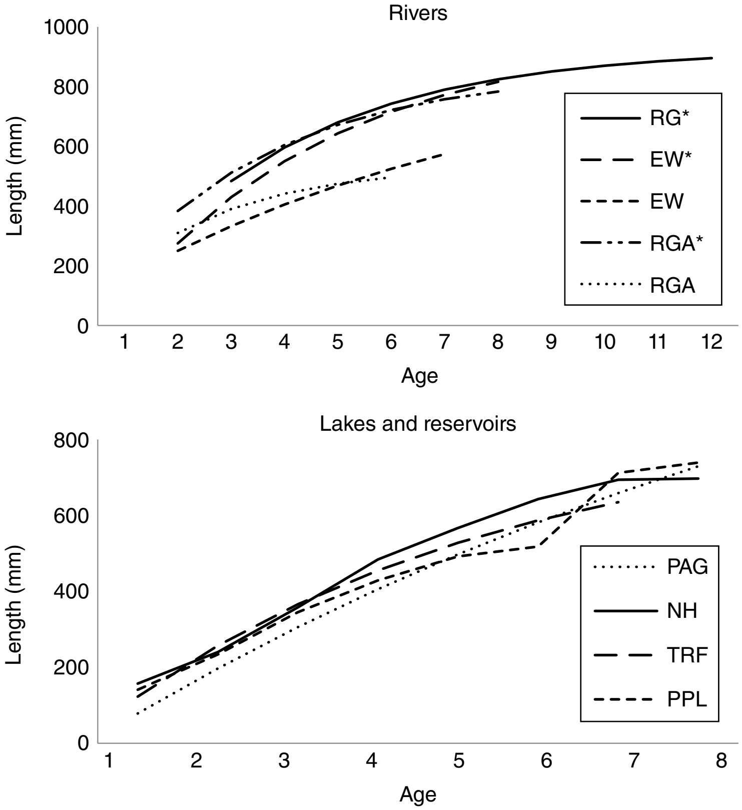

Figure 23.6 Comparison of growth curves for various Patagonian environments. RG: Grande river, RGA: Gallegos river, EW: Ewan river, LI: Limay river, PAG: Piedra del Águila reservoir, NH: Nahuel Huapi lake, TRF: Traful lake, PPL: Pichi-Picun-Leufu reservoir. *Anadromous individuals.

Information on growth has been used for the application of bioenergetics models (Juncos *et al.* 2013) in order to study the consumption of prey, interactions and competition between brown trout, other salmon and perch. Furthermore, predictive models of fishing quality used as a management tool in the fisheries for anadromous trout in the Grande river in Tierra del Fuego also have individual fish growth as a fundamental component (García Asorey 2011, Pascual *et al.* 2010).

Feeding Habits

While there are regional variations in feeding habits, mainly due to the availability of prey, it is possible to make generalizations about the trophic role of the specie in the Patagonian environments. In its adult stage brown trout are top predator with a high preference for larger prey, mainly fish (Macchi *et al.* 1999). This preference results in a narrower trophic niche than other salmonids and native perch that also reach considerable sizes and include fishes in their diets.

Strict Freshwater Populations

In streams and small rivers, juvenile fish feed on insect larvae and to a lesser extent on *Hyalella* amphipods, small *Chilina* gastropods and allochthonous organisms. From 100 mm in length, fish (mainly juvenile stages of salmonids), *Samastacus* and *Aegla* decapods are incorporated into their diet. In larger watercourses and lake environments brown trout assume the role of top predator within fish communities, incorporating much fish prey in their diet (Macchi *et al.* 1999, Ribeiro Guevara *et al.* 2006, Macchi *et al.* 2007; Juncos *et al.* 2015). Macchi *et al.* (1999) studied the feeding habits of brown trout in several lakes and reservoirs in northern Patagonia and found that the preferred prey were the small puyen and Patagonian silverside, while perch and others salmonids also were selected. In continental environments of Tierra del Fuego, adult brown trout is less piscivorous and consumes almost exclusively benthic macroinvertebrates, mainly *Chilina* gastropods and *Hyalella* amphipods (Casalinuovo, unpublished data).

Anadromous Populations

The populations studied in rivers of Tierra del Fuego province provide insight into the understanding of the diet of anadromous brown trout. In Rio Grande, the prey of juvenile and adult residents is mainly *Hyalella*, insect larvae and *Chilina* (O‘Neal 2006, O‘Neal & Stanford 2008, O‘Neal *et al.* 2011). Adults migrating upstream to spawn, however, do not generally feed in freshwater, although it has been found that they can consume prey sporadically, mainly *Hyalella* (O‘Neal & Stanford 2006, 2011).

The only study that considers the trophic function of brown trout in the marine environment of the Argentina continental shelf and its possible impact on other members of the ecosystem was conducted by Ciancio *et al.* (2010). Based on literature data and studies of stable isotopes signatures, these authors infer that the diet of marine brown trout could be based mainly on the consumption of Fuegian sprat (*Sprattus fueguensis*) and cephalopods. Simulations of prey consumption by the brown trout of the Grande and Gallegos rivers in their estuarine areas of distribution indicate that the biomass of prey consumed would not represent a significant value relative to that corresponding to seabirds and other consumers. The authors conclude that the effects of the species, both as predator and competitor are not significant in the current population numbers, although further studies would be needed for more precise spatial and temporal scales.

Interactions with Patagonian Biota

Due to lack of information prior to the introduction of salmonids in general and the fact that the brown trout was disseminated extensively in many basins after the naturalization of other species of the family (since rainbow and brook trout was introduced earlier), it is difficult to assess or identify the impacts produced by this species. Several researchers developed studies aimed to measure the impact of brown trout introductions, not only in Argentine but also Chilean environments. The most noticeable impacts on native biota relate to changes in abundance and spatial distribution, changes in trophic structures and certain adaptations in some population parameters such as growth, depending on the species.

One of the most noticeable effects described is the change of the trophic structure in different habitats where brown trout live. Buria *et al.* (2007) demonstrated experimentally changes in the trophic structure of the benthic community of low order streams of the mountainous area in the presence of rainbow trout. It is likely that juvenile brown trout exert similar influences where they are present, since they often consume the same type of prey (Navone 2006). Brown trout presence induces changes in the benthic community may also have altered the use of food resources and microhabitat of native fish species (Otturi, 2014). Similarly, Perry (2007) and Young *et al.* (2010) conclude that competition for food resources between native fish and salmonids could explain allopatric distribution of the different species in rivers of Chile where brown trout are dominant (Habit *et al.* 2015). The competition for resources could also occur with other species of river ecosystems of Andean Patagonia, such as the potential dietary overlap between the torrent duck (*Merganetta armata armata*), a threatened species, and the juvenile stages of salmonids, since this bird coexists with them in rivers and streams in the Andean region (Fernandez Cánepa 2012).

The piscivorous behavior of brown trout has a noticeable effect on community structure, spatial distribution, growth and abundance of native species and other salmonids. The diet of brown trout in lakes, large rivers and reservoirs of the Patagonia Argentina includes many native and introduced fish species, with larger individuals (about more than 100 mm) being exclusively piscivorous (Macchi *et al.* 1999). The pressure on native fish, especially galaxids, may have generated a change in their trophic position, due to noticeable variations in the type of prey they eat. In lakes with no other predators, brown trout included, adult big puyen are almost exclusively fish eaters, acting even as cannibals and consuming post-larvae and juveniles. In contrast, in the presence of trout, the diet is diversified, consuming less fish and including other items of lower energy value (Habit *et al.* 2015). This, together with the relocation of puyen in deeper layers, could have a major effect on individual growth rates in addition to these fish become part of the diet of salmonids. Also, the high rate of predation of salmonids in general and brown trout in particular may be responsible for the differences in individual growth of small puyen, and it was found that the populations of this species living in lakes with high rates of predation show less longevity and lower growth rates compared to environments where large predators are rare (Macchi 2004). In the Grande River of Tierra del Fuego it has been speculated that in years immediately after being stocked, brown trout fed intensively on native fish and invertebrates to a point where the anadromy was the only option due to the depletion of food supply in the environment (O'Neal 2008), However, this has been debated because it is based on historical assumptions and indirect evidence.

Most of the studies conducted in Argentina found segregation of some type between native fish and introduced salmonids. This segregation is both trophic (Macchi *et al.* 1999, Macchi *et al.* 2007, Lattuca *et al.* 2008, Juncos *et al.* 2012, 2015) reproductive (Cussac *et al.* 1997, Buria *et al.* 2007, Barriga *et al.* 2012 and/or of habitat use (Milano *et al.* 2002, Vigliano *et al.* 2008, Rechencq *et al.* 2010, Milano *et al.* 2013, Barriga *et al.* 2013, Rechencq *et al.* 2014, Juncos *et al.* 2015). Whether this segregation is a mechanism to reduce competition or predation, or if it is a result of broader interactions between species, is the topic of ongoing research (Pascual *et al.* 2002). Another important aspect that has gained attention in recent years is the effect of global warming on the Patagonian fishes. Aigo *et al.* (2008) found a reduction in catches of salmonids and an increase in captures of perch from 1986 to the present, coinciding with an increase in mean annual air temperature. This temperature increase is less favourable for salmonids than for native species, potentially producing new changes in fish communities of Patagonia (Aigo *et al.* 2014).

Management, Exploitation and Economic Importance

Patagonian recreational fisheries are an important economic resource that distributes profits among the various actors involved in the activity (i.e. fishing guides, services providers). They are multi-species fisheries, based on the three most widespread salmonid species in the region: rainbow, brown and brook trout. In jurisdictions external to national parks, species such as perch and Patagonian silverside and, in recent years, the carp are included as target species in the fishery. Some cases of single-species fisheries are the anadromous brown trout of the Gallegos and Grande rivers, those of the rainbow trout environments in the *Meseta* of Santa Cruz province, of which the best known are the Strobel and Cardiel lakes, and some environments where the target species is the chinook salmon as the Caterina river in the same province. These environments are the most valued since they are based around trophy-sized fish, and have permitted the development of business operations through the establishment of fishing lodges in many cases. Several studies determined the economic movement generated by fishing in different areas of Patagonia (Vigliano & Alonso 2002, Urbanski & Sanguinetti 1997, Urbanski & Demicheli 2000), giving values of more than US $ 7 million per fishing season in the Andean region of Neuquén. Vigliano *et al.* (2000) studied the preferences of the fishermen on the different species, noting that the brown trout is popular because it reaches large sizes, and for their willingness to fight when caught.

In the case of anadromous stocks, they have resulted in recreational fisheries of high economic and social value, both locally and regionally (Vigliano & Alonso 2000, Luizón

2009, Casalinuovo *et al.* 2002, Casalinuovo *et al.* 2014). Argentina has two of the most important recreational fisheries of anadromous brown trout in the world located in the Grande and Gallegos, rivers in the provinces of Tierra del Fuego and Santa Cruz respectively. The first of them is currently seen as the best fishery for this species in the world, with remarkable sizes and catch rates (Casalinuovo *et al.* 2002, O'Neal 2008, Luizón 2009, Casalinuovo 2014). Something similar, on a smaller scale occurs in the Gallegos river (Casalinuovo *et al.* 2014). This has led to some coastal *estancias* (ranches) offering accommodation and guiding services usually for foreign anglers who pay between USD 2,500 and 7,500 per fishing week (F. De las Carreras, pers. comm.). Social conflicts with local fishermen regarding access to the fishing grounds in general were resolved through negotiations between the *estancias* and the Government. Ironically, the rest of the Fuegian rivers where have anadromous fishes, in general open fisheries, have not generated an adequate flow of fishermen in relation to the quality of fishing, probably due to the distances involved in accessing them from the national urban centers and the demanding climate that determines that fishermen choose closer, 'friendlier', destinations, outside Tierra del Fuego.

The responsibility for the conservation of the fish fauna and fisheries management in Patagonia Argentina is prerogative of the provinces that are located in that region and the National Parks Administration, in the case of protected areas that are in the region. Different provinces have specific rules and implementation authorities that regulate the sustainable management of their fisheries. In recent years, innovative approaches and encounters, which are aimed at developing a better understanding of ecosystems and appropriate management tools, have been developed. Examples of this are the Honorary Executive Boards for Sport Fishing in the province of Río Negro and the Advisory Board of the Rio Grande in Tierra del Fuego, formed by government agencies, universities and various associations of users which are a key component in the management of fisheries, or the CONICET Thematic Networks (National Council for Research in Science and Technology), such as the Network for the Conservation of Fluvial Ecosystems of Patagonia (Red Ecofluvial), formed by the CONICET, a NGO (The Nature Conservancy), researchers, technologists and technicians, enforcement authorities, aiming for river basin management from an ecosystem perspective, in which the management of fisheries is important as a generator of economic resources and native species conservation target.

Sport fishing is regulated by a regional fishing license, which defines period, sites, number of extractions or harvest limitations, minimum or maximum sizes retainable, etc. to anglers. For years, these management tools have been discussed and agreed upon by the jurisdictional, authorities, who have formed a Technical Committee which meets annually to define the rules to be implemented. Regulations generally aim to protect larger sizes and resident populations through measures such as the release of live specimens and establishing sacrifice quotas. Another tool used, though at a decreasing extent, is the stocking of fish to supplement wild populations or support activity in environments that show limitations for natural reproduction, such as the stocking program in the middle Limay river basin, since the damming of the river has determined the watercourse fragmentation which make impossible the fish to access to suitable spawning sites, and the expenditures of hydroelectric dams have a negative effect on the spawning beds. The knowledge generated in recent years have allowed decisions with greater scientific and technical fundamentals regarding these aspects, because until not long ago, management decisions were based largely on perceptions of users or observations and empirical rules intervention.

Finally, the best knowledge about different biological and ecological aspects of brown trout in our aquatic environments, their relationships with other fish species and their effects on other components of the biota allows deeper understanding of ecosystems. This understanding is critical to successful management, taking into account the changes that occur at the environmental level by global warming and human interventions. Governments are paying more attention to the recommendations of scientists and these are being used in making decisions on a more technical basis. This is auspicious and should be taken as a usual management methodology for fisheries in the whole country. Looking ahead, we believe it is necessary to deepen the studies of population dynamics and the effects of the presence or introduction of species on aquatic ecosystems. The changes caused by environmental effects and of anthropogenic origin naturally require modelling for predictions of changes in the fish fauna, so as to adjust the management guidelines. In this regard it is important to continue studying the populations of brown trout systematically and provide a good base of knowledge to apply to the different situations encountered. To this end, there are in the country excellent trained human resources, universities, research institutes and provincial governments all involved in this issue.

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24

Africa: Brown Trout Introductions, Establishment, Current Status, Impacts and Conflicts

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Introduction

The native range of brown trout *Salmo trutta* includes parts of Europe, Asia and the Atlas Mountains in North Africa (Preface). In sub-Saharan Africa established populations of brown trout are the result of stocking, for the development of angling opportunities for a species familiar to European settlers, with support from Colonial Governments. Although sub-Saharan Africa is generally a subtropical and tropical region, suitably cold, well-oxygenated streams were present in high altitude areas and brown trout were introduced into eight continental African countries, Madagascar and the sub Antarctic Marion Island (Table 24.1, Figure 24.1).

The first successful African introduction of brown trout was into South Africa from Scotland in 1890 to the Boschfontein Hatchery in KwaZulu-Natal Province. In 1892, some 100,000 brown trout ova were imported from Andrews Trout Farm located in Guildford, Surrey, England to the Cape Province (de Moor & Bruton, 1988). Once hatcheries had been established in South Africa, brown trout were distributed from South Africa to Swaziland (1915), Lesotho (most likely between 1907 and 1914), Zimbabwe (1907), Tanzania (1934) and even the sub-Antarctic Marion Island (1964). Kenya received its first brown trout from England in 1905, and the ova were introduced directly into a Gura River headwater stream where in 1909 brown trout were observed spawning (Newton, 2013) and by 1910 a hatchery for supplementary stocking was established under the auspices of the Kenya Angling Association (Coche, 1994). Subsequently, brown trout were introduced to the Ankaratra massif of Madagascar from France in 1926 and the Bale Mountains of Ethiopia from Kenya in 1967 (Table 24.1).

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

Table 24.1 First introductions, current status of Brown trout *Salmo trutta* into Africa.

Date	Country	From	Status	Main reference
1890	South Africa	UK	Established in high altitude streams	DeMoor & Bruton (1988)
1905	Kenya	UK	Established in high altitude streams Mount Kenya and the Aberdares	Newton (2013)
1906	Malawi	South Africa	Extinct	Lewis (2011)
1907	Zimbabwe	South Africa	Established only in the Thomburatedza River, a small tributary of the Pungwe River	Marshall (2012)
No data but likely between 1907 and 1914	Lesotho	South Africa	Established in some rivers	Welcomme (1988)
1914	Swaziland	South Africa	Extinct	Welcomme (1988)
1926	Madagascar	France	Reported as established in high altitude streams in 1933. Current status unknown	Pellegrin (1933)
1934	Tanzania	South Africa	Not established	Eccles (1992)
1964	Marion Island (South Africa)	South Africa	Extinct	Cooper *et al.* (1982)
1967	Ethiopia	Kenya	Established in the Bale Mountains	Gehatun (2007)

The attempted introduction of brown trout into Malawi illustrates the lengths to which people went to facilitate introductions. The first attempts to introduce brown trout to Malawi (then Nyasaland) were made in 1905 and involved efforts to transfer ova from Humshaugh hatchery in Northumberland, northern England, by a sea voyage around Africa to the mouth of the Zambezi River. The fish were then transported, over a 4–5 day period, up the Zambezi and Shire rivers in tropical heat to Chiromo in southern Nyasaland. The fish were then carried, with ice chests to replenish melted ice along the way, by relays of porters up to the Zomba Plateau, a distance of about 200 km. This first attempt failed but a new attempt using rainbow trout in 1906 was successful (Lewis, 2011). Following this success, brown trout ova were shipped out and by the middle of 1909 both brown and rainbow trout were established on the Zomba plateau (Seed, 1949; Lewis, 2011). In 1928 samples from the Mlungusi stream on Zomba Plateau were taken to the Natural History Museum in London due to speculation over which species they actually were. According to Seed (1949) some were confirmed as rainbows though with unnatural markings, one a rainbow parr, and others possible hybrids of brown and rainbow trout. Further stockings were made in 1932, 1933 and 1934 from the Pirie hatchery in South Africa but it is not known whether these were rainbows or browns. Trout were also distributed to other highland parts of the country but only established on Mulanje Mountain and, much later, the Nyika Plateau in the north of the country.

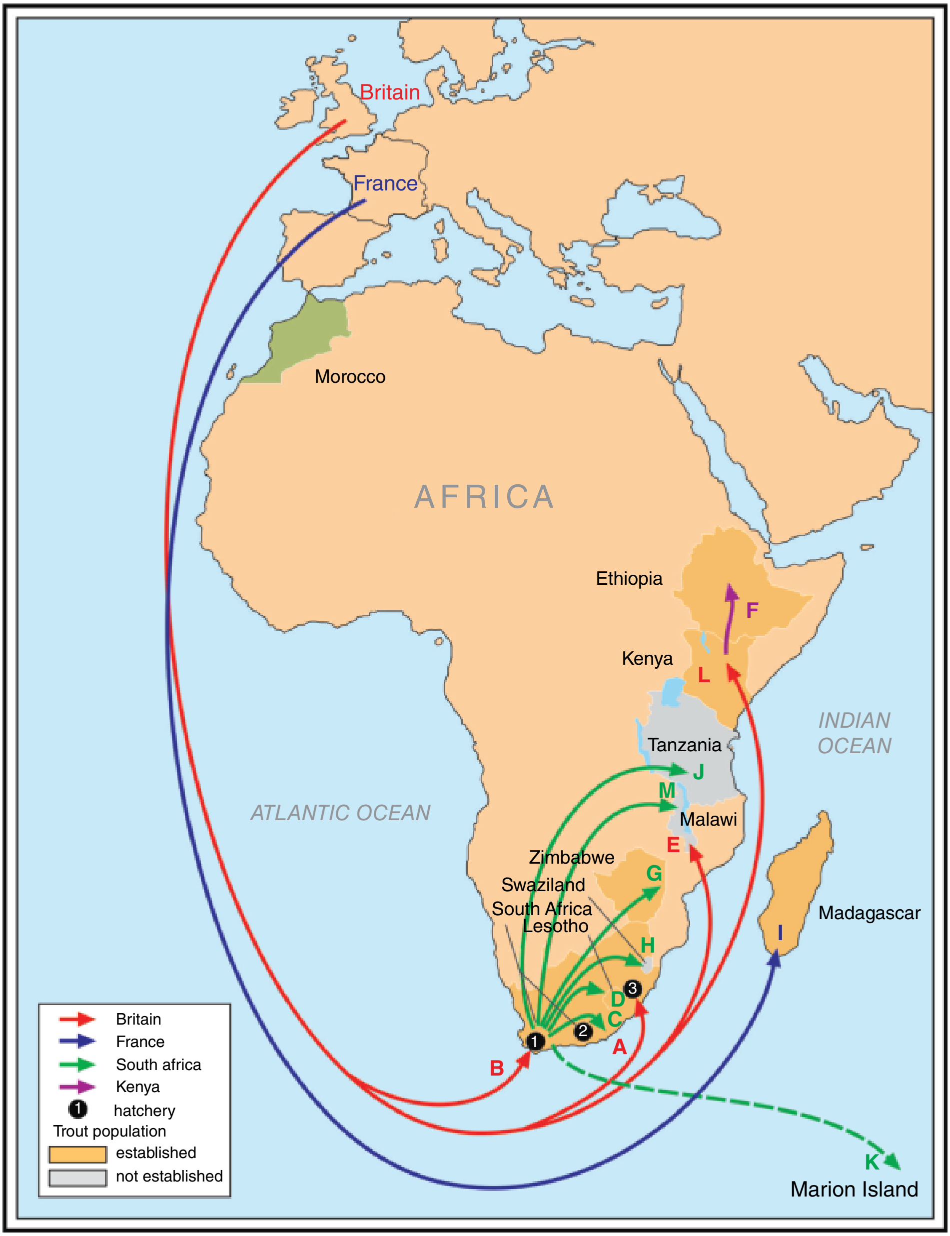

Figure 24.1 Major introduction routes of Brown trout *Salmo trutta* from Britain, France, South Africa and Kenya into African countries: Britain to (A) Natal Province (1890) and (B) the Cape Province (1892) of South Africa (E) Malawi (1906) and (F) Kenya (1905). From South Africa to (C) other localities in South Africa, (D) Lesotho (approx. 1907–14), (H) Swaziland (1914), (G) Zimbabawe (1907), (M) Malawi (1932–34), (J) Tanzania (1934) and (K) Marion Island (1964). From France to (I) Madagascar (1926) and from Kenya to (L) Ethiopia (1967). Early South African hatchery locations (1) Jonkershoek near Stellenbosch in the Western Cape (established 1894); (2) Pirie in the Eastern Cape (1897) and (3) Tetworth Natal (1890).

By the 1970s it was clear that the only trout surviving in the country were rainbows, and a renewed attempt was made to establish brown trout on the Nyika Plateau. In July 1974 an attempt was made to start a hatchery at Chelinda on the plateau and ova were flown up from South Africa (Tweddle, 1981). Both rainbows and browns were reared although there were heavy mortalities due to severe frosts. In April 1975, 27 brown trout were released from the hatchery into the North Rumphi stream, where a single 38 cm specimen weighing 0.63 kg was caught in 1976, undoubtedly one of the original fish stocked. The fish was accepted as a Malawi record (ASOM, 1990) on the basis of confirmed identity from a submitted photo. The fish was in good condition but no other brown trout were ever recorded from the North Rumphi or other Nyika streams, all of which contain lots of rainbow trout, and thus there is no doubt that brown trout no longer occur in Malawi.

Current Status

Brown trout are an important part of sport fisheries and, at least in South Africa, they are often stocked annually to artificially maintain fisheries in rivers, lakes and impoundments. In the context of invasions, it is important to distinguish between these artificial populations and established populations. In this chapter, established populations are defined as those that are self-sustaining, and have survived multiple generations in the wild without supplementary stocking.

A review of available literature indicates a failure to establish in Tanzania, Malawi and Swaziland, and while the current status in Madagascar is unclear, there are recent accounts of establishment from the Bale Mountains (Ethiopian Highlands Ecoregion) in Ethiopia (Getahun, 2007); in mountain streams of the Cherengani Hills, Aberdare Mountains and Mount Kenya (Tana and Asi Ecoregion) in Kenya (Seegers *et al.*, 2003); the Thomburatedza River, a small tributary of the Pungwe River (Zimbabawe Eastern Highlands Ecoregion) in Zimbabawe (Fenwick, 1996); and in several mountain catchments of the Cape Fold, Amatolo-Winterberg, Maloti-Drakensberg and the Southern temperate highveld ecoregions in South Africa (Ellender & Weyl, 2014).

Applying niche models, which use presence to project potential species distribution, is a useful tool in assessing potential distributions or invasion debt. A potential distribution model for brown trout in Africa was built using known occurrence records from a total of 87,246 geo-referenced global native and introduced range occurrence data for brown trout [obtained from the Global Biodiversity Information Facility (GBIF) www.gbif.org/and FishBase www.fishbase.org) and annual mean temperature, mean diurnal range, mean temperature of wettest quarter, annual precipitation and precipitation seasonality. These climatic variables have been widely used in ecological niche modelling of introduced freshwater fish species (Hijmans *et al.*, 2005; www.worldclim.org). This niche model correctly predicted the distribution of brown trout and identified all areas with known and suspected feral populations in its native and introduced ranges as climatically suitable (Figure 24.2). The most important predictor to model performance was annual mean temperature (69%), mean annual precipitation (12%) and mean temperature of the wettest quarter (11%). This indicates that areas of high climatic suitability had a mean annual temperature of approximately 10 °C and high rainfall (>1000 mm y^{-1}).

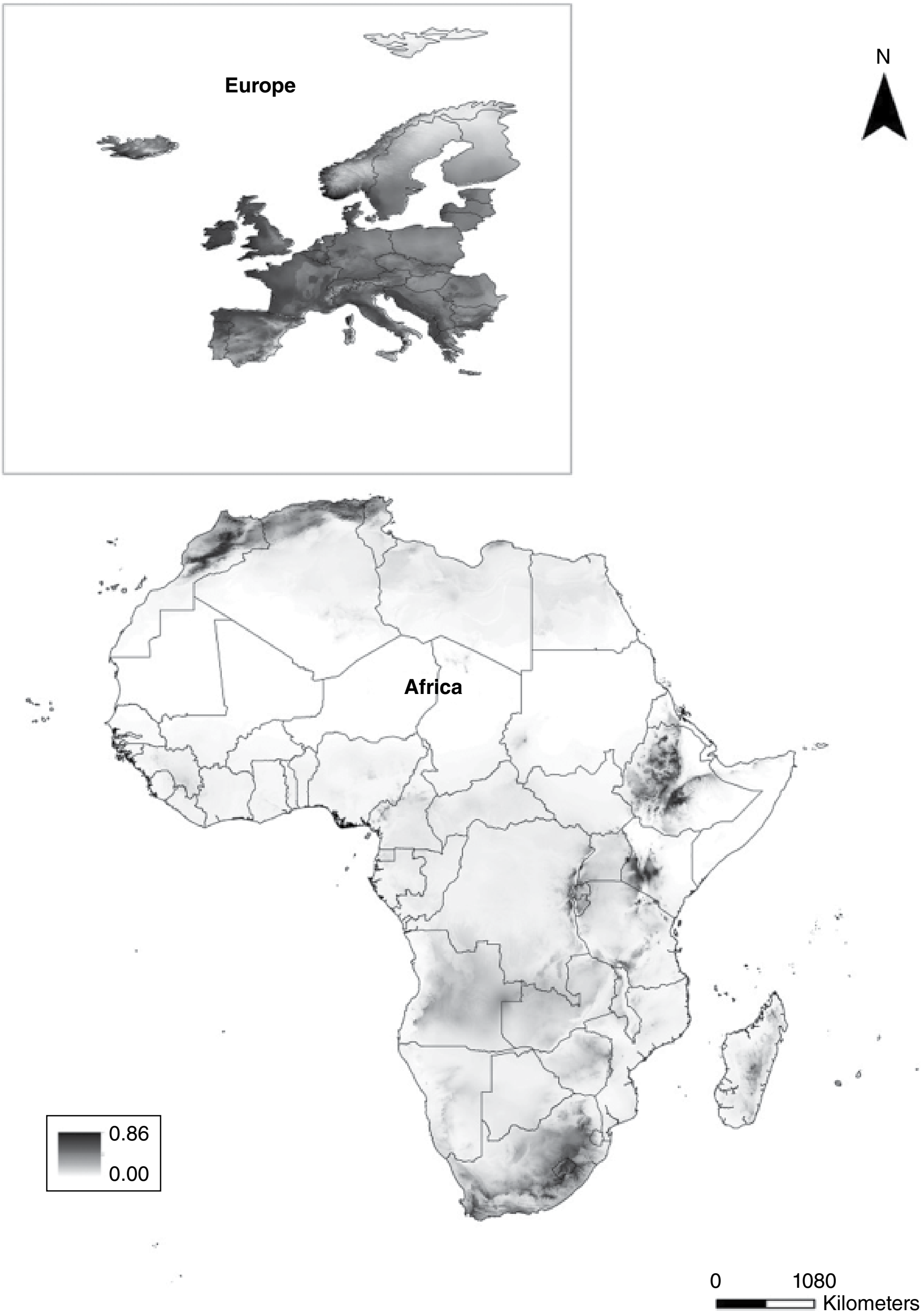

Figure 24.2 The projected distribution of brown trout in its native and introduced ranges based on the application of niche models. Potential distribution is indicated by shaded areas, with black and white indicating high and low probabilities of climatic suitability.

What is evident is that brown trout have not established extensively and now persist only in very small portions of river catchments. As is the case with many introductions, failures are seldom reported and there are subsequently, few data with which to assess the factors responsible for establishment success. In South Africa, focused research programmes on aquatic invasions dating back to the 1980s (de Moor & Bruton, 1988; Ellender & Weyl, 2014) provide a basis on which to make some general observations.

In South Africa, Government support for the introduction of trout facilitated stocking over a wide geographic area and the propagule pressure necessary for establishment. Hatchery infrastructure was developed during the first decade of introduction in three suitable regions i.e., Tetworth Natal (1890); Jonkershoek near Stellenbosch in the Western Cape (1894) and near Pirie in the Eastern Cape (1897) from where stocking was undertaken by Government organisations, private land owners, angling clubs and acclimatisation societies (McCafferty *et al.*, 2012). With the help of these stakeholders, trout were introduced over a wide geographical area which included not only habitats suitable for establishment but also a wide variety of marginal habitats, where brown trout were stocked annually if they failed to establish. This provided the necessary propagule pressure for establishment where environmental conditions were suitable; self-sustaining brown trout populations were reported from within the Breede, Olifants-Doring and Keurbooms Rivers in the Cape Fold Ecoregion; the Buffalo and Keiskamma Rivers in the Amatola-Winterberg Ecoregion; the Mooi, Umkomaas, Umgemi, Umvuti, Orange and Tugela Rivers in the Drakensberg-Maloti Highlands Ecoregion and the Phongolo, Blyde and Incomati catchments in the Southern Temperate Highveld freshwater ecoregion (de Moor & Bruton, 1988; SAIAB unpublished data). Although not formally assessed, there are anecdotal accounts that many of these initially, self-sustaining brown trout populations have since either disappeared or had their range reduced to isolated headwater streams within catchments.

In a review of early introductions, de Moor & Bruton (1988) provide a summary of anecdotal evidence for establishment failure. These include environmental mismatch (temperature, peat stained acidic waters, lack of spawning environments in reservoirs), extirpations through catastrophic events (e.g., droughts, flash floods) and perhaps, failure to compete with rainbow trout as there is no evidence of long-term co-occurrence (de Moor & Bruton, 1988). There are also many examples of populations persisting for multiple generations before local extinction. A good example of this is the trout population introduced to the Van den Boogaard River on sub-Antarctic Marion Island in 1964 to provide food and recreation to Antarctic research station staff (Cooper *et al.*, 1992). Here a small, stunted (max <350 mm L_T) population became established, feeding almost exclusively on an allochthonous diet dominated by snails and spiders. The impoverished nature of the stream and the inability of the population to practice an anadromous life-style because the river enters the sea via a 7 m high waterfall, most likely contributed to the extinction of this population with the last individual recorded in 1984 (Cooper *et al.*, 1992).

While there are many records of introductions and establishment of brown trout on a broad scale in sub-Saharan Africa, what constitutes a typical brown trout invasion and the factors limiting survival and establishment are not entirely known. Data on brown trout distributions in relation to stream thermal regimes, abundance and size structure within the Cata River may provide some insight into this.

The Cata River is a headwater tributary of the upper Keiskamma river system in the Eastern Cape, South Africa, where brown trout persist more than a century after first stocking. From 1903 onwards brown and rainbow trout were introduced throughout the headwaters of upper Keiskamma River system (Figure 24.3). By the 1930s records of brown trout were only available from the Tyume and Cata rivers where they survived until at least the 1970s (de Moor & Bruton, 1988). Currently, more than a century after their first introduction, their distribution is greatly reduced and they now only occupy < 7 km of the Cata River (Figure 24.3), while rainbow trout occur more widely in the upper reaches of the system. Their distributions, however, are mutually exclusive. The Cata River is a small (mean wetted width: 5.2 ± 0.8 m; depth: 0.3 ± 0.2 m), cool

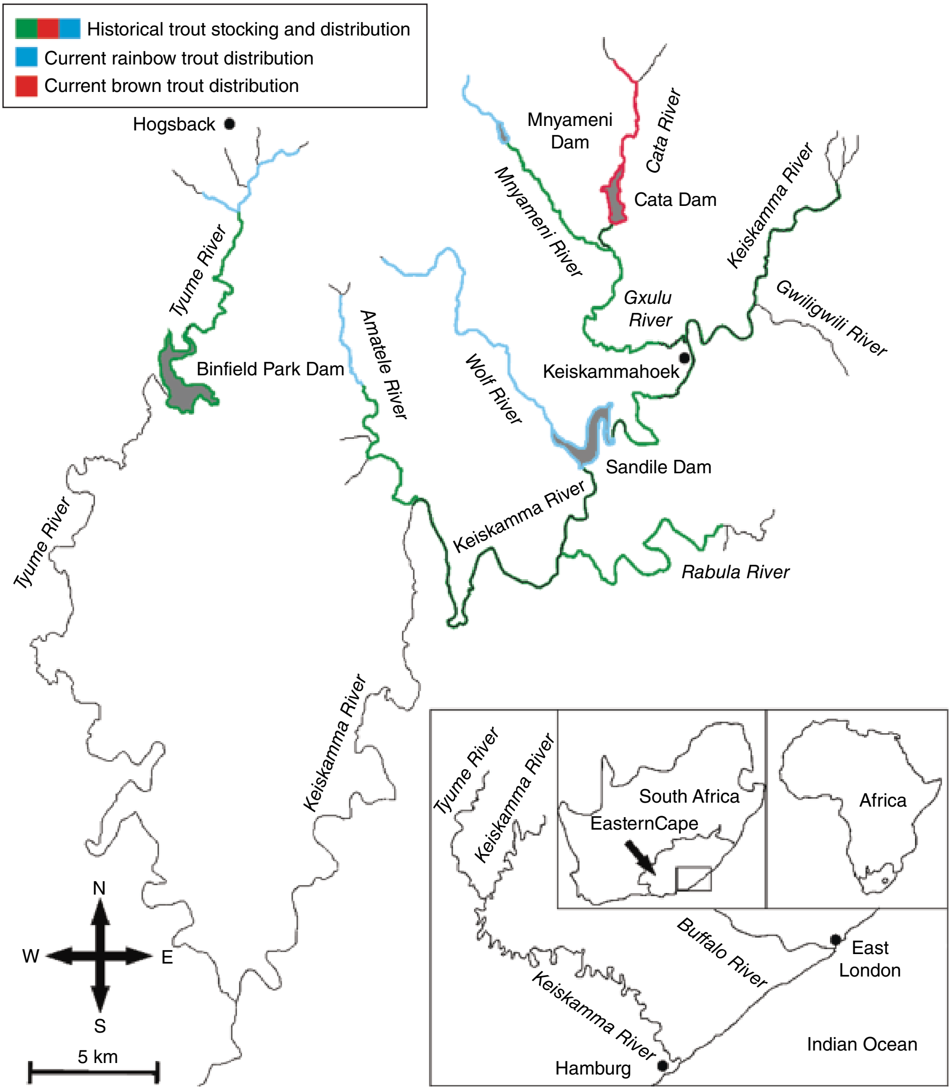

Figure 24.3 Brown trout in the Keiskamma River system, South Africa, a typical African situation. Initially both brown trout and rainbow trout *Onchorhynchus mykiss* were stocked widely throughout the catchment. After the cessation of stocking, brown trout now only occur in a small, isolated stream while rainbow trout have a wider distribution.

(16.2 ± 1.5 °C), clear (3.5 ± 1.7 NTU) third order mountain tributary of Keiskamma River which drains off the Winterberg mountains. The river originates at an altitude of 1900 metres above sea level in montane grassland, and flows over the escarpment through indigenous mist-belt forests and savannah vegetation in the coastal plateau grassland that extends to the base of the escarpment. Brown trout occupy a relatively short reach (~7 km) within the mist-belt forest to the base of the escarpment and do not extend beyond Cata Dam (Figure 24.3). The brown trout population consists of relatively small individuals (95–292 mm FL), however they occur in relatively high abundances (5.79 individuals 100 m^2; Jackson *et al.*, 2016). Despite the relatively small size of individuals occupying the Cata River, two large individuals (length/weight: 560 mm FL, 2.7 kg; 525 mm FL, 2.5 kg) were recorded from the Cata Dam, a 100 ha impoundment on the river, indicating their potential for growth under favourable conditions.

Within the Cata River, brown trout distribution reflects their temperature tolerances and based on a chronic stress threshold exceedance (using a temperature preference of 16.7 °C) using seven-day moving average of daily mean water temperatures (MWAT), the probability of occurrence ranged from 100% at 82 days threshold exceedance to 20% at 120 days threshold exceedance (Ellender *et al.*, 2016). Extrapolating these data over the upper Keiskamma River system indicates that while extensive areas are suitable for brown trout, establishment is patchy and confined to thermal refugia in upper stream reaches. A primary factor contributing to the patchy distribution of suitable thermal conditions is that the upper reaches of the Keiskamma River system have been fragmented by the construction of instream impoundments that increase the temperature in the downstream reaches by up to 3 °C compared to temperatures immediately above the impoundment (accelerating chronic threshold exceedances). The limitation of brown trout to small pockets of thermal refugia may therefore decrease their overall resilience and increase susceptibility to catastrophic events such as floods or droughts that have caused significant declines of brown trout populations in the Bushmans River, Kwa-Zulu Natal, South Africa (de Moor & Bruton, 1988). Such events may cause local extinctions and a lack of connectivity between refugia making recolonisation virtually impossible. This may explain their shrinking distributions and extinction from the Tyume River where they have not been recorded since the 1970s (Gaigher, 1975).

All available evidence suggests that brown trout populations in South Africa are declining, partly as a result of changing instream conditions due to human mediated impacts. This conforms to observations of MacCrimmon & Marshall (1968), who noted that the primary factors affecting the establishment of naturalised populations are water temperature, precipitation, and suitable spawning grounds and that future major expansion in distributions is unlikely in the face of human mediated impacts such as habitat alterations or changing climates. While their distributions may be shrinking and populations declining, where introduced there are documented negative impacts on a broad range of native biota from aquatic invertebrates to frogs and fishes (Ellender & Weyl, 2014).

Ecological Impacts

Although brown trout are considered to be one of the world's worst invasive fishes (Lowe *et al.*, 2000) and have been established in some African countries for over a century (Elliot, 1989; Ellender & Weyl, 2014), their ecological impacts within the continent were, until very recently, unassessed. What little information was published about invasive fishes in Africa, including brown trout, has generally been limited to distribution data in the context of describing the species as a fisheries resource (e.g. Elliot, 1989). Research on brown trout in South Africa over the last five years has, however, added to the growing body of evidence that this species can have negative effects on recipient ecosystems across the globe.

Brown trout are generalist predators, feeding primarily on aquatic invertebrates in their native range, but are able to feed on fish as well as terrestrial invertebrates and vertebrates such as amphibians, reptiles and small mammals (Gillespie, 2001; Budy *et al.*, 2013). This means that their potential impacts, mediated through dietary interactions, can span numerous trophic levels. For instance, in South Africa, they have been linked to the decline, and in some cases local extinction, of native invertebrates, frogs and fish (Karssing *et al.*, 2012; Ellender, 2013; Rivers-Moore *et al.*, 2013; Jackson *et al.*, 2016).

In the Ukhahlamba Drakensberg Park World Heritage Site, South Africa, brown trout and rainbow trout were together implicated in the declining populations of Natal cascade frog (*Hadromophryne natalensis*) in a number of streams (Karssing *et al.*, 2012). The authors compared the abundance of Natal cascade frog tadpoles above and below waterfall barriers to trout invasion and found that their abundance was reduced by factors of 4.7 and 15.7 at sites invaded by rainbow and brown trout, respectively (Karssing *et al.*, 2012). Similarly, invasive brown trout have caused declines in frog abundance in the USA (Chapter 20) and Australia (Chapter 22) and this is thought to be due to predatory behaviour by the trout (Kats & Ferrer, 2003).

In the same region in South Africa, Rivers-Moore *et al.* (2013) and Potgieter (2014) also found subtle differences in invertebrate community structure between upstream and downstream invaded sites. Further, Samways (1994) suggested that brown trout may have been instrumental in the decline in range of many endangered damselfly species in South Africa. Research in South Africa suggests that they can have cascading impacts on decomposition rates (Potgieter, 2014) and ecosystem subsidies through their predatory impact on aquatic invertebrates (Jackson *et al.*, 2016).

In the Drakensberg Park in South Africa for example, the diet of brown trout includes invertebrates such as mayfly larvae, crabs and dragonfly larvae (Crass, 1946). Comparisons of the diet of brown trout with co-occurring Mountain catfish *Amphillius natalensis* using carbon and nitrogen stable isotope analysis have shown that Mountain catfish have a higher nitrogen signature ($\delta^{15}N$) than trout, indicating that they are higher up in the food chain (Figure 24.4; Potgieter, 2014). The nitrogen and carbon ($\delta^{13}C$) signatures of brown trout suggest that they primarily consume benthic invertebrates, including mayfly and caddisfly larvae in the Drakensberg Park, despite their confirmed piscivory in other African river systems (Ellender, 2013). These findings explain the recorded impact of trout on benthic invertebrates and emerging insects (Rivers-Moore, *et al.*, 2013; Jackson *et al.*, 2016) and suggest that their present impact on native fish in Drakensberg Park streams is more likely through competition for resources.

Potgieter (2014) found that brown trout reduced the abundance of shredding invertebrates which caused a decline in the rate that leaf litter was shredded and decomposed, indicating that trout can alter ecosystem function through trophic cascades. In the Drakensberg and the Keiskamma River system, Eastern Cape, trout have also been

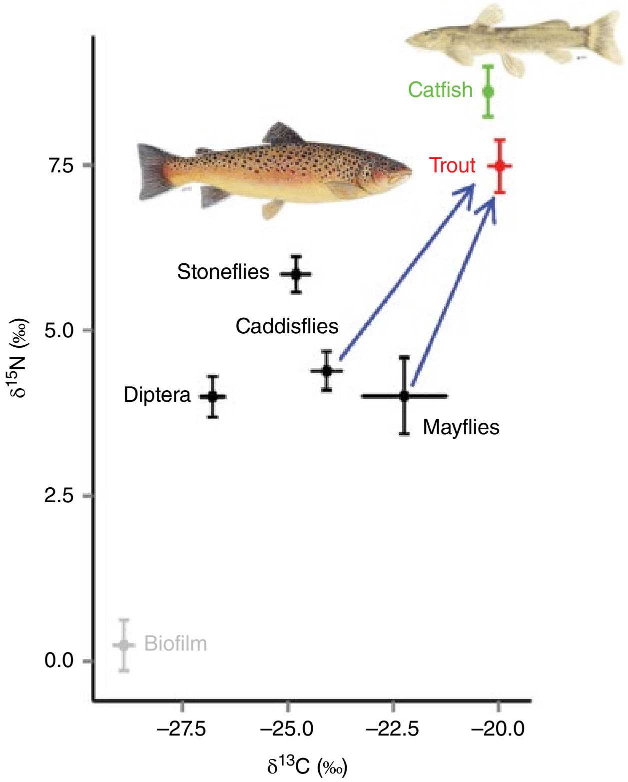

Figure 24.4 Isotope bi-plot of the Sterkspruit stream in the Drakensberg Park redrawn from Potgieter 2014. Data points show population mean ± standard deviation ($n = 3–9$). Blue arrows show assumed trophic links.

revealed to share emerging insects as a resource with riparian spiders, causing a decline in spider abundance at invaded sites (Jackson *et al.*, 2016). Introduced rainbow and brook trout have similarly been associated with declines in emerging aquatic insect subsidies to riparian species in Japan (Baxter *et al.*, 2004) and the USA (Epanchin *et al.*, 2010; Benjamin *et al.*, 2011).

In parts of South Africa, brown trout have also been implicated in the decline of native fishes. Brown trout were considered a contributing factor to the disappearance of the Maloti minnow, *Pseudobarbus quathlambae*, from the Umkomaas River in Kwa-Zulu Natal. Staff at a hatchery stocking brown trout into the stream in 1938 noted a sharp decline in the abundance of the minnow following the introduction of trout; *P. quathlambae* had disappeared from the stream by the 1960s (de Moor & Bruton, 1988). It was, however, noted that severe habitat degradation in the stream's catchment in the 20 years following trout introduction could have equally contributed to the extirpation of *P. quathlambae* from the Umkomaas River (de Moor & Bruton, 1988). A similar minnow species that seems to have suffered direct negative impacts from brown trout is the Border barb, *Barbus trevelyani*. This minnow, endemic to the Keiskamma and Buffalo River systems in south-eastern South Africa, has been extirpated from 24% of its historical global distribution by brown trout and rainbow trout (Ellender, 2013). Outside of Africa, brown trout have caused the decline of several species of *Galaxias* in New Zealand and Australia (Chapters 21 & 22) and this is thought to be due to predatory behaviour and competition for resources, such as space and food (Crowl *et al.*, 1992; Townsend, 2003).

Although brown trout are restricted in their range in South Africa, it is clear that their persistence in certain streams has had long-term negative impacts on the local aquatic ecosystem. In other parts of their African range, however, research on the impacts of their invasion is lacking. Negative impacts of introduced salmonids on native fish and macroinvertebrates have been reported in Zimbabwe (Kadye *et al.*, 2013), and it is likely that similar impacts have occurred in brown trout-occupied streams in African countries such as Kenya, Lesotho, Madagascar and Swaziland, where populations persist without the support of stocking programmes (Welcomme, 1988). Unfortunately, a lack of aquatic ecology research capacity at higher education institutions within these countries, driven by a host of historical socio-economic pressures (Denny, 2001), means that dedicated research into the ecological impacts of brown trout across Africa is unlikely to be pursued in the near future. Nonetheless, the emerging evidence from South Africa suggests it is a topic of research that should not be ignored going forward.

Fisheries and Management

Brown trout and rainbow trout were introduced largely as a consequence of British colonists' dissatisfaction with the lack of indigenous fishes 'suitable' for sport angling and particularly flyfishing (McCafferty *et al.*, 2012). Early successes with brown trout most likely encouraged the subsequent introduction of rainbow trout which, as a result of their higher temperature tolerance, are more widespread than brown trout. Although rainbow trout are more widespread and abundant in Africa, brown trout remain a popular angling species and are still stocked alongside rainbow trout in fisheries. In the African context we will discuss angling in the context of trout, which includes both rainbow and brown trout.

From an angling perspective, trout introductions were very successful and flyfishing for trout is a major component of recreational angling in South Africa (Weyl & Cowley, 2015). Angling organisations such as the Cape Piscatorial Society (established in 1931) and the Federation of South African Flyfishers (FoSAF) were formed to represent angler interests. Literature from these societies, such as the journal *Piscator*, first published by the Cape Piscatorial Society in 1947, includes stocking records, establishment successes, quality of fishing and potential risks to fisheries. In South Africa, these societies represent several thousand members and actively lobby for the interests of their members. Flyfishing for trout has also resulted in considerable tourism development in streams and impoundments. In high altitude areas many private and some public waters are managed as trout fisheries, which forms the basis of a substantial tourism-based local economy in suitable areas (McCafferty *et al.*, 2012). In a continent where poverty eradication, employment and economic empowerment are important national policy objectives, economic opportunities provided by recreational fisheries cannot be ignored when attempting to manage alien invasive species. As a result, trout are considered conflict species in Southern Africa because their management requires weighing up the positive economic benefits against environmental harm (Ellender *et al.*, 2014).

As was the case in many countries, the propagation and distribution of non-native sport fishes was supported by Government agencies that not only funded hatcheries and stocking programmes, but also enforced catch size limits, gear restriction (flyfishing only) and closed seasons to facilitate establishment. In South Africa, the responsibility for these fisheries fell upon the same agencies that were also responsible for conservation (e.g., Natal Parks Board). After surveys in the 1960s revealed that alien sport fishes were having a pronounced impact on native fishes (see Ellender & Weyl, 2014), conservation authorities started to question their role in the demise of the native fishes (Ellender *et al.*, 2014). A 1986 meeting between trout anglers and conservation officials marked the beginning of the withdrawal of government involvement in active stocking and management of alien sport fishes (Ellender *et al.*, 2014). In some cases, conservation authorities devolved some management authority to angling clubs while in others, such as the Eastern Cape Province, management of inland fisheries stopped completely, to the extent that no freshwater angling permits were necessary to fish for alien fishes.

In addition, conservation authorities started a process of rehabilitating rivers through alien fish control projects to better conserve threatened fish species. The first was an eradication of alien invasive smallmouth bass *Micropterus dolomieu* from the Rondegat River but project proposals by the Western Cape provincial nature conservation agency CapeNature to control trout in rivers were met with substantial opposition from trout anglers (Ellender *et al.*, 2014; Weyl *et al.*, 2014; Weyl *et al.*, 2015). As a result, CapeNature were unable to take decisive conservation action regarding trout populations at the time (Weyl *et al.*, 2015). Relationships between conservation authorities and anglers became strained and angling organisations actively lobbied against alien invasive species legislation that they felt would negatively impact directly on recreational angling and associated economic activities.

South African Legislation

Recent legislation for the regulation of introduced species in South Africa began with the National Environmental Management: Biodiversity Act 10 of 2004 (NEMBA), which specifically deals with species and organisms posing potential threats to biodiversity. A 'national list of invasive species' was produced in September 2007 (Government Gazette No. 30293) and included rainbow trout as an invasive species but not brown trout. A revised list of invasive species was released on 3 April 2009, Government Gazette No. 32090 Notice 350, this listed both brown trout and rainbow trout as Category 2 invasive species to be regulated by area (that is the species could be managed in certain areas (rivers or catchments) under permit and was prohibited in other areas) (see Table 24.2). In anticipation of managing under permit in certain areas and prohibiting their introduction to other river systems free of trout, the Department of Environmental Affairs commissioned a collaborative mapping process, co-ordinated by the Southern African Institute of Aquatic Biodiversity, to ascertain the known distribution of trout in South Africa. This mapping included the identification and mapping of areas of high indigenous aquatic biodiversity and potential 'sanctuaries' for endangered indigenous fish.

The effort to map trout distribution and to manage the species by area, however, appeared to be ignored as Government Gazette No. 36683 of 19 July 2013 contained Government Notice R507 in which both rainbow and brown trout were listed as Category 1b invasive species. Category 1b invasive species '*require control by means of an invasive species management programme*'.

Listing trout as Category 1b invasive species understandably raised the ire and concern of trout fishing fraternity and fresh water aquaculture managers who relied on trout for their livelihoods. This concern was due to the definition of control in NEMBA;

Table 24.2 South African legislation regarding brown trout *Salmo trutta*, a Category 2 Alien Invasive species.

Restricted activities	Category 2
a) Importing into the Republic, including introducing from the sea, any specimen of a listed invasive species.	Permit Required
b) Having in possession or exercising physical control over any specimen of a listed invasive species.	Permit Required
c) Growing, breeding or in any other way propagating any specimen of a listed invasive species, or causing it to multiply.	Permit Required
d) Conveying, moving or otherwise translocating any specimen of a listed invasive species.	Permit Required
e) Selling or otherwise trading in, buying, receiving, giving, donating or accepting as a gift, or in any way acquiring or disposing of any specimen of a listed invasive species.	Permit Required
f) Spreading or allowing the spread of any specimen of a listed invasive species.	Permit Required
g) Releasing any specimen of a listed invasive species.	Permit Required
h) The transfer or introduction of specimens of a listed invasive freshwater species from one discrete catchment system in which it occurs, to another discrete catchment system in which it does not occur; or, from within a part of a discrete catchment system where it does occur to another part where it does not occur as a result of a natural or artificial barrier.	Permit Required
i) Discharging of or disposing into any waterway or the ocean water from an aquarium, tank or other receptacle that has been used to keep a prohibited alien species or a listed invasive species.	Prohibited
j) The introduction of any listed invasive species to South Africa's off-shore islands.	Prohibited
k) Catch and release of a listed invasive freshwater fish or listed freshwater invertebrate	Permitted
l) The introduction of a listed invasive fish specimen, or a listed freshwater invertebrate specimen, into a river system	Permit Required

'**control**', in relation to an alien or invasive species, means (a) to combat or eradicate an alien or invasive species; or (b) where such eradication is not possible, to prevent, as far as may be practicable, the recurrence, re-establishment, re-growth, multiplication, propagation, regeneration or spreading of an alien or invasive species.

The change of status of brown trout between the lists of 2007 when the species was not even listed and the list of 2013 where it was listed to be 'combated or eradicated' raised significant concerns amongst those who enjoy the sport of fly-fishing for trout and those whose livelihoods, and the livelihoods of those they employ, depend on trout aquaculture. The draft list of 2013 had created a great degree of uncertainty and animosity from stakeholders in the trout fraternity, and these fears were not easy to allay.

In an attempt to allay these fears and in order to ensure that the regulations pertaining to NEMBA were finally promulgated, the Department of Environmental Affairs revised the proposed listing of many introduced and invasive species. In February 2014 the revised invasive lists and regulations were published for public comment in this draft of the regulations, and brown trout were listed as requiring a permit for introduction into *National Parks, Provincial Reserves, Mountain Catchment areas, Forestry Reserves and rivers; and in other parts of the country, may only be introduced into dams within freshwater systems in which it is has been formally documented to occur.*

As these proposed lists and regulations were drafts prepared for public comment, the National Department of Environmental Affairs, solicited comment from a range of stakeholders not only through a statutory period of 30 days for public comment but through arrangement of meetings with stakeholders. At one such meeting with stakeholders representing industries as diverse as bird-breeders, plant nurseries, pet shop owners and trout fishing fraternity, almost half of the day-long meeting was devoted to discussions around the listing of trout. The trout fraternity representatives argued against the proposed regulations on a number of fronts. Key issues included: that trout did not meet the criteria of an invasive species and a lack of scientific evidence of the risk posed by trout to biodiversity. During the revised comment period the trout fraternity also lobbied its members to submit comments to the Department of Environmental Affairs. The vast majority of comments received from the public during this statutory comment period were concerns regarding the listing of trout. In addition to this lobbying for public support there was a co-ordinated media campaign which challenged the proposed listing of trout. For example, an article by Coan in the Natal Witness (6 May 2015) described that the Federation of South African Fly-fishers planned to stage a number of meetings around the country to highlight concerns regarding the legislation. He stated that 'their position is simple: they believe that the legislation is aimed at destroying the trout-fishing industry'. This and similar commentary in other public media and industry publications raised the degree of antagonism around the issue.

As a result of both political lobbying and increased public antagonism towards the listing of trout, both rainbow trout and brown trout were removed from the revised Alien and Invasive Species regulations promulgated on 1 August 2014 (Government Notice No. 37885, Vol. 590, Regulation Gazette No. 10244) because their inclusion was threatening the passing of legislation on more than 550 other Alien Invasive Species. Although the Department of Environmental Affairs, appeared to have acquiesced and not listed the two trout species there was still a strong belief that, in order to protect areas of conservation significance not yet impacted by trout, trout needed to be regulated to prevent unwanted introductions into these areas. The Department emphasised that the trout industry was already regulated and that permits for a variety of trout related activities were managed either by Department of Fisheries for aquaculture facilities or by Provincial Conservation Departments, which issued permits for stocking of rivers and dams. In order to facilitate progress, the Department of Environmental Affairs suggested a more nuanced approach which would allow the development of aquaculture facilities under permits, and allow for stocking in areas where trout were known to already occur. In order for these regulations and control to work, accurate maps of known distribution of trout needed to be constructed. These maps and legislation governing the use of trout continue to be developed. Conservation Officials appear hopeful that this will meet their needs for biodiversity conservation. The Fisheries Officials do not believe this will hinder aquaculture development, and neither will it impact on the value-chain of fly-fishing.

Conclusion

Brown trout have been in sub-Saharan Africa for more than 100 years. Their presence has resulted in not only the development of sport fisheries and associated economic activities, but also resulted in negative impacts on native biota. As a result, management is necessary. In most areas of Africa where brown trout occur, distributions are restricted, and as quantitative information on its impacts is lacking, no conclusions can be drawn on possible management interventions. South Africa, however, has been developing legislation to manage brown trout populations. The process has however been complicated by the conflicting agendas of the development-driven private enterprises vs the conservation driven agendas of local Nature Conservation authorities; the lack of an overarching national fisheries policy to guide rules; unaligned provincial legislation on trout; strong personalities and opinions on all sides and; the quagmire of finding common ground between conservationists, political lobbyists, lawyers and legislators. Although areas are heavily contested, it is hoped that this process will ultimately result in a 'win-win' for all parties.

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Section 6

Conservation and Management

25

Why Conserve Native Brown Trout?

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Introduction

The book you are reading is a very good example of the amount of research and management effort that has gone into understanding, conserving, and enhancing brown trout populations. The latest studies included in this volume build upon more than a century of scientific research that has been the basis for developing an evidence-based approach to brown trout management. The brown trout is certainly among the most well-studied freshwater fishes – research extends from the behaviour of individual trout to understanding complex social-ecological systems. Although we still have much to learn about brown trout, managers today have much of the basic life history knowledge necessary to make wise management decisions (Elliot 1994, Jonsson and Jonsson 2011, Young *et al.*, Chapter 29, this volume).

Most of the threats to brown trout biodiversity are related to human activities such as habitat degradation, overharvest, or indiscriminant stocking of hatchery fish, and therefore trout management requires managing human influences, behaviours, and attitudes. This short essay addresses some of the ethical justifications for conserving the native biodiversity of brown trout.

Although many important brown trout populations have been extirpated or severely depleted, a considerable amount of the native diversity of the species remains (Vøllestad, Chapter 5, this volume). Many brown trout populations remain abundant enough to support recreational, and in some cases commercial and subsistence fisheries (e.g., Piccolo *et al.* 2012). These remaining native populations, along with successful introductions worldwide ensure that the brown trout as a species is in no danger of extinction.

Researchers realized long ago, however, that the intraspecific diversity of brown trout is driven by local adaption that allows populations to make use of the environmental

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

conditions found in their native watersheds (see Ricker 1972). Recognizing this intraspecific diversity is the key to successful conservation of salmonid biodiversity (Behnke 1992, 2002); such biodiversity provides a 'portfolio effect', buffering metapopulations against environmental change by spreading the risk of local population depletions (Schindler *et al.* 2010). As Darwin long ago told us in '*The Origin of Species*', it is variation within species that is the raw material upon which natural selection works. So although the brown trout as species is more widespread and perhaps more abundant than it has ever been, there is still much concern about the continued extirpation of endemic, locally-adapted native populations. If we wish to conserve a brown trout species that will be resilient to future changes in the biosphere, therefore, we must focus on this intraspecific biodiversity.

Both Atlantic (genus *Salmo*) and Pacific (genus *Oncorhynchus*) salmon and trout establish locally-adapted populations through their celebrated ability to home to their natal streams for spawning (e.g., Taylor 1991; see Primmer 2011). Key life history traits such as age at smolting and maturity, season of spawning, and anadromy versus residency have all been shown to be at least partly under hereditary control (Ricker 1972). Significantly, local adaptation has recently been shown to be under control of a tiny fraction of the genome in Atlantic salmon (Barson *et al.* 2015), at level of sampling unobtainable using previous genetics techniques such as mDNA. Thus, hereditary control of life history traits may be even more important than concluded by earlier researchers (Ricker 1972, Taylor 1991); this has important consequences for salmonid conservation (Piccolo 2016). Such local adaptation, along with considerable phenotypic plasticity, has allowed brown to thrive under a great variety of environmental conditions from icy north European and Icelandic coastal streams to harsh glacier-driven Alpine torrents – both very different from southern populations of the Iberian Peninsula, Sicily or North Africa (see Lobón-Cerviá, Chapter 1, this volume). Adult brown trout can range from a size of 100 g to over 20 kg; some populations migrate long distances in oceans and rivers, others spend their entire lives in a short reach of stream. Sadly, an unknown proportion of the historic native biodiversity of brown trout has already been lost to habitat destruction, overfishing, pollution, and hatchery stocking. Managers are now faced with the urgent task of conserving the remaining populations. Previous chapters of this book have focused on *how* to conserve the remaining biodiversity of brown trout. This final essay focuses on *why* we ought to conserve brown trout – we believe the answer to this question will play an important role in the success of future conservation efforts.

Conservation Values of Brown Trout

The concept of ecosystem services is relatively new, having been introduced by conservation biologists during the initial growth of the discipline (e.g., Ehrlich and Mooney 1983). It was only with the UN's Millennium Ecosystem Assessment (MEA, 2005) that ecosystem services became a well-established justification for conservation, particularly biodiversity conservation. The argument is that loss of biodiversity leads to reduced delivery of ecosystem services – the products of nature that sustain human society. Ecosystem services assign distinctly *anthropocentric* (i.e., *utilitarian*) values to nature. Anthropocentric values are those that are of direct use to humans – the assumption is that value (good and bad) does not exist in nature unless a human is there to experience it. Ecosystem services have been divided into categories such as *provisioning* (e.g., fish for food) or *cultural* (e.g., fish for recreation). When we discuss brown trout in relation to ecosystem services, therefore, it is largely their value to humans as food, sport, or even aesthetics, of which we speak. Over the past few years, however, a considerable debate has taken place among conservation biologists about how we value nature and why we ought to conserve nature. At the heart of this debate is the question of whether nature should be valued for its services to humans (*instrumental value*) or for its own inherent (*intrinsic*) values. Here we discuss this in relation to conservation of brown trout diversity.

> *Conservation is getting nowhere because of our Abrahamic concept of land. We abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong we may begin to use it with love and respect.*
>
> Aldo Leopold, 'A Sand County Almanac'

The American ecologist Aldo Leopold argued that truly enlightened conservation could not take place until humans had learned to recognize nature's intrinsic value. He wrote famously that '*A thing is right when it tends to preserve the integrity, stability and beauty of the biotic community. It is wrong when it tends otherwise*.' By stating that it is *right* to conserve nature (or *wrong* not to do so) Leopold suggested that nature has intrinsic value – humans ought to conserve nature because of its inherent goodness, not because of the good it does for us. A generation of environmental philosophers has followed in Leopold's footsteps, building an indisputable case for intrinsic natural values (see Rolston 2012, Callicott 2014). Many are now convinced that the long-term success of biodiversity conservation will rely upon recognizing both ecosystem services and intrinsic values (Cafaro and Primack 2014, Piccolo 2015, Vucetich *et al.* 2015). Today, the first organizational value for the Society of Conservation Biology (SCB) states: '*There is intrinsic value in the natural diversity of organisms, the complexity of ecological systems, and the resilience created by evolutionary processes*.' Such intrinsic value encumbers upon humans the duty to protect biodiversity because of its inherent good – although it will not always be easy to balance the needs of people and nature, we must give due consideration to the consequences of our actions. We must ask the difficult questions about whether or not we have had it *too* good at the expense of other species.

The next time you hold a native trout in your hand while working or fishing, take a moment to reflect about its history. Consider whether or not you believe that it is an object of value in and of itself. Ask yourself whether the trout pursues a good of its own, as part of the stream ecosystem where its ancestors have lived for millennia, slowly co-adapting with their fellow species as the river has run its course through time. As the brown trout species has been doing since about the time that the human and chimpanzee lineages went their separate ways some 7.5 million years ago. Does the trout need you to recognize its value? Perhaps even more arrogantly, we might ask whether the trout has any value at all if you as a human do not exist to value it. In that case, what good was a trout for the 7 million years they existed before humans arrived on the European continent from Africa? Were all the trout over those 7000 centuries simply value-less objects, waiting for humans to evolve to recognize their true worth? The problem with justifying native trout conservation solely based upon ecosystem services and anthropogenic values is that we fail to recognize the true intrinsic worth of the species or its ecosystem. Although some trout populations may provide significant ecosystem services for humans, some – perhaps most – don't. It is inconceivable, therefore, that the long-term conservation of brown trout biodiversity can be based only upon anthropogenic values. After over 50 years of working on conservation of the native California golden trout (*Oncorhynchus mykiss aquabonita*) Pister (2011) concluded that '*there is a growing need… for an improved environmental ethic …*' if conservation is to succeed.

Conclusion

It's been nearly a century and a half since Darwin (1874) reminded us of the humble origins we share with all life; more than half a century since Leopold (1949) wrote that '*… a land ethic changes the role of Homo sapiens from conqueror of the land-community to plain member and citizen of it*.' This eco-evolutionary worldview opens the door for us to understand nature's intrinsic value. Anyone who has felt the warmth of the sun on a cold day, been fed when hungry, or simply seen the smile of a child, knows that 'good' is not a social construct, but rather an objective experience. But if we are just plain members and citizens of the biosphere, descended from a long line of continuous life, than surely the objective experience of good extends down that line. No one expects a trout to smile, but we ought to recognize that they do indeed pursue a good of their own, independent of any human valuation. Progress in recognizing nature's intrinsic good has been slow but we are progressing all the same. Over the past 50 years a growing number of anglers, managers, and citizens have come to recognize that we have a duty to conserve native trout. Aldo Leopold and a generation of environmental philosophers have urged that the long-term success of conservation must be based in part upon recognition of nature's intrinsic worth and the duty encumbered upon all humans to uphold it. Let us with this new book take another step towards the conservation of brown trout biodiversity by recognizing its unique intrinsic value before it is too late.

> *So much must be done in so short a time to protect the remaining genetic diversity of these fishes that I cannot responsibly suspend judgements about trout biology and management in hope that irrefutable data might one day be collected… If protective management of these species cannot be based on informed professional judgment, many native stocks will disappear before science can vouch for their unique value.*
>
> Robert J. Behnke, 1992. *Native Trout of Western North America*

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Fisheries Management of Stream-Resident Brown Trout Populations – Possibilities and Restrictions

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Introduction

Fishing is an ancient practice in the acquisition of natural resources dating back to the Middle Stone age (Henshilwood *et al.* 2001). Although fishing began as a subsistence practice and later developed as a commercial enterprise, recreational fisheries worldwide have grown in importance in recent decades (Welcomme 2016); many inland recreational fisheries now exceeding commercial fisheries in catch and economic value (Cooke *et al.* 2015). Fishing for trout in most European waters, as in many other regions of the world, is now largely considered as recreational or 'sport', if contact with wild animals can be termed 'sport' at all. However, fishermen nowadays often fish solely for recreation or to experience nature. Therefore, recreational fishing can be considered an important cultural ecosystem service, providing human well-being through contact with nature. In addition to cultural and economic considerations (e.g. Arlinghaus 2004), ethical components are of increasing importance in recreational fisheries. Along with the growing common perception that fishing is a reasonable pastime, animal welfare and nature conservation issues are brought forward that, in extreme cases, deem fishing morally reprehensible (c.f. Arlinghaus *et al.* 2012).

Aside from social perceptions of fishing it is significant that anglers represent the most prominent stakeholder group for aquatic-ecosystem concerns in many areas of the world. Fishermen represent a very valuable source of local ecological knowledge which can be explicitly valuable whenever nature conservationists are in need of support from a larger group of people. Often they are 'the memory of a river', recalling fish sizes, catch rates and ecological conditions. Therefore, many ideas or campaigns to protect or restore freshwater ecosystems are driven by people who enjoy fishing and thus have developed a closer tie to aquatic ecosystems. As testament to their reliable support for nature conservation and their serious interest in 'fish welfare', recreational

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fisheries/fishermen need to work on strategies (1) how to use fish stocks in a sustainable way; (2) how to protect or restore stream habitats; and (3) to practice fishing in a morally/ethically defensible way.

In this chapter we focus on the management of trout rivers and streams and their respective populations of stream resident trout. We first question when and under which circumstances management of trout populations is needed at all and outline a three-step approach for identifying deficits causing impaired fish stocks. A case study of a highly valuable trout fishing beat in the Austrian pre-alpine limestone River Ois is presented to determine biological key parameters one has to consider in order to harvest fish within the realms of natural production. We compare and contrast this example with a second case study, the granite mountain stream River Kleiner Kamp of the Bohemian Massif to set out the need for adaptive management regulations. After commenting on stocking we finally discuss the cornerstones of our understanding of sustainable fisheries management, the tools fisheries management can use and the restrictions or limits sound management has to address.

When is Management Needed?

Among the six major requirements for the existence of brown trout populations according to Elliott (1994) the factors of suitable temperature (1) and oxygen supply (2) are in general intrinsic to the physical attributes of waterbodies. These factors can be difficult to manage locally, and in the case of climate change, they occur at large spatial scales. The availability of food (3) is primarily regulated by the physical and chemical habitat characteristics and the corresponding natural productivity, respectively. In contrast to these three parameters, suitable habitat structures for all life stages (4), gravel for spawning (5) and open migration routes (6) are physical habitat quality prerequisites which can be managed locally, and by all means have to be addressed by fisheries management strategies/concepts. Specifically habitat prerequisites (4–6) are indispensable life-cycle requirements that have been widely anthropogenically-altered throughout much of the natural range of brown trout in Eurasia. Water quality aspects were a major problem in preceding decades but have widely been solved in most Western European countries and are nowadays of reduced relevance. Recent problems related to water quality issues like emerging chemical (e.g. endocrine disruptors, environmental toxins) as well as parasitological problems (e.g. malacosporean parasites), often associated with increasing temperatures, are potential future challenges for fisheries management, but are beyond the scope of this chapter.

The probability that several of the above factors overlap is very likely in Europe, severely complicating the challenge of managing fisheries sustainably. Generally speaking, management is required wherever human activities negatively impact trout habitats or where recreational fisheries use stocks in an unsustainable way. In the end all potential problems of wild trout stocks are related to human activities. Therefore, the need to manage trout is ultimately always associated with human influences, attitudes, behavior and expectations. Contemporary fisheries management in waters dedicated primarily to recreational fishing must furthermore try to merge nature conservation needs and the satisfaction of a still growing number of anglers.

Managing Altered Physical Habitats

As long as the habitat quality of a trout stream is unimpaired the single purpose of fisheries management is to avoid unsustainable use by ensuring sufficient recruitment and avoiding overfishing. How this can be accomplished by implementing sound fishing regulations, based on fish stock data, will be discussed later in the chapter. First, we focus on the typical situation of European streams, altered/impaired habitat.

As viable physical habitats are a prerequisite for vital brown trout populations, as for all organisms, the efforts and possibilities to restore alterations and to reestablish habitat quality towards the natural/pristine status have to be fully exhausted before any other management measures are taken into consideration. The extent of occurring habitat alterations varies as the degree of deterioration and the interplay and severity of different impact combinations can be manifold. The consequences of impaired habitat quality in any case are the reduction of the habitats' carrying capacity due to bottlenecks in the life-cycles of affected populations. To assess the consequences and to derive proper management measures a process we call 'deficit analysis' has to be carried out. Deficit analysis comprises three steps:

1) Analysis of the habitat quality to isolate and specify potential bottlenecks.
2) Analysis of the stock (development).
3) Analysis of preceding management activities.

The first step of a deficit analysis aims to detect the occurring habitat deficits which typically are related to (1) hydrological (water abstraction, hydropeaking, thermal alterations etc.) and/or (2) morphological impacts (bank stabilization measures, instream habitat alteration, longitudinal/lateral barriers etc.). Both types of impacts, and in addition the retention of bedload in upper reaches of the catchment, can have negative consequences for the quality of bed sediments and the availability of food. The analysis of habitat quality in this case is strictly intended for serving fisheries management purposes. This is in many cases congruent or at least in line with processes of river restoration projects, but the scope of river restoration is generally broader, as the fish fauna is just one out of many important aspects related to the ecological integrity of rivers and streams.

The starting point for habitat analysis is set by the life-cycle of the fish species of interest, in our case brown trout. A fish life begins at the spawning ground – therefore the quantity and quality of spawning habitats is a major issue and has to be thoroughly analyzed. Brown trout relies on the availability of loose gravel for spawning and successful recruitment (e.g. Kondolf 2000). Potential spawning habitat deficits are typically related to increased accumulation rates of fine sediments, on the one hand, or to an artificial coarsening of bed sediments, on the other hand. Increased input of fine sediment leads to clogging of the interstitial spaces and consequently degraded gravel beds, hindering redd excavation or the delivery of oxygen-rich water for successful development of incubating eggs. Retention of sediments through torrent control structures and impoundments as well as flushing out gravel due to reservoir management practices lead to coarsening of bed sediments, impeding redd construction. Overall, alterations of natural sediment regimes are a severe and widespread problem in alpine rivers and deficits of suitable spawning habitats are consequently among the major bottlenecks in many rivers and streams (e.g. Pulg *et al.* 2013). Trout fry develop inside interstitial spaces for a period of up to six months (e.g. Crisp 2000). Thus, not only the spawning itself but also the early development after hatching is affected by deteriorated river beds. Even though eggs are able to develop, high losses can occur in the alevin or early fry stage when sealed river beds prevent juveniles from successfully emerging. A further impact on developing eggs is flow alteration due to hydropower; this may result in redds be dewatered, or severe alterations in temperature regimes. Dams may also reduce the downstream transport of suitable spawning gravels, reducing the amount of spawning habitat.

Further on in the life-cycle, early juvenile stages are threatened by a variety of human-induced, hydrological impacts, such as stranding due to hydropeaking surges, reservoir flushing, and thermal changes etc. Morphological alterations due to damming and other river control measures can lower habitat quality for all different life stages. While residual flow stretches mainly reduce the amount of adult fish habitat as the amount of flow and consequently deeper habitats are reduced, many regulated channels lose important habitats for juvenile fish, such as shallow gravel banks or adjacent side arms and backwaters. Another major problem is the disruption of migration pathways, both laterally and longitudinally. Beside weirs and ramps, river bed degradation and, consequently, disrupted connections between main stem and tributaries, hamper spawning migrations and decrease the original longitudinal range of populations. In addition to hindering upstream migration, specifically hydropower dams and the associated turbines can cause high mortality of downstream migrating fish.

This (incomplete) list of possible habitat perturbations reveals why analyzing habitat quality constitutes a major task of fisheries management. As the life-cycle stages of any fish species are related to distinct habitat features, the quality of these features has to be assessed and contrasted with data on fish demographics and distributions. Good-quality habitat data can also be incorporated into recently developed habitat quality models to assess the sensitivity of various life history stages to changes in habitat (see Piccolo and Watz, Chapter 15, this volume). In many cases, fish population structures specifically reflect the habitat situation and help identify potential quality shortcomings.

The most powerful management tool to sustainably support healthy fish populations is habitat restoration. Consequently, especially for the conservation of wild fish stocks, the primary task of fisheries managers is to pursue all options to restore habitat conditions to as close to the pristine situation as possible. A complete introduction to the available measures one can choose would go beyond the scope of this chapter but there is voluminous literature on this topic (e.g. Jungwirth *et al.* 2002, Roni & Beechie 2013). In general, small-scaled mitigation measures, such as the maintenance or improvements of spawning grounds (e.g. Palm *et al.* 2007, Pulg *et al.* 2013), can be carried out and financed relatively easily by people/clubs/agencies responsible for fisheries. However, mitigation or restoration at large- or even catchment-scales needs broader efforts that should nonetheless be supported by fisheries managers. To attain objectives on a larger scale, fisheries managers dealing with common issues (e.g. along the same river) have the chance to gain greater influence when they form coalitions and join with local communities to speak with a common voice. Combining a critical mass of expert and public opinion (see also Young, Gaskell, Jacklin and Williams, Chapter 29, this volume) with the latest sampling and analysis methods is a vital necessity, where riverine water bodies are characterized by a small-scale segmentation of management units (e.g. in Austria).

However, when the habitat quality analyses are completed the results have to be contrasted and merged with the results of step 2, the survey of the current fish stocks. Quantitative electrofishing data must first be generated to enable a comprehensive assessment of the actual population status, e.g. abundances, biomass and population structures. As highlighted in the River Ois case study (see below), yearly surveys and long data series create the best basis and are therefore desired. In many cases data on the fish stock are missing or collected only sporadically. However, it is an important management task to gather stock data. Although the financial expenditure for fish stock surveys is substantial, it will pay off, as in combination with the habitat quality survey potential bottlenecks become detectable and the elimination of habitat deficits will sustainably improve the stocks whereas stocking will remain a continuous management measure, occasioning costs without solving the underlying problems (see below).

Further, to have sufficient knowledge on the actual fish populations and habitat quality provides the opportunity to reflect and evaluate preceding management actions, specifically success or failure of stocking campaigns (see below). The results of all the three steps of deficit analyses provide the basis for the elaboration of management strategies and to derive management actions.

Sustainable Use of Brown Trout Populations

Two fishing beats we want to introduce as case studies for sustainable fisheries management are situated in Austria in the upper reaches of the River Ybbs and the River Kleiner Kamp. Both rivers hold healthy trout populations which enable us here to disregard the previously explained deficit analysis and focus on the population ecological aspects of fisheries management. In this section we will concentrate on the example of the upper Ybbs (called River Ois) which drains from the alpine foothills of the Northern Limestone Alps. Its constrained and largely preserved natural river bed can be characterized as pool-riffle channel-type (Frissell *et al.* 1986; Montgomery & Buffington 1997) with a mean discharge of 4.5 m^3/s (Figure 26.1). The river stretch features a high variance of structural diversity, water depth and heterogeneous substrate conditions. This fishing beat is about 4 km long, the river is about 12 m wide and it comprises a wetted area of about 5.2 hectares. We present here our management approach which was successfully applied over the last decade on rainbow trout (*Oncorhynchus mykiss*), and will be assigned to brown trout in the following years. Until now brown trout has not been harvested in order to survey the natural and unimpaired development of the stock throughout the preceding 10 years (2008–2017).

To highlight the need for adaptive management strategies we include our experience with a trout population in the River Kleiner Kamp, located in the southern reaches of the Bohemian Massif. The character of the respective river is defined by the crystalline substrate and a plane-bed channel type (Montgomery & Buffington 1997). Like the River Ois, the respective section of the River Kleiner Kamp is well-structured, of similar dimensions but of less discharge than the Ois (Figure 26.1).

An important prerequisite for sustainable harvest of fish is the analysis of key parameters related to the population size of the extant, exploited species. As a first step we distinguish two population aspects: The first one estimates stock density, which is typically described as the sum of individuals or the sum of weight for a given area and for

Figure 26.1 Top: Pool-riffle sequences define the character of the Ois River, a trout stream located in the foothills of the Northern Limestone Alps in Lower Austria. (Source: C. Ratschan); Bottom: Granite rocks characterize the River Kleiner Kamp, a well-structured plane-bed trout stream of the southern Bohemian Massif.

defined size classes. The second one is to estimate total stock size and then calculate the number of harvestable fish. To gain these data, regular fish censuses are required. In this context it is critical for fisheries managers to recognize the key relationships that link fish abundance and biomass with density independent factors such as the carrying capacity of a river, which, over the long term, can change due to a variety of natural or anthropogenic influences (Figure 26.2). In other words, changing environmental

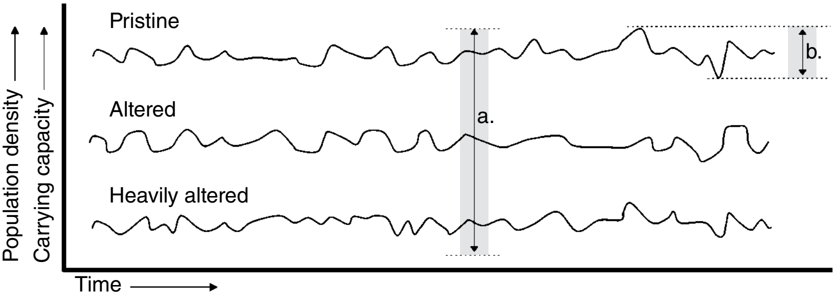

Figure 26.2 Natural and human induced levels and variations of the population densities. (a) The size of a population is a matter of the carrying capacity of the respective water body. The carrying capacity is related to natural conditions and/or anthropogenic influences. In this example three different levels of population density are illustrated, assuming a heavily altered situation of low density up to a pristine situation of high population density. (b) Small scale dynamics of the population density as a consequence of varying density dependent and natural environmental factors.

conditions entail changing population densities. However, historically overexploitation has repeatedly occurred when management practices are tied to habits or routines rather than regular environmental updates (e.g. Sánchez-Hernández *et al.* 2016). Consequently, exploitation of natural resources such as wild fish stocks requires a constant reconsideration of what an ecosystem under current conditions is able to yield (a. in Figure 26.2).

By means of regular stock assessments deeper insights into the magnitude of short-term population dynamics can be gained, which describe a further parameter to be considered (b. in Figure 26.2). Rapidly changing stocks are predominantly regulated by density-dependent factors as well as seasonal environmental (density-independent) influences and could be relevant for determining harvesting quotas.

In the respective river section of the River Ois a quantitative fish sampling campaign is carried out yearly (1997–2016) to assess the named parameters of the salmonid species. Brown trout dominates, holding an average share of 66%. It is followed by the non-native rainbow trout (29%) and European grayling (*Thymallus, thymallus,* 5%). Further species to be found are bullhead (*Cottus gobio*), occasionally Arctic char (*Salvelinus umbla*) and non-native brook trout (*Salvelinus fontinalis*). The discussed fishing beat as well as parts of the River Ois upstream were not stocked since 1997.

The first step in sustainably harvesting brown trout is to capture the demographics of the population. In doing so we see that recruitment in the Ois is subject to extensive natural fluctuations (cf. Unfer *et al.* 2011). According to data from almost two decades of semi-quantitative sampling (cf. Unfer *et al.* 2011), high reproduction success of brown trout occurs every 2.8 years on average. The observed population dynamics can mostly be attributed to hydrological conditions during the incubation period (Unfer *et al.* 2011) and refer to the before mentioned density-independent factors responsible for short-term fluctuations in fish populations (cf. b. in Figure 26.2). Differences in reproductive success are further manifested in the density of the total stock, with fluctuations of up to 200% of the total biomass in the respective time period (see also Table 26.1).

Table 26.1 Biomass and production (kg/ha) of brown trout between 2008 and 2015 in the River Ois. The production (superscript figures) is calculated on the yearly increment of biomass of the respective cohort. Delimitation of size classes follows the age classes.

Size class	Age class	2008	2009	2010	2011	2012	2013	2014	2015
<120 mm	1	1^{+1}	$0.2^{+0.2}$	1^{+1}	2^{+2}	1^{+1}	$0.5^{+0.5}$	$1.4^{+1.4}$	3^{+3}
120–220 mm	2	2	9^{+8}	6^{+6}	11^{+10}	12^{+10}	8^{+7}	10^{+10}	8^{+7}
220–320 mm	3	12	20^{+18}	27^{+17}	39^{+33}	32^{+22}	23^{+11}	29^{+21}	30^{+20}
>320 mm	4	8	$12^{-0.6}$	15^{-5}	$27^{+0.2}$	17^{-22}	12^{-20}	9^{-14}	11^{-18}
Total biomass $^{\text{Total net production}}$		24	41^{+26}	48^{+19}	78^{+45}	63^{+12}	44^{-2}	50^{+18}	53^{+12}

Table 26.2 Abundance and production (Ind/ha) of brown trout between 2008 and 2015 in the River Ois. The production (superscript figures) is calculated on a yearly increment of individuals for the respective cohort. Delimitation of size classes follows the age classes.

Size class	Age class	2008	2009	2010	2011	2012	2013	2014	2015
<120 mm	1	199^{+199}	39^{+39}	114^{+114}	282^{+282}	226^{+226}	85^{+85}	265^{+265}	452^{+452}
120–220 mm	2	48	251^{+52}	109^{+70}	199^{+85}	262^{-20}	203^{-23}	189^{+104}	163^{-102}
220–320 mm	3	69	107^{+59}	190^{-61}	172^{+63}	201^{+3}	146^{-116}	196^{-7}	157^{-32}
>320 mm	4	25	29^{-41}	37^{-70}	59^{-131}	53^{-119}	34^{-167}	25^{-121}	30^{-166}
Total abundance $^{\text{Total net production}}$		341	426^{+110}	450^{+52}	712^{+299}	743^{+90}	468^{-222}	675^{+241}	802^{+153}

Following the determination of stock densities, the yearly production of brown trout has to be considered in order to identify regions in the recruitment curve where harvest becomes possible. Production is defined as the 'amount of tissue elaborated per unit time per unit area, regardless of its fate' (Waters, 1977, Clarke 1946 in Mertz & Myers 1998). Our monitoring data over successive years allows us to illustrate the production balance for single age or size categories. For example, reading cells of the same color on a diagonal from upper left to lower right, the net production (production minus loss) of the 0+ cohort (age class 1 in Table 26.1) from 2010 to 2011 totals 10 kg/ha. The same cohort gains a further increment of 22 kg/ha by the year 2012 before the net production becomes negative (–20 kg/ha) in the subsequent year. Over the long run the described scheme of positive and negative production turns out to be typical, with culminating positive net production in age class 3 and negative net production for older classes.

Along with the increment of biomass an increase of fish abundance can be documented for the transition from age class 1 to age class 2 (Table 26.2), unless fish densities have already been very high in the first year. In the following year fish abundance typically stabilizes, apparently by interacting again with the previous year's level, before it decreases again in age class 4 when fish grow older. General life-cycle characteristics of brown trout become evident in any respective river stretch when one considers

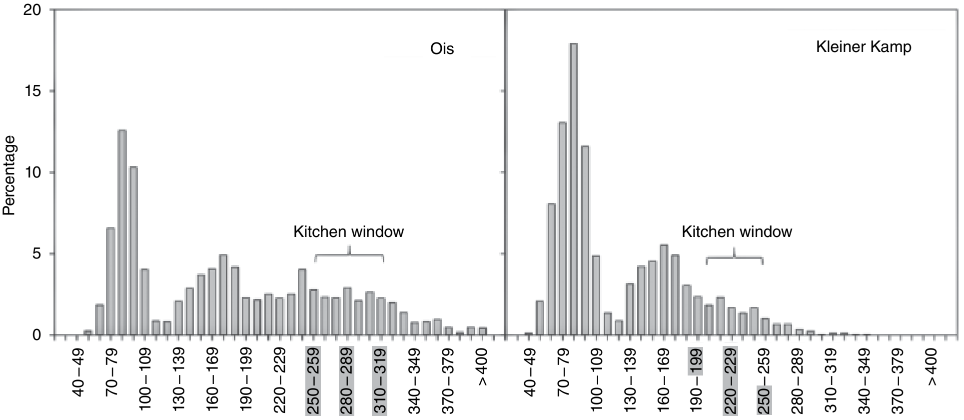

Figure 26.3 Relative length–frequency plots of brown trout in the River Ois and the River Kleiner Kamp showing the suggested 'kitchen windows' in the size class 250–320 mm (Ois) and 200–250 mm (Kleiner Kamp).

long-term stock developments of both biomass and fish abundance. Especially in case of low reproductive success it becomes evident that downstream movement of juvenile stages from the headwaters and tributaries increases production (higher abundances of age class 2 and 3 compared to preceding years). Finally, when fish grow older, natural mortality, outmigration and potentially otter (*Lutra lutra*) predation explain decreasing fish abundance and biomass, hence the negative net production in age class 4.

The natural decrease of fish abundance in size class 4 further supports recommendation that the harvest of fish needs to focus on the most productive, i.e. the third class. Therefore, instead of applying the usually prescribed minimum size of harvestable fish, we recommend a harvest-slot (*kitchen window*) with a minimum fish length of 250 mm and a maximum length of 320 mm (Figure 26.3) that corresponds to an average weight of 200 grams per fish. By the application of harvest slots within a realm of high productivity, fishing mortality becomes a sustainable expansion of natural mortality that leaves enough excess for future generations to persist. The harvest slot furthermore leads to benefits such that fish outgrowing the kitchen window remain in the ecosystem, further developing and releasing their high value for the reproductive success of the population. Also, from a genetic point of view advantages arise, as the removal of intermediate-sized fish potentially decreases the risks of reducing fish genetic heterogeneity (Birkeland & Dayton 2005).

With regard to the River Kleiner Kamp the latest yearly series of stock assessments reveal similar patterns of population dynamics as documented in the example of the Ois, again strongly regulated by the variation of reproductive success (data not shown). It should be noted, however, that the patterns of productivity are differently dispersed among the different age classes. The total biomass is approximately at the same level as in the River Ois, although the highest productivity must be ascribed to younger size classes. Comparing the population structures of the two rivers it becomes evident, that fish of the first age classes in Kleiner Kamp are comparable in growth. However, fish larger than 25 cm are scarce in this population (Figure 26.3). The differences in the population demography consequently imply for an adjusted harvest slot. In order to satisfy anglers but also to protect the population from overfishing the harvest slot has been chosen to be between 200 and 250 mm, Figure 26.3).

When it comes to the determination of harvest quotas, Mertz & Myers (1998) assume that, if fishing mortality is equal to the natural mortality, at least one half of the production of the stock may be harvested. Based on the available data (Table 26.1, total biomass) the average annual total net production $\left(\tilde{x}_{\mathrm{p}} = 19\mathrm{kg}/\mathrm{ha}\right)$ of the whole river Ois fishing beat (5.2 ha) can be calculated as 96 kg per year (2008–2015). Half of the yearly net production divided by an average weight of a harvested fish of 200 grams results in an average possible sustainable harvest of almost 250 brown trout per year. In comparison, the current stock of brown trout in a similar size/age class, e.g. between 22 and 32 cm, averages more than 800 available individuals in the total fishing beat. On average the proposed harvest quota would therefore range between one third to one fourth of the respective stock, which means a sufficient amount of fish remaining to continue and grow bigger, even in years of very low abundance. Additionally, the exploitation of fish within the limits of the 'kitchen window' would reduce the total biomass below the river's carrying capacity, i.e. below unsustainable mortality levels. That increases the chances of survival for smaller fish, and this extra production again can result in surplus or sustainable production (Wallace & Fletcher 2001).

In summary, the example of the River Ois illustrates the necessity to develop fisheries management approaches on basis of careful consideration of (changing) stock quantities. The analysis of quantitative fish data reveals the size and the dynamics that are inherent in the stock and therefore form the basis for management decisions. The differing population structures of the River Kleiner Kamp outline the need for situational regulations. Finally, one must consider that observed dynamics are specific to the local characteristics of a fishing beat, also ascribing relevance to the location of a beat within the distribution boundaries of a species and to the characteristics and the quality of the surrounding catchment.

Stocking Fish – Restrictions and Possibilities

When to Consider Stocking?

If bottlenecks remain after all possibilities to improve the habitat are exhausted, then a fisheries manager has to consider other options to improve the fish stock (cf. Figure 26.4). Not only in Austria, but also in other regions of the world, stocking of artificially propagated fish has been seen as the major (often the only) tool and duty of fisheries management in recreational fisheries (Behnke 2002). Although large amounts of trout of all age classes are still stocked, stocking is about to lose its status as a panacea and is nowadays more and more questioned. The majority of recent scientific literature dealing with stocking fish in riverine environments stresses potential ecological problems and threats deriving from stocking activities (e.g. Christie *et al.* 2014). On the one hand, stocked fish suffer from high mortality and emigration rates after release, so economic success is increasingly in doubt. On the other hand, there is clear proof that propagated fish have negative consequences for wild stocks and populations due to genetic admixture or homogenization as well as to increasing competition for habitat and food (e.g. Fraser 2008, Olden *et al.* 2004).

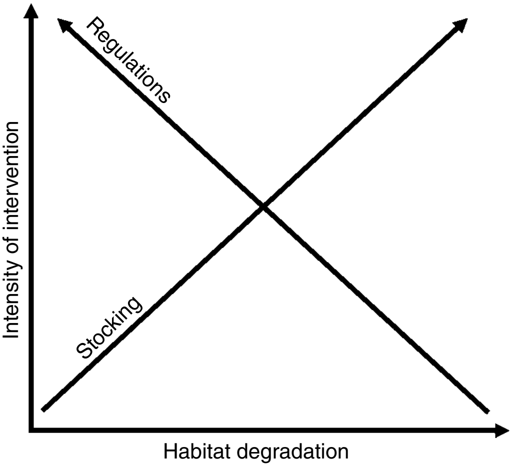

Figure 26.4 Fisheries management actions must be adopted according to the ecological status of a river.

However, if habitat problems remain and essential environmental prerequisites for different life stages are lacking, stocking might be the only option to sustain recreational fishing possibilities. There are different motives to stock (Laikre 1999; Welcomme & Bartley 1998) whereby stocking to mitigate environmental impacts is the most common reason. While compensatory stocking can help to sustain recreational fishing and can be seen as ecologically reasonable, stocking solely to attract or satisfy anglers as well as stocking for enhancement or maintenance can hardly be justified in the context of sound or ecologically orientated fisheries management. Whenever fishes are stocked, one should account for possible negative consequences for the receiving ecosystems and contrast them with potential benefits (mainly socio-ecological). Economic issues or the benefit of the owners of fishing-rights play an important role in Austria, where the right to fish is a private law, and profits are part of the income of the respective fishing right holder. This fact hampers the elaboration and implementation of large-scale, e.g. catchment wide, fisheries management strategies or plans, and stands in contrast to countries where the right to fish is public and ecological or nature conservation issues typically have priority over commercial aspects.

Quality of Stocked Fish

In addition to the negative impacts that stocked fish might have on wild stocks due to resource competition processes, two further major issues have to be considered: aspects of genetic descent as well as deficits deriving from the artificial propagation in hatchery environments. The latter can result in both behavioral and/or phenotypical deficiencies that, in many cases are already genetically fixed. Typically, hatchery fish suffer from various abnormalities as they are kept under hatchery conditions for a period of time. As the time spent in the hatchery environment increases, the process of adapting wild animals to human-controlled environments leads to a wide range of behavioral as well as physiological alterations. In general, domestication results in increased fitness under hatchery conditions but decreased fitness under natural conditions (Berejikian *et al.*

2005) leading to high mortality rates after release (e.g. Weiss & Schmutz 1999). Among the reasons for weak performance of stocked hatchery fish are: Reduced ability to identify and take natural food, missing reaction to variable food availability, increased boldness against novel objects, reduced flight response etc. (e.g. Järvi 2002). About 10–15 years ago researchers postulated that post-release survival has to be enhanced (Maynard *et al.* 2004). However, if large hatchery fish (catchable sizes) are stocked, it might be more favorable, that mid- to long-term survival rates remain low or to generally stock triploid fish, to avoid crossbreeding with wild conspecifics that spreads negative impacts on the genetic integrity of wild populations.

Domestication effects are more likely to be avoided if fish for stocking purposes originate from wild breeders and the duration of their stay in hatcheries is as short as possible. However, stocking of juvenile size classes does not guarantee high survival rates (Pinter *et al.*, 2017) nor can undesired genetic consequences be fully prevented (Christie *et al.* 2016).

Stocking for Conservation

Stocking to achieve conservation aims is the only ecologic reason to release propagated fish. However, fish deriving from artificial propagation will always create repercussions, e.g. reduced reproductive fitness (Araki *et al.* 2007, Christie *et al.* 2014). This is true even if the aim of stocking is the re-establishment of reproducing populations in cases where a habitat bottleneck has been restored or a viable river(-reach) should be recolonized (e.g. after a fish-kill). As stated above, efforts to (re-)establish a population or stock is only meaningful and promising if the habitat prerequisites for self-sustainability are given or habitat quality has been restored. The foremost aim of any conservational stocking campaign should be the initiation of primary (re-)colonization, which implies stocking over a restricted period of time, not continuously. Although the aims of conservational stocking are respectable, the task is far from being simple. The most important precondition is to select or identify a donor-population of suitable genetic origin. In Austria, decades of stocking fish of foreign origin and trans-basin spreading of brown trout (Pinter 2008, Schenekar *et al.* 2014) substantially altered the genetic integrity of wild fish populations, particularly those of salmonid species.

Which Size/Age Classes can be Stocked?

In case a suitable donor population (of local origin and adequate size) is available, the next question is how to carry out the restocking? As it is mandatory to avoid domestication effects as far as possible, the first choice will be to stock fertilized eggs. Eggs can be stocked in ‘artificial nests’ and/or breeding boxes. A major advantage of stocking eggs to avoid domestication is that hatchlings can adapt to the natural environment from the earliest stage on. If potential spawning sites for egg deposition are selected, fish emerging from the nests can home back to their natal site and a regularly used spawning site can be established.

While the optimum life-stage for conservational stocking is evident various problems remain. The first task is to spot a suitable donor population of adequate size and appropriate genetic background. Furthermore, a sufficient number of eggs is needed to be successful, although the extent remains unclear but is in any case high. Large egg numbers are needed to establish a founder population and to compensate for losses of reproductive fitness and further imperfections due to e.g. the inhibition of natural partner selection and modification of other processes of natural selection. We suggest continuing yearly plantings for the duration of a full life-cycle to stabilize the initial stock by more than just one cohort. Survival rates among the cohorts can, of course, vary markedly; as the juveniles are developing on their own and are exposed to natural hazards. The success of stocking juvenile age classes, however, remains unpredictable, as it depends on a variety of environmental and biological factors (e.g. adaptiveness, competitiveness, rearing history of progeny). For example, stocking of 0+ trout in three headwater streams of a Danubian catchment had very low success after wild trout outcompeted the planted strains within the first year after stocking (Pinter *et al.*, 2017). For this study juveniles of a hatchery strain as well as fish derived from wild spawners of local origin were used, and the performance (survival) was contrasted with the resident population.

Monitoring the Success of Stocking

Whenever fisheries managers release fish, they watch them swimming away, convinced that they did a good deed, following the agricultural maxim 'who will reap must sow'. But as already noted, managing fish stocks in riverine environments is a complex challenge. Following a stocking campaign that releases catchable sizes, anglers fishing during the subsequent days are in many cases satisfied. This is because hatchery trout entering natural waters are easy to catch as they soon begin to starve and are therefore prone to take all kinds of bait. Inside the hatchery they received artificial food in good amounts, but in the wilderness they are in many cases neither adept to recognize natural food items nor able to react to varying food availability (Järvi 2002). As high rates of these fish will die or move away soon after release, their economic value is questionable (e.g. Behnke 1989). If it is the overall management aim to satisfy anglers, who like to easily catch naive hatchery fish, the aim might be reached best by regularly releasing hatchery fish, e.g. every second week. If stocking is aimed to support the natural populations, then the targeted purpose would definitely not be achieved. But failure or success can easily be monitored. Nowadays different tagging methods for all size classes of fish are established. Even eyed eggs, e.g. of brown trout, can be marked using chemical dyes (e.g. Unfer & Pinter 2013) or their origin can be classified through molecular-biological methods (e.g. Meraner *et al.* 2013). It is surprising that the majority of fisheries managers spend huge amounts of money for stocking but monitoring studies on the success are scarce and often judged as too expensive.

How to Regulate Fishing

All management perspectives, conservational, economic or fish-ecological, hold that fishing regulations should primarily aim to preserve viable populations. Waters supporting healthy stocks need to be managed without stocking interventions but nevertheless can be harvested in a sustainable way following the necessary regulations (Figure 26.4): Policy can protect the long-term productivity of river ecosystems and fish populations by taking fish following guidelines and catch limits set by natural production and, likewise, by releasing fish in size- and age-classes of limited availability. This follows investment principles of withdrawing only the interest while leaving the fund intact. However, if fish shall be released it would be counterproductive to harm these fish. Therefore, it is mandatory to restrict the gear if management strategies aim to release certain species or size classes. The closer to a pristine habitat situation, i.e. a very good status according to the EU Water Framework Directive (2000), the stricter must be the formulation and implementation of regulations regarding gear restrictions and angling pressure (Figure 26.4). Examples of good practices to minimize hooking mortality include: the use of barbless hooks, bait that can't be swallowed or the minimization of handling procedures of fishes dedicated to release. Regarding fish handling ethical sound practices have to be mandatory in any case.

The example of sustainable harvest in the River Ois represents more than a concept or slogan. It is a realistic management option. On the other hand, at least from an ethical point of view, pure 'catch-and-release' (releasing all caught individuals) is questionable. While it can make sense to release all individuals of a threatened species or to preserve a small stock or population, pure 'catch-and-release' regulations are hard to explain to people who generally conceive of angling as cruel. If people go fishing with the intention to release their entire catch, they are indeed playing with creatures, which is hardly acceptable for animal welfare proponents, irrespective of the debate as to whether fish feel pain or not (e.g. Braithwaite 2010, Rose *et al.* 2014).

Our view is that fishing for brown trout can and should be a reasonable pastime as long as we aim at finessing, catching and taking home healthy and tasty food, as the human race has done for millennia, provided that modesty finds its way into the understanding of the way natural resources are used. In this context a further regulatory lever comes into play: *angling pressure*. Angling pressure can be expressed by days or hours of angling per river length or water surface area. As it can be quantified, so can it be restricted. Limiting angling pressure means that fish are caught less frequently. This helps to avoid learning effects and reduces timidity, which supports angler satisfaction as it will be easier to hook a fish compared to intensively fished beats. Furthermore, limited angling pressure reduces insurance rates and, consequently, hooking mortality. According to Figure 26.4, specifically near-natural habitats have to be protected from overfishing to meet conservational requirements, while altered or artificial water bodies, where in many cases stocking will be a frequently used management tool, can also be burdened with higher pressure. The general scheme of adjusting fishing regulations to fit the ecological status of waterbodies can be used to guide anglers and therefore also angling pressure (Figure 26.4). One cannot forget however that flowing waters remain open ecological systems. Therefore, management actions should always be considered thoroughly in advance, as their effects may reach far beyond the boundaries of a management unit. Finally, as people, specifically children or urban societies, should get the chance to experience angling and to develop a closer relationship to fish and aquatic systems, proper strategies as how to guide as well as foster recreational fishing must be developed, safeguarding the future of this leisure activity and of aquatic ecosystems.

Conclusions

Contemporary management of recreational fisheries needs to balance between the poles of anglers' desire and the sociopolitical and moral obligation to conserve nature. The developmental goals (in between protection and exploitation) have to be set by the relevant authorities, which can be the legislator, the fishing right owner or a fishing club. If we subscribe to adaptive management (e.g. Walters 1986), then the authorities would work with local practitioners and scientists to establish a vision, define what is known and not known, set goals, develop and implement policies, monitor results, and periodically repeat the entire process. Otherwise, we are stuck in the rut of conventional, top–down management. As soon as the goals for a waterbody are defined, the different tools a fisheries manager has can be used. It is our conviction that recreational fishing for trout and environmental conservation can and should be merged, whereby the fisheries have to accept their subordinate role to nature conservation in near natural waters. Subordination, however, does not mean a loss of rights or benefit, but can resemble a successful strategy provided that modest and sustainable harvest schemes are elaborated and angling is carried out in an ethically acceptable way. The example of the River Ois illustrates that if the management of fishing beats located in unimpaired or near-natural river sections is done thoughtfully, the sustainable harvest and continued existence of vital stocks is guaranteed.

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27

Ecology and Management of Stream-Resident Brown Trout in Michigan (USA)

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Introduction

The history of brown trout *Salmo trutta* in Michigan extends back well over a century to 1884, when the first brown trout fry to be successfully introduced into North American public waters were stocked into the Baldwin River, a tributary to Pere Marquette River, which flows into Lake Michigan. Since then, millions of additional brown trout have been stocked in the state, and self-sustaining brown trout populations have become established in rivers throughout Michigan. Stocking of hatchery-reared brown trout continues to be used to create or maintain sport fishing opportunities in streams, inland lakes, and the Great Lakes. Stream-resident populations of brown trout, as well as native and introduced populations of brook trout *Salvelinus fontinalis*, are enjoyed and valued by Michigan anglers and citizens. In this chapter, I provide an overview of the history, ecology, and management of stream-resident brown trout populations in the state of Michigan, USA.

Michigan's Physical Setting

The state of Michigan is situated in the Great Lakes region of Midwestern North America. Michigan is 250,493 km^2 in land area, roughly half the size of the country of Spain 505,990 km^2. In 2014, Michigan's estimated population was 9.9 million people, compared to 46.5 million for Spain. Michigan consists of two large peninsulas, perpendicular to one another, that project into the Great Lakes. This positioning dramatically affects and accentuates climatic differences within each peninsula, as prevailing winds, seemingly minor elevation differences (range 167–604 m), and the proximity to individual Great Lakes can produce considerable variation in local climate conditions. The state's climate can be characterized by ranges in values of several climatic variables, such as growing season length (87–163 days), total annual precipitation (740–900 mm),

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annual average temperature (4.2–9.3 °C), average May–September precipitation (360–500 mm), and average May–September temperature (14.4–19.3 °C) (Albert *et al.*, 1986). Overall, Michigan is characterized by cool–warm summers, cold winters, and precipitation amounts that are fairly evenly distributed throughout the year.

Michigan was totally covered by ice during the Wisconsinan glaciation of the Pleistocene Epoch, and following retreat of the glaciers, was totally ice-free about 10,000 years ago (Farrand & Eschman, 1993). Remnants of glacial activity are the defining features of Michigan as the state is almost entirely covered by glacial drifts (up to 1000 feet deep in places), and has over 58,000 km of rivers (many following former glacial drainageways) and 6,537 lakes greater than 4 ha in size.

Because of its glacial history, Michigan's landscape contains various types of glacial deposits and soil textures in a patchwork that seems to preclude description of streams using the typical longitudinal patterns (cold, high-gradient creeks grading into warm, low-gradient rivers) described by some authors (e.g., Hawkes, 1975; Vannote *et al.*, 1980). These features include end and ground moraines containing particles ranging in texture from clay to boulders, glacial outwash plains and channels consisting of coarse sands and gravels, and flat glacial lakebeds of clay (Figure 27.1). Consequently, some streams have warm headwaters and cooler lower reaches; others are cold upstream and warm downstream, and others alternate between thermal states depending upon characteristics of the landscape (Zorn *et al.*, 2002). Hydrologic conditions in Michigan reach their extremes for streams draining small catchments, and range from extremely-stable, groundwater fed rivers draining deep sand and gravel deposits to hydrologically-flashy tributaries draining clay or bedrock deposits. Using 90% exceedence flow yield per catchment area (Low-flow yield or LFY) as an index for hydrologic stability, Michigan streams show approximately a million-fold range in LFY values between the most stable and flashy streams (Zorn *et al.*, 2002). Some of Michigan's groundwater-fed trout streams, such as the Au Sable and Manistee rivers in the northcentral Lower Peninsula, are among the most hydrologically stable streams in the United States (Zorn & Sendek, 2001; N.L. Poff, Colorado State University, unpublished data).

An understanding of the relationships among Michigan's glacial features, topography, and hydrologic characteristics, in combination with Geographic Information System (GIS) techniques, has led to quantitative and descriptive models of flow conditions and trout stream attributes throughout the state. Michigan trout streams are cooled, and their flow stabilized, by large inputs of groundwater associated with deep deposits of coarse-textured glacial drifts (Wiley *et al.*, 1997). Outwash deposits have exceptionally high hydraulic conductivities, which in combination with elevation head differences provided by adjacent end moraines can provide high rates of groundwater input to nearby channel segments (Hendrickson & Doonan, 1972). Use of surficial geology types (hydraulic conductivity) and slope (hydraulic head) in a GIS environment enabled researchers to model groundwater loading to stream channels throughout Michigan (Wiley *et al.*, 1997; Baker *et al.*, 2003). Looking at the correspondence between the occurrence of coldwater streams in Michigan (Figure 27.2) and Michigan's surficial geology (Figure 27.1), spatial relationships among surficial geology, coldwater streams, and trout distributions within the state are quite apparent. Surface geology also strongly affects land-use patterns in Michigan, as these coarse-textured deposits were ill-suited for initial attempts at agriculture, and ultimately reverted to forests (Figure 27.3).

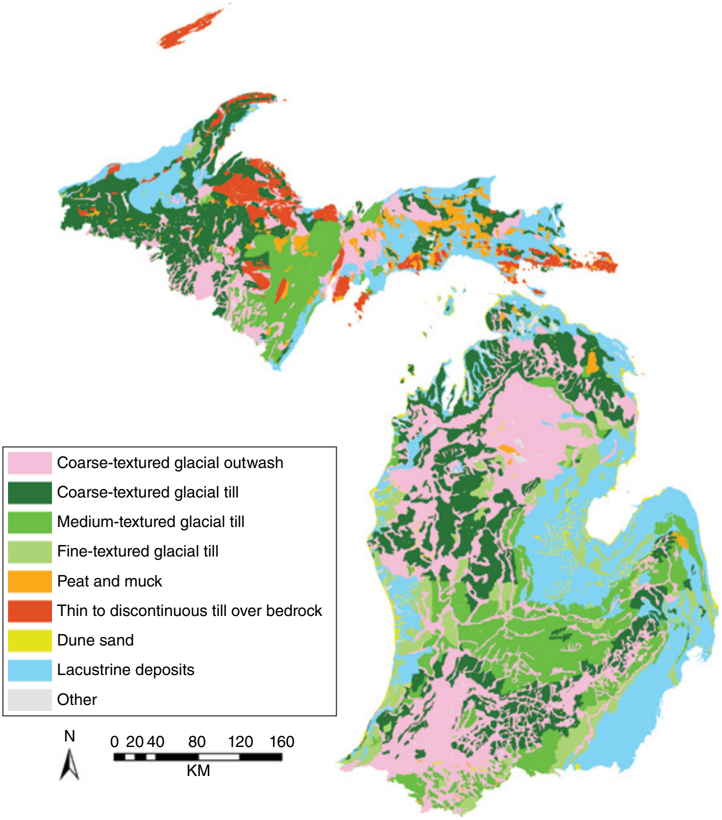


Figure 27.1 Map of surface geology of Michigan (Farrand & Bell, 1982). Michigan trout streams are cooled, and their flows stabilized, by large inputs of groundwater associated with catchments dominated by coarse-textured glacial outwash and tills.

Finer-textured geology, warmer streams, more agriculture, and the majority of Michigan's population occur in the southern third of the state.

Origin of Brown Trout Stream Fisheries

Brown trout were not a member of the original fish communities in Michigan's coldwater streams. Arctic grayling *Thymallus arcticus* have occurred in most major rivers in the northern two thirds of the Lower Peninsula of Michigan (Vincent, 1962). In the Upper Peninsula, records of Arctic grayling only occur for the Otter and Sturgeon rivers on the western side (Vincent, 1962). Arctic grayling were heavily exploited by anglers. For example, in Michigan's Au Sable River it was easy for anglers to catch more than 45 kg of Arctic grayling daily (Huggler, 1981), and anglers often did not reel in their catch until five fish were hooked at once (Day & Donahue, 1951). A small commercial fishery that shipped grayling to the Chicago area was believed to exist in some parts of Michigan (Vincent, 1962). Angling for the species made Michigan a popular tourist

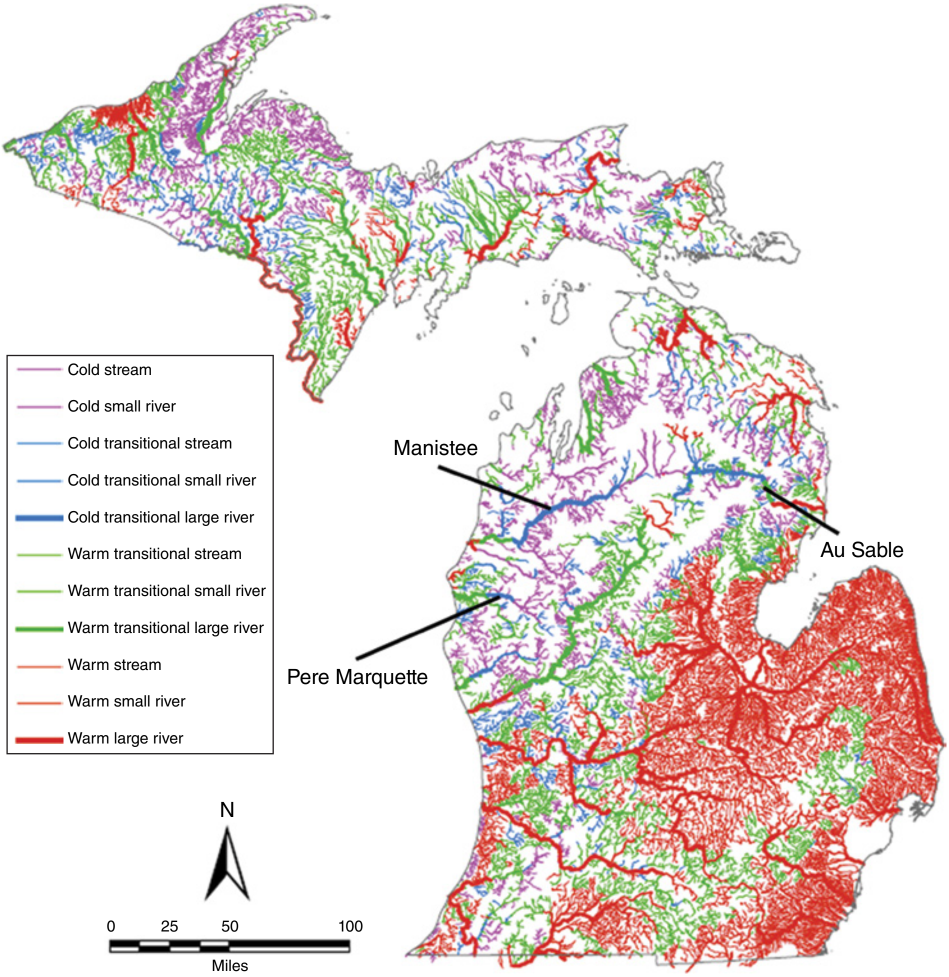


Figure 27.2 Stream classification map of Michigan, showing locations of three prominent trout streams (Zorn *et al.*, 2008).

location in the Midwest, especially once railroad lines were extended into the region (Mershon, 1923). Overexploitation due to intense fishing pressure (described in the accounts such these) is believed to have caused initial declines in Arctic grayling populations throughout the Lower Peninsula (Vincent, 1962).

Unregulated logging also wreaked havoc on Arctic grayling. Nearly the entire state of Michigan was deforested during 1860–1900, and as much land as possible was drained and converted to farming (Whelan, 2004). During the logging period, rivers were the major transportation systems for moving logs to sawmills, and log drives (mass movements of cut logs) occurred on nearly every stream in the state. Log drives required construction of temporary splash dams on streams to create a flood surge in spring for carrying logs downriver over rapids and riffles. These log-laden floods loaded massive amounts of sediment into stream channels, and required large-scale de-snagging operations to

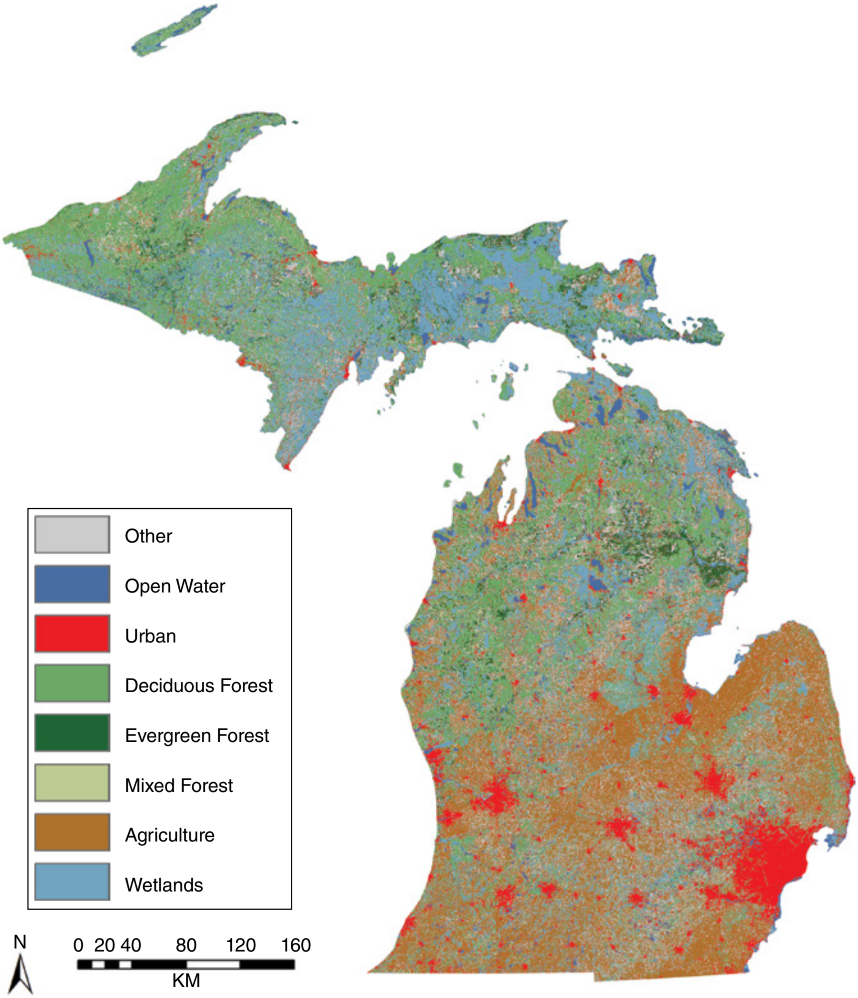


Figure 27.3 Map of 2011 land use and land cover for Michigan (Homer *et al.*, 2015).

remove long-existing log jams (some known to be over 5 miles in length with Native American portage routes) that impeded downstream transport of logs. Lumber mill operations, usually near the river mouth, required additional dams to generate mechanical energy for running saws, and further fragmented streams. Isolation and degradation of stream habitats due to poor forestry practices and dams for lumber or other industry likely contributed to the extinction of Arctic grayling from Michigan's Lower Peninsula by around 1905, and from the UP rivers by 1935 (Westerman, 1974).

Brook trout were native to streams in the Upper Peninsula and the northernmost portion of the Lower Peninsula. As Arctic grayling populations declined, stocking of hatchery-reared brook trout increased. Stocking began in 1879, when 12,000 brook trout fry were stocked into southwestern Michigan streams. The first planting of 20,000 brook trout fry into the Au Sable River occurred in 1885, following the State Board of

Fish Commissioners conclusion that Arctic grayling had disappeared from the river (Westerman, 1974). Brook trout stocking expanded the species range to the extent that the 1885–86 report from the Fish Commissioners stated that 'now the streams of every county in the state but three, whose waters are not suited to this fish, furnish excellent trout fishing' (Westerman, 1974). Rainbow trout *Oncorhynchus mykiss* stocking was also initiated during this period, with the first plant going into the Au Sable River in 1876 (Westerman, 1974).

Fred Mather, superintendent of the New York State Fish Commission, was responsible for introducing brown trout to Michigan. In 1883, he obtained 100,000 brown trout eggs from Herr von Behr, Berlin, Germany, and on April 11, 1884 a portion of the hatched fry were planted in the Baldwin River, a tributary to the Pere Marquette River in northwest Lower Peninsula (Westerman, 1974). This was the first plant of brown trout into public waters in North America. In 1885, the United States Fish Commission received 100,000 Loch Leven (brown trout) eggs from Scotland, sent by Sir James Gibson Maitland, of the Howietown Fishery, Sterlingshire. Of these, 43,000 eggs came to Michigan, and the hatched fry were stocked into Lower Peninsula streams and inland lakes. Brown trout plants from this stock continued in the Lower Peninsula, and the first Upper Peninsula waters (Dead and Chocolay rivers) were stocked in 1894. By the close of the 1896 planting season, after 9 years of stocking, 1,747,000 brown trout fry had been stocked into Michigan waters (Westerman, 1974). Behnke (2002) thought all life-history forms of brown trout (anadromous, riverine and lacustrine) were imported into the U.S., and Michigan certainly has at least two of them, riverine and lacustrine (adfluvial). Stocking of brown trout in Michigan took a 13-year hiatus after the Michigan Fish Commission concluded that brown trout were 'inferior in every respect to either the brook or rainbow' and decided that the hatchery's adult brown trout brood stock should be 'turned adrift' and no further plantings occur. Interest in brown trout eventually returned, due in part to dwindling numbers of brook trout in many streams, and stocking of brown trout fry resumed in 1909 (Westerman, 1974). Fry plants reached 6 million per year by 1926, but then declined in favor of stocking fingerlings which fish culturists and sportsman thought would have a better chance of surviving to the angler's creel (Michigan Department of Conservation, 1928; Westers & Stauffer, 1974). Brown trout have been a highly-important part of Michigan's coldwater fisheries since at least 1920 (Westerman, 1974).

Size at stocking was not the only factor limiting stream trout fisheries in Michigan in the 1920s. Most of Michigan's coldwater streams remained degraded from earlier landscape-level land use changes. Portions of the state were rapidly industrializing, which resulted in issues with municipal and industrial wastes. Hydroelectric dam development peaked during 1930–1949, fragmenting stream habitats and altering temperature and flow conditions of streams (Whelan, 2004). In addition, harvest pressure on inland fish populations increased steadily during the 1930s and 1940s as interest in sportfishing grew rapidly due to increases in leisure time, as a result of changes in labor laws and increases in disposable income (Whelan, 2004). Though harvest regulations existed, regulation compliance was low and enforcement ineffective due to lack of roads, effective communications, and enforcement staff (Whelan, 2004). Thus, spawning populations were low and pressure existed on managers to build populations and increase survival of stocked trout. This also led to initiation of numerous studies of trout and trout streams in Michigan.

Refinements in the Understanding and Management of Trout and Trout Streams

With more than a century of trout management and research in Michigan, a thorough review of past work would be beyond the scope of this paper. In the following paragraphs, I will attempt to summarize the main areas of work and key studies in the earlier decades to trace the progression of knowledge on stream-dwelling brown trout in Michigan. For the most recent decades, I will provide a more detailed summary of stream trout work to provide a more complete view of the scope of our current understanding of brown trout ecology in Michigan streams. Further information on these topics can be found through the cited papers, which serve as gateways for additional investigation. I attempted to cite peer-reviewed studies when possible, and all or nearly all of the agency reports are freely-accessible online through MDNR Fisheries Division's Library and online search tools (e.g., Google).

Early research and management efforts focused on ways to increase trout survival and abundance. Methods for rehabilitating the diversity of stream channel habitats through installation of structures were developed and tested on several Michigan rivers (Hubbs *et al.*, 1932; Tarzwell, 1935). Habitat improvement structures were then built throughout Michigan as large-scale projects and supported by low-cost, federally-funded labor programs such as the Civilian Conservation Corps (Hubbs *et al.*, 1933). Tagging studies were initiated with wild and hatchery brown trout and brook trout to better understand trout survival and movements, which in turn informed stocking and habitat rehabilitation efforts (Shetter, 1936, 1955). This understanding was later enhanced through radio telemetry studies of brown trout movements in Michigan's Au Sable River (e.g., Clapp *et al.*, 1990; Regal, 1992; DePhilip, 2001; Diana *et al.*, 2004). These studies highlighted the importance of the size of fish, water temperature, season, and availability of food and cover in explaining daily and seasonal use of habitat by brown trout.

Additional work occurred to better explain various sources of mortality to trout. Michigan studies (e.g., Leonard & Shetter, 1937) showed that smaller salmonids were the primary item in winter diets of brown trout larger than 30 cm and common mergansers *Mergus merganser*. Alexander (1976) documented predation on trout and estimated daily consumption for several species of birds, mammals, and the northern water snake *Nerodia sipedon*. Predator reductions were attempted, but they had little effect on trout populations or angler catches (Shetter & Alexander, 1970).

Hooking mortality of trout (brook, brown, and rainbow) from different angling methods was quantified, with results showing reduced mortality for fly- and lure-caught trout (Shetter & Allison, 1955, 1958). Such results supported the use of regulations intended to increase trout populations by reducing angling-related mortality on sublegal sized trout. In 1945, Michigan's Discretionary Powers Act was amended, which gave the Conservation Commission the authority to designate experimental fishing regulations on up to 10 streams. This lead to a number of studies on several Lower Peninsula rivers to evaluate effects of various fishing method, minimum size limit, and daily harvest limit restrictions (Shetter & Alexander, 1966; Clark *et al.*, 1981). Establishment of long-term trout population monitoring reaches (index stations), collection of angler harvest data, development of stream electrofishing gear for sampling, and standardization of field sampling and fish aging protocols for these studies were essential for developing an empirical understanding of trout population attributes and dynamics over these longer time periods (McFadden *et al.*, 1976; Gowing & Alexander, 1980; Clark *et al.*, 1980; Clark, 1981). These projects led to development of long-term trout population data sets on several rivers including, the Pere Marquette, Pigeon, Rifle, and North, South, and Main branches of the Au Sable river, and Hunt and Gamble creeks. Many of these study reaches continue to be sampled today.

Opportunities to better describe and understand temporal changes in trout populations became available with the advent of computer technology and annual trout population index data extending back to the 1950s (even earlier for some locations). Of particular interest were declines in brown trout abundance observed at several population index stations on three branches of the Au Sable River during the 1980s. Changes in brown trout growth (and production) on portions of the mainstem and South Branch Au Sable River were found to be associated with water quality improvements that reduced nutrient inputs into river reaches from sewage treatment plants (Merron, 1982). Investigation also occurred into the possibility of introducing brown trout strains from the western United States that were purported to grow faster (Nuhfer, 1988). Effects of spring flow conditions were explored, and a negative relationship between flow conditions in the South Branch Au Sable during the period of brown trout fry emergence and brown trout year class strength was documented (Nuhfer *et al.*, 1994).

Looking at the North, South, and main branches of the Au Sable River, Zorn & Nuhfer (2007a) examined potential influences of various factors hypothesized (by anglers, managers, and researchers) to be influencing long-term trends in brown trout and brook trout density, growth, and survival by age class. These factors included spring flow conditions, age class abundance the prior year, density of piscivorous brown trout, woody habitat condition, summer water temperature, predator abundance, nutrient availability, and changes in voluntary release rates of angler-caught trout. Regression models developed for these species emphasized the influence of year class strength on older age classes, with year class strength being positively related to spawner abundance for both species and negatively related to high spring streamflow conditions for brown trout. Age class density was also positively associated with higher large woody debris (LWD) levels in streams. Annual growth increments of brown trout and brook trout were often negatively related to increased age class density and large woody debris, and positively associated with elevated total phosphorus levels, cool summers, and warm winters. Annual survival of trout from age-0 to age-4 was negatively related to intra- and inter-specific age-class density, and in 3 of 7 models, positively associated with levels of large woody debris. Their findings emphasized the importance of year class strength to trout population dynamics as well as the need to include collection of regional- and local-scale habitat data in studies of trout population dynamics.

Following up on this work, Zorn & Nuhfer (2007b) assessed the potential for regional synchrony in brown trout and brook trout population dynamics among Michigan rivers. They found a high degree of synchrony in average May stream discharge (approximating the time of brown trout fry emergence) among many trout streams, particularly those in the northern portion of Michigan's Lower Peninsula. Significant correlations in long-term densities of brown trout and brook trout year classes occurred among several rivers in this area, and predicted numbers of days to 50% swim-up of brown trout fry for four of these streams (based on water temperature data) were similar and temporally synchronous. Their findings complemented similar studies done elsewhere (e.g., Strange *et al.*, 1992; Gowan & Fausch, 1996; Cattanéo, 2002; Lobón-Cerviá, 2004), but the Michigan findings were distinct due to the low-gradient, stable flow nature of the rivers studied. This work underlies the Michigan Department of Natural Resources (MDNRs) use of a network of long-term, population index sites for describing temporal trends in trout populations and the spatial extent of observed trends (Wills *et al.*, 2006). Data from these index sites are freely-available online through the MDNR Fisheries Division's Stream Fish Population Trend Viewer (Zorn *et al.*, 2014).

Larger brown trout in Michigan streams are piscivorous, a trait they share with larger brown trout in populations introduced elsewhere (Budy *et al.*, 2013). Michigan brown trout likely became piscivorous fairly soon after their introduction to Michigan waters as a 7 kg fish was caught by an angler in 1940 (Westerman, 1974); large brown trout certainly occurred in Michigan waters prior to this record. Their ability to outcompete other stream trout in Michigan's low gradient streams may in part explain why the Michigan Fish Commission in 1896 stated they were 'inferior in every respect to the brook or the rainbow', and released their brown trout brood stock. Westerman (1974) noted that brown trout competes closely with brook trout (both spawn in the fall and inhabit similar stream types), but the brown trout has the edge since it is more carnivorous, grows much larger, is more aggressive (monopolizes choice pools), and is more wary of anglers. He noted that 'there are small streams where the brown trout has taken over to the complete exclusion of the brook trout' (Westerman, 1974). For this reason, Westerman (1974) stated that the Michigan Department of Natural Resources (MDNR) Fisheries Division had 'been reluctant in planting them in waters where brook trout have continued to be abundant'. This still the case for many Upper Peninsula rivers with resident brook trout populations. Fausch & White (1981) documented behavioral dominance of brown trout over brook trout in a Michigan stream, and negative influences of brown trout density on brook trout age classes were described in Michigan's Au Sable River (Zorn and Nuhfer, 2007a). In addition, statewide patterns in brook trout densities were negatively associated brown trout density based on causal modeling (Zorn & Wiley, 2010) and regression modeling results (Zorn *et al.*, 2004). Mean lengths at age of brown trout from late summer surveys conducted at 24 MDNR index sites between 2002–2013 were as follows: age-0 (80 mm); -1 (167); -2 (247); -3 (322); -4 (391); -5 (468); -6 (522); -7 (569); -8 (633); -9 (638) (T. Zorn, MDNR Fisheries Division, unpublished data).

In the 1990s, geographic information system (GIS) technology provided Michigan researchers and managers the capability to study landscape-scale and spatial aspects of trout habitat. Spatial data layers describing Michigan's surficial geology, land cover types, groundwater inputs, and connectivity among stream reaches and lentic habitats, combined with site-based stream discharge, temperature, and fish survey data led to development of models for statewide prediction of exceedence flow values (Seelbach *et al.*, 2010), summer water temperatures (Wehrly *et al.*, 2006), and fish species distribution and abundance (Zorn *et al.*, 2004; Steen *et al.*, 2008) for Michigan rivers. Detailed long-term temperature measurements from electronic data loggers allowed Michigan researchers to describe thermal tolerances of stream trout (Wehrly *et al.*, 2007; Zorn *et al.*, 2011), and effects of temperature and ration on juvenile trout growth (Hinz & Wiley, 1997, 1998). These data also contributed to descriptions and plots of associations between fish density and mean July water temperature, stream size, and hydrology for all common stream fishes in Michigan (Lyons *et al.*, 2009; Zorn *et al.*, 2009). The understanding of hydrologic differences among Michigan streams, in combination with information describing river size, connectivity, slope, and water quality attributes (e.g., summer water temperature), led to development of a river valley segment classification (Seelbach *et al.*, 2006), and associated stream temperature (Wehrly *et al.*, 2003) and fish community (Zorn *et al.*, 2002) classifications. Valley segments are generally quite large (e.g., 3–60 km) and characterized by relatively homogenous hydrologic, limnologic, channel morphology, and riparian dynamics (Seelbach *et al.*, 1997). Valley segment characteristics often change sharply (and segment boundaries occur) at stream junctions, slope breaks, and boundaries of local landforms. The valley segment classification underpins fish community assessment and management efforts on all Michigan rivers, including trout streams (Wills *et al.*, 2006; Zorn *et al.*, 2008).

Management of Stream-Resident Brown Trout in Michigan

Populations of resident brown trout, as well as native and introduced populations of brook trout, occur throughout much of Michigan and are cherished by anglers and citizens alike. These populations support valuable sport fisheries, and while outside their native range, are considered naturalized rather than invasive. In fact, the high value placed on wild trout populations and the rivers that sustain them led to the formation of Trout Unlimited, a national coldwater conservation organization, on the banks of the Michigan's Au Sable River in 1959.

Recreational fishing is an important activity in Michigan, with the state ranking in the top four states in the United States in terms of total annual angler numbers (1.74 million), annual angling effort (over 28.2 million total fishing days), total annual angler expenditures (US$2.46 billion in retail sales and $4.2 billion overall effect), and angling-related jobs (37,989) (Southwick Associates, 2012). In 2011, Michigan's rivers and streams provided and estimated 8,159,000 days of angling for approximately 586,000 anglers, many of whom fished for trout and salmon (United States Fish and Wildlife Service, 2013). Recreational fisheries are a huge economic engine for the state, and along with recreational boating, provide one of the largest and highest-value uses of Michigan's aquatic resources.

Active management is needed to sustain Michigan's stream fisheries to ensure that they provide world class angling opportunities for future generations. To this end, MDNR Fisheries Division's mission is to 'To protect and enhance Michigan's aquatic life and habitats for the benefit of current and future generations' (Michigan Department of Natural Resources, 2013). Management of brown trout in Michigan occurs through several programs (resource assessment, fishing regulations, habitat protection and management, and fish stocking), each of which will be discussed below.

Resource Assessment

Michigan's streams are a valuable, productive, and sustainable resource. For example, the 5,100 km of Michigan's 'top quality' coldwater streams alone support wild populations of brook and brown trout estimated at over 10.7 million fish (Anonymous, 1967; Gowing & Alexander, 1980). The number of naturally reproduced age-1 brook trout and brown trout in these streams alone (estimated at over 2.7 million fish) is about 3.4 times greater than the number produced annually by MDNR Fisheries Division hatcheries for stocking in streams (Wills *et al.*, 2006). In addition, many of these streams serve as important spawning and rearing grounds for other highly-prized adfluvial salmonids caught in the Great Lakes and tributary streams (e.g., steelhead [rainbow trout], Chinook salmon *Oncorhynchus tshawytscha*, and coho salmon *Oncorhynchus kisutch*). Abundant natural production of wild fishes provides forage for many species of wildlife (Alexander, 1976) and humans.

Assessing Michigan's trout stream resources is a daunting task, given 58,000 km of streams (31,000 km of which support trout) and over 1,500 managed trout streams in the state. In addition, state fisheries biologists are also responsible for 11,000 inland lakes (more than 100 of which are managed for trout) and 43% of Great Lakes waters that lie within Michigan's jurisdiction. Given the scope of aquatic resources and limited staff in Michigan (MDNR Fisheries Division currently has 159 full-time permanent employees), MDNR Fisheries Division biologists must make the best use of limited information they have available on individual waters. Decisions regarding individual waters are usually made by local biologists, with each of the state's eight management units typically having one to three biologists and a crew of about three technicians. Management unit crews survey trout populations and habitat, often with volunteer assistance from other agencies, non-profits, or individuals. Great Lakes assessment is done by MDNR Fisheries Division's Research Section. Universities (under permit from the MDNR) also conduct surveys that typically focus on specific research questions.

Fortunately, MDNR Fisheries Division has a long history of surveys and over time many waters have been sampled at least once, with more important waters being sampled multiple times. The earliest surveys on streams in Michigan were conducted by the University of Michigan's Museum of Zoology, with sampling crews typically using seines, recording every species that was captured, and preserving individual fish as voucher specimens. As early as 1947, MDNR research crews conducted mark-recapture electrofishing to estimate trout populations at index sites on streams as part of various studies (see previous section). Prior to the mid-1980s, MDNR management unit surveys on streams generally targeted game fish species (usually trout), collecting data on species abundance and size distribution, sometimes recording anecdotal information on occurrence and abundance of non-game species, though rarely to species level. The purpose of surveys was varied and surveys commonly occurred for the following reasons: to assess game fish abundance or growth; to assess the survival of stocked fish: to assess potential of waters for trout stocking; to assess the effects of habitat improvement efforts; to obtain information at locations where no data were available; and to assess the effects of development or land use change on fish populations. Electrofishing gear (backpack or tow-barge electrofisher) was typically used, and there was no statewide standardization of field or data methods. The amount and types of surveys varied by management unit, as each unit had different types of streams, different management concerns, and local issues. An improved stream assessment program was needed to enable MDNR to better understand and track Michigan's stream resources, and to provide managers with science-based, quantitative decision support tools for management.

In 2002, MDNR Fisheries Division initiated the Stream Status and Trends Sampling Program (SSTP). This statewide program has several features that make it a significant advance over MDNR's previous stream survey efforts (Wills *et al.*, 2006). First, it employed a two-pronged approach to sampling. A network of fixed sites (population index stations) was established throughout the state as a high-resolution system for describing temporal trends in important resources (i.e., coldwater and smallmouth bass streams) and testing hypotheses related to changes in those resources. In addition, a stratified random sampling design is used for conducting an inventory of all streams in Michigan, and to provide information for quantitatively describing and comparing different types of systems. Michigan's statewide river valley segment classification (Seelbach *et al.*, 2006) provided the strata for sample site selection and data summarization. These data will allow fishery managers to describe typical fish community and habitat conditions for each type of stream (defined by valley segment attributes) in Michigan. All SSTP surveys incorporate the following important features: (1) a state-level (centralized) approach to sample site selection; (2) standardized and detailed field sampling protocols and forms for fish and habitat data collection; (3) data collected on all fish species and habitat at each survey; (4) detailed written data entry instructions; (5) a centralized database for data entry and summarization; and (6) biologists charged with statewide oversight of this program. Fish population trend data from fixed sites are freely-available online at MDNR's Stream Fish Population Trend Viewer website (http://www.mcgi.state.mi.us/fishpop/#; Zorn *et al.*, 2014). Written summaries from the random sampling component of the SSTP are available (Wills *et al.*, 2015), and efforts are underway to develop an online decision support tool from these data. Data for both online tools will be refreshed annually, so biologists and the public continuously have the latest and best data available for managing Michigan streams and trout populations. The SSTP is scheduled to use 40% of each unit's stream surveying effort, with the remaining 60% available for use at each management unit's discretion.

Fishing Regulations

Stream-resident populations of brown trout and brook trout in Michigan are managed as recreational fisheries. The need for regulations to protect Michigan's stream trout from excessive angler harvest was identified early on, and formally acknowledged shortly after 1873, when the Michigan legislature established the first Board of Fish Commissioners. George H. Jerome, Michigan's first Superintendent of Fisheries, reported in 1873:

> *that waters once abounding with fish can become barren by excessive, or ill-timed, or barbarous fishing, or all together, is too obviously, painfully true. …Go where we will, lakes streams and rivers, which scarcely a generation ago gave great joy and profit to riparian owner and general angler, now scarcely excite their thought or notice. …Laws, too, prescribing closure times and regulating the utensils and methods of capture, whether by seine or weir, or spear or hook, grow out of the very necessities of the case and can no more be dispensed with than can the rudder be detached from the ship and she ride on in safety.*
>
> (Michigan Fish Commission, 1873)

In 1881, the first regulation was adopted for trout in Michigan streams, a 152-mm minimum size limit for brook trout and Arctic grayling (Clark *et al.*, 1981). Beginning in 1889, the open fishing season for trout was set from May through August. The first 'special regulation' was enacted in 1901, and increase of the minimum size limit to 203 mm on the Au Sable River. In 1903, the statewide minimum size limit was increased to 178 mm for brook trout, brown trout, rainbow trout, Atlantic salmon, and Arctic grayling, and the daily possession limit was set at 50 trout (Clark *et al.*, 1981). In 1907, the first flies-only rule was adopted on the North Branch of the Au Sable River. In 1952, the daily possession limit for trout in most rivers was reduced to 10 fish, and in 1969 it was reduced to five fish (Clark *et al.*, 1981).

Despite many regulation changes and evaluations on individual waters, the basic structure of these early regulations (e.g., fishing seasons, minimum size limits, and location-specific gear restrictions) remains similar to what it was over 100 years ago. Trout fishing regulation changes occur periodically on individual streams as fishery managers obtain new information (e.g., water temperature or fish community survey data) to better assess the suitability of waters for trout populations. The MDNR periodically reviews and modifies statewide trout regulations to ensure they remain aligned with current knowledge of trout biology and preferences of Michigan trout anglers (e.g., importance of catch vs. harvest rates for trout). Associated with each regulation change are extensive opportunities for public engagement and comment. Public input processes routinely start with focus groups of anglers and fishing group representatives, and then involve the general angling public using press releases, public meetings, and online surveys. In general, MDNR's resident stream trout regulations strive to maintain productive and sustainable trout populations, be readily understood and enforceable, and provide an array of angling opportunities. Regulations are enforced by MDNR's Law Enforcement Division, rather than Fisheries Division.

The principle types of fishing regulations are creel limits, fishing and harvest closures, gear or fishing method restrictions, and size limits. Creel limits require anglers to release caught fish once they reach the creel limit, but these restrictions are generally not effective unless limits are set low enough that many anglers reach the limit. Still, creel limits are useful for preventing individuals from harvesting more fish in a day than the general public feels would be reasonable, and contribute to a more equitable distribution of fish among the angling public. In Michigan, the 2015 daily creel (or possession) limit on most streams is five trout, with no more than three trout being longer than 381 mm. Fishing and harvest closures occur on most Michigan streams from October 1st to the last Saturday in April, in large part to protect brown trout and brook trout which are spawning on riffles in fall (and are more vulnerable to anglers), and to minimize angler use of rivers while trout eggs are incubating.

Recreational fishing gear or method restrictions may be used to enforce principles of fair chase, assuring that fish are captured individually and with sufficient difficulty. Such restrictions may also be used to prevent spread of potentially invasive bait species into waters where they are not desired. More importantly, these restrictions are often used to reduce mortality of fish that may not be legally harvested. For example, on river reaches designated as 'flies only' or 'artificial lures and flies only' (where high catch rates are the objective), use of live bait is not allowed because early Michigan-based studies determined that hooking mortality is much higher with live bait than artificial lures and flies (Shetter & Allison, 1955; Shetter & Allison, 1958). The most common gear and method restrictions applied on Michigan streams are restrictions on the use of bait, number of points per hook (treble vs. single hooks), and barbless hook requirements.

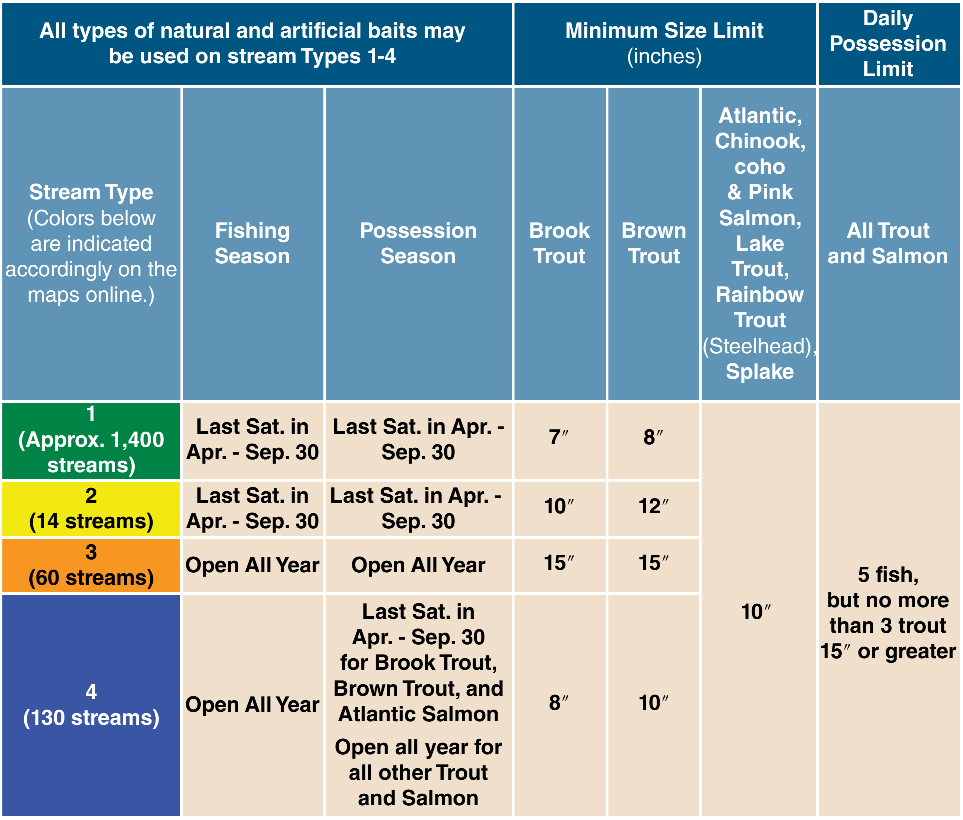
Minimum size limits (MSL) require anglers to release fish that are not large enough to be legally harvested. The best MSL for a particular fishery depends upon the intensity of the fishery, growth and survival rates of trout, and whether protection is needed to assure there are enough spawners to saturate spawning habitats. In contrast with creel limits and gear and method restrictions, MSLs have been shown to be effective in lowering angling and total mortality of trout populations (Shetter, 1969; Hunt, 1970). In his work on brook trout in Lawrence Creek, Wisconsin, Hunt (1970) noted that 'The size limit, if wisely applied is the best single regulation for preventing excessive angler harvest of brook trout populations. The size limit applies to every trout caught, and it can be related to a rather stable biological parameter, growth rates of trout populations.' The MDNR Fisheries Division focuses almost entirely on selecting the appropriate MSL's for each species and stream. Minimum size limits for brown trout and brook trout vary among different types of streams, due to differences in growth rates of trout among streams.

Since anglers are a key component in fishery management, an understanding of angler behavior, preferences, and attitudes is needed in order for management to be effective. For example, in a survey of trout anglers fishing Michigan's Au Sable River, Gigliotti (1989) found that most trout anglers fishing in special regulation areas believed that their fishing area was being neglected by fishery managers if the violation rate was, in their opinion, too high. Additional Michigan-based efforts have been undertaken or are ongoing to help MDNR better understand trout angler behavior and opinions. Knoche (2014) used a choice experiment survey of Michigan trout anglers to examine the willingness of anglers to make tradeoffs between changes in driving distance to a fishing site and changes in attributes available at fishing sites (e.g., trout species available, trout size and catch rates). He found that on average, trout anglers prefer higher catch rates, shorter travel distances to a fishing site, and are highly averse to strict fishing regulations such as catch-and-release only and artificial flies only regulations. However, 13–23% of anglers showed a strong preference for strict regulations. Melstrom *et al.* (2015) found that Michigan anglers are more likely to fish streams in watersheds that they think hold abundant brook trout populations. In preparation for development of its first inland trout management plan, MDNR Fisheries Division recently conducted a survey of resident trout anglers (Carlson and Zorn, in press).

Another issue that complicates management of trout populations in Michigan streams is that we know little about the actual harvest from nearly all of our streams, and especially our smaller ones. Thus, many of our assumptions on harvest may be incorrect. It is exceptionally difficult and expensive to estimate angler harvest on most of our streams due to many factors including the sheer number of trout streams in Michigan, multiple access points along most rivers, agency staff limitations, and changes in angler behavior (e.g., voluntary release rates of legal-sized trout caught) over time which limit the utility of older harvest estimates in predicting effects of proposed regulation changes on stream trout populations.

Michigan's sport fishing regulations for brown trout in streams represent an effort to optimize stream and trout population characteristics (e.g., self-sustaining vs. stocked populations, trout growth potential) while taking angler preferences and demographic factors into account (e.g., availability of stream trout fisheries in the area, potential angling pressure). Michigan trout streams generally fall into one of five regulation types.

Most of Michigan's trout streams (about 1,400 streams and about 27,000 km) are classified as Type 1. Type 1 streams are generally small, with stable flows, cold, summer temperatures, and are often difficult to fish (Figure 27.4). They usually have self-sustaining populations of relatively slow-growing trout, though some streams may be stocked. Some are tributaries to larger, thermally-marginal rivers and serve as seasonal coldwater refugia for trout from such rivers. Many Type 1 streams are narrow and most commonly fished with bait or spinners, because streamside vegetation makes fly-casting difficult. Trout in Type 1 streams would benefit from protection during the spawning season, because fish may concentrate when spawning areas are limited and be vulnerable to experienced anglers. Type 1 streams have fishing and harvests seasons that extend from the last Saturday in April to September 30, a 203-mm MSL for brown



All types of natural and artificial baits may be used on stream Types 1-4			Minimum Size Limit (inches)			Daily Possession Limit
Stream Type (Colors below are indicated accordingly on the maps online.)	**Fishing Season**	**Possession Season**	**Brook Trout**	**Brown Trout**	**Atlantic, Chinook, coho & Pink Salmon, Lake Trout, Rainbow Trout** (Steelhead), **Splake**	**All Trout and Salmon**
🟩 1 (Approx. 1,400 streams)	Last Sat. in Apr. - Sep. 30	Last Sat. in Apr. - Sep. 30	7″	8″	10″	5 fish, but no more than 3 trout 15″ or greater
🟨 2 (14 streams)	Last Sat. in Apr. - Sep. 30	Last Sat. in Apr. - Sep. 30	10″	12″		
🟧 3 (60 streams)	Open All Year	Open All Year	15″	15″		
🟦 4 (130 streams)	Open All Year	Last Sat. in Apr. - Sep. 30 for Brook Trout, Brown Trout, and Atlantic Salmon Open all year for all other Trout and Salmon	8″	10″		

Figure 27.4 Sport fishing regulations for Michigan trout streams in 2014 showing season dates, allowable fishing methods, minimum size limits, and daily possession limits for each stream type. Other fishing regulations (e.g., Gear Restricted) are specific to individual waters and not shown.

trout and a 178-MSL for brook trout, and a daily possession limit of five trout with no more than three individual trout being longer than 381 mm.

Type 2 trout streams are generally larger than Type 1 streams, often have less stable flows, and being warmer have somewhat faster-growing trout (Figure 27.4). Depending on the magnitude of groundwater inputs, some Type 2 streams contain self-sustaining trout stocks, while others are supported by stocking. Because of their potential to support higher catch rates of larger trout, these streams have higher MSLs (305 mm for brown trout and 254 mm for brook trout). Bait is allowed because these streams often have other fish species of interest to anglers. Season and possession restrictions are the same as Type 1 streams. Fourteen streams (about 300 km) have Type 2 regulations.

Type 3 streams typically receive seasonal runs of adfluvial fish from the Great Lakes, and therefore are open to fishing and harvest all year (Figure 27.4). Resident brown trout and brook trout fisheries are usually minor or non-existent in Type 3 streams, but if these species occur they receive substantial protection from a 381-mm MSL. Type 3 regulations occur on 60 streams (about 1300 km).

Michigan's 130 Type 4 streams (about 3100 km) vary greatly in size, exhibit flows ranging from moderately stable to quite variable, and have summer water temperatures that may be above optimal levels for trout (Figure 27.4). Trout growth may be average to above average, but survival and natural recruitment will generally be low. Trout fisheries in Type 4 streams may be represented only by seasonal runs of Great Lakes salmonids or supported by stocking. For these reasons, fishing is permitted year-round, but harvest of brown trout and brook trout can only occur from the last Saturday in April to September 30, and the 254-mm MSL for brown trout is higher than for Type 1 streams. The Type 1 MSL applies to brook trout in Type 4 streams, since they are expected to occur rarely or not at all.

Gear restricted regulations occur on 19 stream reaches, and may be employed for a variety of purposes. Most of these streams are fairly large, high-quality, stable-flow streams, with trout growth that is average to above average, and have the capacity to support high densities of trout. These reaches employ gear restrictions (flies-only, or lures and flies only) and high MSLs or no-kill regulations to maintain larger populations and higher catch rates of larger-sized trout. To encourage recruitment of new anglers, many allow year-round fishing and daily harvest of one 203–305 mm trout by children under 12. Two streams are located in the metropolitan Detroit area (Paint Creek, Huron River) and have the potential for high angler use and recruitment of urban anglers to stream trout fishing. Therefore, these streams also have gear, season, and trout size restrictions that allow for high use, while maintaining relatively high catch rates and some harvest. Michigan law limits application of gear restricted regulations to a maximum of 341 km of rivers in Michigan, and 296 km of streams currently have gear restricted regulations.

It is generally accepted that appropriate use of gear restricted and catch-and-release regulations will contribute to higher catch rates of larger-sized trout in streams (Arlinghaus *et al.*, 2007). Early evaluations of special regulations were pioneered on Michigan's Au Sable River (Shetter *et al.*, 1954), and other Michigan evaluations followed (e.g., Shetter and Alexander, 1962; 1966; Latta, 1973). These short-term evaluations found a mix of fish population and fishery responses, depending on the stream, while noting reduced angler use of special regulations stretches. It is very difficult to demonstrate effects of regulations in short-term field studies due to the inherent variability of trout populations over such time scales (Wiley *et al.*, 1997), and longer-term (decadal) changes in regional climate, water quality, and habitat quality in Michigan streams (Alexander *et al.*, 1979; Zorn and Nuhfer, 2007a; 2007b). A more recent and rigorous evaluation of catch-and-release regulations in the South Branch Au Sable River by Clark and Alexander (1992) conclusively showed that flies-only, catch-and-release regulations produced a better population of larger brown trout than would have occurred with just flies-only regulations. They were no detectable effects on the brook trout population. They also noted an increasing trend in voluntary release of trout over time, with anglers in the mid-1970s releasing about 40% of trout caught, but 80-90% of fish by 1990. Like earlier studies, they noted a decrease in fishing pressure in the catch-and-release reach. Fishing pressure in gear-restricted reaches today may be different, as several reaches (e.g., those on the Au Sable, Manistee, and Pere Marquette rivers) are thought to be quite heavily fished compared to nearby trout waters without such regulations.

In addition to state-licensed recreational anglers, Michigan trout streams are open to fishing by several Native American tribes. Each tribe sets its own regulations for stream resident brown trout and brook trout, and some tribes provide reports of harvested fish to MDNR Fisheries Division as per terms of the 2007 Inland Consent Decree (United States v. Michigan, 2007). Tribal harvests of brown trout appear to be very small (e.g., fewer than 10 fish) based on information provided to MDNR thus far.

Habitat Protection and Management

The protection, restoration, and maintenance of stream habitats are critical, given the immense capacity of Michigan streams to support self-sustaining trout populations and provide recreational benefits to citizens. In Michigan, this is accomplished through collaboration between MDNR, the Michigan Department of Environmental Quality (MDEQ), several federal regulatory agencies, and concerned anglers, citizens, and partners throughout the state. Documenting effects of habitat degradation also provides critical information for supporting habitat protection work. I will highlight some of the major efforts for these topics below.

Much protection is afforded to trout streams through a number of state and federal laws and rules (Michigan Department of Environmental Quality, 2015). Two key laws are the Federal Clean Water Act of 1972 and the Michigan Rivers and Streams Acts (Public Act 451). These laws require permits before activities that could potentially harm aquatic resources are undertaken. In addition, select river reaches receive additional riparian zone protection through the Federal Wild and Scenic Rivers Act and the State Natural Rivers Act. The MDEQ typically administers the permit processes associated with these laws, with MDNR Fisheries Division staff reviewing permits and providing recommendations for denial, approval, or modification of the proposed activities. Permits are required for changes to stream water quality including temperature impacts to streams (e.g., from dams, power generation facilities, surface runoff, etc.), changes to dissolved oxygen concentrations (e.g., from confined animal feeding operations, agricultural activities, or other sources of nutrients), and discharge of chemicals from industry or water treatment facilities. In Michigan, coldwater streams get special protections such as maintenance of a required minimum dissolved oxygen concentration of 7 mg/L. The MDNR also plays a support role in guiding MDEQ-led efforts to assess and clean up areas contaminated by toxic chemicals. To educate Michigan citizens about potential hazards of excess consumption of fish from contaminated waters, the MDNR and Michigan Department of Community Health collaborate to produce an online fish consumption advisory document that addresses all waters and locations where limited fish consumption is recommended (Michigan Department of Community Health, 2015).

Various activities have potential to cause significant structural harm to Michigan streams and aquatic communities. Oil and natural gas exploration and extraction activities occur throughout much of Michigan, and mines for metallic and non-metallic deposits occur in the Upper Peninsula of the state. Michigan DNR comments on permits submitted for these activities to prevent adverse water quality and physical habitat impacts on streams. The MDNR Fisheries Division provides input on development activities that could adversely affect stream habitat or hydrology, including changes to streambanks or riparian wetlands, dam construction or modification, road-stream crossings, and other construction activities. Where public forest lands are harvested, MDNR input ensures forested riparian habitats remain intact to protect water quality.

On some small coldwater streams, limiting tree harvests in riparian zones may discourage colonization by beaver *Castor canadensis*, since their dams can elevate water temperatures to unsuitable levels for trout on marginal systems.

Excess sedimentation of streams can result from inappropriate activities associated with roads, agriculture, construction, urbanization, dams, and logging. The MDNR Fisheries Division (Alexander & Hansen, 1988) undertook a study to document the effects of increased sedimentation (comparable to what might occur with improper road maintenance activities in northern Michigan) on the brook trout population in Hunt Creek, a small coldwater stream in the northeastern portion of Michigan's Lower Peninsula. They found that the abundance of brook trout declined more than 50% due to excess sand sedimentation. In response to habitat degradation, Alexander & Hansen (1988) rehabilitated age-1 and older brook trout densities in Hunt Creek to previous levels by excavating sediment traps, which were oversized, periodically-excavated reaches of stream channel that reduced current velocity and facilitated deposition and capture of sand bedload. Their findings led to construction of more than 150 sediment traps on stream reaches in Michigan alone. Unfortunately, evaluations of sediment traps in Michigan and Wisconsin by others (e.g., Avery, 1996; Zorn & Wills, 2012; Wills, 2013) have not shown the positive responses to sediment traps noted by Alexander and Hansen (1988). Nuhfer (2004) noted that fall abundance of age-0 brook trout in the reach of Hunt Creek that was impacted nearly 25 years earlier by excess sand bedload had recovered to only 55% of pre-impact levels, despite the use of sand traps. Despite the negative sediment trap results, these collective efforts provided valuable data to support prevention of excessive sediment in Michigan streams.

Many Michigan trout streams are considered to be lacking in woody habitat (large woody debris or LWD) dating back to when the state was originally cutover and its rivers used for log drives in the mid-late 1800s. Since then, much of riparian forest habitat in the state is relatively young (re-growing) or being actively managed, and large senescent trees that would fall into rivers are less abundant than in old growth systems. As a result, inputs of LWD to trout streams are often limited, and people have added LWD to Michigan rivers to restore some of this lost habitat since at least the 1920s (Hubbs *et al.*, 1932).

Efforts to restore lost habitat complexity in Michigan streams range from construction of an individual log complex (or logjam) as a group service project, to construction of dozens of habitat structures on a stream reach, to placement of hundreds of whole trees in rivers using helicopters. Since permits are required for these activities, fairly complete records are available from MDEQ (as far as rivers receiving permits) going back to 1991. These data show LWD-related activities (bank stabilization or fish structure installation) occurring on an average of 21.5 streams per year (MDEQ, unpublished data). Numbers of permits for LWD activities have varied from year to year with no obvious trend over time. Except for federally-funded projects on United States Forest Service lands (which comprise 36% of LWD projects since 1991), all LWD-related activities are conducted by non-governmental organizations (their actions guided by MDNR fisheries biologists) and funded by various grants (MDEQ, unpublished data). Reviews of fish responses to LWD (e.g., Roni *et al.*, 2015) and Michigan (e.g., Zorn & Nuhfer, 2007a; Wills & Dexter, 2011) have shown that when other aspects of habitat are suitable, brown trout density and survival were positively associated with increased woody habitat in stream reaches.

Nearly all Michigan watersheds with trout streams have been impaired by dams since the initial ones were constructed for grain milling in the early 1800s or to facilitate log drives and power mills in the mid-late 1800s. Built for various purposes (e.g., recreation, power generation, and navigation) many of Michigan's roughly 2500 dams are approaching the end of their lifespan, and today dam removal likely outpaces dam construction. Over 100 dams are used for power production, though hydropower provides only about 1.5% of Michigan's power generation because Michigan's rivers are relatively small, with low-gradient. Dams adversely affect trout populations in Michigan rivers through a variety of mechanisms including impounding rare high-gradient stream reaches, fragmenting habitats, disrupting transport of sediment and woody debris, destabilizing daily flows, reducing seasonal flow fluctuations which shape habitat, altering downstream temperatures (e.g., warming in summer), and blocking seasonal (or daily) movements of trout among habitats. The MDNR Fisheries Division works with MDEQ, federal regulators (in particular the Federal Energy Regulatory Commission), dam owners, and concerned citizens to remove dams (when possible), modify dam operations to minimize adverse effects of dams, and to seek restitution for damages that existing dams cause to stream habitats and biota. For example, re-licensing of a suite of large dams owned by Consumers Energy and Wisconsin Electric Power Company during the 1990's resulted in dam removals, changes to run-of-river (rather than peaking) flow operations at several dams, improvements in public access and facilities on impounded and riverine reaches affected by dams, improvements in the monitoring dam of operations and river flows, and establishment of corporate-funded mitigation funds for projects that help address local and system-wide impacts of these large dams.

During the 1990s, the MDNR Fisheries Division initiated a study of the effects of migratory rainbow trout (steelhead) from the Great Lakes on the resident brown trout population in Hunt Creek, to help inform fish passage decisions for Great Lakes salmonids in Michigan streams. They found that survival of age-0 brown trout declined significantly in the presence of steelhead, which resulted in densities of age-1 and older brown trout being 46% lower the two species co-occurred (Nuhfer *et al.*, 2014). These results and other studies in the region (e.g., Lessard & Hayes, 2003; Dodd *et al.*, 2003; Januchowski-Hartley, 2013) are informing fish passage decisions at small dams, sea lamprey barriers, or the more than 67,000 road-stream crossings in Michigan with culverts that potentially provide barriers to upstream movement of aquatic organisms.

Regulation of water use in Michigan and the Great Lakes has become a prominent habitat protection issue during the last decade. In 2008, a progressive water management system to protect the waters of the Great Lakes basin, the Great Lakes – St. Lawrence River Basin Water Resources Compact, was adopted by each of the Great Lakes states and provinces, the U.S. Congress, and signed by the President (Hamilton & Seelbach, 2011). This federally-ratified regulatory framework for the Great Lakes is enforceable against interstate movement of Great Lakes water, and applies a common resource-based conservation standard to new or increased large capacity water withdrawals from the Great Lakes basin waters (including groundwater).

Application of this framework in Michigan involved stream classification and model development to determine when proposed water withdrawals (individually or cumulatively) would adversely affect stream fish communities (Hamilton & Seelbach, 2011; Zorn *et al.*, 2008). To this end, fish community responses to flow reduction were

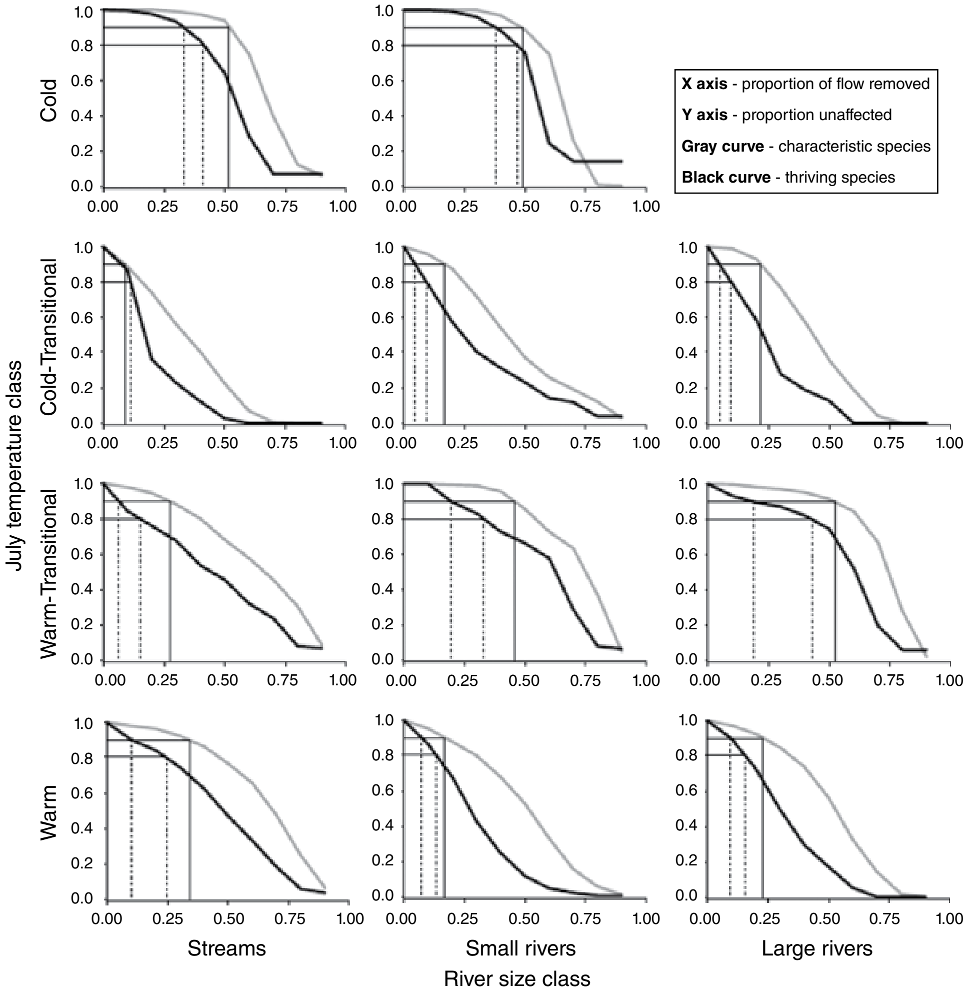


Figure 27.5 Curves describing fish community responses to water withdrawal for Michigan's 11 river types, as defined by size and July temperature characteristics. The black curve describes the proportion of Thriving Species thriving at each increment of flow reduction. The gray curve quantifies the proportional change in Characteristic Species Remaining and Characteristic Species Abundance metrics, and is an average of their values at each level of water withdrawal. The x-axis is the proportion of flow removed, and the y-axis is the proportional change from the original metric value. The right-most vertical line in each plot identifies the flow associated with an adverse resource impact (ARI), while other vertical lines identify water withdrawal levels associated with other management actions to be taken in anticipation of river base-flow yield values approaching the ARI level. See Zorn *et al.* (2012) for further details.

estimated for each type of stream in Michigan (Zorn *et al.*, 2012; Figure 27.5). These modeling results provided the basis for legislating maximum percentages of flow reduction that would be allowed for each type stream in Michigan (Hamilton & Seelbach, 2011). Modeling results for resident trout streams were consistent with other Michigan-based studies which indicated trout populations were somewhat resilient to short-term flow reduction in streams with high groundwater inputs (Nuhfer & Baker, 2004; Wills *et al.*, 2006; Nuhfer *et al.*, 2017), but more vulnerable in marginal, cold-transitional streams (Gowan, 1984).

Fish Stocking

Most populations of stream-resident brown trout in Michigan are self-sustaining. For example, only 78 of over 1600 streams managed for trout in Michigan were stocked with brown trout in 2014 (Table 27.1). With suitable coldwater habitat, sound inventory data and tools to guide management, and adequate habitat protection and fishing regulations, stocking is unnecessary in many Michigan streams.

The move towards supporting self-sustaining populations is a significant shift in management philosophy from the 1950–1964 ‘Legal-size trout era’, when legal-sized trout were stocked into streams during weeks surrounding the opening day of trout harvest season to maximize the proportion of stocked fish creeled by anglers (Westers & Stauffer, 1974; Whelan, 2004). The ‘Legal-size trout era’ followed research findings from the ‘Fingerling era’ (1930–1949) which showed higher returns from plants of legal-size (greater than 178 mm), compared to 102–152 mm fingerlings (yearlings) that had been held in hatcheries for one winter (Westers & Stauffer, 1974). Of course, the ‘Fingerling era’ followed the ‘Fry era’ (1873–1929), and began because fish culturists and sportsman thought they would receive better returns from stocking trout fingerlings than fry.

Most brown trout are reared at two state fish hatcheries (Oden and Harrietta), with some rearing also occurring at Thompson State Fish Hatchery up until 2016. Three strains of brown trout are currently raised: (1) Gilchrist Creek strain fish are from captive-reared brood stock originally obtained from a wild (naturalized), stream-resident population of brown trout in Gilchrist Creek, Michigan; (2) Sturgeon River strain brown trout are also from captive brood stock originally sourced from the Sturgeon River which has a mix of wild, stream-resident fish and adfluvial brown trout that migrate from Burt Lake, in the northern Lower Peninsula; and (3) Wild Rose strain brown trout which were originally obtained from the Wild Rose State Fish Hatchery in Wisconsin, though this strain likely has its roots in Michigan, as it is thought that they came, in part, from brood stocks held at the Harrietta State Fish Hatchery.

The MDNR Fisheries Division Hatchery Program uses state-of-the art technology to efficiently produce high-quality, relatively disease-free trout with high genetic integrity. Protected water supplies and rigorous biosecurity and disinfection procedures at hatcheries minimize the incidence and spread of disease. For example, whirling disease plagues the western United States but Michigan sees little expression of it for these reasons, and because of the high resistance of brown trout to Mercer (MRSA) infection, likely a result of them co-evolving with the disease, and a lack of the least resistant clade/lineage of *Tubifex tubifex* (the proximate hosts for this pathogen) in our waters (G. Whelan, MDNR, personal communication). Brown trout are all reared from captive broodstocks, but use of the Gilchrist Creek and Sturgeon River strains reflects a movement of Michigan’s hatchery system towards naturalized strains of brown trout that can be periodically refreshed through broodstock collection in rivers as opposed to domesticated strains (e.g., Wild Rose) that cannot. To maximize genetic diversity and minimize genetic drift, each hatchery year class of brown trout consists of more than

Table 27.1 Total number of streams stocked with brown trout, total number of brown trout stocked, and weighted average length of brown trout stocked into inland streams in Michigan by year (MDNR Fisheries Division, unpublished data).

Year	Number of streams stocked	Total fish stocked	Average length (cm)
1979	87	457,393	15.7
1980	89	489,781	14.0
1981	83	398,099	12.6
1982	87	421,825	13.7
1983	101	868,481	15.0
1984	102	784,082	14.7
1985	102	505,526	16.8
1986	105	679,256	15.9
1987	105	658,830	14.7
1988	104	910,607	13.8
1989	107	945,769	14.9
1990	100	781,870	14.3
1991	94	753,496	15.2
1992	99	817,061	14.7
1993	96	770,017	17.3
1994	93	744,606	17.3
1995	96	694,371	16.4
1996	92	684,111	16.4
1997	92	744,955	15.8
1998	87	781,656	15.2
1999	86	765,976	15.1
2000	80	813,195	14.1
2001	77	865,539	14.0
2002	76	745,409	14.9
2003	84	795,232	16.1
2004	79	691,502	15.5
2005	78	750,567	16.5
2006	78	748,296	16.5
2007	77	558,273	16.6
2008	77	675,002	15.6
2009	78	818,727	15.1
2010	78	723,139	15.6
2011	74	805,938	14.3
2012	80	1,152,699	13.2
2013	74	663,641	15.5
2014	78	681,851	16.4
Averages:	88.2	726,299	15.3

100 unique families produced from one-to-one pairings of male and female fish. While males and females of different age classes are always used to create new captive brood lots, rearing logistics do not always allow this to happen for fish produced for stocking. New brood lots are formed, typically every other year, by obtaining a random tablespoon of eggs from each pairing and rearing these separately from ones to be stocked. These hatchery procedures are based upon recommendations of the U.S. Fish & Wildlife Service's Fish Genetics course, developed by geneticist, Dr. Robb F. Leary.

The quality and performance of brown trout reared in MDNR hatcheries has been evaluated in both the hatchery and field (e.g., Nuhfer, 1996; Wills, 2005). From fishery managers' experience and these evaluations, we have identified commonly-occurring situations in Michigan where each strain generally performs best. Sturgeon River strain brown trout are stocked in situations where there is potential for a lake or stream fishery, and adfluvial spawning runs. The Gilchrist Creek strain is primarily used to provide river-resident brown trout fisheries in streams where water quality is good for multiyear survival of stocked fish, but natural reproduction is lacking (most often due to lack of spawning habitat). Wild Rose strain fish are preferred in situations where survival beyond one summer is questionable and a put-grow-and-take fishery is desired. Wild Rose also seem to be a good fit for stocking in lakes where piscivorous fish are present, and larger size at stocking is critical for enhancing survival of stocked fish.

Brown trout are stocked into streams as yearlings. A mean of 729,299 brown trout, averaging 153 mm in length, have been stocked annually into streams in Michigan since 1979, with no obvious trend in numbers or average sizes of fish stocked into streams since the 1980s (Table 27.1).

Streams where brown trout are now typically stocked provide suitable habitat for year-to-year survival of stocked fish, but have limited or no natural reproduction of trout; often due to high summer temperatures, excessively high spring flows which impair reproduction, or lack of suitable spawning substrates. The number of streams stocked has declined over the last few decades, going from a high of 107 streams in 1989 to a low of 74 in 2013. Plants on individual streams are discontinued when surveys identify a self-sustaining trout population at a site, when fisheries data indicate survival of stocked trout is poor, or when habitat data suggest the stream is thermally unsuitable. Brown trout are also stocked into inland lakes and the Great Lakes (46% of brown trout stocked since 2000), but these populations are beyond the scope of this report.

Acknowledgments

Several excellent accounts provided much of the historical information in this report, especially Westerman (1974), Clark *et al.*, (1981), and Whelan (2004). Ken Yeh provided the surface geology and land use maps. This manuscript was improved by the thoughtful reviews of Gary Whelan, Brian Gunderman, and Dan Sampson.

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28

History, Conservation and Management of Adfluvial Brown Trout Stocks in Finland

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Introduction

Freshwater brown trout is considered endangered (EN in IUCN classes) in southern Finland and near threatened (NT in IUCN classes) in northern Finland (Rassi *et al.*, 2010). However, this assessment does not separate resident and migratory forms, and in general the migratory populations are more endangered than the resident ones. Tens of lake-migrating (i.e. adfluvial) inland brown trout populations were lost during the 20th century due to damming of most major spawning rivers and intensive land use in their watersheds, and many of the remaining small populations did not tolerate the heavy fishing mortality in their feeding areas. The contemporary migratory populations mainly exist because of intensive supportive breeding programs. A number of resident populations have also vanished due to dredging of creeks and ditching of forests and wetlands, while some of the original populations have been lost due to stocking of brown trout from non-local strains.

Typically, Finnish inland fisheries are mixed-stock and mixed-species fisheries without any effective controls over fishing effort. The most important forms of lake fishing are gillnet fishing and trolling, with use of more effective gears such as seine nets and trawls restricted to professional fishermen, and in rivers fishing is done mainly by rod with both effort and bag limits. Economically brown trout is the most important species in river fishing in inland watersheds, but in lake fishing its importance is relatively small compared to non-salmonid fishes (Finnish Game and Fisheries Research Institute, 2011).

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

Most current management actions aim to support intensive recreational fishing, but increasingly also to increase the natural reproduction and to restore the wild adfluvial spawning stocks. In this chapter, we review biogeographically the history of the most important Finnish adfluvial brown trout stocks, main issues in the management of fisheries and trout environments, and using a simple age-structured population model evaluate the potential sustainable catches from two important stocks. Finally, we identify research needs in order to improve both fisheries management and understanding of crucial life-history phases.

Environment of Adfluvial Brown Trout in Finland

Human activities have modified most aquatic environments in Finland. Only about 30% of the lake surface area and 20% of rivers achieve pristine ecological status. Between the assessments of 2008 and 2013, the status of lakes deteriorated slightly, whereas that of rivers somewhat improved (Ministry of the Environment, Finnish Environment Institute and Finnish Game and Fisheries Research Institute, 2013).

In boreal environments, adfluvial brown trout typically requires oligotrophic, clear-water lakes with a surface area of some tens of square kilometers and a sufficiently deep hypolimnion with well-oxygenated water all the year round (Vehanen & Aspi, 1996). Water chemistry rarely limits the existence of migratory trout except for some highly humic and acidic waters in Eastern Finland, even though the waters in southern and central Finland have become browner during this century due to the warmer autumns and associated increased leaching of humic materials (see Kritzberg & Ekström, 2012; Sarkkola *et al.*, 2013). Most Finnish large lake environments including their outlets are also good feeding habitats for adfluvial brown trout. A good feeding lake typically supports an abundant stock of small-sized prey fishes such as vendace (*Coregonus albula*), smelt (*Osmerus eperlanus*) or sticklebacks (mainly *Pungitius pungitius*) (Lind, 1978). There are at least 115 such lakes with strong vendace populations in Finland (Sipponen *et al.*, 2006).

Finnish lakes are typically divided into several basins, separated by slowly flowing straits and relatively short rapids. Brown trout is often found in both lakes and in lake outlets. Outlet streams typically have a low gradient and few natural migration barriers, and their hydrology is stabilized by the presence of several lake basins. The maximum water temperature in lake outlets is normally 21–26 °C in summer, and the water temperature stays above zero in winter, thus reducing the formation of anchor ice typically present in other types of boreal streams in November–February. Food resources in lake outlets are typically good for juvenile trout because of abundant filter feeding insects, mainly Trichoptera and Diptera larvae (Malmqvist & Eriksson, 1995; Syrjänen *et al.*, 2011a).

Seven Important Watersheds and Adfluvial Trout Stocks

Until the beginning of the 20th century brown trout probably occurred in most lakes with surface area ≥ 50 km^2. Spawning stocks were most likely strong especially in the seven most important watersheds (Figure 28.1), but lake-migrating brown trout has

Figure 28.1 The seven most important Finnish watersheds for adfluvial brown trout: Kok = Kokemäenjoki, Kym = Kymijoki, Vuo = Vuoksi, Oul = Oulujoki, Kou = Koutajoki, Tuu = Tuulomajoki, and Paa = Paatsjoki. The locations of the River Oulankajoki (Ou) and the Rautalampi watercourse (Ra) are also marked.

likely never been particularly abundant in Finnish lakes due to the limited availability of habitats suitable for reproduction.

There are currently five large watersheds with significant lake areas and existing wild brown trout stocks in southern and north-eastern Finland; these are the watersheds of the rivers Kokemäenjoki, Kymijoki, Vuoksi, Oulujoki and Paatsjoki (Figure 28.1). In addition, the spawning rivers of the northern Tuulomajoki and Oulankajoki watersheds are located in Finland, while the most important feeding areas in these watersheds, lakes Nuortti and Pääjärvi, are located in Russia.

There are almost no scientific data available concerning the status of wild adfluvial trout stocks in Finland before the 1970s; only some catch reports from recreational or subsistence fishing in earlier decades exist.

Kymijoki Trout Stocks in the 20th Century

The best historical data are available for the Kymijoki watershed, which is used here as an example of the typical development of adfluvial stocks in Finland during the past century. In the early 20th century, the fishing of adfluvial brown trout often occurred in spawning rivers. The largest, and probably exceptional, documented catch on the single lifting of a longline having 800 hooks in Lake Päijänne, the largest lake in the Kymijoki watershed (Figure 28.1), was 41 brown trout in 1922, and the weight range of the fish was 3–12 kg (Hurme, 1965). The total annual trout catch was several thousands of fish or more in Lake Päijänne in the 1920s (Hurme, 1965). However, these catches likely indicate striking developments in fishing methods rather than sustainable catches.

Gillnets were taken into common use in lakes in the 1950s and 1960s, and have been used in both recreational and professional fishing ever since. However, as early as 1928–1959 some specialized individual fishermen were reported to have captured several thousands of kilograms of brown trout with gillnets (Kovanen *et al.*, 1994; Eloranta, 1993). The largest documented individuals among those early catches were ca. 15 kg in weight (Pentti Valkeajärvi, Konnevesi Fisheries Research Society, unpublished) indicating that these gillnetting pioneers were targeting nearly virgin, unfished populations.

As a consequence of rapidly developing fishing gear, increasing fishing pressure and cumulative environmental damage, artificial breeding methods were developed from the 1920s onwards. Some spawners for artificial breeding were captured with gillnets or hand nets in the rivers and hatchery-reared offspring were released as newly hatched fry in May or June to the rivers. In eight rivers in the Kymijoki watershed, 1,623 spawners were caught, marked and released after breeding in 1921–1945. The mean weight of 630 males and 993 females was 4.7 kg and 4.3 kg, respectively (Pentti Valkeajärvi, Konnevesi Fisheries Research Society, unpublished). As only some unknown proportion of the trout catch was recorded, the total catch to hatcheries must have been larger.

In addition, spawners were fished for food, both legally with rod (Eloranta, 1993) and traps, and illegally with gigs and gillnets in rivers (Kovanen *et al.*, 1994). However, at that time rod fishing was restricted and rod fishers were very few. The annual rod catch was some tens of kilograms per river, or some hundreds of kilograms in the largest rivers. The largest individuals caught were 8–12 kg in weight (Eloranta, 1993).

Some rough estimates can be given for the size of the spawning stocks in the Kymijoki watershed before damming of rivers and modern lake fishing. There were approximately 45 outlet rivers from lakes, or separate riffle sections in the few longer rivers, having a mean discharge of 10–150 m^3s^{-1} in the watershed. Trout most likely occurred in all of these and still occurs as resident in all of the rivers that remain undammed. If the annual number of lake-migrating spawners was 50 to 150 fish per river (see Järvi, 1936), there must have been in total 2250 to 6750 migratory spawners in the Kymijoki watershed, translating to 10–30 tonnes with the mean fish weight of 4.5 kg. However, before the time of documented catches, the number of repeat spawners and very large individuals may well have been even higher. In addition, there were about 20 rivers in the watershed with a mean discharge of 1–10 m^3s^{-1}, and resident trout still spawn in most of these. Thus, the total annual spawning stock of migratory trout in the Kymijoki watershed could have been roughly 3 000–12 000 fish and 15–50 tonnes. Now, due to unregulated lake fishing, poaching and river damming, the total adfluvial brown trout spawning stock in the whole watershed is at maximum only a few hundred fish (Syrjänen & Valkeajärvi, 2010).

Vuoksi, Kokemäenjoki and Oulujoki Stocks

In the Kokemäenjoki and Oulujoki watersheds (Figure 28.1), adfluvial brown trout was probably common at the beginning of the 20th century. However, in these watersheds, the total lake area is smaller than in the Kymijoki watershed. In contrast, the Vuoksi watershed includes the largest Finnish lake areas, like Lake Saimaa, and historically the largest riffle areas in Finnish rivers, but trout spawners and parr partly shared the same habitats with landlocked Atlantic salmon (*Salmo salar* L.) in the three largest rivers, leading to potential interspecific competition (Kaijomaa *et al.*, 2003). In addition, Arctic charr (*Salvelinus alpinus* L.) occurred in many lakes in the watershed (Seppovaara, 1969; Kolari & Hirvonen, 2013). Based on the historical size of the lake and river areas, it can be supposed that the size of adfluvial stocks in the Vuoksi watershed was probably similar to those in the Kymijoki watershed.

Several records of brown trout are found in historical documents. In the Kokemäenjoki watershed, eleven trout with the mean size of 8 kg were caught with a net in 1864 (Koskinen, 1981). Ahlgren (1967) mentioned that he caught several trout of 9 kg or more in a river. Hurme (1966) reported that the average size of captured trout in a lake was more than 5 kg in the 1930s, but 4 kg in the 1940s (Hurme, 1966). The record individual of 12.7 kg was caught in 1893 (Hurme, 1966). However, wild adfluvial brown trout has thereafter disappeared from the Kokemäenjoki watershed.

Currently, a small number of migratory brown trout spawn annually in the rapids of the Heinävesi watercourse in the Vuoksi watershed (Rajala & Hentinen, 2014) but the total number of spawners in the Vuoksi watershed is at most a hundred fish. In the Vuoksi watershed, the record fish of 13 kg was caught in the 1930s (Pautamo, 2003). Nearly all major spawning rivers in both the Vuoksi and Kokemäenjoki watersheds have been dammed, and until recently, recreational fishing on lakes has been almost unregulated.

In the Oulujoki watershed, both Baltic salmon (*Salmo salar*) and sea trout migrated to the River Oulujoki and the rivers upstream from Lake Oulujärvi to spawn. Several separate adfluvial brown trout stocks lived in Lake Oulujärvi and in the watercourses upstream, and wild resident trout populations still exist in some of the small tributaries of the system. Wild migratory individuals are now rare and occur mainly in some pristine lakes and rivers of Kuhmo area. All the main stem rivers have been dammed for hydropower without fishways since the late 1950s.

Koutajoki, Tuulomajoki and Paatsjoki Stocks

In the River Koutajoki (Kovda in Russian) watershed (Figure 28.1), the main brown trout spawning river system, the Oulankajoki (Olanga in Russian side), runs from west to Lake Pääjärvi (Pyaozero in Russian), the central lake of the basin, located in northwest Russia. Some other rivers flowing into the lake also support adfluvial brown trout stocks (Huusko *et al.*, 1990). In the westernmost part of the watershed there is a subbasin, Lake Kitkajärvi, draining through the River Kitkajoki into the River Oulankajoki. The Jyrävä Falls, located approximately in the middle course of the River Kitkajoki, prevent upstream migration of fish, thus isolating the Lake Kitkajärvi basin from the downstream fish populations.

In the first half of the twentieth century, a record of the daily catch by a recreational fisherman in Lake Kitkajärvi and the River Kitkajoki recorded up to ten large (2 – 7 kg in mass) trout (Hänninen, 1921). In the 1950s and 1960s, an extensive gill-net fishery developed both in the lake and the river with the consequence that the trout stock collapsed by the early 1970s (Keränen, 1978). The present annual spawning population of large adfluvial trout is extremely sparse (Hyytinen, 1985; Huusko & Saraniemi, 2003).

The changes in brown trout stock dynamics in the river-system of the Oulankajoki and Lake Pääjärvi basin have been less dramatic. Until the 1960s, trout was mainly harvested from Lake Pääjärvi, and there was little river fishing. Fishing in the lake was greatly reduced in the 1960s due to hydropower construction, including raising the water level of Lake Pääjärvi by several meters (Litinskaya, 1976; Khalturin, 1971, Huusko *et al.*, 1990). From the 1970s onwards, recreational fishing of trout increased heavily in the River Oulankajoki and its tributaries, and has remained high (Huusko, 1990; Sutela & Huusko, 1998; Wendelin *et al.*, 2015).

Due to the different past timings of harvesting between the lake and the river, the total harvest remained at a sustainable level in the twentieth century, and the trout stock of the River Oulankajoki system remained viable. However, from the late 1990s onwards trout fishing in Lake Pääjärvi has rapidly increased, and fishing effort and fishing mortality in both the rivers and the lakes are now so high that the trout stock has declined. The record individual trout of 13 kg was caught in the lower reach of the River Oulankajoki (Vjatseslav Shirokov, Northern Fisheries Research Institute (SevNIIRH), Petroskoi, Russia, personal communication).

The River Tuulomajoki watershed was historically one of the largest and most important salmon rivers running to the Barents Sea (Pautamo, 1996). However, following construction of two major hydroelectric plants in the 1930s to 1960s, salmon abundance declined strongly (Pautamo, 1996, Kazakov & Veselov, 1998) and salmon populations now persist only in a few tributaries located below the second dam (Karppinen *et al.*, 2002). The upper Tuulomajoki system, above the two dams, still supports adfluvial brown trout stocks. Their feeding area is Lake Notozero (Nuorttijärvi in Finnish), which is basically a large reservoir lake located above the second dam. Spawning of brown trout takes place in several near pristine headwater tributaries on both the Finnish and Russian sides.

In the Tuulomajoki watershed, the hydroelectric development and water regulation has probably had a negative effect on the adfluvial brown trout stocks, but unfortunately there is no reference information from the period before the regulation. In recent years the annual spawning stock in the most important Finnish tributary, the River Luttojoki, is estimated to be only a few hundred individuals ranging in size from 1 to 5 kg (Aalto *et al.*, 1998; Orell *et al.*, 2011). Snorkeling counts of trout spawners have indicated some positive development during the last few years (Orell *et al.*, 2015), but the patchy occurrence of both spawners and parr indicates that brown trout has not succeeded in colonizing the juvenile production areas in large main stems that were utilized by salmon before the damming.

Historically, adfluvial brown trout was naturally common in the northern Lake Inari in the Paatsjoki watershed but likely less abundant than the Arctic charr (*Salvelinus alpinus*). Inlets to the lake, like the Rivers Ivalojoki and Juutuanjoki are long rivers with large riffle areas offering substantial spawning and parr habitats for adfluvial brown trout. It is not known if the Inari trout also used the outlet river, Paatsjoki, for spawning before its damming in the 1940s. The largest trout caught have included a 10-kg fish in the River Juutuanjoki in 2010, and a 13-kg trout in a Lake Inari gill net fishery in 2012 (Erno Salonen, Natural Resources Institute Finland, unpublished). Wild adfluvial trout is still common in Lake Inari.

River Channel Modification and Heavy Exploitation

Dam Building and Channel Dredging

In the early 20th century, hundreds of dams for mills, sawmills and timber floating were built in small streams and in side channels of larger rivers. Almost all river channels were dredged, mostly for log transport. Although small dams and dredging did not completely prevent reproduction of trout, migratory trout stocks declined significantly. Only certain rivers in the Kymijoki and Vuoksi watersheds are known to have supported relatively strong stocks until the 1950s.

The most intensive period of construction of hydropower dams in Finland was in the 1960s and the 1970s. Initially, most power companies had obligations to construct fishways alongside dams to facilitate the migration of aquatic biota. However, these obligations were often challenged and faced protracted civil-actions, so that only a handful of fishways were ever actually constructed. Unfortunately, the early fishways did not function as expected, and consequently the hydropower companies were later obliged to compensate the fisheries losses by direct payments or programs of stocking salmonids. Despite these compensatory actions, the migratory trout stocks in the watersheds of the Rivers Kokemäenjoki, Kymijoki, Vuoksi and Oulujoki (Figure 28.1) significantly declined.

One result of the high demand for electricity is that nine of the outlets from the ten largest Finnish lakes, each with surface area of 250–4400 square kilometers, are now dammed. The amplitude of the water level regulation in outlets is typically close to or less than one meter, but is up to three meters (average amplitude 1.7 m) in Lake Oulujärvi. In the largest watershed, Vuoksi, almost all large rivers (mean discharge $> 50\,m^3s^{-1}$), and most of the smaller rivers (mean discharge $1–50\,m^3s^{-1}$), are dammed for hydroelectricity production. The Kokemäenjoki and Oulujoki watersheds are dammed even more intensively: hydropower dams prevent fish migrations to the largest lakes, but the upper river systems still provide both small feeding lakes and spawning habitat for wild resident brown trout populations. Around half of the large and small rivers in the Kymijoki watershed are still undammed, and most of the human-impacted channels have been restored. In the Oulankajoki, Tuulomajoki and Paatsjoki watersheds, most rivers are still unmodified and in a near-pristine state, except for the River Kuusinkijoki which has been dammed for hydroelectricity production and suffers from both river dredging and intensive water level fluctuations.

Intensive Subsistence Fishing

Southern migratory brown trout stocks collapsed between the 1960s and the 1990s (Figure 28.2A) not only in dammed rivers but also in watercourses that were free from migration barriers (Valkeajärvi *et al.*, 2013). This was due to nearly unregulated and intense recreational fishing on lakes, mainly with gillnets and trolling (Syrjänen & Valkeajärvi, 2010). Most of this intensive fishing was for consumption and could be classified as subsistence fishing, whereas more recreation-oriented fishing has increased only very recently. A local license from shareholders' associations was needed for each gillnet, but the maximum number of licenses (gear units) that were available for sale, were never reached in practice. Thus, a recreational gillnetter could have used a 300 m or even longer gillnet set. Also, rod fishing with originally strong consumption orientation became popular in rivers in the 1970s and 1980s, and at that time the minimum size limit for brown trout was first 300 mm and later 350 mm, i.e. less than the size at maturity of migratory or even resident individuals. In addition, illegal fishing with hook and line with worm bait, gigging and gillnetting continued in rivers relatively intensively.

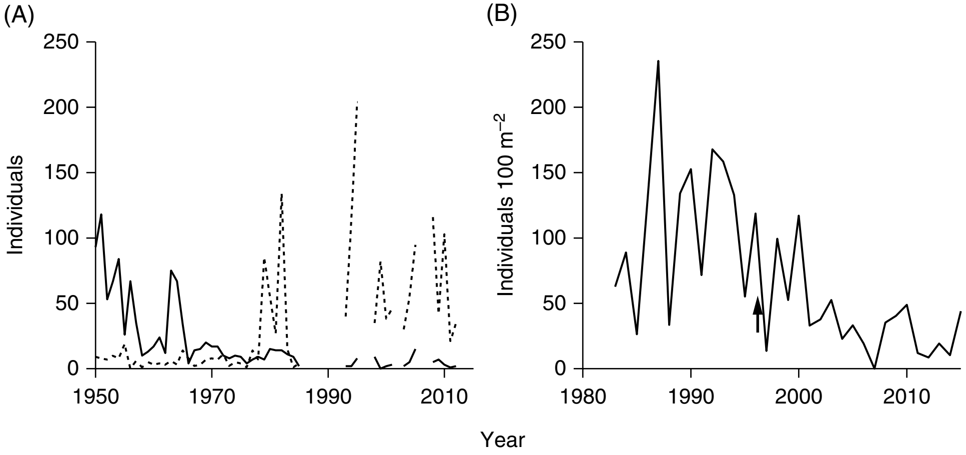

Figure 28.2 (A) Annual number of brown trout in the fishway of the dammed River Vaajakoski, flowing from Lake Leppävesi to Lake Päijänne (redrawn from Valkeajärvi *et al.*, 2013). Solid line indicates trout of 600 mm long or more and dotted line trout shorter than 600 mm. Extensive stocking of 2- and 3-year-old trout into lakes began in the 1970s. In the 1950s, all trout in the fishway were wild or stocked as alevins, but in the 2010s over 90% of trout have been of hatchery origin. (B) Density of 0-year-old brown trout, estimated by electrofishing, in Kivikoski, the main spawning area of adfluvial trout of the Arvaja watercourse in the Kymijoki watershed (Jukka Syrjänen and Anssi Eloranta, Konnevesi Fisheries Research Society, unpublished). The arrow indicates the time of channel restoration.

From the 1950s onwards, land owners changed their traditional seine and longline fishing to gillnet fishing targeting mainly whitefish, vendace, European perch (*Perca fluviatilis* L.), pikeperch (*Sander lucioperca* L.) and pike (*Esox lucius* L.). Salmonids were most often caught as by-catch. In inland waters, the total recreational biomass yield of brown trout was approximately 257 tonnes in 2010. This catch is relatively small compared to the perch (6033 tonnes), pike (6422 tonnes), and pikeperch (2632 tonnes) catches (Finnish Game and Fisheries Research Institute, 2011).

Some recreational gillnet experts (formerly classified also as subsistence fishermen) targeted trout in lakes and were able to catch a hundred or more trout per year. The known record catch is 800 trout in a year by one single gillnetter in the 1980s (Pentti Valkeajärvi, Konnevesi Fisheries Research Society, unpublished). No bag limits were set for lake fishing. Thus, fishing was entirely open-access at least to land-owners, and hatcheries produced large quantities of fish to compensate for intensive fishing (also referred to as ’lake ranching’). The high level of lake fishing effort and catch is well illustrated by the fact that Finland has the highest fish catch from inland waters of all European countries (Sipponen *et al.*, 2006).

Recreational lake fishing was so intense from the 1970s to the 2000s that migratory stocks would have vanished because of fishing mortality alone, even without the impact of damming. The last southern wild adfluvial brown trout stock persists in low numbers in the Heinävesi watercourse in the Vuoksi watershed, and is supported by parr stocking. The second-to-last adfluvial stock died out in the Arvaja watercourse in the Kymijoki watershed in the 1990s (Figure 28.2B) (Syrjänen & Valkeajärvi, 2010), and now only resident trout spawn in the watercourse.

Because of continuous stocking, recreational fishing of brown trout is still common in most medium to large lakes and rivers throughout the country. Roughly two thirds of the recreational trout catch in lakes is harvested with gillnets (both targeted catch and by-catch) and one third with trolling targeting brown trout and landlocked Atlantic salmon (Syrjänen *et al.*, 2010, 2011b). Commercial fishermen operate only on the largest lakes focusing mainly on vendace and pikeperch, and catch only a small proportion, roughly 10 – 20%, of the total trout catch as by-catch (Syrjänen *et al.*, 2011b). Only in the northern Lake Inari in the Paatsjoki watershed (Figure 28.1) is adfluvial brown trout one of the most important species in commercial fisheries.

Nowadays Lake Inari, including its tributaries, is the only Finnish area which still has moderately abundant wild adfluvial stocks in several rivers (Swatdipong *et al.*, 2013) although the majority of the catch is nevertheless based on intensive stocking programs. The annual total mixed-stock catches of wild and stocked brown trout in Lake Inari have been respectively 3–25 and 12–35 tonnes in the 21st century (Niva *et al.*, 2015).

Management of Inland Brown Trout Fisheries

Fisheries Administration

Fishing rights in Finland are bound to land ownership except for the so-called general fishing rights that empower free, open-access angling and rod fishing with one rod, line and lure in all still waters and non-salmonid rivers other than some put-and-take fisheries. Most fishing rights are owned by private citizens, who form shareholders’ associations according to their land ownership (Sipponen *et al.*, 2006). The water area managed by a single association is typically small, only some tens to at maximum some thousands of hectares. Associations are formed by registered villages, and there are 10,500 registered villages in Finland (Sipponen *et al.*, 2006). The number of shareholders in each association is from less than ten to some thousands. Because of the small size of the shareholder associations, a single lake can include tens of small shareholder associations with conflicting interests. This mosaic-like structure of local fisheries management is a substantial problem in Finnish inland fisheries.

The complex, mosaic-like ownership structure has prevented rational, whole watershed level management of fishing waters and especially migratory fishes. The fisheries regions established in the 1980s represented intermediate public, but non-governmental administration that brought together shareholders' associations, recreational fishers and other stakeholders. As this system has also proved somewhat inefficient, even larger fisheries region management units will be established in 2018 – 2019. The number of these regions will then be 100–150 in the whole country. Each region will have to prepare a management plan which will guide the practical decisions of individual shareholders' associations.

The governmental regional fishery administration operates currently in Centres for Economic Development, Transport and the Environment (ELY Centres). The ELY administration discusses actively with shareholders' associations and economic fisheries regions, and regions must get their management plans accepted in the ELY administration. As required by the new fishing law which came into force at the start of 2016, the ELY Centres have established regional co-operative advisory groups having representation from the key national associations, research institutes and old fisheries regions, first to support the formation and then, the operation of the new fisheries region management units.

Shareholders' associations formed regional consulting private Fishery Centres in the 1950s –1980s. Originally Fishery Centres functioned as associations, but many of them have changed their function to company-based businesses with the aim of making some financial profit. Fishery Centres established their operations in private fish farming and transmission of hatchery fish to shareholders' associations, and often in the practical operation of fishery regions. Fishery Centres formed a nation-wide association, the Federation of Finnish Fisheries Associations. In addition, recreational angling clubs have formed a nationwide Finnish Federation for Recreational Fishing that also has local representation in Fisheries Regions.

Overview of Compensatory Efforts

Historically, the Finnish inland fisheries management dogma was to compensate for the overfishing through intensive stockings instead of managing levels of harvest to meet the production capacity of natural stocks. Stocking to running waters with newly hatched fry began as early as the 1920s. Until the 1980s to 1990s, several hundreds of thousands of parr and smolts, and also eggs, fry, and mature hatchery trout, were stocked annually into lakes and inland rivers. The hatcheries of Fishery Centres, of power companies, and of the National Resources Institute Finland, all produce fish for stocking.

Brown trout is still one of the most important species in stocking according to the economic value in inland waters. The great majority of trout individuals living in lakes are currently of hatchery origin, i.e. emerged and raised in hatcheries and subsequently stocked (or released) into lakes and rivers. Even in the Kymijoki watershed, around 95% of trout in lakes are of hatchery origin, and not more than 5% are wild, i.e. emerged from natural redds made by spawners (Valkeajärvi *et al.*, 2013). Also in Lake Inari, the proportion on hatchery individuals rose to 65–88% in lake catch in 2004–2010 (Niva *et al.*, 2015). The Tuulomajoki watershed is now the only notable watershed for adfluvial trout, where all fish are wild and no stocking takes place.

The marking of hatchery-origin trout by adipose fin clipping begun in the Kymijoki watershed in 2005, and the practice spread to other watersheds and to some coastal areas of the Baltic Sea in the 2010s. The recent fishery legislation requires adipose fin clipping for stocked fish of one-year old or older from 2017 onwards. So, fishermen can increasingly distinguish caught stocked trout from wild ones when fishing. This is likely to decrease the bycatch mortality of wild individuals in rod fisheries but not alter the situation significantly in gillnet fishing. In lake fishing, the first recommendations to release wild fish were included in the management plans of some fisheries regions in the 2010s. But of course, wild trout tangled in gillnets as by-catch typically die quickly, and only a small proportion of gillnetted and released trout recovers and survives (see Buchanan *et al.*, 2002; Ng *et al.*, 2015). The release of wild trout gradually became a routine rule in most southern rivers only after 2005.

Following strong public pressure from non-governmental organizations (NGOs), the length limit of southern brown trout, wild and stocked, was increased from 400 mm to 600 mm by a national statute of the Ministry of Agriculture and Forestry in 2014. The new fishery legislation imposes the protection of wild individuals in Southern Finland. However, the legislation does still not include any bag limits for stocked trout or wild trout in the north in lake fishing. Historically, there was practically no limit for the number of gillnets per recreational fisherman, but in the 2016 fishing law, the total length limit of gillnets is 240 meters per boat or household, which is still very high by international comparisons.

Most often, the license for a 30 m long gillnet costs 2–3 euros for a calendar year, and there is no demand to report the fishing effort or catch. River mouths, lake outlets and straits in lakes have only small or non-existent areas with fishing restrictions. Therefore, the bycatch mortality of wild trout will likely not decrease enough to allow the stocks to recover in the near future without strong local actions.

Extensive Stocking Programs

The first experimental stocking of newly hatched and one-summer-old brown trout had taken place already in 1892 (Brofelt, 1920). In the first trout hatcheries, spawners caught in various watercourses within a region were mixed with each other as early as the 1920s. Thus, the original locally adapted and likely genetically distinct stocks were lost and mixed with the stocked fish within the watersheds, or in some cases even among the watersheds. Since then, stocking of brown trout continued mainly with eyed eggs and newly hatched alevins into streams until the 1950s (Halme & Strandman, 1967).

Stocking of 2–3-year-old juveniles has been the most commonly used method in the management of freshwater brown trout stocks in Finland. In the 1960s and 1970s, with the development of the hatcheries, older and larger hatchery fish could be reared. As larger fish were assumed to survive better and produce a better stocking result, the practice changed to favour stocking of 2–3-year-old trout directly into lakes, rivers and manmade reservoirs. In the 1990s more than one million individual brown trout ≥2-year-old were released per year (Vehanen, 1998) (Figure 28.3).

Currently, the hatcheries run by the Natural Resources Institute Finland maintain 12 vulnerable and\or important adfluvial brown trout brood stocks from five watersheds; Kymijoki, Vuoksi, Oulujoki, Oulankajoki and Paatsjoki (http://www.rktl.fi/vesiviljely/viljeltavat_kalat/tuotantolajit_kannat/). The main task of the state hatchery program is to maintain the adfluvial stocks that generally do not reproduce naturally. After the restoration of migration routes and reproduction areas it may be possible to restore, at least partially, the natural reproduction in their native areas. Hatchery stocks have relied on completely hatchery-maintained broodstocks since the 1990s, as only a very few spawners returning from lake migration could be caught to hatcheries in the Kymijoki and Vuoksi watersheds. Nevertheless, the hatchery brood stocks have been renewed occasionally by collecting wild parr from the rivers and growing them to maturity in hatcheries.

At present, freshwater brown trout stocking in Finland can be divided to four general categories. They are (1) stocking for mitigation; (2) stocking for enhancement; (3) stocking for restoration; and (4) creation of fisheries (The Salmon Advisory Committee, 1991; Cowx, 1994).

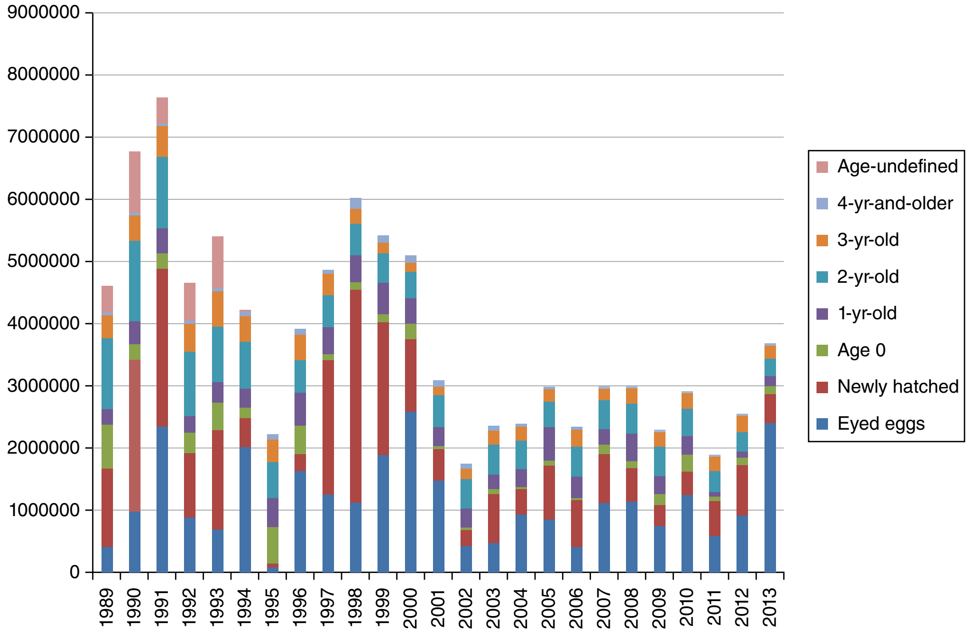

Figure 28.3 Total numbers of brown trout stocked into Finnish inland waters in 1989–2013 (data Pekka Korhonen, Natural Resources Institute Finland).

Stocking for mitigation is carried out in lakes and river reservoirs where the nursery areas have been lost due to migration barriers and habitat degradation. Mitigation stocking is a usually done for compensation for the flow regulation and constructions or other actions weakening the stocks (Vehanen, 1998). In Finland, the environmental policy follows the ‘pollutor pays’ principle, and mitigations are thereby funded and organized by hydropower, forestry or waste management companies. The number of fish and their sizes used for compensation are typically set by the court of law.

Enhancement stocking is carried out to supplement an existing stock where parr or smolt production is less than the lake or river can sustain, and the factor limiting the production cannot be identified. It is very common to compensate for a weak natural trout population in Finnish rivers by releasing hatchery fish. Typically, fish are released as eyed eggs or as up to 2-year-old parr. Enhancement (to increase fishable biomass, not spawning biomass) stocking is also done by stocking 2–3-year-old smolts directly to their feeding areas in lakes and reservoirs (Vehanen, 1998).

Stocking for restoration is carried out when the factor limiting production is removed, and the vanished or weakened stock is to be restored using eyed eggs, parr or mature brood fish. Characteristic examples could be the brown trout nursery and spawning areas that are blocked behind migration barriers.

Fisheries in lakes and reservoirs are created and maintained by lake stocking of hatchery smolts typically of 2–3 years old. Moreover, in many rivers and small lakes, the intensive rod fishery is maintained by stocking of 4–6 years old trout (400–600 mm in length), aimed to be caught within the same season. However, there are no statistics about the economic importance of this action in the whole country, and many of the local river fisheries have shifted from stocking brown trout to stocking rainbow trout, *Oncorhynchus mykiss* (Walbaum), due to its cheaper price, lack of length limit, and lesser genetic damage on the original brown trout population (see e.g. Hansen, 2002; or Madeira *et al.*, 2005).

Variable Results from Stocking

Results from monitoring of lake and reservoir stocking of brown trout have been reported since the 1960s based on the tag returns of Carlin-tagged trout groups (Toivonen *et al.*, 1983, 1991; Ahonen, 1993; Valkeajärvi, 1993; Huusko *et al.*, 1994; Makkonen *et al.*, 1996). The main principle in lake stockings has been to maximize the benefits to fisheries, i.e. seeking the highest possible catch as numbers of fish (Vehanen, 1998). Especially in the 1960s and 1970s, this resulted in wide use of regionally non-native brown trout stocks. Therefore, most regional native stocks have been assumed to have become genetically mixed with hatchery stocks. A change to using only trout native to the watershed has been taking place during the past two decades, but is still not required by law or by any formal regulations.

According to the Carlin tag returns, stocking results have been highly variable. There are some success stories, like Lake Inari where stocking of native brown trout has an important role in restoring and mitigating the lake’s brown trout stocks. In general, however, the results have not been satisfactory in biological terms. The average yield from all the tagging groups in the 1960s was less than 100 kg/1000 released fish, and in most areas just some tens of kilograms in the 1970s (Toivonen *et al.*, 1983, 1991). Thus, the mean trout biomass yield caught by fishermen was typically smaller than the total biomass of stocked fish.

However, the proportion of unreported tags was not estimated in these studies. Valkeajärvi (1993) considered that the real catch of originally tagged hatchery trout was 1.5–4 times as much as the yield estimated from tag returns in various cases in the Kymijoki watershed. Even with these corrections, most stockings of tagged trout have produced at maximum a yield that equals the total stocked biomass. Large clearwater lakes in the Kymijoki watershed with abundant vendace stocks gave the best yields of 200–500 kg/1000 trout released. However, later research has revealed that the yields per number of stocked fish have decreased over time also in these most productive areas in the 21st century (Syrjänen *et al.*, 2010).

Why has Stocking not Been More Successful?

One important reason for generally low yields from stocking, and in many cases failure to restore the natural life-cycle of brown trout, is the uncontrolled recreational trolling and subsistence fishing with gillnets. Stocked brown trout typically become entangled in gillnets during the first year after release and before they become sexually mature (Syrjänen *et al.*, 2010, 2011b; see Chapter 28). Of the tag returns for 2-year-old stocked and tagged trout, 80–90% arrives within two years from stocking. Most tag returns for trout stocked as 3-year-old smolts arrive during the stocking year (Syrjänen *et al.*, 2010, see Figure 12.4 in Huusko *et al.*, page 279 of this book).

In addition to problems with fishing, several other reasons have been found to explain the poor stocking results. In lake stocking there are differences between lake-types: lakes with suitable physical characteristics (e.g. water quality, size, depth) and fish community structure (niche for brown trout) give better yields (see Lind, 1978; Vehanen & Aspi, 1996). Stocking results have also been found to fluctuate with the strength of the typical prey fish stocks (Vehanen, 1995; Niva & Julkunen, 1998; Hyvärinen & Huusko, 2006). The number of fish released per area (stocking density) and the size of released fish also affects the stocking result (Vehanen, 1998). Hyvärinen (2004) concluded that the timing of stocking, together with the availability of seasonally varying suitability of prey fish and size-dependent predation played a large role in determining the optimal release window for lake stocked brown trout.

Ecological Impacts of Stocking

Lake-dwelling brown trout is a pelagic predator that can have a significant impact on vendace stocks when vendace stocks are sparse (Koivurinta & Marjomäki, 1995). Thus, the recommended stocking density is typically ca. 0.5 fish ha^{-1} only when vendace is abundant. Hatchery-reared brown trout can also have negative ecological effects on wild trout populations in streams and rivers: they can compete with wild fish and decrease the fitness of wild conspecifics (Vehanen *et al.*, 2009, Huusko & Vehanen, 2011). Thus, the ecological impacts of stockings should be considered before releases are made.

Ways to Improve Stocking Results

Salmonid juveniles from plain hatchery environments have shown lower survival compared with wild conspecifics when released to a complex natural environment (Weiss & Schmutz, 1999; Hyvärinen & Rodewald, 2013). Enriched rearing methods, i.e. providing a more variable rearing environment in the hatchery, improve the ability of hatchery trout to learn to forage on live prey (Brown *et al.*, 2003) and to survive in the natural environment (Rodewald *et al.*, 2011; Hyvärinen & Rodewald, 2013; Härkönen *et al.*, 2014), but these methods have not yet been taken into general practice in private hatcheries.

Importance of the Development Stage of Stocked Fish

The densities created by stocking 1–3-year-old fish, newly hatched brown trout larvae or eggs, have varied widely. The main reasons put forward are the habitat quality in the river basin, sedimentation rate, droughts and floods increased by forest and bog ditching, nutrient loading from the watershed (Mäki-Petäys *et al.*, 1999; Sutela & Vehanen, 2010; Louhi *et al.*, 2011, see Restoration of Rivers for Migratory Fish in this chapter), and the genetic quality of the stocked fish.

In the beginning of the 21st century the numbers of stocked brown trout have declined, and in recent years the use of eyed eggs for stocking into rivers has again increased (Figure 28.3). There are two main reasons for these trends: firstly, the results from lake stockings have been relatively poor, and secondly, there has been a change in the national management strategy from fish stocking to actions to restore the natural reproduction of salmonid fishes (e.g. Ministry of Agriculture and Forestry, 2012).

Stocking eyed-eggs to suitable areas has been a method to mitigate, enhance and restore brown trout stocks during the juvenile period in flowing waters. Syrjänen *et al.* (2008) used incubation experiments to determine the egg-to-fry survival in two lake-outlet streams in the Kymijoki watershed. The survival of embryos and hatched alevins was overall very high, from 83 to 98% until mid-April, probably because of the good water quality and high oxygen concentration of these near-natural rivers.

Niva *et al.* (2012) released eyed eggs marked with Alizarin Red dye above the bottom gravel in 2008–2011 in nine tributaries of the northern rivers Ivalojoki and Juutuanjoki, flowing into Lake Inari, with a stocking volume of 1–12 liters per tributary. Like Syrjänen (2008), they also reported good results in these near pristine rivers: in electrofishing the densities of one-summer-old brown trout were more than double in the supplemented areas compared to the average density of wild brown trout in the area (Niva *et al.*, 2012). However, in sites where the density of wild juveniles was high, results from stocking of eyed eggs was poor, indicating competition or predation by the wild parr.

In contrast, the results of incubation experiments have been poor in human-altered and polluted environments. For example, Laine *et al.* (2001) reported a survival rate of brown trout eggs of only 0.2 to 9.0% in three northern Finnish streams influenced by peatland drainage. The high mortality of incubating eggs in small streams, even close to 80%, has also been linked to low winter discharge levels caused by intensive drainage of watersheds for forestry purposes (Louhi *et al.*, 2010). In the Vuoksi watershed, Korsu *et al.* (2003) reported a survival rate of 57% for brown trout eggs in a slightly acidic stream (lowest pH 5.7), but only 11 and 27% in two highly acidic streams (pH 4.8 and

5.0, respectively). Syrjänen *et al.* (2015) found only a low to moderate impact of egg-stocking in 17 rivers situated in the Kymijoki, Vuoksi and Kokemäenjoki watersheds, due to stock-related (large variation in total parr density between years), method-related (placing egg boxes and egg pockets in unsuitable microhabitats), and other extrinsic factors leading to high mortality.

In conclusion, stocking eyed-eggs is a potential method for restoring brown trout populations in pristine environments provided that stocking is done by experienced personnel who can find suitable microhabitats for the egg boxes or pockets. When the environment does not support early development of larvae, stocking of older parr and smolts usually proves the most efficient way to support the stock.

Restoration of Rivers for Migratory Fish

The most radical exploitation of Finnish rivers took place between 1850 and 1970 when a great majority of rivers and streams were channelized to facilitate water transport of timber. At its maximum, the total length of dredged channels in Finland amounted to approximately 20 000 km, of which 13 000 km were still in use by the 1950s (Lammassaari, 1990). Timber floating had ceased by the end of the 1980s, and legislation imposing restoration on channelized rivers and streams was soon established. Following this, intensive restoration programs have been initiated in all parts of the country to return the degraded streams closer to their pre-channelization state.

Methods and Results from the Past Three Decades

As elsewhere in Fennoscandia, habitat restoration in Finland has mostly been motivated by the enhancement of recreational fisheries through the provision of better living conditions for migratory fish, especially brown trout. Fisheries management has a more than 30-year tradition of adding boulders (largest diameter 50–150 cm) into the river bed, constructing in-stream structures, such as weirs, flow deflectors, boulder dams, and adding spawning gravel into streams (Yrjänä, 1998; Nilsson *et al.*, 2005). The construction work in large streams and rivers as well as the re-opening of side channels are usually conducted using excavators. Until very recently, the installation of large wood was rarely used as a restoration measure, although it is a common practice in many other parts of the world (e.g. Hunter, 1991; Lisle, 2002). This is likely the major shortcoming of early restoration measures, as headwater streams in northern Fennoscandia are almost devoid of large woody debris (LWD) due to a history of intensive forestry. Manual addition of LWD would compensate for the lack of mature riparian forests (e.g. Lazdinis & Angelstam, 2005).

Otherwise, the measures commonly used in river restoration are known to be highly effective at enhancing streambed complexity and decreasing flow velocity (Muotka & Syrjänen, 2007; Gardeström *et al.*, 2013), thus potentially increasing the availability of habitat for juvenile salmonids (Koljonen *et al.*, 2013). Nevertheless, the biotic responses have been weak or completely lacking for most species groups including brown trout (reviewed in Nilsson *et al.*, 2015). Vehanen *et al.* (2010) reported no detectable benefits of in-stream restoration for age 0 and 1 trout, including both wild and stocked fish, but the density of age 2 and older fish increased slightly in three years. The study was based on monitoring fish densities in six boreal streams each of which had three differently treated stream sections: (i) restored with boulders; (ii) restored with boulders and LWD; and (iii) channelized (no added structures). Monitoring was carried out for three years before restoration treatments and for three years afterwards. Importantly, the authors highlighted the importance of added LWD-structures in creating critically needed refuges against drought in relation to the extreme weather conditions which boreal streams are likely to face with increasing frequency according to climate change scenarios (see Kämäri *et al.*, 2015).

At present, the monitoring of fish densities in all the study sites of Vehanen *et al.* (2010) has continued for 12 years after the restorations, and the restoration structures have had a slight positive effect on the abundance of all age classes of brown trout (Louhi *et al.*, 2016). The strongest impact was seen in the densities of 2-year-old and older fish in LWD-restored sections, highlighting the urgent need for LWD-measures to be included in future restorations. Moreover, trout densities were low even after over 10 years of post-monitoring; e.g. the mean density of age 1 trout, including both wild and stocked fish, even in LWD-restored sections was still only 3.0 fish 100 m^{-2}, indicating that positive outcomes are not easy to achieve by restoring the channels alone. Selected actions should also be carried out in the catchment area.

Stocking of young salmonids is a common fisheries management action integrated into restoration projects in Finland, which aims to enhance the recovery of salmonid populations in streams with initially low population size. Luhta *et al.* (2012) monitored the densities of age 1 and older trout in four pre-restored, four under-management, 10 post-management, and three reference streams during 2000–2005. The measures included the combination of typical in-stream restoration measures (described above), and a 5-year stocking programme with 1-year-old brown trout. The constant annual stocking density was 6 individuals per 100 m^{-2}, which is well within the lower end of the range of densities reported in Finnish streams (Korsu *et al.*, 2007). The trout densities were significantly higher in post- than in pre-management streams indicating population establishment. However, the absolute juvenile trout density in post-management streams was significantly lower than in the near-pristine reference streams. Furthermore, the success of re-building managed brown trout population varied, indicating stream-specific responses to management measures. Based on the results and population genetic considerations, stocking should be used along with restoration programs only when wild brood fish are completely absent.

Role of Restoration Now and in the Future

The new Strategy for Restoration of Waters was launched by the Finnish Ministry of the Environment in 2013 (Olin, 2013), and presents the measures and means for promoting restoration of waters in improving ecological and chemical status of waters to be used hence forwards. According to the Strategy, restoration measures are seen as a way to contribute to the achievement of a good ecological status for water bodies as required by the EU Water Framework Directive (WFD).

At present, however, restoration projects typically aim to increase both the availability of in-stream fish habitat and its heterogeneity, and their objectives are not sufficiently integrated with other ecosystem-based management targets. For example, Finnish river basins are intensively used for forestry, agriculture and peat mining purposes, and aquatic ecosystems are facing loadings of particulate organic matter, fine sand and nutrients. The national legislation imposes the best suitable water protection methods, such as overland flow areas, sedimentation pits, or plugging the old forest ditches of the forest drainage network, to be used in the context of land-use changes. However, the methods applied vary across sites and the effects on aquatic ecosystems have not yet been evaluated. Therefore, future restoration projects should be closely linked with actions in river basins to mitigate the detrimental effects of land-use induced disturbance on aquatic ecosystems.

As in other countries (Bernhardt *et al.*, 2007), the ecological monitoring of restoration projects is rarely done in Finland, and if such monitoring exists the resultant data are not always stored in common databases available for nationwide management or research purposes. Due to the lack of adequate monitoring, no wider consensus of the effectiveness of restorations on brown trout or other fish populations exists. Nevertheless, stream restoration in its present form has a strong public acceptance in Finland, mainly because it is considered beneficial for commercially important fish, ecotourism, and the well-being of local people (Olkio & Eloranta, 2007; Marttila *et al.*, 2016). Thus, numerous restoration projects are currently underway in Finland, and many more are expected.

A Simple Population Model as a Tool to Evaluate Alternative Management Scenarios

In order to evaluate the current fisheries management practices and to build scenarios for potential sustainable future catches with improved management, two important wild adfluvial brown trout stocks, the Rautalampi watercourse stock in the Kymijoki watershed and the River Oulankajoki stock in North-East Finland/Russia were modeled as examples.

The Rautalampi watercourse includes a series of lakes and connecting rapids and river sections that discharge into Lake Päijänne (Valkeajärvi *et al.*, 1997). Both rod (mainly trolling) and gillnet fishing are allowed in lake areas without any effective restrictions on total effort. The management was based on a 400 mm minimum size limit until 1.1.2014, when the minimum size limit was increased to 600 mm. However, on 1.1.2016 the minimum size limit of stocked brown trout with clipped adipose fins was decreased to 500 mm. A recommendation to release all wild trout had been applied since the early 2000s, but since 1.1.2016 the wild brown trout have been protected by law south from 64°00 N. Fishing in some of the exclusively rented privately-owned rapids (e.g. Äyskoski, Siikakoski, Karinkoski, Kellankoski) is currently based on obligatory catch-and-release while in other rapids different combinations of bag limits and size limits are in use for stocked fish. In addition to the releases of large fish for the purpose of put-and-take fisheries, intensive stocking of 1–3-year-old parr and smolts is used to compensate for the high fishing mortality occurring mainly in the feeding areas.

The River Oulankajoki stock includes three sub-stocks of the Finnish rivers Kuusinkijoki, Oulankajoki and Kitkajoki and all small tributaries that discharge into these rivers, but for simplicity these stocks were modeled as one. All the stocks mix during their feeding migration to Lake Pääjärvi in Russia and during the early spawning migration into the River Oulankajoki. There is intensive angling in the rivers, but in Lake Pääjärvi only very restricted professional fishing occurs legally. The minimum size limit in the River Oulankajoki system is 600 mm everywhere (total length in Finland, standard length in Russia). In Finnish rivers there is a daily bag limit of one trout and an annual bag limit of five trout. In addition, brown trout has been completely protected in the upper River Oulankajoki since 2015. Parr are stocked into the River Kuusinkijoki, but their contribution to the spawning stock is small.

Model Description and Parameterization

A stochastic, age-structured population model was used to simulate the population dynamics of brown trout in discrete time with annual updates under different harvesting scenarios. Individual growth was based on density-dependent adjustment of Von Bertalanffy -type growth (Jenkins *et al.*, 1999). The maximum age considered was 15 years, as the maximum lifespan of piscivorous brown trout in harvested populations is typically ca. 12 years (Johnsson *et al.*, 1999). For simplicity, recruitment of trout to the end of age 0 was modeled using Beverton–Holt-type recruitment (Beverton & Holt, 1957) that is based on the ecologically feasible idea of finite reproduction areas. The populations were modeled without any supportive stocking to examine their natural production capacity.

The seasonal order of events was (1) all mortality; (2) growth; (3) reproduction. Thus, N_t (see below) corresponds to the population size at the end of the year. The model corresponds structurally to Leslie-matrix models and as such to earlier models built for brown trout (Gouraud *et al.*, 2001). In order to add ecological realism to the otherwise age-structured model, some key biological functions depend on fish size at a given age (at the end of the year). All the parameters of the model are presented in Table 28.1.

Number of individuals at age $a+1$ at year $t+1$ is described by:

$$N_{a+1,t+1} = e^{-Z_a} N_{a,t} \tag{1}$$

where the total instantaneous mortality rate Z_a is defined as the sum of natural mortality M_a and fishing mortality F. Natural mortality was age-dependent to capture the higher mortality rate during the parr and smolt migration phase in comparison to the lake phase, but for simplicity the fishing mortality was assumed to depend only on the size of the fish:

$$Z_a = M_a + f_a F, \tag{2}$$

where $f_{p,a}$ is the proportion of fish recruited to fishing at age a (in year t), and defined for fish at age a as:

$$f_{a,t} = \frac{1}{1+e^{-(l_{a,t}-l_{min})/l_{var}}} \tag{3}$$

where $l_{a,t}$ is the total length of fish in the end of the year t and at age a, and l_{min} is the minimum size limit and l_{var} the variation over minimum size in recruitment to fishing.

Table 28.1 All parameters and their source of origin in the order of appearance in the text. *Different values were used for parr: River Oulankajoki: $L_\infty = 713.7$ mm, $k = 0.099$, $t_0 = -1.093$; Rautalampi watercourse: $L_\infty = 1071.1$ mm, $k = 0.0866$, $t_0 = -0.873$.

Parameter name	**Symbol**	**Value, Oulanka stock**	**Value, Rautalampi stock**	**Source**
Natural mortality, parr	M_{1-3}	0.68	0.47	Literature/electrofishing
Natural mortality, migrating smolts	M_4	1.4	1.0	Assumed based on literature
Natural mortality, adults	M_{5-15}	0.4	0.19	Assumed based on environmental characterististics
Fishing mortality rate	F	0.5	3.0	Mark-recapture data
Minimum size limit	l_{min}	600 mm	400 mm	Fishing regulations
Variation over minimum size limit	l_{var}	50 mm	50 mm	Approximated based on the gillnet mesh sizes used
Von Bertalanffy's asymptotic size*	L_∞	855 mm	734 mm	Individual catch data
Von Bertalanffy's growth constant*	k	0.238	0.246	Individual catch data
Von Bertalanffy's zero time size*	t_0	1.84	0.270	Individual catch data
Intake capacity, constant	c_0	1	1	Choice makes no difference
Intake capacity, exponent	c_1	0.76	0.76	Elliott 1976
Allometry constant, slope, g mm^{-1}	μ_0	0.00000151	0.0000118	Individual catch data
Allometry constant, exponent	μ_1	3.32	2.99	Individual catch data
Functional response, smoother	υ_o	100	100	Set to reduce growth variation to ca. 10%.
Annual food availability	C_{max}	Variable	Variable	Found by matching the growth rate between the data and the model
Egg to 0-y parr survival	φ	0.053	0.03	Literature/electrofishing data
Proportion of females	κ	0.67	0.61	Catch data
Proportion of mature individuals spawning	λ	0.5	0.5	Mark–recapture data
L_{50}-value	l_{mat}	551.9 mm	560 mm	Individual catch data, literature
Variation in L_{50}	l_{mvar}	39 mm	39 mm	Individual data
Fecundity, slope	α_1	1.3 g^{-1}	1.364 g^{-1}	Literature
Beverton-Holt carrying capacity	β_0	400000	12000	Estimation based on total suitable habitat area and observed parr densities
Beverton-Holt constant	β_1	400000	12000	Set initially for maximal value giving 100% survival

Lobón-Cerviá *et al.* (2012) estimated that the average daily mortality rate of 2–3 year-old riverine brown trout in two distinct populations was 0.0031 day^{-1} which corresponds to an instantaneous natural mortality rate of 1.13 y^{-1}. Electrofishing data from the Oulanka system did not support such high mortality, and parr mortality in the River Oulankajoki model was assumed to be 50% annually (Table 28.1).

The average smoltification age for brown trout in both the Rautalampi and Oulanka stocks was estimated to be 3.5 years. No direct data on smolt survival during downward migration and the first months in the lake were available, but given reports of very high mortality of hatchery-reared salmonid smolts (c.f. Kekäläinen *et al.*, 2008) we assumed an additional 50% mortality to occur at age 4 (Table 28.1). According to Carlson *et al.* (2008), the monthly survival of 4-year-old brown trout could be as low as 92% corresponding to an annual natural mortality rate of 1.0 y^{-1}. In contrast, Brown (2004) estimated that annual natural mortality rate of brown trout in an Australian river was 0.44 y^{-1}. Because the lake environment is assumed to be relatively safe for a large brown trout while spawning migrations are risky, we assumed $M = 0.4$ y^{-1} for fish at ages 5–15 years.

Brown trout were assumed to grow according to von Bertalanffy's growth function multiplied by a variable C_p accounting for density-dependence in growth. The growth function giving the length-at-age l_a is

$$l_a = L_\infty \left[1 - e^{(-(k(a-t_0)))}\right] C_{p,t-1}. \tag{4}$$

In equation 4 L_∞ is the asymptotic length of fish (mm), k the growth factor and t_0 the time when the fish is 0 mm long. The age sub-index is not shown in the equation, but we used different parameters L_∞, k and t_0 for parr (trout of 0–3 in age) and for older trout (4 years and older, see Table 28.1). Von Bertalanffy parameters were estimated using the FSA-package in R 3.2.0 (The R Foundation for Statistical Computing). The River Oulankajoki parr growth data (N = 1066) were based on back-calculated lengths (with −1 correction for age) of ascending brown trout captured by fish traps in Vartiolampi in the River Oulankajoki. For the Rautalampi watercourse, parr growth rate was estimated using parr samples electrofished from six smaller rivers (Könkköjoki, Arvaja, Saajoki, Tarhianjoki, Multianjoki and Koivujoki) in the Kymijoki watershed (N = 882 individuals). The growth rate of 4-year-old and older River Oulankajoki trout was estimated from a sample of fish captured both in the Lake Pääjärvi and in the River Oulankajoki (see Table 12.3 in Huusko *et al.*, page 282 in this book). For the Rautalampi model, we used recapture data from Carlin-tagged stocked fish (N = 1758 recaptures in 1990–2009).

In order to calculate the growth factor C_p, the total metabolic scope C_{tot} of the population at year t was calculated as:

$$C_{tot,t} = \sum_{a=0}^{15} c_0 m(l)^{c_1} N_t, \tag{5}$$

where c_0 and c_1 are the constants defining food intake allometry and $m(l)$ is the mass of individual as defined by its length:

$$m(l) = \mu_0 l^{\mu_1} \tag{6}$$

where constants μ_0 and μ_1 define the allometry between body length and mass. These were estimated using a non-linear regression (N = 618 for the River Oulankajoki and N = 1503 for the Rautalampi watercourse). The realized growth variable $C_{p,t}$ at year t is calculated using the linear Holling Type 1 functional response with a dampening function that reduces the realized impact of food availability variation on growth:

$$C_{p,t} = \frac{(\upsilon_0 - 1) + \frac{C_{max}}{C_{tot,t}}}{\upsilon_0}, \tag{7}$$

where υ_0 is the functional response constant defining how steeply the growth rate responds to changes in food availability and to C_{max}, i.e. annually available resource amount. Dampening the direct linear function response was necessary because otherwise heavy harvesting would have translated to unrealistically fast individual growth rate among the few surviving individuals.

The total number of offspring produced by the population, S_t, is calculated as:

$$S_t = \varphi \kappa \lambda \sum_{a=0}^{15} o_a g_a N_{a,t}, \tag{8}$$

where φ is the survival of eggs to 0-year-old parr (to the end of the first year), κ is the proportion of females, λ the proportion of mature individuals spawning annually (without correction for the first spawning), o_a the proportion of mature individuals at age a, g_a the fecundity of individuals at age a and $N_{a,t}$ the number of individuals in the age class a at year t. According to Keränen *et al.* (1974), 1.7% of eggs survive to 1-year-old (from emergence) parr and 0.4% of eggs survive to smolt phase in the Oulanka system. We further adjusted the parameter φ based on the electrofishing records to yield an average density for ca. 7 0-year-old individuals of $100\,\mathrm{m}^{-2}$ in the total area available for reproduction (approximated to be 125 ha) in the Oulanka model. For the Rautalampi watercourse trout, 3% egg survival to the end of the first year was assumed.

The proportion of mature individuals at age a depends on the length-at-age as:

$$o_a(l_a) = \frac{1}{1 + e^{-(l_a - l_{mat})/l_{mvar}}}. \tag{9}$$

In equation 9, l_{mat} is the L_{50} (size at which 50% of individuals are mature) and l_{mvar} the variation around the maturation size. L_{mat} for the River Oulankajoki stock was estimated using logistic regression explaining maturity with length (N = 618). L_{mvar} was estimated visually by matching the steepness of the estimated logit function and the observed frequency of mature individuals in the model in the initial conditions.

The fecundity of an individual at body mass m is defined as:

$$g(m) = \alpha_1 m, \tag{10}$$

where α_1 is the slope to define how realized fecundity changes with body mass (eggs g^{-1}). The total recruitment to year $t + 1$ is then defined by:

$$N_{0,t+1} = \frac{\beta_0 S_t}{\beta_1 + S_t} \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(x-1)^2}{2\sigma^2}}, \tag{11}$$

when positive but otherwise zero, and where the Beverton-Holt constant β_0 defines the total carrying capacity of the environment for 0-year-old parr (from the emergence), estimated using information on the total availability suitable spawning and parr habitat and first summer mortality in the respective system. The β_0 in the River Oulankajoki was assumed to be 400 000 (32 individuals $100\,\mathrm{m}^{-2}$). x is derived randomly by MS Excel and the variance σ was set to 0.1.

Fisheries catch at age a at year $t+1$ is derived by Baranov's catch equation:

$$C_{a,t+1} = \frac{f_{a,t}F}{Z_a}\left(1 - \mathrm{e}^{-(M_a + f_{a,t}F)} N_{a,t}\right). \tag{12}$$

The river catch is estimated by Equation 12 by replacing $N_{a,t}$ with $N_{a,t}o_a\lambda$, *i.e.* with the numbers of individuals on their spawning run annually. The total catch per year (as well as the river catch) is obtained by summing age-specific catches:

$$C_t = \sum_{\mathrm{a}=1}^{15} C_{a,t}. \tag{13}$$

The total yield is obtained by multiplying the annual catches by the average body mass of the captured fish as:

$$Y_t = \sum_{\mathrm{a}=1}^{15} C_{a,t}\,\mu_0 {l_{avg}}^{\mu_1}, \tag{14}$$

where l_{avg} is the average length between ages *a–1* and *a*. Average size of captured fish was calculated by dividing the yield by the catch.

The total stock size is obtained by summing the numbers of individuals at a certain year. The total stock biomass is obtained by summing the products of the age-specific body mass (m_a) and the age-specific number of individuals (N_a), and numbers and total mass of spawners are obtained by multiplying the above mentioned variables by the proportion of mature (o_a) and migrating (λ) fish. All individuals at the age of 15 die for natural reasons without offspring.

Implementation and Analysis

The model was built in Microsoft Excel. First, 1000 individuals were introduced at age 0 and the model was run for 200 years without any fishing mortality ($F=0$, $Z=M$). Within this time the population dynamics reach equilibrium (assessed graphically). Then, the population is harvested for 400 years during which time the population reaches a new population dynamic equilibrium. Finally, the model is run for 100 additional years (with harvesting) that are used to derive the average and standard deviation values for the variables of interest. It should be noted that all values for year $t+1$ are the same as for year t in the equilibrium.

To capture the long-term variation, ten model runs were used to derive the final average and S.D. values (as averages of 100 year average and S.D. values). The population census occurs at the end of the year. The factor setting density-dependence in growth, $C_{p,t+1}$, was set to 1 at the starting conditions by refining the total food availability until the parameter converged.

For 2014, the spawning population size of the River Oulankajoki stock was estimated to be 1173 (no error estimate available) individuals. In 2013, the river catch was 334 individuals (Wendelin *et al.*, 2015). Based on this information, the fishing mortality rate at the starting conditions was assumed to be 0.5 y^{-1}. The fishing mortality at the starting conditions was assumed to be 0.3 y^{-1} for the Rautalampi stock because the approximated current fishing mortality rate, 3.0 y^{-1} did not allow the simulated population to be established.

Model Results and Further Needs for Stock Assessment

Oulanka Stock, Current Status

Assuming the natural mortality rates as specified in the model parameterization (Table 28.1) and $F = 0.5$, the predicted annual total catch was 544 ± 25 fish (average mean ± average S.D. over ten model runs) and the river catch was 217 ± 11 fish. The average size of caught fish was 3059 g ± 36 g, the total stock biomass 14370 kg ± 485 kg (192,230 ± 11,940 individuals) and 3116 ± 821 smolts started growth in Lake Pääjärvi annually. The average density of 0-year-old parr was 7.75 ± 0.8 ind. 100 m^{-2} which corresponded to a survival of 2.05% from egg-to-1-year-old parr, and of 0.13% from egg-to-smolt. The total spawning run consisted of 1040 ± 51 individuals. The assumed fishing mortality of 0.5 $year^{-1}$ led to growth overfishing, and $F = 0.3^{-1}$ would maximize the biomass yield (Figure 28.4A).

Oulanka Stock, Potential Improvements for Management

Decreasing the minimum size limit to 500 mm would decrease catches by at least 10% and increase the risk of recruitment overfishing at F values ≥ 0.2. Increasing the minimum size limit to 700 mm would decrease the risk of recruitment overfishing and slightly improve yield at current and higher than current fishing mortality rates. Stopping fishing completely would result in an increased spawning run size of 3922 ± 146 individuals and an increased number of surviving smolts of 7760 ± 1945 individuals $year^{-1}$.

The model is very sensitive to changes in egg survival, and an improvement in environmental conditions so that egg survival (until the end of the first year) increased to 10% would have dramatic effects on the yield (Figure 28.4A). In conclusion, the model shows that the Oulanka brown trout stock is very sensitive to environmental drivers but also to overfishing, and its management should ensure that the annual instantaneous fishing mortality rate does not exceed 0.4 y^{-1} (1/3 of the number of fish). Similarly, actions that reduce fishing-induced and natural mortality of parr, smolts and undersized individuals are expected to a have strong positive impact on both the catches and the spawning population.

To verify the model parameters and the predicted outcomes would require assessment of the actual total smolt run size and experimental evaluation of the strength of density-dependence in egg to parr survival (stock–recruitment relationship). Information about the number of descending smolts could help to disentangle the sources of mortality of immature fish, and as such determine the true potential maximum sustainable catch. The main message of the model is clear: the optimal fishing mortality rate lies between 0.2 and 0.4, which would require a decrease from the current

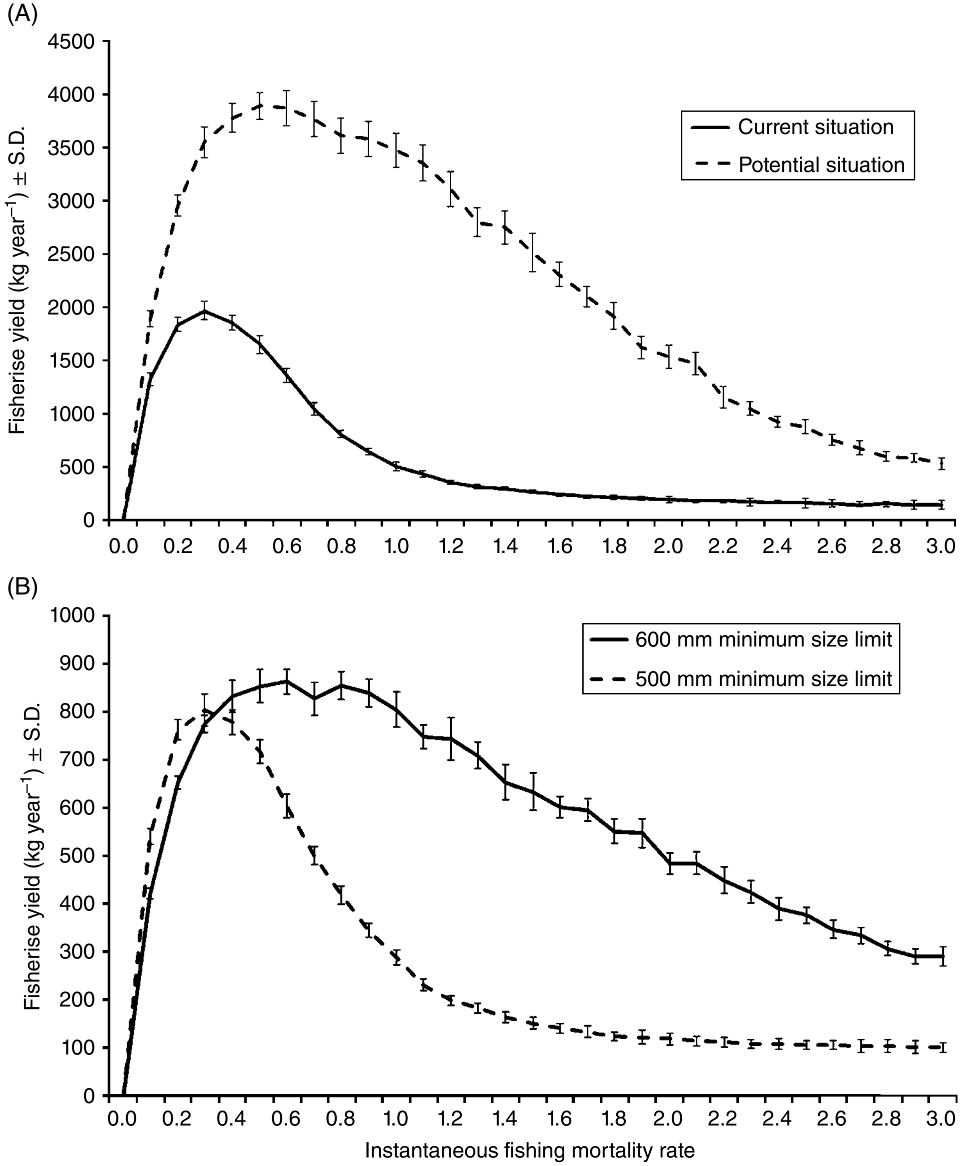

Figure 28.4 (A) Modeled total fisheries yields from the River Oulankajoki brown trout stocks as a function of annual instantaneous fishing mortality rate (equal for mature fish in the rivers and immature fish in the feeding areas) assuming two different scenarios for egg to parr survival (5.3% as the current situation and 10% as a potential situation). In both scenarios a minimum size limit of 600 mm was applied. (B) Modeled fisheries yield from the Rautalampi watercourse brown trout stock as a function of annual instantaneous fishing mortality rate (equal for mature fish in the rivers and immature fish in the feeding areas) with 500 mm and 600 mm minimum size limit. The initial growth conditions were set with $F = 0.3$, as only the released density-dependence saves the population from extinction at $F = 3.0\ y^{-1}$ and minimum size limits < 600 mm by increasing growth rates and as such maturation rates.

fishing pressure. Any further increase in fishing mortality leads to a stock decline and reduced catches unless egg-to-smolt survival can be substantially improved through management actions in the spawning and parr habitats.

Rautalampi Stock, Current Status

According to the model, the historical combination of a 400 mm minimum size limit and a fishing mortality rate of 3.0 y^{-1} drives the population to extinction. Correspondingly, the contemporary fisheries catches in lakes are based on stocking, whereas river catches mainly include resident trout. This corresponds well with the observed size of trout redds in the rapids and rivers of the Rautalampi watercourse (Syrjänen *et al.*, 2014a). The average length of redds was significantly smaller in the Rautalampi watercourse and in other rivers and watercourses in the Kymijoki watershed than in the River Oulankajoki, the Heinävesi watercourse, Lake Inari tributaries, or known Swedish spawning rivers of adfluvial brown trout. Syrjänen *et al.* (2014a) concluded that most spawners are probably resident in the Rautalampi watercourse and elsewhere in the Kymijoki watershed.

Rautalampi Stock, Potential Improvements for Management

Assuming a potentially sustainable $F = 0.3$ and a minimum size limit of 600 mm, the Rautalampi stock would be able to recruit naturally. The stock would be able to produce an annual total catch of 280 ± 9 individuals and a river catch of 104 ± 4 individuals (average mean ± S.D. over ten model runs). The catch would correspond to a total yield of 766 kg ± 24 kg with an average size for a captured fish of 2701 g ± 20 g (Figure 28.4B). The total biomass of migrating adults would be 1,933 kg ± 62 kg and the total population size 25 023 ± 1,203 fish. The annual number of smolts surviving until the feeding migration would be 849 ± 154, and the spawning run would consist of 770 ± 29 individuals.

Given the current approximated instantaneous fishing mortality rate of 3 y^{-1}, the current level of gillnet fishing and the minimum size limit of 500 mm imposed from 1.1.2016, the wild brown trout stock is not expected to recover. Only 10 ± 1 fish are expected to spawn annually and produce a total (bycatch) yield of 101.2 kg ± 12.7 kg. The total population would consist of 1048 ± 107 individuals of which the majority would be parr, as only 28 ± 14 smolts would be expected to start lake feeding annually.

If the minimum size limit in gillnet fishing was also 600 mm, fishing would be sustainable even at the current level with zero bycatches of undersized individuals ($F = 3.0$). However, the maximal fisheries yield would be obtained with a drastically reduced fishing mortality rate of $F = 0.3$ (Figure 28.4B). In order to ensure the viability of the wild brown trout stock, the minimum size limit should be at least 600 mm and the instantaneous fishing mortality rate should be kept below 1.0 y^{-1}.

The Key is Adjusting the Fishing Mortality

Despite its relative simplicity, our model was able to capture the basic mechanisms of density-dependence and sources of mortality that regulate population dynamics. Despite the inherent inaccuracies in the model analyzed in annual time steps, the model provides two important insights. First, due to very high and variable natural mortality during the juvenile phase (Elliott, 1993), brown trout populations are sensitive to adverse environmental drivers during the egg and parr stages. Second, due to late maturity, very fast growth and low fecundity, harvesting of migratory brown trout should take place at a large size and at a relatively low rate which would safeguard the necessary numbers of spawners. Due to the fast growth rate of brown trout, there are no biological reasons why stocked fish should have a different minimum size limit than wild trout. Based on the model, the 500 mm size limit imposed from 1.1.2016 has no biological foundations, and actually prevents recovery of the wild stock due to bycatch mortality in the gillnet fishery which is regulated based on the 500 mm minimum size limit.

The model pinpoints the importance of resolving stock-recruitment relationships for migratory brown trout and incorporating environmental drivers such as temperature into them. Lethal summer or winter temperatures, or exceptional flow or food conditions, can have severe impacts on the recruitment of brown trout (Elliott, 1993). Similarly, global climate change will impose long-term threats to populations that already suffer from extreme summer temperatures (Jonsson & Jonsson, 2009).

The most important message from the modeling exercise for the fisheries management is that the wild brown trout stocks do not tolerate the current heavy mortality in Finnish large lakes due to intensive gillnetting and trolling. The model also shows that the capacity of wild brown trout stocks to support significant fisheries catches is very limited: the estimated sustainable catch of the Rautalampi watercourse brown trout stock, only about 280 fish annually, likely comes as a surprise for most local fisheries managers and recreational anglers. However, the Rautalampi watercourse makes up roughly one sixth of the total area of contemporary trout lakes and one fourth of the free rivers in the Kymijoki watershed. Also the maximal smolt production was estimated conservatively (max 958 ± 180 smolts without any fishing corresponding to 12,000 0-year-old parr). Therefore, the potential sustainable catch in the whole Kymijoki watershed could be ca. 2000 fish annually.

The model results do give some hope for the recovery of the wild brown trout stocks. The wild populations can tolerate annual removal of one third of the fish provided there is no bycatch of fish below 600 mm. However, the 600 mm minimum size limit alone, without effort limitations and other measures to reduce bycatch mortality of undersized individuals cannot guarantee recovery of the stocks and sustainable fishing. Unfortunately, the minimum size limit of 500 mm imposed from 1.1.2016 does not support the recovery of the wild Rautalampi watercourse brown trout stock if the bycatch mortality on wild individuals cannot be reduced significantly.

Based on the model scenarios for sustainable fishing, the spawning population should consist of at least 450 migratory individuals in each large river in the River Oulankajoki system (1350 fish in total) and of at least 320 individuals in the Rautalampi watercourse to ensure viable and productive populations; even higher spawner numbers might help to cope with environmental stressors and in the maintenance of genetic diversity. The simple model we built in MS Excel also shows that local fisheries management could easily adopt knowledge-based approaches if such simple models could be taken into practice by educating local fisheries managers.

Conclusions

The adfluvial brown trout will probably remain one of the most important fishes in recreational fishing in Finland during the forthcoming decades despite climate change. The biomass catch of the species will remain low, but the experiences of catching, and often releasing, are likely to maintain a trout as a highly-valued catch by recreational fishermen. The potential economic value of river fishing for brown trout is much higher than is currently obtained, but realizing that potential involves a trade-off with consumptive lake fishing. Given the limited capacity of wild brown trout stocks to produce harvestable fish and the high demand for fish by gillnetting and trolling, supportive stocking will likely continue to be an important management practice in the future.

To enable wild brown trout stocks to recover and to ensure their future, lake fishing methods and fishing culture should change radically to become sustainable, and restoration of small streams with road culverts and other obstacles in their channels should continue at a large scale. In addition, population genetic analyses should be conducted to identify the last original wild populations, especially before any stocking with hatchery material. Field surveys of channel conditions and fish populations in small potential spawning streams could be conducted in the watershed of each large lake. Private water owner organizations clearly should take a stronger role in monitoring the current trout stocks.

One of the greatest current concerns in fisheries is the genetic impact of fishing on harvested stocks. In the watersheds of Kymijoki, and probably of Kokemäenjoki and Vuoksi, most wild trout individuals display resident life history (Syrjänen & Valkeajärvi, 2010; Syrjänen *et al.*, 2014b). Residency might be just an ecological, phenotypically plastic non-genetic response to a low number of spawners and parr (Olsson *et al.*, 2006; Wysujack *et al.*, 2009), or a maternal effect of females mediated by egg hormones to the behavior of their offspring (Burton *et al.*, 2013). In either case, the migratory life-style might be restored by facilitating the recovery of the river-resident subpopulations and/or migratory subpopulations to higher population sizes. However, if the reason is a fishing-induced genetic change in populations and the loss of 'migratory genes' (Thériault *et al.*, 2008; Eldridge *et al.*, 2010), the migratory subpopulations can probably be reestablished only by introducing new gene material from migratory hatchery stocks or from non-native wild migratory stocks. Anyhow, the full recovery of migratory populations will take at least 20 – 30 years, and it will not happen without supportive research projects and strict and rational decisions from fishery administrations.

International comparative studies are needed to relate the management policy and the condition of wild stocks of salmonid fishes in Finland and other countries. The varying aspects of end users, the recreational fishers, and the economic value of rod fishing, should be surveyed at the same time to build socially sustainable fisheries management policies (Beard *et al.*, 2016).

The status of Finnish migratory salmonid stocks is poor among European countries having suitable environments for these species. All salmonid species, including adfluvial brown trout, Arctic char, landlocked Atlantic salmon, sea-migrating brown trout and Baltic salmon, in all watersheds flowing eventually into the Baltic Sea have been or are endangered (Rassi *et al.*, 2010), and the only Finnish fish stock that has ever risen in its conservation status category is the Baltic salmon due to the recovery of River Torniojoki salmon stock as a consequence of tighter international fishing restrictions (Romakkaniemi *et al.*, 2003).

River damming and watershed ditching have weakened the reproduction environments of salmonids, but this has happened in all European countries and most North-American states, to some extent even more intensively than in Finland. The major factor distinguishing Finland from other countries in salmonid management is the very intensive fishing due to the lack of direct controls over fishing effort and the resulting high fishing mortality. Open access to recreational fishing, with the right to use gears and methods that are restricted to commercial fishing in many other countries, is most likely the main reason the remaining migratory wild stocks have been driven practically to extinction. Thus, the recovery of wild stocks of adfluvial brown trout, as well as of other salmonid fishes, depends strongly on the fishing politics and the attitudes of recreational fishers and citizens in the forthcoming decades. In addition, NGOs (see Cooke *et al.*, 2013) working for wild salmonid stocks are still relatively few and lack influence, but their calls for sustainable policies are increasing in volume.

Social awareness of the poor state of wild populations of migratory salmonid fishes has increased in the 2010s. Currently, there is intense public discussion and activity in social media by fisheries, conservation and animal rights oriented NGOs as well as other advocacy groups about the management goals and management policies for salmonids. The discussion focuses mainly on management measures such as minimum size limits, acceptability of catch-and-release in recreational fishing, and building of fishways. The increasing call from the public has already led to new regulations such as the increased minimum size limit at the start of 2014 showing that the social media and public pressure have affected the way recreational fisheries are managed. As recreational fisheries continue their shift from consumption-orientation to more recreation-based orientation, fisheries management should develop simultaneously and also evaluate the monetary values of wild and viable brown trout populations, while ensuring ethical aspects of fishing with necessary novel regulations for catch-and-release fishing. Native salmonids offer considerable potential for the tourism-based bioeconomy, but this potential will not be realized as long as the stocks are valued simply by their biomass yield.

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Brown Trout Management for the 21st Century

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Introduction

The brown trout is uniquely placed to inform freshwater fisheries and river ecosystem management in the 21st century. As a popular sport fish reliant on good water quality and functioning river ecosystems, brown trout enjoys enduring interest from anglers, the public and government agencies. With a native range centred in Europe, it has the longest recorded management history of any freshwater fish (Buckland, 1863; Halford, 1902; Buckland-Nicks *et al.*, 2012). It has a global distribution due to intentional and accidental introductions (MacCrimmon & Marshall, 1968), and is thus managed across a wide range of environmental and socio-political contexts as an iconic component of native biodiversity, a highly valued non-native sport fish, and a harmful invasive species (Varley & Schullery, 1998; McDowall, 2006). Finally, brown trout is one of the best-studied fishes, and is used as a model system for investigating questions spanning the sub-disciplines of ecology (Elliott, 1996; Crisp, 2000; Hendry & Stearns, 2003; Harris & Milner, 2007).

Brown trout management has traditionally been species and angling centric. Fisheries managers adjust harvest regulations, impose gear restrictions, and modify stocking programmes in an effort to maximise the socioeconomic value of trout fisheries. While we address these three traditional management issues, our goal is to advance beyond this historic view by framing brown trout management in a broader ecological and socio-political context. This goal is motivated by a number of developments. First, government agencies and non-governmental organisations (NGOs) increasingly manage trout as components of biological communities embedded in wider aquatic ecosystems (Convention on Biological Diversity, 1992; Water Framework Directive, 2000). Second, salmonid and river ecosystem management are closely linked, conceptually and operationally. Third, there has been a cultural shift among trout managers and anglers away from stocked, harvest fisheries to wild, catch-release fisheries.

Brown Trout: Biology, Ecology and Management, First Edition. Edited by Javier Lobón-Cerviá and Nuria Sanz.

For these reasons, trout management in the 21st century will be more about navigating socio-political institutions to protect and restore river ecosystems than manipulating trout populations through harvest and stocking.

We proceed with four goals. We begin by developing a graphically distilled conceptual framework for 21st century trout management. We do this by constructing three 'management filters': river ecosystem processes, trout biology and socio-political factors. Together, these filters summarise how management interventions are identified, prioritised, constrained and delivered across spatiotemporal scales. We next consider these management filters alongside contemporary approaches to river catchment management (Roni *et al.*, 2008; Beechie *et al.*, 2010; Roni *et al.*, 2013a; Roni *et al.*, 2013b). We then briefly consider harvest regulations, gear restrictions and stocking in the context of the management filters. Finally, we use text boxes to highlight issues, case studies and recommendations central to trout management in the 21st century. Given the size of the relevant literatures, we make no attempt to exhaustively reference the topics covered. While we focus on wild riverine brown (and sea) trout in its native European range, because the challenges of trout management transcend taxonomic and geographic boundaries, we draw freely from the literatures on other species and regions. Our views on trout management are inevitable shaped by our collective experience in (mostly) the United Kingdom and United States. We endeavour, however, to overcome any taxonomic, geographical and cultural biases to provide a framework that will benefit wild trout management everywhere.

Trout Management Filters

There are practical and conceptual reasons for developing graphical trout management filters. Despite the value of interdisciplinary catchment assessments (Steel *et al.*, 2004; Bartz *et al.*, 2006; Roni & Beechie, 2013), in practice most management interventions are delivered without the benefit of such exhaustive analyses. This is particularly true where angling groups and NGOs are actively involved in trout and catchment management. There is thus a need to distil the key elements of formal catchment assessments into a broadly applicable trout management framework. Doing this by constructing management filters is motivated by Benda *et al.*'s (2002) recipe for avoiding 'train wrecks' in catchment management. They argue for an effective collaboration between scientists from at least three disciplines: surface water hydrology, geomorphology, and riverine ecology. They represent this interdisciplinary approach graphically by placing relevant processes and concepts from each discipline into two-dimensional spaces with spatial scale and temporal scale as axes. We suggest trout management will benefit from a similar interdisciplinary approach using three two-dimensional management filters (Figure 29.1): river ecosystem processes, trout biology, and political, social and economic factors.

We stress two points before describing the management filters. First, they are representative rather than exhaustive. The filters capture those processes, factors and concepts that are key drivers for, and constraints to, effective trout management. Furthermore, the spatiotemporal scales across which processes and factors are depicted graphically are simplified; we focus on those scales most relevant to trout management. Second, by constructing the filters and, in the following section, considering them alongside Roni *et al.*'s (2008) river catchment management hierarchy, we aim to highlight

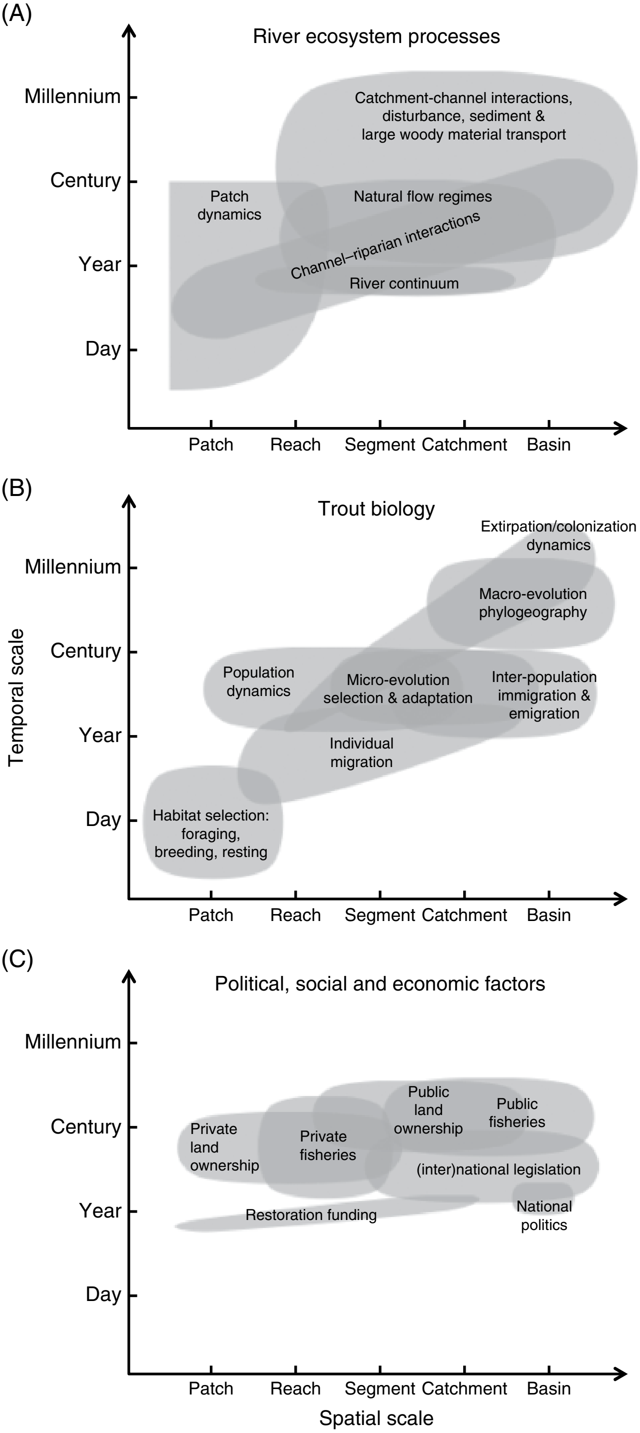

Figure 29.1 Effective trout management is motivated and constrained by elements of river ecosystem ecology, trout biology and socio-political factors. Two dimensional spatiotemporal management filters distil the key elements of these three drivers and can help government agencies, non-governmental environmental organisations and anglers effectively manage trout without the benefit of exhaustive multi-disciplinary catchment analyses. These management filters and their elements are discussed throughout the text.

that effective trout management does not require exhaustive analyses by interdisciplinary teams of river ecologists, trout biologists and social scientists. Angling clubs, NGOs and government agencies with limited financial and technical resources can apply general principles to effectively manage trout across a range of ecological and socio-political scenarios.

River Ecosystem Processes

River ecosystems are shaped by physical, biological and chemical processes operating across spatiotemporal scales (Vannote *et al.*, 1980; Townsend, 1989; Poff *et al.*, 1997; Ward *et al.*, 2001; Allan, 2004; Benda *et al.*, 2004; Thorp *et al.*, 2006; Rice *et al.*, 2008; Beechie *et al.*, 2010; Winemiller *et al.*, 2010; Hladyz *et al.*, 2011). The processes operate in directional, dendritic channel networks and the terrestrial catchments they drain. River ecosystem structure and function are determined in the physical domain by catchment geology and land use, climate, flow regimes, stochastic disturbance events, longitudinal connectivity between channel segments, and lateral connectivity between channels and hill slopes, riparian zones and floodplains (Figure 29.1A). The biological components of structure and function emerge from the assemblages of species able to colonise and persist in these dynamic physiochemical conditions. Effective river ecosystem management takes a spatially hierarchical approach to protect and restore natural processes, connectivity and catchment conditions (Benda *et al.*, 2002; Woolsey *et al.*, 2007; Roni *et al.*, 2008; Beechie *et al.*, 2010; Fullerton *et al.*, 2010; Beechie *et al.*, 2013).

The physical, chemical and thermal character of trout habitat across channel networks depends on processes operating across spatiotemporal scales. The recruitment of sediment and organic matter from the catchment to channel networks depends on lateral connectivity. In headwater streams, sediment and organic matter are typically introduced episodically during disturbance and high-flow events (e.g. wind storms, tree fall, landslides and debris flows). In large low-gradient valley-bottom channels, sediment and Large Woody Material (LWM; i.e. >0.2 m diameter and >2 m length) recruitment occurs more regularly as channels erode and deposit banks (Craig *et al.*, 2008). Sediment transport through channel networks depends on longitudinal connectivity, flow regimes, geology and channel network structure (Rice *et al.*, 2008). These large-scale sediment dynamics, as modified by LWM dynamics, drive the formation and loss of habitat patches (e.g. riffles and pools) at smaller spatiotemporal scales (Townsend, 1989; Winemiller *et al.*, 2010). These physical processes provide the template for biological (e.g. macroinvertebrate communities) and chemical (e.g. nutrient cycling) ‘river continuums’ that operate over intermediate spatiotemporal scales (Vannote *et al.*, 1980; Minshall *et al.*, 1983; Naiman *et al.*, 1987).

The processes that determine the distribution and character of trout habitat across channel networks depend on catchment conditions, particularly those of riparian zones, where linkages between terrestrial and aquatic ecosystems are strongest (Gregory *et al.*, 1991; Young, 2000; Richardson *et al.*, 2010; Wasson *et al.*, 2010). Channel-riparian interactions affect river ecosystems and trout habitat through processes operating across spatiotemporal scales (Figure 29.1A). Riparian vegetation stabilises channel margins, reduces water temperature through shading, provides allochthonous energy to aquatic food webs, and filters fine sediment and dissolved nutrients in surface and subsurface flow. Riparian-derived LWM forms debris jams that retain sediment and organic matter in smaller channels, provides scour-points that regulate habitat patch formation in mid-size channels, and creates side-channel and off-channel habitat in larger valley bottom channels. The spatiotemporal extent and importance of channel-riparian interactions combined with the often degraded condition of riparian zones make riparian zone protection and restoration a common focus of river ecosystem and trout management (Gregory *et al.*, 1991; Naiman & Décamps, 1997; Young, 2000; Richardson *et al.*, 2010; Wasson *et al.*, 2010; Eros *et al.*, 2012).

Trout Biology

The behavioural, population, and evolutionary ecology of riverine trout can also be represented in a spatiotemporal management filter (Figure 29.1B). Over hourly to monthly time scales, individuals of a given age-class move within and among habitat patches to feed, breed, rest, and avoid predators and thermal stressors (Heggenes, 1996; Dunham *et al.*, 2002; Leung *et al.*, 2008; Rosenfeld & Taylor, 2009; Ayllón *et al.*, 2014). Over their lifetime (typically 2 to 10 years) individuals may remain in a single reach, or migrate throughout watersheds, basins, and near-shore marine environments (Jonsson & Jonsson, 2011). In the demographic (rather than genetic) sense, populations fluctuate from years to decades at the reach to catchment scale. Demographic dynamics may be uncorrelated at smaller spatial scales when driven by stochastic patch dynamics (Milner *et al.*, 1993; Gresswell *et al.*, 2006), or synchronous at larger spatial scales when driven by interrannual variation or directional trends in thermal and hydrological conditions (Hari *et al.*, 2006; Lobón-Cerviá, 2007; Almodóvar *et al.*, 2012; Kanno *et al.*, 2015). From the segment to basin scale, depending on longitudinal connectivity and life histories, populations are connected via immigration and emigration (Garant *et al.*, 2000). Micro-evolutionary dynamics and adaptive divergence can occur from segment to basin spatial scales depending on population genetic structure (Meier *et al.*, 2011; Keller *et al.*, 2012; Meier *et al.*, 2014). Over longer time scales, macro-evolutionary processes result in phylogeographic structure from the catchment to inter-basin scale (Bernatchez, 2001; Apostolidis *et al.*, 2011). These demographic and genetic population processes result in part from extirpation/colonisation dynamics operating from small (e.g. temporary losses due to local disturbance) to large (e.g. post-glacial colonisation of entire basins) spatiotemporal scales.

The scale-dependent processes captured by the trout biology management filter have been formally integrated with those represented in river ecosystem management filter through the 'landscape to riverscape' approach to fish conservation and management (Fausch *et al.*, 2002). This perspective has motivated the development of increasingly spatially explicit approaches that mechanistically link catchment conditions, in-channel processes and stream fish community ecology (Erős *et al.*, 2011; Troia & Gido, 2013; Erős & Campbell Grant, 2015; Le Pichon *et al.*, 2015). Honouring the parlance and legacy of Fausch's influential synthesis, considering the third management filter provides an even broader 'landscape to riverscape to socialscape' approach to trout management.

Political, Social and Economic Factors

The socio-political factors influencing trout management in the 21st century operate across a range of spatiotemporal scales (Naiman, 2013) (Figure 29.1C). At the largest spatial scale, international legislation guides the national governments ultimately responsible for trout management. By ratifying the Convention on Biological Diversity (Convention on Biological Diversity, 1992), nations committed to managing trout and their habitat using Precautionary and Ecosystem Approaches. Across much of the brown trout's native range, European Community member states are compelled under the Water Framework Directive (Water Framework Directive, 2000) to restore (and maintain) all (except heavily modified) riverine Water Bodies to Good Ecological Status (GES), which is determined in part by fish communities. A subset of European river ecosystems are additionally protected as Natura 2000 sites under the Habitats Directive (Habitats Directive, 1992). In addition to these international policy drivers, brown trout management is affected (positively and negatively) by land and river channel management legislation at national/international levels. The degree to which these policy drivers are enforced, funded and implemented to support effective trout management varies spatially between nations and temporally within nations as government priorities change through political cycles.

Because most management interventions involve accessing land and river channels, and/or changing fisheries regulations, spatiotemporal variation in the ownership of land, channels and fisheries imposes important controls on trout management (Figure 29.1C). Private land is typically (but not always) owned at smaller spatial scales than public land. For example, individual citizens may own structures in single habitat patches (e.g. a weir that prevents trout migration), whereas government agencies may own and manage entire catchments on behalf of all citizens. Similarly, where riverine trout fisheries are privately owned, angling clubs usually hold fishery rights at the reach to segment scale, creating a patchwork of fisheries rights at the catchment to basin scale. In some cases, this patchwork may include small sections under government ownership, but freely accessible riverine trout fisheries are typically owned and managed at larger spatial scales.

Trout management requires money, particularly for interventions contributing to river ecosystem restoration. For example, protecting riparian zones with bank-side fencing costs €5–10 k per kilometre of channel, while removing (or installing a fish pass on) a large migration barrier typically costs between €100 k and €1 m. The amount of capital available for trout management is important, but so is the spatiotemporal scale at which funding is made available (Figure 29.1C). Large, catchment-scale restoration programmes require funding over decadal time scales, which is at odds with government planning and funding cycles. Management interventions are often conceived and delivered over shorter time-scales, and funded at levels determined by annual budgets and short-notice release of government underspend. This unfortunate reality imposes conceptual and logistical constraints on restoration interventions, particularly when governments fund NGOs to deliver projects on the ground.

Regardless of the challenges associated with legislation, land/fishery ownership, and funding, support from local communities, landowners and anglers is critical for effective trout management. Private landowners often have small but important parcels scattered among larger public ownerships, but private parties may also control entire catchments that should be integrated into larger management plans. Angling organisations and NGOs (i.e. voters) can compel governments to deliver sometimes controversial restoration programmes, and provide support for long-term monitoring efforts. Of course, not all citizens and landowners care about wild trout and river ecosystems, or, if they do, they may care more about exercising legally protected rights incompatible with effective trout management. Government agencies ultimately responsible for managing wild trout must meet these challenges by balancing at least three approaches: facilitating collaborative consultations built around the multiple Ecosystem Services provided by healthy river catchments; challenging inappropriate land use and fisheries practices in the face of socio-political inertia; and resolving 'public over private' concerns via the enforcement of eminent domain and the compulsory purchases of privately owned land and channels.

Trout Habitat Management

In recent decades, salmonid and river ecosystem management have developed in parallel to become a *de facto* multidisciplinary field combining pure and applied aspects of the physical, biological and social sciences. Large literatures from the relevant subdisciplines are summarised in a number of books (Elliott, 1996; Williams *et al.*, 1997; Crisp, 2000; Harris & Milner, 2007; Darby & Sear, 2008; Kemp, 2010; Roni & Beechie, 2013). This body of work underscores the importance of catchment-scale assessments focussed on the interface between natural catchment processes (Figure 29.1A), trout biology (Figure 29.1B), and socio-political and economic factors (Figure 29.1C). In reality, many (if not most) management interventions are delivered opportunistically as individual projects without the benefit of multidisciplinary catchment assessments, strategic planning or long-term funding. Our aim in this section is thus to illustrate how the management filters can support effective trout management in the face of these constraints.

We do this by exploring how the three management filters mutually inform a widely embraced prioritisation scheme developed through exhaustive analysis of interventions aimed (principally) at restoring riverine salmonid habitat (Roni *et al.*, 2002; Roni *et al.*, 2008; Roni *et al.*, 2013a). The four-part prioritisation hierarchy is simple and flexible, and when applied alongside the management filters can support effective trout management across geographical, biological and socio-political contexts. The first step is to identify and *protect* high quality riverine habitats where key ecosystem processes function in natural or near-natural conditions. The next step is to *provide* adequate water quantity and quality by ensuring flow regimes, and thermal/chemical conditions are suitable for trout. The next priority is to *restore* natural catchment processes dependent on longitudinal and lateral habitat connectivity. The final priority is to *enhance* in-channel habitat until natural catchment processes sustain functional and resilient river ecosystems, which should then be protected from subsequent degradation.

Considering this prioritisation scheme alongside the management filters highlights a number issues. First, the prioritisation scheme is a flexible guide rather than a strict formula; trout/river ecosystem management is often an unhappy marriage between ecological principles (Figure 29.1A,B) and socio-political reality (Figure 29.1C). It may be necessary, for example, to deliver a project out of ideal sequence, if doing so builds the socio-political momentum or organisational capacity required to further broader objectives. That said, ill-conceived (or poorly communicated) interventions can jeopardise long-term management objectives if socio-political backlash compromises organisational influence and capacity. Second, when considered across scales, restoration interventions rarely fit neatly into a single scheme category. For example, establishing riparian zone buffers may improve water quality, restore lateral channel-bank connectivity, increase soil water retention, and enhance in-channel habitat, and these outcomes will manifest at different spatiotemporal scales. Third, across much of its native European range (and elsewhere) trout habitat restoration is often delivered by NGOs with funding from government agencies. Considered together, the management filters and prioritisation scheme highlight the benefits and challenges of this increasingly common arrangement.

Protecting High Quality Habitats

Identifying and protecting high quality riverine habitat is the first priority for effective trout management (Box 29.1) (Williams *et al.*, 2007; Williams *et al.*, 2011). At the basin scale and above, protecting ecologically functional river catchments with phenotypically diverse trout populations will protect the genetic and adaptive diversity necessary to maximise ecological and evolutionary resilience in the face of anthropogenic pressures and climate change (Waples, 1995; Jensen *et al.*, 2008; Waples & Hendry, 2008; Wenger *et al.*, 2011). At this scale, protected areas should be large enough to render the chance of extirpation due to demographic and environmental stochasticity miniscule (Lande, 1993), and spaced to allow emigrants from protected refugia to rescue populations in adjacent areas (Pulliam, 1988; Dunham & Rieman, 1999). Similar principles justify protecting high quality habitats at smaller spatial scales. At the patch to catchment scale (Figure 29.1B), high quality habitats and trout 'hot spots' can increase population resilience, and seed adjacent habitats through individual migration over ecological time scales (Vøllestad *et al.*, 2012). Demographic interactions between trout in protected areas and the wider habitat matrix will depend on trout life histories and longitudinal connectivity (Dunham & Rieman, 1999; Rieman & Dunham, 2000). Where trout are anadromous or migratory, adult straying will regularly provide immigrants to other (sub) catchments, as constrained by natural and artificial migration barriers (Schtickzelle &

Box 29.1 Protect the Best, Restore the Rest

The highest priority for trout management is to protect the best remaining habitats from degradation. The best remaining habitats may be defined as those areas that currently support strong trout populations, habitats where ecosystem processes are functioning at levels that maintain and support good trout habitat, or headwater regions that produce cold, clean water and Large Woody Material in support of downstream trout populations. Historically, valley bottom and mainstem river habitats were the most productive portions of the catchments, but these areas are usually the first to be degraded by land use change or pollution. Therefore, protection efforts most often focus on headwaters or more remote areas away from urban areas and agricultural pressures. As remaining high quality habitats are identified and protected, efforts may proceed to adjacent downstream areas of the catchment to restore natural flow regimes, riparian areas, and in-channel habitats. Ideally, protected areas should be identified on the basis of benefits to the wider aquatic ecosystems rather than single species. Where there are intact native freshwater communities, efforts should focus on protecting these larger functioning aquatic systems (Williams *et al.,* 2011).

Quinn, 2007). For non-migratory populations in smaller headwater streams, protected areas, even if geographically adjacent, may be functionally isolated over time scales relevant to management legislation (Figure 29.1C). For these populations, extirpation probability will be related to habitat area and connectivity (Dunham *et al.*, 1997; Morita & Yamamoto, 2002), and carefully considered translocation interventions that mitigate the effects of anthropogenic habitat fragmentation may be appropriate (Griffith *et al.*, 1989; Young, 1999; Young *et al.*, 2005; Olden *et al.*, 2011).

Protecting high quality trout habitat requires powers and resources typically available only to government agencies, though NGOs can affect the process through lobbying. In general, however, trout management NGOs will contribute by delivering interventions that improve the condition and expand the spatial influence of protected areas. In the United States, for example, many trout populations are protected in designated National Parks, Monuments and Wilderness Areas. High quality river corridors are protected by the Wild and Scenic Rivers Act. The habitat of imperilled species can be protected through the designation of Critical Habitat areas for threatened or endangered species under the U.S. Endangered Species Act. Although not native to the U.S., brown trout occurs in some protected areas, and so benefits from protective measures for sympatric native trout. Depending on the local biological and socio-economic context, wild brown trout in the U.S. may be highly valued as sport fish, or managed as an invasive species harmful to native fishes.

Across the brown trout's native European range, dozens of river catchments are designated as Special Areas of Conservation (SAC) under the Habitats Directive, and thus receive special protection from activities that damage river ecosystems. However, *Salmo trutta* is not listed as a species whose 'conservation requires the designation of SAC' (Annex II), nor 'in need of strict protection' (Annex IV), nor whose 'taking in the wild and exploitation may be subject to management measures' (Annex V). This is presumably because brown trout's life history diversity, wide geographic range and locally high abundance render extinction implausible. Atlantic salmon, *Salmo salar*, and two endemic trout species (*S. marmoratus* and *S. macrostigma*) are listed in Annex II; if anadromous brown trout had its own scientific name, it would likely be listed as well. Because SAC rivers are protected based on the conservation status of designated habitat types and species, benefits to brown trout from the SAC network depend in part on distributional overlaps with designated species, particularly Atlantic salmon. For example, in a SAC river designated for Atlantic salmon, development that disrupts longitudinal connectivity and alters flow regimes in headwater trout streams (e.g. depleted reach hydropower schemes) is permissible, even if those trout migrate to/through salmon bearing reaches to complete their life-cycle. Regardless of species identity or status, that SAC rivers are not managed and protected at the catchment scale is incongruous with the scale of relevant processes and contemporary views of river ecosystem management (Figure 29.1A). That said, high quality trout habitat unquestionably receives some level of protection from the European network of protected SAC rivers.

The Water Framework Directive (WFD) requires European Community member states to protect and enhance the status of aquatic ecosystems across Europe, and should thus affect the management of all brown trout habitat across much of its native range. The Directive is delivered and monitored at the spatial scale of the Water Body, which is a 'discrete and significant element' such as a 'stream, river or canal' or part thereof (i.e. roughly the reach to catchment scale of Figure 29.1B). All riverine Water Bodies must be restored to and maintained in Good Ecological Status (GES) as determined by monitored Biological Quality Elements, one of which is the fish community. Most member states have developed fish community classification tools for which the presence and abundance of brown trout increases the index score. Fish communities are assessed relative to those expected in a similar water body not affected by anthropogenic factors. In essence, if brown trout should be present but is not, or should be abundant but is rare, a water body will be less likely to achieve GES. Because of its wide natural distribution and intolerance of poor water quality, brown trout is perhaps the single most important fish species for WFD classification across Europe. To paraphrase a leading scientist involved in the development of WFD fish classification tools, 'If trout are abundant, the water body shouldn't be failing.' The WFD's requirement that member states maintain water bodies in GES suggests that in the coming decades billions of Euros should be spent protecting high quality habitat across the brown trout's native range.

The reality may be quite different. Beyond the lack of funding and political will to address the fundamental causes of river ecosystem degradation (Moss, 2008; Scheuer & Naus, 2010), member states are compelled to target limited resources toward bringing failing water bodies into GES rather than protecting water bodies already achieving Good or High Status. This is because the European Commission measures WFD compliance based on the proportion of water bodies falling on the better side of the Moderate/Good Status boundary. As a result, member states are unlikely to invest limited funds in protecting Good or High Status Water Bodies. Using limited funds to restore degraded habitats rather than protect high quality habitats is, if ecologically questionable, politically understandable. As of 2012, fewer than half of the riverine water bodies in Europe were classified as Good or High Ecological Status (European Commission, 2012), so the challenge is daunting.

Government agencies and NGOs can work together to circumvent the legislative mandate to target WFD resources away from protecting high quality trout habitat. At the segment to basin scale, collaborative interventions can target two types of water bodies: those failing to achieve GES based on biological monitoring, but that are actually in relatively good ecological condition; and failing water bodies adjacent to water bodies with high quality trout habitat. The first approach takes advantage of classification uncertainty/inaccuracy to protect and improve existing high quality habitats. The second expands the spatial influence of high quality habitats by restoring adjacent habitats that may currently act as demographic 'sinks' maintained by immigration (Pulliam, 1988). These approaches to protecting high quality trout habitat require that government agencies ultimately responsible for delivering the WFD embrace uncertainty in status classification and resist the (very strong) temptation to 'chase' water body scale classification targets over six-year WFD reporting cycles.

Providing Water Quantity and Quality

Many of the World's rivers are impacted by flow modification and degraded water quality (Foley *et al.*, 2005; Nilsson *et al.*, 2005; Woodward *et al.*, 2012), and in the brown trout's native European range, water abstraction and water quality are leading causes for failure under the WFD (European Commission, 2012). Humans modify flow regimes directly by removing water from channel networks (e.g. for hydropower, consumption and agriculture), and indirectly through land use that alters hydrological processes (e.g. urbanisation and deforestation). Water quality is compromised by direct point source pollution inputs (e.g. industrial and sewage discharge), and by diffuse pollution associated with land use (e.g. urban and agricultural run-off). These simplified dichotomous categories are useful, but the effects of water quantity and quality stressors on brown trout and their habitat are complex and interactive. For example, agriculture can increase peak and decrease baseline flows by reducing hydrologic retention across a catchment, reduce chemical water quality through point and diffuse pollution, and reduce thermal water quality by removing riparian zone vegetation. Acknowledging these complexities, here we focus on direct flow regime modification because indirect mechanisms are addressed in the next section (*Restoring natural catchment processes*), and on diffuse pollution because point source pollution is typically regulated by specific legislation, whereas diffuse pollution is often addressed through collaborative working between government agencies, NGOs, and private land and fisheries owners.

There are mature literatures on the effects of altered flow regimes on river ecosystems (Poff *et al.*, 1997; Haxton & Findlay, 2008; Vaughan *et al.*, 2009; Arthington *et al.*, 2010; Poff & Zimmerman, 2010), fish communities in general (Mims & Olden, 2013; Rolls & Arthington, 2014), and brown trout and related salmonids in particular (Hatfield & Bruce, 2000; Rosenfeld *et al.*, 2007; Armstrong & Nislow, 2012; Milner *et al.*, 2012; Nislow & Armstrong, 2012; Wilding *et al.*, 2013). This body of work provides a clear message: modifying natural flow regimes, and the structures used to do so (e.g. dams, weirs, intakes) are generally bad for trout and aquatic communities. There are several established approaches to restoring flow regimes sufficient to support physical, biological and chemical processes of river ecosystems (Poff *et al.*, 2010a; UKTAG, 2013; Davies *et al.*, 2014). The European Commission has recently synthesised this research to support WFD delivery (European Commission, 2015). These syntheses and on-going efforts to protect and restore natural flow regimes underscore four important realities. First, while we now have frameworks for assessing how modified flow regimes affect wild trout, the idiosyncrasy of river ecosystems and complexity of trout ecology make identifying widely transferable ‘flow rules’ challenging. Progress will rely on studying the hydrobiology of wild trout in natural flow regimes, delivering well-designed case studies (Arthington *et al.*, 2010), and conducting comparative analyses using data from standard monitoring programmes (Acreman & Ferguson, 2010). Second, because abstraction licenses are often legally protected and provide ecosystem services more widely valued than wild trout (e.g. drinking water, agricultural production, hydropower), changing them for the benefit of trout is difficult, time consuming and expensive. Third, when the second challenge is successfully overcome, funding is rarely available to conduct monitoring across the spatial and temporal scales required to meaningfully address the first challenge. Fourth, these challenges must be addressed in the face of historic, current and future hydropower development, which has a myriad of impacts on brown trout, including the extirpation of migratory and anadromous populations.

In the context of these realities, protecting and restoring natural flow regimes will be a challenging priority for trout management in the 21st century. Variation in brown trout life history and behaviour (Figure 29.1B) reflects (in part) the combined effects of individual plasticity and evolutionary adaptation associated with natural flow regimes (Figure 29.1A). It is thus reasonable to assume that more natural flow regimes will benefit trout, though there may be cases where flow modification can positively affect demographic indices (e.g. decreasing the frequency/magnitude of peak flows during fry emergence may increase early juvenile survival). Notwithstanding such nuances, efforts to protect and restore flow regimes will benefit from a number of general principles. First, the provision of some water to currently dry channels can be prioritised over naturalising the flow regimes of already wetted channels (Bradford *et al.*, 2011). Increasing the amount of trout habitat will almost certainly increase population size and resilience, whereas the consequences of modifying flow regimes in existing habitats are less certain. This simple first principle comes with an equally simple qualification: there is no point creating wetted channels where other conditions needed by trout (e.g. temperature and water quality) will not be met. Second, consistent with the first priority of protecting high quality habitats, priority should be given to restoring flow regimes in rivers with good rather than degraded physical habitat. Third, addressing other catchment-channel processes and enhancing in-channel habitat may yield 'trout returns' where modifying impounding structures and/or changing abstraction licenses is prohibitively difficult. For example, sediment regimes can be naturalised by moving gravel from above to below impounding barriers, restoring riparian zones can mitigate the thermal consequences of low flows, and increasing in-channel complexity by introducing pool-scouring LWM can increase the area of usable habitat during low flow periods. Fourth, the complexity of river ecosystems warrants targeting limited monitoring resources to situations where outstanding scientific questions can be meaningfully addressed (Davies *et al.*, 2014). The science of trout management will benefit more from answering questions well in few cases than poorly in many. Fifth, because human demand for water is likely to increase, it seems inevitable that trout managers (and society) will be confronted with the decision of whether to remove more water from already abstracted sites or to alter natural flow regimes at additional sites. Given habitat protection is the highest trout management priority, and that abstraction usually requires impounding structures that disrupt longitudinal connectivity, we suggest it will typically be more sensible to further degrade already abstracted rivers than modify currently natural flow regimes of additional rivers.

The degree to which these ecological principles affect decisions at the interface of water and trout management will depend on socio-political factors (Figure 29.1C). Where water and trout fisheries are managed by government agencies as shared public resources, it may be easier to deliver ecologically rational management decisions at relevant spatial scales (Figure 29.1A,B). For example, where trout fisheries are privately owned, it will be politically difficult to sacrifice an already impacted population (i.e. a fishery) to further abstraction in order to protect another from new abstraction. Where trout fisheries are publicly owned, anglers may be more supportive of ecological triage in order to protect other freely accessible fisheries. More generally, manipulation of flow – either toward or away from a natural regime – can affect trout populations that co-exist with species of higher conservation concern. If water management decisions are based principally on species-specific criteria, trout may suffer more, or benefit less, than if more holistic ecosystem-based criteria guided decision making (Poff *et al.*, 2010b). That said, trouts may often provide useful focal species around which to develop socially compelling flow and river ecosystem restoration programmes (Box 29.2).

Temporal trends in water quality across the brown trout's native European range have differed between rural and urban areas during the last half-century. While human

Box 29.2 Conservation Targets: Single Species or Whole Communities?

Traditionally, management efforts focus on single species that are desirable, imperilled, or for some other reason receive management priority. Trouts are common targets for single species management if for no other reason than we often know more about their status and habitat needs compared to other aquatic species. Focusing on single species can often result in small projects designed to benefit species in isolated patches. But the cost of approaching conservation by sequentially addressing the patch-scale habitat needs of individual species can be substantial. Restoring larger and more high-quality habitat patches within an interconnected stream network increases trout population size and facilitates the potential to restore migratory life histories, leading to more large fish and greater population resilience (Haak & Williams, 2013). Increasing the size and number of habitat patches can also help protect a greater diversity of habitats and species. Because trouts are well known compared to many riverine species, and are sensitive to habitat degradation, they are a useful focal species for larger stream ecosystem conservation efforts that benefit wider communities (Dauwalter *et al.*, 2011).

population growth and the intensification of agricultural and other natural resource industries have driven declines in rural water quality, the combination of de-industrialisation and improved controls over point-source discharges have led to improvements in the water quality of Europe's urban rivers (European Commission, 2012). Salmonids have returned to rivers from which they were long absent (Perrier *et al.*, 2010; Griffiths *et al.*, 2011), and urban trout fisheries are growing in popularity (Box 29.3). While many of the principles discussed here apply to water quality management of urban streams, a proper treatment of this rapidly maturing and important field is beyond the scope of this chapter (Wenger *et al.*, 2009). We focus our discussion on rural water quality, and do so in the following section because interventions that restore catchment processes often improve water quality.

Box 29.3 The Rise of Urban Trout Fisheries

The combination of de-industrialisation and stricter environmental legislation during the end of the 20th century improved urban water quality throughout much of the brown trout's native European range. Trout have returned to waters from which they had been absent for decades, and the increasing popularity of urban trout angling has the potential to engage millions of citizens in river restoration. In the UK, urban trout fishing is now a popular pastime, with a recently published guidebook (Pike, 2012) and companion website (urbantrout.net) promoting a 'fish where you live' ethos. Complementing this trend, the Wild Trout Trust's Trout in the Town project recruits urban residents to adopt, protect and restore their local trout streams – with trout fishing emerging as a key engagement tool (http://www.wildtrout.org/content/trout-town). Urban fishing for a totemic species reliant on healthy river systems will become increasingly important for progressing brown trout management in the 21st century. The apparent incongruity of wild trout (an icon of pristine rural watercourses) thriving in Europe's post-industrial rivers will engage electorates and provide strong motivation for governments to fund river restoration.

Restoring Catchment Processes

The concept of connectivity provides a useful focus for restoring river ecosystems for the benefit of wild trout (Ward, 1989; Fausch *et al.*, 2002; Zitek *et al.*, 2008; Fullerton *et al.*, 2010; Bracken *et al.*, 2013; Erős & Campbell Grant, 2015). The processes that shape river ecosystem structure and function depend (in part) on two types of connectivity: longitudinal connectivity through channel networks, and lateral connectivity between those networks and the catchments they drain. Humans degrade river ecosystems by decreasing and increasing connectivity. Examples include the interference to movements of fish, sediment and organic matter through channel networks due to impounding structures (reduced longitudinal connectivity). Alternatively, agricultural practices that create overland flow pathways deliver diffuse pollution and alter flow regimes (increased lateral connectivity). Restoring connectivity-dependent processes often involves increasing longitudinal connectivity through channel networks, increasing channel-floodplain lateral connectivity, and decreasing lateral connectivity across catchments The first universal challenge is to identify, prioritise and deliver cost-effective interventions that: are appropriate for the physical character of channel segments and catchments (Figure 29.1A), are consistent with trout biology (Figure 29.1B), and accomodate socio-political constraints (Figure 29.1C) (Roni & Beechie, 2013). The nearly universal second challenge is to meet the first without the benefit of multi-disciplinary catchment analyses or long-term strategic funding programmes (Box 29.4).

Restoring longitudinal connectivity by removing in-channel structures that disrupt fish migration is the cheapest and fastest way to benefit wild salmonids in anthropogenically fragmented catchments (Garcia de Leaniz, 2008; Kemp & O'Hanley, 2010).

Box 29.4 Effectively Funding River Ecosystem Restoration: A Case Study

The spatiotemporal disconnect between river ecosystem processes and the allocation of restoration funding presents a fundamental impediment to effective trout management. The Bonneville Power Administration manages 31 federal hydropower facilities throughout the Columbia River basin in the Pacific Northwest of the United States. The Bonneville Environmental Foundation (BEF), established in 1999, provides financial support to businesses and NGOs working to mitigate the impacts of the hydropower network. Following five years of 'standard' annual project-by-project funding for river restoration interventions, the BEF convened an expert panel to review the effectiveness of the programme (Reeve *et al.*, 2006). The panel concluded that, '…short-term funding was likely to promote site-specific interventions and discourage rigorous, sustained monitoring and a watershed-scale approach'. In response, the BEF now supports catchment restoration efforts based on four enhanced criteria: a minimum 10-year restoration-funding agreement; an explicit time table of interventions; binding, contractual language for delivery and monitoring; iterative assessment and adaptive management through independent expert peer-review. This long-term, large-scale approach to agency-NGO collaboration builds NGO capacity, delivers superior restoration outcomes, and contributes to our scientific understanding of catchment-river-salmonid interactions. The BEF funding approach provides an effective, but as yet rarely implemented, model for collaborative trout management in the 21st century.

Doing so is simple in principle: identify human-made barriers that disrupt migration, prioritise them according to ecological impact and removal cost, then remove them in sequence. The impact of barriers on upstream salmonid migration is clear, but barriers can also disrupt downstream migration (Marschall *et al.*, 2011; Svendsen *et al.*, 2011; Gauld *et al.*, 2013). Thus, current elaborations of the simple 'bottom-up' prioritisation rule that consider up-stream passage efficiency, channel network structure and habitat quantity/quality (Steel *et al.*, 2004; Kemp & O'Hanley, 2010; Erős *et al.*, 2011; Nunn & Cowx, 2012; McKay *et al.*, 2013) should begin to account for two-way migration impacts (Calles & Greenberg, 2009). Of course, in-channel structures can also alter flow and thermal regimes, disrupt the movement of sediment and organic matter, and modify in-channel and riparian habitats (Mueller *et al.*, 2011). The degree and spatial extent of these impacts will vary within and between catchments, and how these impacts inform barrier prioritisation will also depend on wider biodiversity objectives. In reality, even from a narrow ecological/financial perspective, barrier prioritisation can be anything but simple.

Removing impassable mainstem dams will often be the highest ecological priority, but doing so requires substantial capital and many years of negotiation, particularly when they provide ecosystem services (e.g. hydroelectric power, irrigation) valued by politically empowered stakeholders. However, recent progress in the Pacific Northwest of the United States demonstrates a growing willingness to remove large dams like those that are a major threat to wild brown trout in some parts of Europe (e.g. Scandinavia). But most fragmenting structures in the brown trout's native European range are old, small weirs that provide little tangible benefit to society. There are tens of thousands of such weirs that can be removed to benefit wild trout. Beyond the challenge of prioritising barriers for removal, there are various operational, ecological and socio-political issues that warrant consideration. From an operational perspective, bankside infrastructure and land may need to be protected as channel profiles adjust following barrier removal, and sediment in weir pools may need to be tested and removed if contaminated. From an ecological perspective, weirs may provide barriers to the spread of invasive aquatic species and thus deliver conservation benefits to wild trout and other species (Peterson *et al.*, 2008). The principal impediments to restoring longitudinal connectivity are socio-political. There is a persistent perception among fisheries managers and anglers that if some upstream-migrating adult trout are able to pass a weir at some flows, the weir is not worth removing. Private fishery owners often value the angling opportunities provided by impeded migration below weirs and holding water above weirs. Private weir owners are often legally empowered to prevent removal, and are more likely to do so when tempted by financial gain from hydropower development. Citizens like the look and sound of historic weirs to the degree that some are legally protected by heritage legislation. Finally, fish passes provide socially acceptable ecological half-measures that once installed make barrier removal less unlikely. Despite these complications, there is a growing appreciation across Europe for the unmatched value of barrier removal (European Centre for River Restoration, 2015). Still, meaningfully restoring longitudinal connectivity in Europe and elsewhere will require political and financial commitments that national governments, as yet, appear unwilling to make.

The management filters provide two insights into the challenge of restoring longitudinal connectivity. First, the relevant river ecosystem processes (e.g. LWM and sediment transport) and trout biology elements (e.g. migration, immigration and emigration) operate at larger spatiotemporal scales than restoration funding is typically administered. Second, these processes and elements operate at spatiotemporal scales coincident with variations in land and fisheries ownership. Effectively accommodating these realities requires combining a catchment perspective with realistic opportunism. While removing a large mainstem barrier may be the highest ecological priority, such removals can be sufficiently problematic to stoke conflict and erode stakeholder enthusiasm. For NGOs and angling clubs, removing small weirs in headwater streams has numerous socio-economic advantages: it is relatively cheap, infrastructure and channel realignment issues are simpler to overcome when fewer land/weir owners are affected, and successfully delivering smaller projects builds organisational capacity and stakeholder support. Doing so also makes ecological sense. Headwater streams are often important spawning and rearing areas for the migratory (and sea) trout targeted as adults in main-stem fisheries. Restoring headwater connectivity can increase the size and resilience of resident trout populations (Fagan, 2002; Morita & Yamamoto, 2002), a benefit that will become increasingly important as a warming climate drives trout to higher elevations (Hari *et al.*, 2006; Almodóvar *et al.*, 2012). Even removing fragmenting structures in fishless headwaters can benefit trout by naturalising sediment and organic matter transport dynamics into lower fish-bearing reaches (Meyer *et al.*, 2007; Wipfli & Baxter, 2010). Of course, realistic opportunism does not diminish the importance of removing fragmenting structures in larger main-stem channels. Finally, how ownership patterns affect efforts to restore longitudinal connectivity will depend on some combination of societal will and governmental commitment. Our experience in Europe and North America suggests citizens have yet to compel governments to impose their powers of eminent domain and compulsory purchase upon private weir/dam owners to restore longitudinal connectivity for the benefit of river ecosystems and trout.

If restoring longitudinal connectivity is challenging, restoring lateral connectivity is daunting. The degree and spatial scale of rural catchment degradation across much of the brown trout's native European range demands a persistent optimism that interventions delivered at small spatiotemporal scales (Figure 29.1C) will yield catchment scale benefits over the long term (Figure 29.1A). This optimism is challenged further by the EU spending over 40% of its budget on Common Agricultural Policy subsidies that ineffectively *encourage* rather than *require* rural landowners to take the most basic measures to restore lateral connectivity for the benefit of river ecosystems and trout. In England for example, dirt tracks and cattle can freely enter trout-bearing streams, riparian zone protection is voluntary, and rural landowners can dredge and channelise small streams with only symbolic regulatory oversight. These catchment management issues are not unique to Europe, but the long history of degradation and predominance of private land ownership in this region makes addressing them particularly challenging. Still, thousands of NGOs, fishing clubs and landowners are working collaboratively (often supported by EU funding) to restore lateral connectivity across the brown trout's native range.

The management filters provide two complementary guiding principles for restoring lateral connectivity-dependent processes in the face of spatiotemporal disconnects between ecological, biological and socio-economic factors (Figure 29.1). First, restore lateral connectivity at the catchment scale 'from the top down'. Second, focus on protecting and restoring riparian zone vegetation. These simple principles do not negate the need to restore connectivity between valley bottom channels and their floodplains

(Ward *et al.*, 2001; Fullerton *et al.*, 2010), or reduce upslope hydrological connectivity (Allan, 2004; Withers & Jarvie, 2008). They do, however, provide practitioners an ecologically sound framework with which to restore lateral connectivity at the patch to reach scale in a manner likely to yield long term, catchment scale benefits. Small streams represent the majority of channel length in directional hydrologic networks: restoring connectivity-dependent physical, thermal, chemical and biological conditions upstream will benefit downstream reaches, but the converse does not hold. Riparian zones are where the connection between catchments and channel networks is strongest. They influence every component of river ecosystem structure and function, their effect on channels is inversely related to channel width, and riparian zone-channel interactions operate across the spatiotemporal scales relevant to trout biology (Figure 29.1A,B).

The top–down riparian-zone approach to restoring lateral connectivity comes with socio-political advantages and challenges. From an angling perspective, small streams are less likely to be fished, thus minimizing trade-offs between riparian zone fences and access, and between riparian zone vegetation and back-casts! It can be difficult, however, to convince anglers and government agencies to allocate resources to channels that are neither fished nor sampled for WFD status compliance. Private landowners may be more willing to allow the riparian zones of small streams to be protected by fencing because they are often less vulnerable to over-bank flooding, which reduces maintenance costs. However, the cumulative length of small streams means protecting them with fencing may be costly and fragment fields. None of these challenges are insurmountable, and by letting ecological principles guide top–down landowner engagement, agencies, anglers and NGOs can restore lateral connectivity in a strategically opportunistic manner.

Enhancing in-Channel Habitat

The scientific consensus places in-channel habitat enhancement as the lowest priority for river ecosystem restoration, but directly modifying habitat can have both sociological and ecological benefits. There is understandable appeal to a few people doing in a day - e.g. creating a LWM jam or stabilising an eroding bank -what might take a recovering catchment decades to achieve through natural processes. In-channel habitat enhancement was popular during the emergence of river restoration as an applied science. Its dubious reputation is rooted in ill-conceived projects delivered without regard to catchment processes and channel dynamics (Frissell & Nawa, 1992; Stewart *et al.*, 2009). Habitat enhancement involves learning by doing, and we now have decades of experience. For example, the California Department of Fish & Wildlife's habitat restoration manual, first published in 1991 as a 'how to' manual for in-channel habitat enhancement, now includes in its 4th edition chapters on catchment assessment, fish passage and upslope erosion (California Department of Fish and Wildlife, 2010). Improved techniques and well-monitored case studies provide compelling evidence that habitat enhancement, reconnection and creation can benefit salmonid populations from the patch to catchment scale (Solazzi *et al.*, 2000; MacInnis *et al.*, 2008; Ogston *et al.*, 2015).

Habitat enhancement is popular in the brown trout's native European range, with interventions ranging from low-cost, patch-scale projects to large, multi-million Euro reach-scale channel reconfigurations (European Centre for River Restoration, 2015). The popularity of patch-scale projects may be justified when specific habitat features are manipulated in smaller streams (Stewart *et al.*, 2009; Hering *et al.*, 2015). Many rural catchments are sufficiently degraded, with little prospect of timely recovery, that stakeholders may lack patience for habitat to recover through natural processes. For example, it can be difficult to wait for LWM to recruit to the channel when a catchment's trees have been replaced by livestock, riparian zones are not being protected or restored, and in-channel LWM is removed by government agencies in the name of flood defence. Beyond providing immediate benefits for channel processes and trout, habitat enhancement projects can also engage private fishery owners who might be hesitant to invest in top–down restoration. To avoid repeating past 'failures', it is important that experienced practitioners design enhancement projects that work with (rather than against) natural channel processes. For example, placing small pieces of LWM in a channel with large substrate is unlikely to result in a scour pool that will hold large trout. The work of the Wild Trout Trust in the UK exemplifies how government agencies, NGOs and angling clubs can work collaboratively to deliver habitat enhancement projects that benefit river ecosystems, engage stakeholders, and improve trout fisheries (Box 29.5).

It seems less likely that large-scale channel reconfiguration projects will deliver ecologically cost-effective benefits to river ecosystems and wild trout. Across Europe (and elsewhere), many of these projects aim to transform relatively short, urban/semi-urban, heavily modified reaches to a more natural state (European Centre for River Restoration, 2015). While such high-cost projects may be ecologically justified when they include the removal of high-priority migration barriers, they are otherwise difficult to justify given the spatial scales at which river ecosystem processes and relevant aspects of trout biology operate (Figure 29.1A,B). It will often make more ecological sense to spend limited resources strategically restoring connectivity across higher quality catchments than transforming a short concrete canal into a semi-natural urban park. With new legislation and directives compelling national governments to invest in river restoration, deciding how to best spend limited financial resources will be a central challenge for trout management in the 21st century. Notwithstanding the obvious socio-political

Box 29.5 The Wild Trout Trust: A Model for Angler Engagement

NGOs will play a central role in 21st century trout management, especially where fisheries are privately owned. Founded in 1998, the Wild Trout Trust (WTT, www.wildtrout.org) employs a network of experts to educate, engage and support groups interested in protecting and enhancing wild trout and their habitat in the United Kingdom. Delivery partners include landowners, angling clubs, government agencies and other NGOs. The lack of regulatory responsibilities allows the WTT to deliver independent evidence-based restoration advice. The trust uses membership communications, angling publications, social media, and public presentations to engage with a broad network of river restoration practitioners. Funding sources range from project grants with specific outcomes to broad 'memoranda of understanding' to guide the development of larger restoration programmes. The core 'on the ground' activity of the WTT is the Advisory Visit and Practical Visit (AV/PV) programme, which provides habitat surveys, practical training, organisational advice, support for funding applications, and help with securing relevant consents. Central to all the Trust's work is the idea that trout do not exist in a vacuum, but rely on and reflect the ecological integrity of rivers and their catchments.

benefits of high-profile urban projects, a rational 'ecological triage' approach to allocating resources away from highly degraded channels seems sensible. As funding will likely remain limited, government agencies, anglers and NGOs will need to carefully balance social and ecological benefits when conceiving and funding habitat enhancement work.

Trout Fisheries Management

The management filters can also inform the three elements of traditional riverine trout fisheries management: harvest regulations, gear restrictions, and stocking. Before discussing these, we highlight two non-angling fishery issues that affect the abundance of sea trout. First, in many coastal areas of Europe sea trout in marine/estuarine environments are harvested by targeted fisheries and/or as by-catch of fisheries targeting other species. In some areas, marine harvest can be a principal threat to sea trout stocks (Working Group for Baltic Salmon and Sea Trout, 2013). Second, there is now a compelling body of peer-reviewed evidence, much of it from Europe, that salmonid aquaculture poses a threat to wild anadromous salmonids via a variety of mechanisms (Fleming *et al.*, 2000; Heuch *et al.*, 2005; Ford & Myers, 2008; Costello, 2009; Revie *et al.*, 2009; Krkosek *et al.*, 2013). A number of European nations (e.g. Ireland, Norway, UK) will struggle for the foreseeable future to balance the economic benefits of Atlantic salmon aquaculture against the threat to wild sea trout. Where marine harvest and aquaculture threaten wild sea trout populations, anglers and NGOs may contribute to the debate, but the ultimate responsibility for dealing with these threats lies with government agencies.

Until the late 20th century, most riverine brown trout fisheries fell into three broad categories: wild unmanaged catch-and-kill fisheries, where exploitation rates depend on angling pressure; wild-bag-limit fisheries, where exploitation rates are determined by a combination of angling pressure and harvest regulations; supplemented put-and-take fisheries, where stocking is used to increase the number of harvestable trout available to anglers. In recent decades, a combination of imposed policies, educational campaigns and a change in angling culture has led to an increase in catch-and-release fisheries for wild brown (and other) trout throughout their native and introduced ranges (Cooke *et al.*, 2013b). On balance, catch-and-release angling will clearly benefit wild trout, possibly to the detriment of native fish species where trout are non-native (McDowall, 2006; Young *et al.*, 2010). Indeed, even where wild trout are rare/threatened, the socioeconomic benefits (and, through engagement and investment, the ecological benefits) of catch-and-release angling may outweigh any negative impacts associated with stress/mortality experienced by released trout (Cooke *et al.*, 2014).

Where exploitation rates are low, recreational fisheries are unlikely to dramatically impact wild trout populations, but high exploitation rates may drive population declines and evolutionary changes in traits related to catchability (Biro & Post, 2008; Post *et al.*, 2008; Post, 2013). Ignoring the potential evolutionary consequences of fisheries induced mortality (Heino *et al.*, 2013), it is essentially declines in the abundance and size of trout that motivate imposed and voluntary catch-and-release angling. Regardless of the motivational balance between conservation and fishery quality, two factors will principally determine the ecological efficacy of catch-and-release angling: the impact of catch-and-release and associated gear restrictions on individual fish, and the spatial scale at which such measures are implemented. Being captured and released is stressful for fish and increases their chance of dying (Davie & Kopf, 2006; Cooke *et al.*, 2013a). Released fish may also learn how to avoid being caught and become more selective, diminishing (for some anglers) the fishery benefits of catch-and-release (Askey *et al.*, 2006). Capture induced-mortality rates of released fish is low in general [mean = 18% from a survey of n = 274 estimates, (Bartholomew & Bohnsack, 2005)], and for salmonids in particular (Gargan *et al.*, 2015; Havn *et al.*, 2015). Mortality rates likely vary with hook type (circle-v-J, single-v-treble), fishing method (bait-v-lure), water temperature, fight duration, handling time, and release method (Meka, 2004; Bartholomew & Bohnsack, 2005; Raby *et al.*, 2015). Though scientific and sociological nuances may attract academic attention (Cooke & Suski, 2005; Cooke *et al.*, 2012; Nguyen *et al.*, 2013), the survival rate of released fish certainly exceeds that of harvested fish, and that difference can almost certainly be increased by using common sense: use single, barbless, circle-hooked flies; land fish quickly; do not remove fish from the water; release fish quickly.

The spatial scale at which enlightened harvest regulations and gear restrictions are implemented is also important. While the population level impacts of catch-and-release may remain poorly quantified (Kerns *et al.*, 2012), catch-and-release and/or gear restrictions are unlikely to be ecologically effective when implemented at spatial scales small relative to the target population/stock (e.g. a 3 km catch-and-release reach in the middle of a 37 km harvest fishery).

As with harvest regulations and gear restrictions, there has been encouraging progress on the issue of stocking in recent decades. Belatedly heeding a decades-old warning (Reisenbichler & McIntyre, 1977), there is now a clearly articulated evidence-based scientific consensus that stocking is incompatible with the goal of protecting the ecological and evolutionary integrity of wild salmonids, except (perhaps) as a last-resort intervention to rescue populations at immediate risk of local extirpation (Araki & Schmid, 2010; Neff *et al.*, 2011; Palme *et al.*, 2012; Rand *et al.*, 2012; Young *et al.*, 2104). The views of many anglers understandably lag behind the science (van Poorten *et al.*, 2011). For over a century, fisheries managers have sold stocking as a panacea (Meffe, 1992), and dispelling this myth in favour of more responsible interventions remains challenging (Young, 2013). Government agencies are making admirable progress in implementing evidence-based stocking policies (Box 29.6), and guidelines are available for situations where stocking continues in wild populations because of socio-political inertia (Recovery Implementation Science Team, 2009; Wild Trout Trust, 2012; Atlantic Salmon Trust, 2014).

Traditional trout fisheries management issues underscore the importance of spatiotemporal overlap between relevant trout biology and socio-political factors (Figure 29.1B,C). Where fisheries are privately owned by clubs legally empowered to set angling regulations, government agencies may be left to negotiate harvest, gear and stocking policies, or rely on lengthy and costly legal procedures to impose unpopular conservation measures. In the United Kingdom for example, we know of many situations where sea trout exploitation rates and gear restrictions vary among private fishing clubs along a river, and downriver clubs refuse to reduce their harvest rates for shared (angler and trout) benefit. In contrast, where rivers and trout are managed as freely accessible shared public resources, agencies can work collaboratively with anglers to develop spatially rational harvest, gear and stocking management plans that offer a range of opportunities available to all anglers (Oregon Department of Fish and Wildlife,

Box 29.6 A Changing Tide: Trout Stocking in the United Kingdom

Since the time of Darwin, anglers and fisheries managers have stocked trout into rivers in hope of improving fisheries or mitigating the impacts anthropogenic habitat destruction. Research over recent decades has culminated in an evidence-based scientific consensus that stocking fish into viable populations is generally incompatible with the goal of protecting wild trout. While trout management has lagged behind this consensus for socio-political reasons, recent developments in the United Kingdom reflect a broader trend toward enlightened trout management. In Scotland, the recommendations of the Wild Fisheries Review include a presumption that stocking will not take place where there are viable wild salmonid populations (Scottish Government, 2014). Between 2010 and 2015, England and Wales enacted a policy that allows only sterile female triploid brown trout to be stocked in open systems with wild brown trout (Environment Agency, 2015). In 2014 Natural Resources Wales made the historic decision to end sea trout (and salmon) stocking in Wales, freeing resources to support collaborative delivery of habitat restoration interventions (Natural Resources Wales, 2014). Trout stocking will justifiably continue throughout the 21st century, both for rescuing populations from imminent extirpation and supporting harvest fisheries. However, the century will also see the end of habitually supplementing viable wild populations with hatchery fish.

2014). When all anglers have equal access to public fisheries, it will often be easier (but by no means easy!) to establish fishery networks that deliver conservation (e.g. wild, single-barbless, catch-and-release rivers) and harvest (e.g. hatchery supplemented, variable-gear, catch-and-kill rivers) objectives across biologically and socially meaningful spatial scales.

Conclusions

Trout management in the 21st century will be fundamentally different than in the century before. What for decades involved fisheries biologists and anglers using traditional fishery interventions to increase (or through mismanagement reduce) the number and size of trout, trout management now involves government agencies working collaboratively with multiple stakeholders to restore river catchments in the context of multiple ecosystem-based legislative drivers. The ultimate motivation for some may still be to catch more big fish, but this angling end will increasingly be achieved by taking an ecosystem approach to managing trout, be they brown in Europe, or other species elsewhere. This relatively recent conceptual and practical transformation presents challenges, but wild trout and their habitat will ultimately benefit from this broader ecological and socio-political perspective.

The central challenge for trout management in the 21st century is not scientific but socio-political; we mostly know what to do, but societies are mostly not ready to genuinely restore river ecosystems (Lackey, 2009; European Commission, 2012). The 20th century saw European governments enact legislation limiting the amount of pollutants that could be poured into rivers. Societies decided that rivers could no longer be used as sewers, and urban water quality quickly improved across much of the brown trout's native range. The beginning of the 21st century has welcomed legislation calling on governments to restore the *ecology* of the rivers where trout live; clean water is a necessary but insufficient condition for healthy river ecosystems. Meeting the promise of these new initiatives will require that societies value the Ecosystem Services provided by healthy river catchments (e.g. reduced flood risk, cheaper drinking water, nutrient cycling, biodiversity, *more trout*) to a degree that demands fundamental changes in ecosystem-based sectors (e.g. agriculture, forestry, mining, flood defence) that continue to damage river ecosystems (Sweeney *et al.*, 2004; Thorp *et al.*, 2010; Acuña *et al.*, 2013). Unfortunately, the combination of broad electoral pressure and strong government leadership (Kenward *et al.*, 2011) necessary to mobilise the 'grand public works' scale of investment required to protect and restore river ecosystems has yet to materialise.

Despite these challenges, the 21st century looks promising for trout management. Our scientific understanding of interactions between catchments, rivers and trout is mature and growing. Legislative drivers, be they consensual or enforceable, ecologically sound or flawed, have never been better. Angler appreciation of wild, catch-and-release trout fisheries is growing alongside society's wider appreciation for the intrinsic (and material) value of biodiversity. Fishery-inspired NGOs have become professional organisations effectively bridging the gap between government agencies and stakeholders to deliver informed catchment and trout management interventions (Newson, 2011; Williams *et al.*, 2015). These NGOs are increasingly capable of working collaboratively with government, industry and stakeholders to fund and deliver large-scale management initiatives framed around the multiple Ecosystem Services provided by healthy river catchments (Box 29.7). Together, these developments mean that trout management in the 21st century will be less about deciding how many trout to kill or stock, and more about collaboratively seizing the opportunities and negotiating the challenges presented by the *new* trout management.

We hope the combination of management filters and the *protect-provide-restore-enhance* prioritisation scheme will help government agencies, NGOs and anglers deliver effective trout management in the face of multiple future challenges. The first arises

Box 29.7 The Rise of NGOs: Rivers Trusts in the United Kingdom

The 21st century will see environmental NGOs play a central role in restoring river ecosystems for the benefit of wild trout. The Rivers Trust movement in the UK exemplifies this trend (Rivers and Fisheries Trusts of Scotland, 2015; The Rivers Trust, 2015). With national networks supporting independent bottom–up community initiatives, there are now over 80 Trusts working collaboratively with government agencies, stakeholders and volunteers to restore river catchments. Free from the regulatory burden shouldered by government agencies, Rivers Trusts are able to engage effectively with industry, landowners and anglers to deliver on the promise of the Water Framework Directive and other legislative drivers. The Trusts have transformed river restoration and outpaced government agencies in working with industry to fund restoration programmes built around Paid Ecosystem Services (Westcountry Rivers Trust, 2015). Success in the UK has led to growing influence at the European level. As important as any legislation or government initiative, the rise of Rivers Trusts and similar organisations across Europe provide hope for brown trout management in the 21st century.

from the spatiotemporal disconnect between relevant river ecosystem processes (Figure 29.1A) and restoration funding (Figure 29.1C). While legislative drivers should motivate long-term planning, until funding for catchment restoration transcends political and financial-year cycles, agencies and NGOs will need to rely on strategic opportunism to deliver catchment-scale restoration at the patch-to-reach scale. Ironically, the second challenge in the brown trout's native European range is the WFD. The Directive will clearly benefit river ecosystems and wild trout, but logical incongruences compromise its effectiveness. Annual status assessments, the six-year reporting cycle, and reliance on temporally dynamic Biological Indicators combine to encourage short-term thinking and 'status chasing' by government agencies. Assessing Ecological Status at the water body rather than catchment scale encourages small-scale thinking and delivery. The focus on improving poor rather than protecting high quality habitats is ecologically dubious and potentially wasteful. The third challenge is also an opportunity. Lingering conflicts between government agencies and anglers can impede effective management interventions to a degree determined in part by patterns of fishery ownership and the position of fisheries management in government agency structures (Box 29.8). We suspect that trout management in the 21st century will, for better or worse, increasingly rely on NGOs that can diffuse these conflicts by acting as independent, non-regulatory advisers able to engage with stakeholders and collaboratively deliver ecologically sound interventions.

We conclude with the requisite reference to the central environmental crisis of the 21st century: climate change. It is now clear the World's governments will not take actions sufficient to avoid fundamental changes to the planet's thermal and hydrological regimes. Trout will suffer (Wenger *et al.*, 2011). Populations and sub-species at the southern ends of ranges will be most vulnerable, and managed relocations will likely be

Box 29.8 To Fisheries Agency or Not to Fisheries Agency?

Governments manage trout through a variety of organisational structures. In some jurisdictions, trout management is delivered by fisheries agencies with narrow remits and independent budgets. Elsewhere, trout management is the responsibility of agencies with broad remits that include the licensing and regulation of development activities that damage trout and their habitat. The single agency approach may provide management and/or financial efficiencies, but typically leads to a cascade of consequences detrimental to trout management. First, when embedded within agencies whose principal responsibility is to deliver wider political priorities, fisheries management can become marginalised, diminished, and treated as a 'conservation nuisance' to be overcome. Second, debates that might benefit from public exposure are negotiated behind closed doors before being presented with a single voice to stakeholders as the 'best environmental outcome'. Third, anglers justifiably come to view the agency responsible for managing trout fisheries as that which allows, or even promotes, the destruction of trout habitat and river ecosystems. Fourth, the loss of trust and credibility in turn makes it difficult for agencies to gain the support of anglers for scientifically justified management interventions. Having independent fisheries agencies focused on conserving wild trout and their habitat may not remove all these barriers to effective management. It does, however, appear to be the more promising approach.

required to conserve certain evolutionary lineages (Olden *et al.*, 2011). For trout and trout managers, there is hope for two reasons. First, trout have behaviours and life histories well suited for persisting in dynamic and changing environments (Figure 29.1B). Second, the same management interventions that benefit trout in a today's climates will help them cope with climate change (Beechie *et al.*, 2013; Williams *et al.*, 2015). Protecting and expanding areas of high quality habitat, restoring longitudinal and lateral connectivity, and restoring riparian zones will enhance population persistence, facilitate range adjustment, and increase the amount of high quality habitat with suitable thermal regimes. Climate change does not require that we do anything differently, only that we do it more urgently and across larger spatial scales. We hope this contribution helps that happen.

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Understanding Brown Trout Population Genetic Structure: A Northern-European Perspective

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Appendix

In two appendix tables I summarize all the data used in the various analyses. One table presents estimates of genetic diversity and the other table presents data on pairwise F_{ST}values. The files are (will be) available in xlsx or txt format.

Comments on the genetic diversity file: The populations are classified as either anadromous or freshwater resident, and if they are samples in rivers or lake. Further I classify marker type (allozyme, microsatellite, SNP, AFLP), marker number, number of individuals sampled and the different estimates (H_o – observed heterozygosity, He – expected heterozygosity, AR – allelic richness, N_e – effective population size). Reference numbers refer to the list of references below.

Comments on F_{ST} file: The two populations are named, together with information on the presence or absence of barriers to migration (0/1), shortest waterway distance between populations, and geographic scale (1 = within watershed, 2 = among watershed, 3 = among regions or larger). Marker type and number of markers used are also given, together with the estimated F_{ST}. Reference numbers refer to the list of references below.

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Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Slupia River	Poland	River	Anadromous	SNP	39	12	0.234	0.271			1	2013
Vistula River	Poland	River	Anadromous	SNP	39	12	0.389	0.346			1	2013
Bornholm	Denmark	River	Anadromous	SNP	20	50	0.267	0.256	1.870	103.3	2	2014
Slupia River	Poland	River	Anadromous	SNP	22	50	0.261	0.269	1.957	159.2	2	2014
Vistula River	Poland	River	Anadromous	SNP	21	49	0.266	0.270	1.913	185.2	2	2014
Neman River	Lithuania	River	Anadromous	SNP	22	50	0.199	0.219	1.957	26.5	2	2014
Riguldi River	Estonia	River	Anadromous	SNP	21	50	0.247	0.246	1.913	71.2	2	2014
Loo River	Estonia	River	Anadromous	SNP	18	50	0.354	0.345	1.783	56.8	2	2014
Valkla River	Estonia	River	Anadromous	SNP	18	50	0.298	0.305	1.783	197.6	2	2014
Jukkola River	Russia	River	Anadromous	SNP	19	50	0.257	0.271	1.826	51	2	2014
Rompet River	Russia	River	Anadromous	SNP	19	50	0.293	0.290	1.826	450.7	2	2014
Krobæk River	Denmark	Lake	FW resident	allozyme	4	37		0.300			3	1996
Krobæk River	Denmark	Lake	FW resident	allozyme	4	36		0.330			3	1996
Guddalselva	Norway	River	Anadromous	msats	11	79	0.685	0.719	7.542		5	2007
Granvinelva	Norway	River	Anadromous	msats	11	50	0.600	0.600	5.894		5	2007
Granvinelva	Norway	River	Anadromous	msats	11	39	0.582	0.599	6.028		5	2007
Opo	Norway	River	Anadromous	msats	11	46	0.647	0.643	7.074		5	2007
Vosso	Norway	River	Anadromous	msats	11	48	0.642	0.674	6.795		5	2007
Steinsdalevla	Norway	River	Anadromous	msats	11	53	0.656	0.666	7.679		5	2007
Eio	Norway	River	Anadromous	msats	11	56	0.697	0.689	7.435		5	2007
Etne	Norway	River	Anadromous	msats	11	58	0.646	0.709	8.028		5	2007
Etne	Norway	River	Anadromous	msats	11	63	0.647	0.700	8.273		5	2007
Jølster Li	Norway			msats	9	63.2	0.420	0.480	7.300	20	6	2009
Jølster L2	Norway			msats	9	77.9	0.430	0.460	7.000	63	6	2009
Jølster L3	Norway			msats	9	18.7	0.500	0.490	5.400		6	2009
Jølster R1	Norway			msats	9	67.4	0.440	0.510	6.400	33	6	2009
Jølster R2	Norway			msats	9	48	0.520	0.500	7.100	15	6	2009

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Røldal L1	Norway			msats	9	70.4	0.440	0.430	5.900	536	6	2009
Røldal L2	Norway			msats	9	83	0.410	0.420	6.100	316	6	2009
Røldal L3	Norway	Lake		msats	9	71.3	0.400	0.400	5.900	29	6	2009
Røldal R1	Norway	Lake		msats	9	67.6	0.530	0.540	8.000	20	6	2009
Røldal R2	Norway	Lake		msats	9	73	0.550	0.560	8.100	16	6	2009
Olden L1	Norway	Lake	FW resident	msats	9	67.6	0.500	0.530	7.300	18	6	2009
Olden L2	Norway	Lake	FW resident	msats	9	71.9	0.560	0.590	8.000	29	6	2009
Olden R1	Norway	Lake	FW resident	msats	9	69.3	0.570	0.580	6.200	209	6	2009
Lough Melvin	Ireland	Lake	FW resident	allozyme	46	202		0.066			7	1991
Lough Melvin	Ireland	Lake	FW resident	allozyme	46	341		0.072			7	1991
Lough Melvin	Ireland	Lake	FW resident	allozyme	46	13		0.038			7	1991
Vejle	Denmark	River	Anadromous	msats	9	37	0.636	0.709	8.000		8	2002
Vejle	Denmark	River	Anadromous	msats	9	50	0.705	0.716	8.000	795	8	2002
Kovads	Denmark	River	Anadromous	msats	9	35	0.662	0.672	6.750		8	2002
Kovads	Denmark	River	Anadromous	msats	9	50	0.686	0.676	6.625	547	8	2002
Karup	Denmark	River	Anadromous	msats	9	44	0.628	0.673	8.000		8	2002
Karup	Denmark	River	Anadromous	msats	9	67	0.657	0.690	7.625		8	2002
Karup	Denmark	River	Anadromous	msats	9	49	0.712	0.689	6.875		8	2002
Karup	Denmark	River	Anadromous	msats	9	72	0.703	0.699	6.750	671	8	2002
Kolding	Denmark	River	Anadromous	msats	9	50	0.668	0.686	6.750		8	2002
Odder	Denmark	River	Anadromous	msats	9	39	0.625	0.639	6.000		8	2002
Brandstrup bæl	Denmark	River	Anadromous	allozyme	12	35		0.082			9	1993
Tirsbæk	Denmark	River	FW resident	allozyme	12	35		0.071			9	1993
Tirsbæk	Denmark	River	Anadromous	allozyme	12	35		0.078			9	1993
Klokkedalså	Denmark	River	FW resident		12	35		0.084			9	1993
Klokkedalså	Denmark	River	Anadromous		12	35		0.093			9	1993
Krobæk	Denmark		FW resident		12	37		0.114			9	1993
Bisballe bæk	Denmark		FW resident		12	40		0.097			9	1993
Kilde dollerup	Denmark		FW resident		12	35		0.084			9	1993

Dolleruå bæk	Denmark		FW resident		12	35		0.103		9	1993
Kapeldal bæk	Denmark		FW resident		12	35		0.131		9	1993
Gjelbæk	Denmark	Lake	FW resident		12	38		0.074		9	1993
Dollerup Møllebæk	Denmark	Lake	FW resident		12	40		0.105		9	1993
Blanktjärnen	Sweden	Lake	FW resident		12.1	104	0.313	0.311	74	10	2012
Fiksno	Norway	Lake	FW resident	allozyme	40	100	0.012			11	1991
Gryteelvi	Norway	Lake	FW resident	allozyme	40	50	0.003			11	1991
Langejolo	Norway	Lake	FW resident	allozyme	40	50	0.003			11	1991
Dyrvo	Norway	Lake	Anadromous	allozyme	40	40	0.031			11	1991
Dyrvo	Norway	Lake	Anadromous	allozyme	40	106	0.028			11	1991
Dyrvo	Norway	Lake	Anadromous	allozyme	40	65	0.030			11	1991
Teigdalselvi	Norway	Lake	Anadromous	allozyme	40	42	0.035			11	1991
Teigdalselvi	Norway	Lake	Anadromous	allozyme	40	20	0.030			11	1991
Blanktjärnen	Sweden	Lake	FW resident	allozyme	74	1415	0.059		97	12	1996
Flyn	Sweden	Lake	FW resident	allozyme	74	1456	0.061		52	12	1996
ôstra Trollsvatten	Sweden	Lake	FW resident	allozyme	74	1551	0.052		480	12	1996
Västra Trollsvatten	Sweden	Lake	FW resident	allozyme	74	1477	0.056		140	12	1996
Haravattsån I	Sweden	River	FW resident	allozyme	74	636	0.030		64	13	2003
Haravattsån II	Sweden	River	FW resident	allozyme	74	1392	0.058		243	13	2003
Pleutajokk	Sweden	Lake	FW resident	allozyme	35	51	0.023			14	1983
Tärnasjön	Sweden	Lake	FW resident	allozyme	35	76	0.032			14	1983
Svärfarbäcken	Sweden	River	FW resident	allozyme	35	28	0.053			14	1983
Dajmanjaure	Sweden	Lake	FW resident	allozyme	35	100	0.039			14	1983
Njuonajaure	Sweden	Lake	FW resident	allozyme	35	65	0.017			14	1983
Dajmanjåppe	Sweden				35	97	0.013			14	1983
Saxvatten	Sweden				35	144	0.013			14	1983
Sipmeggejaure	Sweden				35	106	0.004			14	1983
Hetenjaure	Sweden				35	108	0.023			14	1983
Uretjaure	Sweden				35	96	0.000			14	1983

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Östertjärn	Sweden				35	100	0.017				14	1983
Bågede	Sweden				35	68	0.041				14	1983
Svaninsån	Sweden				35	50	0.028				14	1983
Jeriken	Sweden	Lake			35	99	0.012				14	1983
Bursvatten	Sweden	Lake			35	58	0.015				14	1983
Bunnersjöane I	Sweden	Lake	FW resident	allozyme	35	125	0.038				14	1983
Bunnersjöane II	Sweden	Lake	FW resident	allozyme	35	140	0.018				14	1983
Visjön	Sweden	Lake	FW resident	allozyme	35	48	0.010				14	1983
Dalsjön	Sweden	Lake	FW resident	allozyme	35	68	0.023				14	1983
Långån	Sweden	River	FW resident	allozyme	35	60	0.039				14	1983
Häggsjön	Sweden	Lake	FW resident	allozyme	35	54	0.036				14	1983
Västra Trollsvatten	Sweden	Lake	FW resident	allozyme	35	205	0.039				14	1983
Västra Trollsvatten	Sweden	Lake	FW resident	allozyme	35	100	0.037				14	1983
Östra Trollsvatten	Sweden	Lake	FW resident	allozyme	35	100	0.034				14	1983
Östra Trollsvatten	Sweden	Lake	FW resident	allozyme	35	101	0.035				14	1983
Blanktjärnen	Sweden	Lake	FW resident	allozyme	35	100	0.027				14	1983
Blanktjärnen	Sweden	Lake	FW resident	allozyme	35	106	0.024				14	1983
Haravattsån	Sweden	River	FW resident	allozyme	35	94	0.026				14	1983
Lilla Stensån	Sweden	River	FW resident	allozyme	35	162	0.003				14	1983
Stora Fulvern	Sweden	Lake	FW resident	allozyme	35	107	0.024				14	1983
Slorudsälven	Sweden	River	FW resident	allozyme	35	51	0.017				14	1983
Greåna	Sweden	River	FW resident	allozyme	35	65	0.024				14	1983
Barlingshultsälven	Sweden	River	FW resident	allozyme	35	71	0.031				14	1983
Rämåna	Sweden	River	FW resident	allozyme	35	135	0.030				14	1983
Sandaälven	Sweden	River	FW resident		35	123	0.030				14	1983
Karlsforälven	Sweden	River	FW resident		35	72	0.029				14	1983
Bunnersjöane I	Sweden	Lake	FW resident		54	125	0.028				15	1979
Bunnersjöane II	Sweden	Lake	FW resident		54	140	0.011				15	1979
Flåm	Norway	River	Anadromous		32			0.058			16	1992

Aurland	Norway	River	Anadromous		32	0.052	16	1992
Vossavatn	Norway	Lake	FW resident		32	0.077	16	1992
Gjetingsdal	Norway	Lake	FW resident		32	0.050	16	1992
Øyre A	Norway	River	Anadromous		32	0.072	16	1992
Øyre R	Norway	River	FW resident		32	0.027	16	1992
Enes	Norway	River	Anadromous	allozyme	32	0.050	16	1992
Vatnastøl	Norway	Lake	FW resident	allozyme	32	0.016	16	1992
godal	Norway	Lake	FW resident	allozyme	32	0.030	16	1992
Gygrastol	Norway	Lake	FW resident	allozyme	32	0.053	16	1992
Mehl	Norway	River	Anadromous	allozyme	32	0.053	16	1992
Myrdal	Norway	Lake	FW resident	allozyme	32	0.070	16	1992
Guddalselva	Norway	River	Anadromous	allozyme	32	0.060	16	1992
Hildal	Norway	Lake	FW resident	allozyme	32	0.102	16	1992
Opsanger	Norway	Lake	FW resident	allozyme	32	0.042	16	1992
Fosså	Norway	River	Anadromous	allozyme	32	0.063	16	1992
Kalven	Norway	River	Anadromous	allozyme	32	0.053	16	1992
Vosso	Norway	River	FW resident	allozyme	32	0.053	16	1992
Matre	Norway	River	Anadromous	allozyme	32	0.072	16	1992
Årung	Norway	River	Anadromous	allozyme	32	0.052	16	1992
Suldal	Norway	River	Anadromous	allozyme	32	0.051	16	1992
Langang	Norway	River	Anadromous	allozyme	32	0.065	16	1992
Bygland	Norway	Lake	FW resident	allozyme	32	0.064	16	1992
Løyning	Norway	Lake	FW resident	allozyme	32	0.068	16	1992
Svartatjønn	Norway	Lake	FW resident	allozyme	32	0.028	16	1992
Tunhovd	Norway	Lake			32	0.068	16	1992
Bjornes	Norway	Lake			32	0.081	16	1992
Setningen	Norway	Lake			32	0.053	16	1992
Slidre	Norway	Lake			32	0.014	16	1992
Tomaselv	Norway				32	0.076	16	1992

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Lågen	Norway				32			0.049			16	1992
Våla	Norway	Lake			32			0.068			16	1992
Gausa	Norway	River			32			0.059			16	1992
Rinda	Norway	Lake			32			0.045			16	1992
Vismunda	Norway	River			32			0.041			16	1992
Bråstad	Norway	Lake	FW resident	allozyme	32			0.029			16	1992
lena	Norway	Lake	FW resident	allozyme	32			0.033			16	1992
Stenseng	Norway	Lake	FW resident	allozyme	32			0.033			16	1992
Bruvoll	Norway	Lake	FW resident	allozyme	32			0.023			16	1992
Skanselv	Norway	Lake	FW resident	allozyme	32			0.032			16	1992
Båhus	Norway	Lake	FW resident	allozyme	32			0.028			16	1992
Brumunda	Norway	Lake	FW resident	allozyme	32			0.026			16	1992
Loch Ave	Scotland	Lake	FW resident	allozyme	34	33	0.071				17	1990
Blar Ghour	Scotland	Lake	FW resident	allozyme	34	10	0.089				17	1990
Tangy Loch	Scotland	Lake	FW resident	allozyme	34	17	0.043				17	1990
Rannoch Moor	Scotland	Lake	FW resident	allozyme	34	14	0.063				17	1990
Pool B	Scotland	Lake	FW resident	allozyme	34	15	0.060				17	1990
Pool C	Scotland	Lake	FW resident	allozyme	34	10	0.079				17	1990
Loch an Easlachlan	Scotland	Lake	Anadromous	allozyme	34	10	0.015				17	1990
Loch Crocach	Scotland	Lake	Anadromous	allozyme	34	10	0.018				17	1990
loch Veyatie	Scotland	Lake	Anadromous	allozyme	34	12	0.055				17	1990
Loch Druim Suardalain	Scotland	Lake	Anadromous	allozyme	34	13	0.054				17	1990
Locj Gillaroo	Scotland	Lake	Anadromous	allozyme	34	14	0.026				17	1990
Loch Awe	Scotland	Lake	Anadromous	allozyme	34	14	0.027				17	1990
Loch Beannnach	Scotland	Lake	Anadromous		34	14	0.016				17	1990
Loch Assynt	Scotland	Lake	Anadromous		34	14	0.054				17	1990
Fionn Loch	Scotland	Lake	Anadromous		34	12	0.065				17	1990
Loch Beag A'Chocair	Scotland	Lake	Anadromous		34	15	0.047				17	1990
Loch Quoich	Scotland	Lake	Anadromous		34	16	0.065				17	1990

Loch Ness	Scotland	Lake	Anadromous		34	17	0.044			17	1990
Leven	Scotland	Lake	Anadromous		34	18	0.044			17	1990
Triasheno	Russia	River	Anadromous		38	57	0.062		1.320	18	1995
Vorob'yev	Russia	River	Anadromous		38	170	0.063		1.290	18	1995
Svyatoe Lake	Russia	River	Anadromous		38	56	0.091		1.240	18	1995
Medja River	Russia	River	FW resident	allozyme	38	28	0.055		1.180	18	1995
Burrishoole	Ireland	Lake	Anadromous	allozyme	9	52		0.189	1.890	19	1992
Lough Feeagh	Ireland	Lake	Anadromous	allozyme	9	31		0.203	1.890	19	1992
Fairy Glen	Ireland	River	FW resident	allozyme	9	50		0.253	2.000	19	1992
Newport River	Ireland	River	Anadromous	allozyme	9	42		0.152	1.780	19	1992
Crumlin	Northern Ireland	River	FW resident	allozyme	28	41	0.079			20	1986
Crumlin	Northern Ireland	River	FW resident	allozyme	28	24	0.076			20	1986
Glenavy	Northern Ireland	River	FW resident	allozyme	28	37	0.065			20	1986
Ballinderry	Northern Ireland	River	FW resident	allozyme	28	33	0.055			20	1986
Upper Bann	Northern Ireland	River	FW resident	allozyme	28	52	0.070			20	1986
Callan	Northern Ireland	River	FW resident	allozyme	28	22	0.059			20	1986
Callan	Northern Ireland	River	FW resident	allozyme	28	76	0.057			20	1986
Fury	Northern Ireland	River	FW resident	allozyme	28	19	0.092			20	1986
Blackwater	Northern Ireland	River	FW resident	allozyme	28	21	0.083			20	1986
Blackwater	Northern Ireland	River	FW resident	allozyme	28	59	0.079			20	1986
Ballinderry	Northern Ireland	River	FW resident	allozyme	28	65	0.122			20	1986
Ballinderry	Northern Ireland	River	FW resident	allozyme	28	89	0.092			20	1986
Moyola	Northern Ireland	River	FW resident	allozyme	28	58	0.099			20	1986
Clady/Grillagh	Northern Ireland	River	FW resident	allozyme	28	26	0.071			20	1986
Main	Northern Ireland		FW resident		28	26	0.059			20	1986
Main	Northern Ireland				28	29	0.091			20	1986
Aghanure	Northern Ireland				28	45	0.075			20	1986
Aghanageeragh	Northern Ireland				28	42	0.101			20	1986
Glenwhirry	Northern Ireland				28	33	0.082			20	1986

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Glenwhirry	Northern Ireland				28	39	0.091				20	1986
Rathmore	Northern Ireland				28	43	0.077				20	1986
Iskelly	Northern Ireland				28	36	0.071				20	1986
Straid	Northern Ireland				28	25	0.073				20	1986
Straid	Northern Ireland				28	109	0.091				20	1986
Straid	Northern Ireland	River	FW resident	allozyme	28	36	0.059				20	1986
Ballyclare	Northern Ireland	River	FW resident	allozyme	28	23	0.122				20	1986
Palantine	Northern Ireland	River	FW resident	allozyme	28	38	0.075				20	1986
Ballymartin	Northern Ireland	River	FW resident	allozyme	28	48	0.097				20	1986
Ballymartin	Northern Ireland	River	FW resident	allozyme	28	58	0.085				20	1986
Clady	Northern Ireland	River	FW resident	allozyme	28	79	0.261				20	1986
Clady	Northern Ireland	River	FW resident	allozyme	28	42	0.099				20	1986
Clady	Northern Ireland	River	FW resident	allozyme	28	40	0.093				20	1986
Lough Neagh	Northern Ireland	Lake	FW resident	allozyme	28	243	0.090				20	1986
Lough Neagh	Northern Ireland	Lake	FW resident	allozyme	28	89	0.077				20	1986
Svartavasstjønn	Norway	Lake	FW resident	allozyme	22	77		0.024			21	1991
Skansbekken	Norway	River	FW resident	msats	8	34	0.625	0.626	5.120	111.5	22	2014
Bausbakkelva	Norway	River	FW resident	msats	8	35	0.579	0.613	5.110	83	22	2014
Brumunda	Norway	River	FW resident	msats	8	30	0.588	0.607	4.780		22	2014
Brumunda	Norway	River	FW resident	msats	8	34	0.588	0.600	4.690	443.3	22	2014
Vesleelva	Norway	River	FW resident	msats	8	30	0.615	0.662	5.360	85.2	22	2014
Flagstadelva	Norway	River	FW resident	msats	8	29	0.616	0.594	4.380	30.8	22	2014
Flagstadelva	Norway	River	FW resident	msats	8	35	0.621	0.628	5.060	358.4	22	2014
Flagstadelva	Norway	River	FW resident	msats	8	35	0.609	0.641	5.560	1222.3	22	2014
Finsalbekken	Norway			msats	8	30	0.611	0.669	5.230	242.7	22	2014
Måsabekken	Norway			msats	8	41	0.680	0.653	5.590	42.4	22	2014
Måsabekken				msats	8	33	0.629	0.629	5.050	120.6	22	2014
Vikselva				msats	8	30	0.633	0.678	6.190	12.2	22	2014
Vikselva				msats	8	30	0.729	0.685	6.130	53.8	22	2014

Labelva				msats	8	17	0.757	0.705	5.880	71.7	22	2014
Labelva				msats	8	19	0.717	0.672	4.680	8.6	22	2014
Färsån	Sweden			msats	5	383	0.540	0.530			23	2000
Färsån	Sweden			msats	5	254	0.500	0.520			23	2000
Amm Brook, Amm house weir	England		Anadromous	msats	9	32	0.742	0.708	6.077		24	2009
Ashburn, Belford Hill	England	River	FW resident	msats	9	36	0.645	0.611	5.238		24	2009
Dury Brook, Dury Farm	England	River	Anadromous	msats	9	33	0.712	0.674	5.145		24	2009
East Dart, Postbridge	England	River	Anadromous	msats	9	21	0.656	0.685	5.590		24	2009
East Webburn, Bagpark Estate	England	River	Anadromous	msats	9	28	0.690	0.639	5.364		24	2009
East Webburn, Dunstone Bridge	England	River	Anadromous	msats	9	57	0.677	0.671	5.727		24	2009
East Webburn, Veton Bridge	England	River	Anadromous	msats	9	49	0.671	0.672	6.021		24	2009
East Webburn, Wooder Manor	England	River	Anadromous	msats	9	77	0.633	0.639	5.603		24	2009
Gatacombe River	England	River	FW resident	msats	9	34	0.647	0.647	4.118		24	2009
Harbourne, Hatcheries Fish Farm	England	River	Anadromous	msats	9	41	0.701	0.733	6.614		24	2009
River Hems	England	River	Anadromous	msats	9	40	0.711	0.720	6.548		24	2009
Holly Brook	England	River	Anadromous	msats	9	29	0.684	0.703	6.234		24	2009
Cherry Brook, Lower Bridge	England	River	Anadromous	msats	9	58	0.713	0.689	5.783		24	2009
Ruddycleave, Bowden Farm	England	River	FW resident	msats	9	90	0.585	0.555	4.047		24	2009
Ruddycleave, Ruddycleave Cottage	England	River	FW resident	msats	9	36	0.679	0.626	4.535		24	2009
Ruddycleave, Pudsham Down	England	River	FW resident	msats	9	96	0.546	0.544	4.062		24	2009
River Swincombe, Wydemeet	England	River	Anadromous	msats	9	76	0.741	0.706	6.084		24	2009
Cherry Brook, Upper Bridge	England	River	Anadromous	msats	9	68	0.692	0.699	5.837		24	2009
West Dart, Cockern Tor	England	River	Anadromous	msats	9	114	0.696	0.688	5.480		24	2009
River Webburn, Mistresses Piece	England	River	Anadromous	msats	9	32	0.654	0.662	5.769		24	2009
West Webburn, Pondsworthy Bridge	England		Anadromous	msats	9	122	0.692	0.686	5.777		24	2009
West Webburn, Lower Cator Bridge	England		Anadromous	msats	9	29	0.671	0.666	5.893		24	2009
Dokka lower				allozyme	17	55	0.193				25	2001
Bjerkreimselva				allozyme	17	50	0.191				25	2001
Kvassheimsåna				allozyme	17	50	0.198				25	2001

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Salangen				allozyme	17	50	0.231				25	2001
Dokka upper				allozyme	17	50	0.162				25	2001
Vikedalselva	Norway			allozyme	17	5	0.141				25	2001
Grunnåa	Norway			allozyme	17	50	0.213				25	2001
Brunkåa	Norway			allozyme	17	20	0.175				25	2001
Svoletjørn	Norway	River	FW resident	allozyme	17	55	0.119				25	2001
Krokavatn	Norway	Lake	FW resident	msats	11	29	0.680	0.660	4.050		27	2008
Krokavatn	Norway	Lake	FW resident	msats	11	98	0.650	0.650	4.060		27	2008
Krokavatn	Norway	Lake	FW resident	msats	11	48	0.650	0.650	3.970		27	2008
Skavatn	Norway	Lake	FW resident	msats	11	18	0.500	0.530	3.920		27	2008
Skavatn	Norway	Lake	FW resident	msats	11	50	0.600	0.620	4.700		27	2008
Kollsvatn	Norway	Lake	FW resident	msats	11	23	0.450	0.540	4.060		27	2008
Kollsvatn	Norway	Lake	FW resident	msats	11	69	0.560	0.620	4.760		27	2008
Kollsvatn	Norway	Lake	FW resident	msats	11	96	0.600	0.620	4.850		27	2008
Kollsvatn	Norway	Lake	FW resident	msats	11	48	0.630	0.660	5.000		27	2008
Litlosvatn	Norway	Lake	FW resident	msats	11	17	0.480	0.510	4.250		27	2008
Litlosvatn	Norway	Lake	FW resident	msats	11	57	0.560	0.600	4.540		27	2008
Litlosvatn	Norway	Lake	FW resident	msats	11	86	0.580	0.600	4.840		27	2008
Kvennsjøen	Norway	Lake	FW resident	msats	11	22	0.490	0.490	3.950		27	2008
Kvennsjøen	Norway	Lake	FW resident	msats	11	50	0.520	0.520	4.260		27	2008
Øvre Krokavatn	Norway	Lake	FW resident	msats	11	36	0.460	0.460	4.050		27	2008
Ringedalsvatn	Norway	Lake	FW resident	msats	11	34		0.550	4.640		28	2007
Løyningsvatn	Norway	Lake	FW resident	msats	11	47		0.580	4.870		28	2007
Krokavatn	Norway	Lake	FW resident	msats	11	44		0.650	4.010		28	2007
Skavatn	Norway			msats	11	49		0.620	4.960		28	2007
Kollsvatn	Norway			msats	11	46		0.660	5.320		28	2007
Litlosvatn				msats	11	48		0.610	5.060		28	2007
Kvennsjøen				msats	11	45		0.550	4.540		28	2007
Midtre Grøndalsvatn				msats	11	46		0.580	4.570		28	2007

Mår				msats	11	50	0.550		4.390		28	2007
Dimmedalsvatn		Lake		msats	11	50	0.660		4.900		28	2007
Nordmannslågen	Norway	Lake		msats	11	36	0.680		5.690		28	2007
Ringedalsvatn	Norway	Lake		AFLP		34	0.160				28	2007
Løyningsvatn	Norway	Lake	FW resident	AFLP		47	0.210				28	2007
Krokavatn	Norway	Lake	FW resident	AFLP		44	0.160				28	2007
Skavatn	Norway	Lake	FW resident	AFLP		49	0.180				28	2007
Kollsvatn	Norway	Lake	FW resident	AFLP		46	0.180				28	2007
Litlosvatn	Norway	Lake	FW resident	AFLP		48	0.170				28	2007
Kvennsjøen	Norway	Lake	FW resident	AFLP		45	0.210				28	2007
Midtre Grøndalsvatn	Norway	Lake	FW resident	AFLP		46	0.180				28	2007
Mår	Norway	Lake	FW resident	AFLP		50	0.150				28	2007
Dimmedalsvatn	Norway	Lake	FW resident	AFLP		50	0.170				28	2007
Nordmannslågen	Norway	Lake	FW resident	AFLP		36	0.180				28	2007
Ringedalsvatn	Norway	Lake	FW resident	msats	11	35	0.520	0.550	4.640		29	2007
Løyningsvatn	Norway	Lake	FW resident	msats	11	50	0.540	0.580	4.870		29	2007
Kollsvatn	Norway	Lake	FW resident	msats	11	50	0.620	0.660	5.320		29	2007
Litlosvatn	Norway	Lake	FW resident	msats	11	50	0.570	0.610	5.060		29	2007
Kvennsjøen	Norway	Lake	FW resident	msats	11	50	0.520	0.550	4.540		29	2007
Øvre Krokavatn	Norway	Lake	FW resident	msats	11	36	0.460	0.460	4.190		29	2007
Midtre Krokavatn	Norway	Lake	FW resident	msats	11	36	0.480	0.470	4.060		29	2007
Nedre Krokavatn	Norway	Lake	FW resident	msats	11	34	0.410	0.470	3.720		29	2007
Øvre Bjørnavatn	Norway	Lake	FW resident	msats	11	50	0.540	0.550	4.150		29	2007
Nedre Bjørnavatn	Norway	Lake	FW resident	msats	11	50	0.440	0.500	3.680		29	2007
Dimmedalsvatn	Norway	Lake	FW resident		11	50	0.710	0.660	4.900		29	2007
Bessvatn	Norway	Lake	FW resident		11	13	0.650	0.670	5.030		29	2007
Bellbekken	Norway	River	FW resident		15	575	0.757	0.757	10.330		30	2010
Bellbekken	Norway	River	FW resident		15	451				104.3	31	2012
Skjern River	Denmark		Anadromous		74	53	0.710	0.740	9.370		32	2011

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Varde River	Denmark				74	36	0.720	0.760	10.000		32	2011
Sneum River	Denmark	River	Anadromous		74	35	0.700	0.760	10.220		32	2011
Storaa River	Denmark	River	FW resident		74	34	0.720	0.760	10.410		32	2011
Kongeaa River	Denmark	River	Anadromous		74	33	0.720	0.730	11.300		32	2011
Ribe River	Denmark	River	FW resident		74	31	0.670	0.730	9.710		32	2011
Granvinelva	Norway	River	Anadromous	msats	74	32	0.630	0.680	7.760		32	2011
Guddalselva	Norway	River	FW resident	msats	74	32	0.690	0.770	9.660		32	2011
Tejn River	Denmark	River	Anadromous	msats	74	32	0.660	0.720	7.990		32	2011
Laesaa River	Denmark	River	FW resident	msats	74	32	0.700	0.720	8.010		32	2011
Karup River	Denmark	River	Anadromous	msats	74	32	0.680	0.730	8.470		32	2011
Skals River	Denmark	River	FW resident	msats	74	32	0.680	0.740	9.110		32	2011
Villestrup River	Denmark	River	Anadromous	msats	74	32	0.690	0.760	10.040		32	2011
Lilleaa River	Denmark	River	FW resident	msats	74	32	0.720	0.770	10.700		32	2011
Kolding River	Denmark	River	Anadromous	msats	74	32	0.710	0.760	10.010		32	2011
Lake Hald	Denmark	Lake	FW resident	msats	74	32	0.670	0.730	8.690		32	2011
Lake Mossoe	Denmark	Lake	FW resident	msats	74	32	0.660	0.730	9.410		32	2011
Normannslågen	Norway	Lake	FW resident	msats	18	47	0.240	0.220	2.490		33	2013
Olavsdalselva	Norway	River	FW resident	msats	19	43	0.270	0.220	2.310		33	2013
Midtre Grøndalsvatn	Norway	River	FW resident	msats	19	30	0.300	0.210	1.680		33	2013
Skavatn	Norway	Lake	FW resident	msats	15	19			5.730		34	2014
Gjuvsjå	Norway	Lake	FW resident	msats	15	40			6.420		34	2014
Pålsbufjorden pop12	Norway	Lake	FW resident	msats	13	80	0.656	0.668	6.400		35	2012
Pålsbufjorden pop3	Norway	Lake	FW resident	msats	13	88	0.226	0.231	4.700		35	2012
Tunhovdfjorden pop23	Norway	Lake	FW resident	msats	13	49	0.226	0.220	2.000		35	2012
Tinnsjøen Måna	Norway			allozyme	13	121		0.322	2.000		36	2006
Tinnsjøen Måna	Norway			allozyme		82		0.350	2.000		36	2006
Tinnsjøen Mår	Norway			allozyme		103		0.368	2.000		36	2006
Tinnsjøen Gøyst	Norway			allozyme		42		0.325	2.000		36	2006
Tinnsjøen Austbygdåi	Norway			allozyme		107		0.339	2.000		36	2006

Tinnelva	Norway			allozyme		22	0.332	2.000	36	2006
Tunhovdfjorden	Norway	Lake	FW resident	allozyme		59	0.390	2.000	36	2006
Slidrefjorden	Norway	Lake	FW resident	allozyme		43	0.021	1.300	36	2006
Skaupsjøen	Norway	Lake	FW resident	allozyme		50	0.354	2.000	36	2006
Møsvatn	Norway	Lake	FW resident	msats	8	35	0.680	9.000	37	2002
Kvenna	Norway	River	FW resident	msats	8	35	0.650	9.300	37	2002
Hondle	Norway	River	FW resident	msats	8	36	0.600	8.300	37	2002
Skinåi	Norway	River	FW resident	msats	8	14	0.710	5.600	37	2002
Tunhovdfjorden	Norway	Lake	FW resident	msats	8	21	0.630	7.600	37	2002
Azika	Russia	River	Anadromous	msats	10	44	0.650	4.160	38	2009
Azika	Russia	River	Anadromous	msats	10	36	0.640	4.060	38	2009
Gorodjonka	Russia	River	FW resident	msats	10	33	0.670	3.940	38	2009
Khrevitsa	Russia	River	FW resident	msats	10	79	0.650	3.840	38	2009
Lemovzha	Russia	River	Anadromous	msats	10	61	0.570	3.260	38	2009
Lubenka	Russia	River	Anadromous	msats	10	13	0.700	3.880	38	2009
Solka	Russia	River	Anadromous	msats	10	33	0.640	3.790	38	2009
Solka	Russia	River	Anadromous	msats	10	29	0.630	3.820	38	2009
Solka above	Russia	River	FW resident	msats	10	48	0.670	3.980	38	2009
Sumka	Russia	River	Anadromous	msats	10	32	0.680	3.820	38	2009
Ukhora	Russia	River	Anadromous	msats	10	42	0.660	4.050	38	2009
Vidon	Russia	River	Anadromous	msats	10	33	0.620	3.780	38	2009
Vruda	Russia	River	Anadromous	msats	10	28	0.670	4.220	38	2009
Vruda	Russia	River	Anadromous	msats	10	12	0.700	4.350	38	2009
Lohijoki	Russia	Lake	FW resident	msats	10	28	0.570	3.400	38	2009
Ur'ja	Russia		Anadromous		10	19	0.600	3.310	38	2009
Surnujoki	Finland				15	15	0.610	4.420	39	2010
Siuttajoki	Finland				15	53	0.540	3.740	39	2010
Niipijoki	Finland				15	15	0.540	3.220	39	2010
Naamajoki	Finland				15	18	0.450	3.060	39	2010

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Kielajoki	Finland				15			21	0.640	4.260	39	2010
Kaamajoki	Finland	Lake	FW resident		15			22	0.690	5.100	39	2010
Muddusjärvi	Finland	Lake	FW resident		15			29	0.580		39	2010
Nellimjoki	Finland	Lake	FW resident		15			15	0.610	4.120	39	2010
Juutuanjoki - Kettukoski	Finland	Lake	FW resident		15			23	0.580	4.430	39	2010
Juutuanjoki - Vaskojoki	Finland	Lake	FW resident	msats	15			43	0.620	4.420	39	2010
Juutuanjoki - Kurtujoki	Finland	Lake	FW resident	msats	15			11	0.630	4.000	39	2010
Juutuanjoki - Ala Menesjoki	Finland	Lake	FW resident	msats	15			16	0.630	5.080	39	2010
Juutuanjoki - Ylä Menesjoki	Finland	Lake	FW resident	msats	15			21	0.640	4.660	39	2010
Juutuanjoki - Lankojoki	Finland	Lake	FW resident	msats	15			28	0.550	4.200	39	2010
Juutuanjoki	Finland	Lake	FW resident	msats	15			28	0.560	3.630	39	2010
Juutuanjoki	Finland	Lake	FW resident	msats	15			82	0.570	3.990	39	2010
Nukkumajoki	Finland	Lake	FW resident	msats	15			19	0.660	4.670	39	2010
Ivalojoki - Alakosi and Pajakoski	Finland	Lake	FW resident	msats	15			24	0.690	5.340	39	2010
Ivalojoki	Finland	Lake	FW resident	msats	15			21	0.610	4.510	39	2010
Ivalojoki - Appisjoki	Finland	Lake	FW resident	msats	15			29	0.620	4.300	39	2010
Ivalojoki - Kyläjoki	Finland	Lake	FW resident	msats	15			33	0.630	4.410	39	2010
Ivalojoki - Taimenjoki	Finland	Lake	FW resident	msats	15			29	0.670	4.920	39	2010
Ivalojoki - Pikku Rullajoki	Finland	Lake	FW resident	msats	15			30	0.660	4.770	39	2010
Ivalojoki - Karvajoki	Finland	Lake	FW resident	msats	15			31	0.610	4.340	39	2010
Ivalojoki	Finland	Lake	FW resident	msats	15			48	0.640	4.710	39	2010
Ivalojoki	Finland	Lake	FW resident	msats	15			50	0.610	4.500	39	2010
Ivalojoki	Finland	Lake	FW resident	msats	15			66	0.620	4.400	39	2010
Ivalojoki - Joupinniva and Helkikoski	Finland	Lake	FW resident	msats	15			25	0.600	4.040	39	2010
Ivalojoki - Lismajoki	Finland				15			32	0.550	3.340	39	2010
Ivalojoki - Naskamajoki	Finland				15			22	0.520	3.210	39	2010
Ivalojoki - upper Naskamajoki	Finland				15			18	0.520	3.520	39	2010

Nellimjoki - Kontosjoki	Finland				15			13	0.610	4.530	40	2013
Sarmijoki	Finland				15			19	0.670	5.280	40	2013
Juutuanjoki - Ahvenjoki	Finland				15	19		0.610	4.370		40	2013
Storaa River	Denmark		Anadromous		21	34	0.740	0.790	7.900		41	2009
Skjern River	Denmark		Anadromous		21	39	0.790	0.800	8.100		41	2009
Varde River	Denmark		Anadromous		21	31	0.760	0.820	8.400		41	2009
Sneum River	Denmark		Anadromous		21	13	0.680	0.770	7.400		41	2009
Kongeaa River	Denmark	River	Anadromous	msats	21	35	0.780	0.810	8.000		41	2009
Ribe River	Denmark	River	Anadromous	msats	21	18	0.740	0.770	7.400		41	2009
Gloppenelva	Norway	River	Anadromous	allozyme	9	56	0.189	0.198			42	2006
Mørkridselva	Norway	River	Anadromous	allozyme	9	60	0.138	0.143			42	2006
Aurlandselva	Norway	River	Anadromous	allozyme	9	179	0.141	0.145			42	2006
Flåmselva	Norway	River	Anadromous	allozyme	9	45	0.161	0.160			42	2006
Årøyelva	Norway	River	Anadromous	allozyme	9	23	0.178	0.181			42	2006
Oselva	Norway	River	Anadromous	allozyme	9	59	0.248	0.239			42	2006
Øyreselva	Norway	River	Anadromous	allozyme	9	118	0.222	0.234			42	2006
Sima	Norway	River	Anadromous	allozyme	9	43	0.176	0.187			42	2006
Kapeldal River	Denmark	River	FW resident	msats	8	22	0.682	0.694	5.625	79	43	2005
Kapeldal River	Denmark	River	FW resident	msats	8	41	0.620	0.658	5.270		43	2005
Krobæk River	Denmark	River	FW resident	msats	8	83	0.599	0.630	5.034	56	43	2005
Krobæk River	Denmark	River	FW resident	msats	8	40	0.549	0.617	4.855		43	2005
Krobæk River	Denmark	River	FW resident	msats	8	50	0.589	0.582	4.755		43	2005
Dollerup Møllebæk	Denmark	River	FW resident	msats	8	109	0.666	0.653	5.053		43	2005
Nordre Finnvikelv Tributary	Norway	River	FW resident	msats	6	58	0.600	0.530			44	1999
Nordre Finnvikelv	Norway	River	FW resident	msats	6	74	0.520	0.520			44	1999
Nordre Finnvikelv	Norway	River	FW resident	msats	6	71	0.540	0.510			44	1999
Nordre Finnvikelv	Norway		FW resident		6	61	0.490	0.480			44	1999
Nordre Finnvikelv	Norway		FW resident		6	57	0.440	0.430			44	1999
Mörrumsån	Sweden		Anadromous		7	50	0.660	0.660	5.430		45	2007
Vejle River	Denmark		Anadromous		7	40	0.580	0.680	6.140	166	45	2007
Vejle River	Denmark				7	50	0.690	0.690	6.860	390	45	2007

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Karup River	Denmark		Anadromous		7	47	0.590	0.640	6.430	222	45	2007
Karup River	Denmark		Anadromous		7	68	0.620	0.660	6.000	499	45	2007
Karup River	Denmark		Anadromous		7	49	0.680	0.660	5.710	240	45	2007
Karup River	Denmark		Anadromous		7	72	0.670	0.670	5.430	581	45	2007
Kovads River	Denmark		Anadromous		7	36	0.630	0.640	5.860	381	45	2007
Kovads River	Denmark	River	Anadromous	msats	7	50	0.660	0.650	5.290	755	45	2007
Odder River	Denmark	River	Anadromous	msats	7	40	0.580	0.620	5.140		45	2007
Kolding River	Denmark	River	Anadromous	msats	7	50	0.630	0.660	5.570		45	2007
Vellens River	Denmark	River	Anadromous	msats	7	49	0.640	0.680	7.140	235	45	2007
Vellens River	Denmark	River	Anadromous	msats	7	22	0.690	0.670	5.140	158	45	2007
Vellens River	Denmark	River	Anadromous	msats	7	50	0.620	0.670	5.860	271	45	2007
Blykobbe River	Denmark	River	Anadromous	msats	7	45	0.620	0.590	5.710	104	45	2007
Blykobbe River	Denmark	River	Anadromous	msats	7	46	0.680	0.680	7.000	4235	45	2007
Blykobbe River	Denmark	River	Anadromous	msats	7	50	0.630	0.670	4.860	371	45	2007
Dondals River	Denmark	River	Anadromous	msats	7	29	0.730	0.680	5.140	98	45	2007
Dondals River	Denmark	River	Anadromous	msats	7	18	0.720	0.690	5.000	168	45	2007
Dondals River	Denmark	River	Anadromous	msats	7	50	0.580	0.580	4.140	151	45	2007
Tejn River	Denmark	River	Anadromous	msats	7	41	0.680	0.680	6.000	490	45	2007
Tejn River	Denmark	River	Anadromous	msats	7	47	0.630	0.650	6.860	1038	45	2007
Tejn River	Denmark	River	Anadromous	msats	7	23	0.640	0.620	4.860	106	45	2007
Tejn River	Denmark	River	Anadromous	msats	7	50	0.540	0.610	6.140	177	45	2007
Grodeby River	Denmark	River	Anadromous	msats	7	40	0.620	0.620	4.570	164	45	2007
Laesaa River	Denmark	River	Anadromous	msats	7	50	0.670	0.630	5.000	405	45	2007
Baggeaa River	Denmark	River	Anadromous	msats	7	40	0.590	0.650	6.000	96	45	2007
Blanktjärnen	Sweden		FW resident	allozyme	14	2694	0.314	0.313		63	46	2011
Dalälven	Sweden		Anadromous	allozyme	17	93		0.280	2.100		47	2003
Dalälven	Sweden		Anadromous		8	135		0.670	6.500	60	47	2003
Lake Hald	Denmark		FW resident		10	37	0.676	0.712	7.560		48	2008
Lilleaa River	Denmark				10	35	0.769	0.746	8.980		48	2008

Norring Møllebæk River	Denmark		FW resident		10	36	0.690	0.710	6.510		48	2008
Karup River	Denmark		Anadromous		10	36	0.692	0.721	7.480		48	2008
Tjærbæk River	Denmark		Anadromous		8	48	0.692	0.699			49	2001
Flads River	Denmark		Anadromous		8	59	0.628	0.712			49	2001
Mern River	Denmark		Anadromous		8	59	0.656	0.676			49	2001
Karup River	Denmark	River	Anadromous	msats	8	50	0.700	0.679			49	2001
Esrum River	Denmark	River	Anadromous	msats	8	54	0.632	0.689			49	2001
Trollsvattnet	Sweden	Lake	FW resident	allozyme	14	4140		0.284		121	50	2013
Trollsvattnet	Sweden	Lake	FW resident	allozyme	14	4140				193	50	2013
Trollsvattnet	Sweden	Lake	FW resident	msats	7	382		0.503			50	2013
Lake Hald	Denmark	Lake	FW resident	msats	44	32	0.674	0.680		153	51	2014
Lake Mossoe	Denmark	Lake	FW resident	msats	44	32	0.664	0.670		252	51	2014
Lilleaa River	Denmark	River	Anadromous	msats	44	32	0.739	0.740		288	51	2014
Storaa River	Denmark	River	Anadromous	msats	44	34	0.740	0.750		244	51	2014
Skjern River	Denmark	River	Anadromous	msats	44	53	0.749	0.760		259	51	2014
Varde River	Denmark	River	Anadromous	msats	44	36	0.756	0.760		245	51	2014
Sneum River	Denmark	River	Anadromous	msats	44	35	0.734	0.740		429	51	2014
Kongeaa River	Denmark	River	Anadromous	msats	44	33	0.735	0.740		1317	51	2014
Ribe River	Denmark	River	Anadromous	msats	44	31	0.692	0.700			51	2014
Skals River	Denmark	River	Anadromous	msats	44	32	0.686	0.690		74	51	2014
Karup River	Denmark	River	Anadromous	msats	44	32	0.697	0.700		537	51	2014
Villestrup River	Denmark	River	Anadromous	msats	44	32	0.698	0.700		369	51	2014
Kolding River	Denmark	River	Anadromous	msats	44	32	0.712	0.720		771	51	2014
Steindalsbekken	Norway	River	Anadromous	allozyme	15	80	0.209				52	2001
Fjelldalselva	Norway		Anadromous	allozyme	15	80	0.211				52	2001
Pendalsbekken	Norway		Anadromous	allozyme	15	73	0.232				52	2001
Sævelibekken	Norway		Anadromous		15	79	0.201				52	2001
Allemannsbekken	Norway		Anadromous		15	52	0.248				52	2001
Songebekken	Norway				15	80	0.184				52	2001

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Mørefjærbekken	Norway		Anadromous		15		80	0.216			52	2001
Langangsvassdraget	Norway		Anadromous		15		80	0.220			52	2001
Esna	Estonia		FW resident		13		48	0.670	0.650	5.000	53	2015
Esna	Estonia		FW resident		13		60	0.630	0.630	4.950	53	2015
Kivioja	Estonia		FW resident		13		41	0.440	0.430	2.580	53	2015
Körtsioja	Estonia	River	FW resident	msats	13		41	0.680	0.670	5.320	53	2015
Kuusalu	Estonia	River	FW resident	msats	13		47	0.660	0.600	5.410	53	2015
Männiku	Estonia	River	FW resident	msats	13		82	0.600	0.590	4.300	53	2015
Männiku	Estonia	River	FW resident	msats	13		33	0.640	0.630	5.120	53	2015
Piirsalu	Estonia	River	FW resident	msats	13		27	0.660	0.650	5.480	53	2015
Preedi	Estonia	River	FW resident	msats	13		50	0.530	0.530	3.910	53	2015
Preedi	Estonia	River	FW resident	msats	13		172	0.550	0.550	4.050	53	2015
Tatra	Estonia	River	FW resident	msats	13		29	0.470	0.470	3.030	53	2015
Valkla	Estonia	River	FW resident	msats	13		27	0.690	0.620	4.740	53	2015
Valkla	Estonia	River	FW resident	msats	13		45	0.630	0.620	5.410	53	2015
Vodja	Estonia	River	FW resident	msats	13		65	0.620	0.640	5.100	53	2015
Vodja	Estonia	River	FW resident	msats	13		31	0.630	0.640	5.110	53	2015
Völingi	Estonia	River	FW resident	msats	13		22	0.550	0.510	4.110	53	2015
Tjærbæk River	Denmark	River	Anadromous	msats	8		48	0.692	0.699		55	2000
Karup River	Denmark	River	Anadromous	msats	8		50	0.700	0.680		55	2000
Karup River	Denmark	River	Anadromous	msats	8		77	0.669	0.688		55	2000
Esrum River	Denmark	River	Anadromous	msats	8		54	0.632	0.689		55	2000
Stamperenden	Denmark	River	Anadromous	msats	8		51		0.620		56	2001
Mörrumsån	Sweden	River	Anadromous	msats	8		50		0.680		56	2001
Karup River	Denmark		Anadromous		8		70	0.658	0.691		57	2002
Skjern River	Denmark		Anadromous		8		63	0.694	0.690		57	2002
Odder River	Denmark		Anadromous		9		66	0.082	0.086		58	1996
Odder River	Denmark				9		70	0.073	0.066		58	1996
Stampemølle Å	Denmark				9		72	0.063	0.068		58	1996

Asbæk Å	Denmark		Anadromous		9	74	0.068	0.071			58	1996
Kragebæk	Denmark		Anadromous		9	72	0.072	0.071			58	1996
Assedrup Å	Denmark		Anadromous	allozyme	9	72	0.076	0.075			58	1996
Fiskebæk	Denmark		Anadromous	allozyme	9	69	0.076	0.072			58	1996
Färsån	Sweden		FW resident	msats	5	51	0.530	0.540			59	2001
Eldsjöbäcken	Sweden	River	FW resident	msats	5	45	0.550	0.550			59	2001
Gulån	Sweden	River	FW resident	msats	5	52	0.530	0.490			59	2001
Öravatsbäcken	Sweden	River	FW resident	msats	5	60	0.500	0.480			59	2001
Borgforsen	Sweden	River	FW resident	msats	5	49	0.450	0.500			59	2001
Laxsjöbäcken	Sweden	River	FW resident	msats	5	59	0.220	0.240			59	2001
Lycktorpsbäcken	Sweden	River	FW resident	msats	5	32	0.040	0.040			59	2001
Färsån	Sweden	River	FW resident	msats	5	27	0.520	0.560			59	2001
Eldsjöbäcken	Sweden	River	FW resident	msats	5	47	0.490	0.530			59	2001
Borgforsen	Sweden	River	FW resident	msats	5	36	0.530	0.520			59	2001
Abbert	Ireland	Lake	FW resident	msats	12	48	0.540	0.530	4.130	186	60	2010
Baelnabrack	Ireland	Lake	FW resident	msats	12	48	0.630	0.650	5.180	238	60	2010
Black	Ireland	Lake	FW resident	msats	12	48	0.590	0.600	4.790		60	2010
Cong	Ireland	Lake	FW resident	msats	12	46	0.560	0.590	5.030	17.3	60	2010
Cornamona	Ireland	Lake	FW resident	msats	12	48	0.590	0.630	5.280	850	60	2010
Cross	Ireland	Lake	FW resident	msats	12	48	0.610	0.600	4.660	199	60	2010
Drimneen	Ireland	Lake	FW resident	msats	12	36	0.620	0.620	4.780		60	2010
Grange	Ireland	River	FW resident	msats	12	48	0.710	0.810	7.500	123	60	2010
Oughterard	Ireland	Lake	FW resident	msats	12	48	0.630	0.670	5.920	44.5	60	2010
Rena River (Løpet)	Norway	River	FW resident	allozyme	10	71	0.135	0.135			61	1999
Deset	Norway		FW resident	allozyme	10	26	0.119	0.128			61	1999
Søre Osa	Norway		FW resident	allozyme	10	42	0.057	0.056			61	1999
Nordre Osa	Norway		FW resident		10	44	0.102	0.108			61	1999
Ulvåa	Norway		FW resident		10	33	0.106	0.100			61	1999
Slemma	Norway		FW resident		10	57	0.100	0.104			61	1999

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Villa I	Norway		FW resident		10		52	0.114	0.112		61	1999
Villa II	Norway		FW resident		10		50	0.076	0.089		61	1999
Deia	Norway		FW resident	allozyme	10		36	0.033	0.040		61	1999
Flåtesøbekken	Norway		FW resident	allozyme	10		30	0.118	0.107		61	1999
Tinnsjøen Måna	Norway		FW resident	msats	9		32	0.630	0.660		62	2006
Måna 1	Norway	River	FW resident	msats	9		27	0.600	0.610		62	2006
Måna 2	Norway	River	FW resident	msats	9		25	0.570	0.600		62	2006
Måna 3	Norway	River	FW resident	msats	9		58	0.650	0.580		62	2006
Måna 4	Norway	River	FW resident	msats	9		28	0.630	0.650		62	2006
Måna 5	Norway	River	FW resident	msats	9		29	0.620	0.650		62	2006
Måna 6	Norway	River	FW resident	msats	9		26	0.640	0.660		62	2006
Møsvatn	Norway	Lake	FW resident	msats	9		37	0.640	0.620		62	2006
Säverå	Sweden	River	Anadromous	msats	8		49		0.690		63	2008
Ume-Vindelälven	Sweden	River	Anadromous	msats	8		45		0.690		63	2008
Öreälven	Sweden	River	Anadromous	msats	8		31		0.690		63	2008
Tuohijoki	Finland	River	FW resident	msats	12		18		0.660	4.380	64	2015
Repojoki	Finland	River	FW resident	msats	12		64		0.660	4.520	64	2015
Tolosjoki	Finland	River	FW resident	msats	12		33		0.650	4.450	64	2015
Sallijoki	Finland	River	FW resident	msats	12		26		0.650	4.230	64	2015
Umeälven A	Sweden	River	Anadromous	msats	8		59	0.680	0.680	5.060	65	2012
Umeälven B	Sweden	River	Anadromous	msats	8		75	0.680	0.690	5.270	65	2012
Laisälven A	Sweden	River	Anadromous	msats	8		45	0.690	0.690	4.810	65	2012
Laisälven B	Sweden	River	Anadromous	msats	8		44	0.720	0.680	5.000	65	2012
Ammaarnäs	Sweden	River	FW resident	msats	8		55	0.560	0.590	4.310	65	2012
Giertsbäcken	Sweden		FW resident		8		31	0.560	0.570	3.790	65	2012
Krokforsen	Sweden		Anadromous		8		27	0.368	0.660	4.790	65	2012
Gargån	Sweden		FW resident		8		45	0.480	0.490	3.680	65	2012
Krycklan	Sweden				8		39	0.700	0.690	4.570	65	2012
Matjokkbäcken	Sweden				8		30	0.690	0.700	4.840	65	2012

Rågobäcken above	Sweden		FW resident		8	19	0.470	0.440	2.670		65	2012
Rågobäcken below	Sweden		Anadromous		8	15	0.720	0.680	5.130		65	2012
Renforsen	Sweden		Anadromous		8	46	0.620	0.670	5.050		65	2012
Piteälven	Sweden		Anadromous		8	32	0.650	0.710	4.930		65	2012
Sikån	Sweden		Anadromous		8	68	0.590	0.610	4.570		65	2012
Hundforsen	Sweden	River	FW resident	msats	8	33	0.550	0.570	4.260		65	2012
Varjisån	Sweden	River	Anadromous	msats	8	30	0.670	0.680	4.570		65	2012
Stockforsälven	Sweden	River	FW resident	msats	8	28	0.640	0.650	4.420		65	2012
Trehannick	England	River	Anadromous	msats	23	47	0.750	0.770	9.890		66	2015
Stannon	England	River	Anadromous	msats	23	44	0.790	0.780	11.150		66	2015
Gwills	England	River	Anadromous	msats	23	49	0.760	0.750	9.510		66	2015
Kestle Mill	England	River	Anadromous	msats	23	45	0.730	0.740	8.920		66	2015
Tregony	England	River	Anadromous	msats	23	42	0.770	0.780	10.250		66	2015
Geen Mill	England	River	Anadromous	msats	23	46	0.750	0.760	10.010		66	2015
Tehidy Brook	England	River	Anadromous	msats	23	41	0.700	0.700	6.870		66	2015
Roseworthy Farm	England	River	Anadromous	msats	23	40	0.690	0.700	7.790		66	2015
St Erth	England	River	Anadromous	msats	23	43	0.620	0.620	6.200		66	2015
Porthcocllum	England	River	Anadromous	msats	23	39	0.610	0.610	6.230		66	2015
Drym Farm	England	River	Anadromous	msats	23	42	0.650	0.650	6.680		66	2015
Clowance wood	England	River	Anadromous	msats	23	27	0.640	0.630	6.340		66	2015
Cuccurian	England	River	Anadromous	msats	23	46	0.680	0.650	6.960		66	2015
Trythogga	England	River	Anadromous	msats	23	45	0.740	0.740	9.360		66	2015
Noongallas	England	River	Anadromous	msats	23	45	0.700	0.700	7.300		66	2015
Drym Farm	England	River	Anadromous	msats	7	30			7.620	53.1	67	2011
Binnerton	England		Anadromous		7	25			5.610	27.3	67	2011
Relubbus	England				7	30			6.900	80.8	67	2011
St Erth	England				7	36			8.110	20.9	67	2011
Tehidy Brook	England				7	39			8.440	54.2	67	2011
Vellens River	Denmark				7	50	0.562	0.669	5.857	47.9	68	2003

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Blykobbe River	Denmark				7	50	0.609	0.674	5.571	24.3	68	2003
Døndals River	Denmark		Anadromous		7	50	0.580	0.563	4.143	44.5	68	2003
Tejn River	Denmark		Anadromous		7	48	0.542	0.608	6.143	57.7	68	2003
Læsaa River	Denmark		Anadromous		7	50	0.669	0.626	5.000		68	2003
Grødeby River	Denmark		Anadromous		7	40	0.621	0.620	4.571		68	2003
Baggeaa River	Denmark	River	Anadromous	msats	7	40	0.595	0.648	6.000		68	2003
Vellens River	Denmark	River	Anadromous	msats	7	22	0.688	0.667	5.143		68	2003
Otra at Evje	Norway	River	FW resident	allozyme	9	122	0.208	0.185	1.800		69	1997
Bjornes	Norway	Lake	FW resident	allozyme	9	76	0.190	0.242	1.700		69	1997
Brumunda	Norway	River	FW resident	allozyme	9	87	0.076	0.075	1.400		69	1997
Otra at Bygland	Norway	River	FW resident	allozyme	9	95	0.203	0.188	1.600		69	1997
Tunhovdfjorden	Norway	Lake	FW resident	allozyme	9	45	0.191	0.206	1.700		69	1997
Otra at Vennesla	Norway	River	FW resident	allozyme	9	41	0.291	0.242	1.700		69	1997
Aurlandselva	Norway	River	Anadromous	allozyme	9	87	0.177	0.157	1.800		69	1997
Langangsvassdraget	Norway	River	Anadromous	allozyme	9	60	0.193	0.179	1.700		69	1997
Øyreselva	Norway	River	Anadromous	allozyme	9	102	0.239	0.211	1.800		69	1997
Årungselva	Norway	River	Anadromous	allozyme	9	19	0.185	0.153	1.600		69	1997
Svartavasstjønn	Norway	Lake	FW resident	allozyme	22	77	0.025				70	1987
Vistula	Poland	River	Anadromous	msats	5	40	0.713	0.751	7.600		71	2002
Rega	Poland	River	Anadromous	msats	5	40	0.665	0.750	8.000		71	2002
Rega	Poland	River	Anadromous	msats	5	40	0.708	0.735	6.600		71	2002
Skjern River	Denmark	River	Anadromous	msats	8	62	0.689	0.690	5.980		72	2006
Videbæk	Denmark	River	FW resident	msats	8	23	0.460	0.449	2.970		72	2006
Lille Skærbæk	Denmark	River	FW resident	msats	8	75	0.560	0.600	4.660		72	2006
Sønder Felding	Denmark		FW resident		8	42	0.518	0.543	3.740		72	2006
Storaa River	Denmark				8	29	0.658	0.694	6.020		72	2006
Torneälven	Sweden				10	151		0.680	6.220		73	2015
Kalixälven	Sweden				10	48		0.660	5.470		73	2015
Piteälven	Sweden				10	38		0.720	6.320		73	2015

Byskeälven	Sweden				10	23	0.730	6.570	73	2015
Säverå	Sweden		Anadromous		10	54	0.720	6.460	73	2015
ôreälven	Sweden		Anadromous		10	32	0.710	6.110	73	2015
Bråviken	Sweden		Anadromous		10	52	0.720	6.460	73	2015
Emån	Sweden		Anadromous		10	54	0.700	6.690	73	2015
Mörrumsån	Sweden	River	Anadromous	msats	10	29	0.680	6.220	73	2015
Vähäjoki	Finland	River	Anadromous	msats	16	19		5.900	74, 75	2013
Purilanjoki	Finland	River	Anadromous	msats	16	15		1.700	74, 75	2013
Helikanjok	Finland	River	Anadromous	msats	16	30		4.600	74, 75	2013
Punassuon Lohoja	Finland	River	Anadromous	msats	16	16		2.400	74, 75	2013
Kiskonjoki upstream	Finland	River	FW resident	msats	16	38		3.400	74, 75	2013
Kiskonjoki-Perinönjoki downstream	Finland	River	Anadromous	msats	16	49		4.300	74, 75	2013
Kiskonjoki-Perinönjoki upstream	Finland	River	FW resident	msats	16	25		5.700	74, 75	2013
Karjaanjoki Mustionjoki	Finland	River	Anadromous	msats	16	23		3.000	74, 75	2013
Ingarskilanjoki	Finland	River	Anadromous	msats	16	186		4.500	74, 75	2013
Siuntionjoki	Finland	River	Anadromous	msats	16	54		4.200	74, 75	2013
Siuntionjoki Passilankoski	Finland	River	Anadromous	msats	16	15		4.700	74, 75	2013
Mankinjoki	Finland	River	Anadromous	msats	16	130		5.200	74, 75	2013
Espoonjoki	Finland	River	Anadromous	msats	16	72		4.800	74, 75	2013
Sipoonjoki	Finland	River	Anadromous	msats	16	46		3.000	74, 75	2013
Mustijoki	Finland	River	FW resident	msats	16	31		2.400	74, 75	2013
Pervoonjoki	Finland	River	FW resident	msats	16	51		4.400	74, 75	2013
Virojoki	Finland	River	Anadromous	msats	16	80		2.900	74, 75	2013
Urpalanjoki	Finland/Russia	River	Anadromous	msats	16	40		6.200	74, 75	2013
Santajoki	Finland/Russia		Anadromous		16	19		4.400	74, 75	2013

(*Continued*)

Location	Country	Habitat	Life history	Marker type	Marker no	Individuals	Ho	He	AR	Ne	Reference	Publ year
Rakkolanjoki	Finland/Russia				16			13		3.300	74, 75	2013
Mustajoki	Finland/Russia				16			376		4.700	74, 75	2013
Kilpeenjoki	Finland/Russia				16			11		3.600	74, 75	2013
Notkopuro	Russia				16			51		5.600	74, 75	2013
Inojoki	Russia				16				25	5.700	74, 75	2013
Pikkuvammeljoki	Russia	River	Anadromous	msats	16				49	4.900	74, 75	2013
Vammeljoki	Russia	River	Anadromous	msats	16				39	5.400	74, 75	2013
Kuokkalanpuro	Russia	River	Anadromous	msats	16				23	5.500	74, 75	2013
Rajajoki	Russia	River	Anadromous	msats	16				20	4.500	74, 75	2013
Luga	Russia	River	Anadromous	msats	16				59	4.900	74, 75	2013

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Slupia River	Vistula River	0	SNP	39	0.130		2	Poland	1	2013
Bornholm	Slupia River	0	SNP	23	0.085		2	Baltic	2	2014
Bornholm	Vistula River	0	SNP	23	0.063		2	Baltic	2	2014
Bornholm	Neman River	0	SNP	23	0.089		2	Baltic	2	2014
Bornholm	Riguldi River	0	SNP	23	0.023		2	Baltic	2	2014
Bornholm	Loo River	0	SNP	23	0.085		2	Baltic	2	2014
Bornholm	Valkla River	0	SNP	23	0.071		2	Baltic	2	2014
Bornholm	Jukkola River	0	SNP	23	0.126		2	Baltic	2	2014
Bornholm	Rompoti River	0	SNP	23	0.157		2	Baltic	2	2014
Slupia River	Vistula River	0	SNP	23	0.010		2	Baltic	2	2014
Slupia River	Neman River	0	SNP	23	0.030		2	Baltic	2	2014
Slupia River	Riguldi River	0	SNP	23	0.078		2	Baltic	2	2014
Slupia River	Loo River	0	SNP	23	0.129		2	Baltic	2	2014
Slupia River	Valkla River	0	SNP	23	0.078		2	Baltic	2	2014
Slupia River	Jukkola River	0	SNP	23	0.101		2	Baltic	2	2014
Slupia River	Rompoti River	0	SNP	23	0.174		2	Baltic	2	2014
Vistula River	Neman River	0	SNP	23	0.008		2	Baltic	2	2014
Vistula River	Riguldi River	0	SNP	23	0.061		2	Baltic	2	2014
Vistula River	Loo River	0	SNP	23	0.099		2	Baltic	2	2014
Vistula River	Valkla River	0	SNP	23	0.064		2	Baltic	2	2014
Vistula River	Jukkola River	0	SNP	23	0.091		2	Baltic	2	2014
Vistula River	Rompoti River	0	SNP	23	0.163		2	Baltic	2	2014
Neman River	Riguldi River	0	SNP	23	0.065		2	Baltic	2	2014
Neman River	Loo River	0	SNP	23	0.116		2	Baltic	2	2014
Neman River	Valkla River	0	SNP	23	0.050		2	Baltic	2	2014
Neman River	Jukkola River	0	SNP	23	0.065		2	Baltic	2	2014
Neman River	Rompoti River	0	SNP	23	0.141		2	Baltic	2	2014

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Riguldi River	Loo River	0	SNP	23	0.093		2	Baltic	2	2014
Riguldi River	Valkla River	0	SNP	23	0.056		2	Baltic	2	2014
Riguldi River	Jukkola River	0	SNP	23	0.089		2	Baltic	2	2014
Riguldi River	Rompoti River	0	SNP	23	0.140		2	Baltic	2	2014
Loo River	Valkla River	0	SNP	23	0.052		2	Baltic	2	2014
Loo River	Jukkola River	0	SNP	23	0.132		2	Baltic	2	2014
Loo River	Rompoti River		SNP	23	0.116		2	Baltic	2	2014
Valkla River	Jukkola River		SNP	23	0.063		2	Baltic	2	2014
Valkla River	Rompoti River		SNP	23	0.089		2	Baltic	2	2014
Jukkola River	Rompoti River		SNP	23	0.073		2	Baltic	2	2014
Karup River	Tjærbæk River			7	0.038			Denmark	4	2000
Karup River	Flads River			7	0.043			Denmark	4	2000
Tjærbæk River	Flads River			7	0.037			Denmark	4	2000
Jølster R1	Jølster L1				0.030		1	Norway	6	2009
Jølster R1	Jølster L2				0.024		1	Norway	6	2009
Jølster R1	Jølster L3				0.019		1	Norway	6	2009
Jølster R1	Jølster R2				0.002		1	Norway	6	2009
Jølster R1	Røldal L1	1			0.361		2	Norway	6	2009
Jølster R1	Røldal L2	1			0.372		2	Norway	6	2009
Jølster R1	Røldal L3	1			0.391		2	Norway	6	2009
Jølster R1	Røldal R1	1	msats	9	0.266		2	Norway	6	2009
Jølster R1	Røldal R2	1	msats	9	0.258		2	Norway	6	2009
Jølster R1	Olden R1	1	msats	9	0.214		2	Norway	6	2009
Jølster R1	Olden L1	1	msats	9	0.266		2	Norway	6	2009
Jølster R1	Olden L2	1	msats	9	0.229		2	Norway	6	2009
Jølster L1	Jølster L2	0	msats	9	0.014		1	Norway	6	2009
Jølster L1	Jølster L3	0	msats	9	0.017		1	Norway	6	2009

Jølster L1	Jølster R2	0	msats	9	0.008	1	Norway	6	2009
Jølster L1	Røldal L1	1	msats	9	0.391	2	Norway	6	2009
Jølster L1	Røldal L2	1	msats	9	0.403	2	Norway	6	2009
Jølster L1	Røldal L3	1	msats	9	0.421	2	Norway	6	2009
Jølster L1	Røldal R1	1	msats	9	0.293	2	Norway	6	2009
Jølster L1	Røldal R2	1	msats	9	0.279	2	Norway	6	2009
Jølster L1	Olden R1	1	msats	9	0.209	2	Norway	6	2009
Jølster L1	Olden L1	1	msats	9	0.258	2	Norway	6	2009
Jølster L1	Olden L2	1	msats	9	0.221	2	Norway	6	2009
Jølster L2	Jølster L3	0	msats	9	0.001	1	Norway	6	2009
Jølster L2	Jølster R2	0	msats	9	0.030	2	Norway	6	2009
Jølster L2	Røldal L1	1	msats	9	0.390	2	Norway	6	2009
Jølster L2	Røldal L2	1	msats	9	0.399	2	Norway	6	2009
Jølster L2	Røldal L3	1	msats	9	0.420	2	Norway	6	2009
Jølster L2	Røldal R1	1	msats	9	0.294	2	Norway	6	2009
Jølster L2	Røldal R2	1	msats	9	0.282	2	Norway	6	2009
Jølster L2	Olden R1	1	msats	9	0.245	2	Norway	6	2009
Jølster L2	Olden L1	1	msats	9	0.297	2	Norway	6	2009
Jølster L2	Olden L2	1	msats	9	0.251	2	Norway	6	2009
Jølster L3	Jølster R2	0	msats	9	0.024	1	Norway	6	2009
Jølster L3	Røldal L1	1	msats	9	0.359	2	Norway	6	2009
Jølster L3	Røldal L2	1		9	0.368	2	Norway	6	2009
Jølster L3	Røldal L3	1		9	0.396	2	Norway	6	2009
Jølster L3	Røldal R1	1		9	0.251	2	Norway	6	2009
Jølster L3	Røldal R2	1		9	0.242	2	Norway	6	2009
Jølster L3	Olden R1	1		9	0.218		Norway	6	2009
Jølster L3	Olden L1	1		9	0.270		Norway	6	2009
Jølster L3	Olden L2	1		9	0.227		Norway	6	2009

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Jølster R2	Røldal L1	1			0.376			Norway	6	2009
Jølster R2	Røldal L2	1			0.388			Norway	6	2009
Jølster R2	Røldal L3	1			0.407			Norway	6	2009
Jølster R2	Røldal R1	1			0.275			Norway	6	2009
Jølster R2	Røldal R2	1			0.264			Norway	6	2009
Jølster R2	Olden R1	1			0.203			Norway	6	2009
Jølster R2	Olden L1	1			0.255			Norway	6	2009
Jølster R2	Olden L2	1	msats	9	0.219		2	Norway	6	2009
Røldal L1	Røldal L2	0	msats	9	0.000		1	Norway	6	2009
Røldal L1	Røldal L3	0	msats	9	0.005		1	Norway	6	2009
Røldal L1	Røldal R1	0	msats	9	0.082		1	Norway	6	2009
Røldal L1	Røldal R2	0	msats	9	0.079		1	Norway	6	2009
Røldal L1	Olden R1	1	msats	9	0.368		2	Norway	6	2009
Røldal L1	Olden L1	1	msats	9	0.408		2	Norway	6	2009
Røldal L1	Olden L2	1	msats	9	0.370		2	Norway	6	2009
Røldal L2	Røldal L3	0	msats	9	0.006		1	Norway	6	2009
Røldal L2	Røldal R1	0	msats	9	0.083		1	Norway	6	2009
Røldal L2	Røldal R2	0	msats	9	0.081		1	Norway	6	2009
Røldal L2	Olden R1	1	msats	9	0.378		2	Norway	6	2009
Røldal L2	Olden L1	1	msats	9	0.420		2	Norway	6	2009
Røldal L2	Olden L2	1	msats	9	0.382		2	Norway	6	2009
Røldal L3	Røldal R1	0	msats	9	0.102		1	Norway	6	2009
Røldal L3	Røldal R2	0	msats	9	0.096		1	Norway	6	2009
Røldal L3	Olden R1	1	msats	9	0.396		2	Norway	6	2009
Røldal L3	Olden L1	1	msats	9	0.434		2	Norway	6	2009
Røldal L3	Olden L2	1	msats	9	0.397		2	Norway	6	2009

Røldal R1	Røldal R2	0	msats	9	0.007		1	Norway	6	2009
Røldal R1	Olden R1	1	msats	9	0.247		2	Norway	6	2009
Røldal R1	Olden L1	1	msats	9	0.288		2	Norway	6	2009
Røldal R1	Olden L2	1	msats	9	0.251		2	Norway	6	2009
Røldal R2	Olden R1	1	msats	9	0.253		2	Norway	6	2009
Røldal R2	Olden L1	1	msats	9	0.278		2	Norway	6	2009
Røldal R2	Olden L2	1	msats	9	0.235		2	Norway	6	2009
Olden R1	Olden L1	0	msats	9	0.065		1	Norway	6	2009
Olden R1	Olden L2	0	msats	9	0.051		1	Norway	6	2009
Olden L1	Olden L2		msats	9	0.059		1	Norway	6	2009
sonaghen	gillaroo		allozyme	46	0.030		1	Irland	7	1991
sonaghen	ferox		allozyme	46	0.118		1	Irland	7	1991
gillaroo	ferox		allozyme	46	0.085		1	Irland	7	1991
Vejle	Kovads			9	0.053			Denmark	8	2002
Vejle	Karup			9	0.025			Denmark	8	2002
Vejle	Kolding			9	0.002			Denmark	8	2002
Vejle	Odder				0.040			Denmark	8	2002
Kovads	Karup				0.052			Denmark	8	2002
Kovads	Kolding				0.049			Denmark	8	2002
Kovads	Odder				0.039			Denmark	8	2002
Karup	Kolding				0.024			Denmark	8	2002
Karup	Odder				0.051			Denmark	8	2002
Kolding	Odder				0.041			Denmark	8	2002
Haravattsån I	Haravattsån II	0	allozyme	74	0.133	2	1	Sweden	13	2003
Skansbekken	Bausbakkelva	0	msats	8	0.031		2	Norway	22	2014
Skansbekken	Brumunda	0	msats	8	0.025		2	Norway	22	2014
Skansbekken	Brumunda	0	msats	8	0.029		2	Norway	22	2014

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Skansbekken	Vesleelva	0	msats	8	0.031		2	Norway	22	2014
Skansbekken	Flagstadelva	0	msats	8	0.040		2	Norway	22	2014
Skansbekken	Flagstadelva	0	msats	8	0.023		2	Norway	22	2014
Skansbekken	Flagstadelva	0	msats	8	0.015		2	Norway	22	2014
Skansbekken	Finsalbekken	0	msats	8	0.030		2	Norway	22	2014
Skansbekken	Måsabekken	0	msats	8	0.038		2	Norway	22	2014
Skansbekken	Måsabekken	0	msats	8	0.043		2	Norway	22	2014
Skansbekken	Vikselva	0	msats	8	0.058		2	Norway	22	2014
Skansbekken	Vikselva	0	msats	8	0.029		2	Norway	22	2014
Skansbekken	Labelva	0	msats	8	0.083		2	Norway	22	2014
Skansbekken	Labelva	0	msats	8	0.110		2	Norway	22	2014
Bausbakkelva	Brumunda	0	msats	8	0.024		2	Norway	22	2014
Bausbakkelva	Brumunda	0	msats	8	0.012		2	Norway	22	2014
Bausbakkelva	Vesleelva	0	msats	8	0.019		2	Norway	22	2014
Bausbakkelva	Flagstadelva	0	msats	8	0.023		2	Norway	22	2014
Bausbakkelva	Flagstadelva	0	msats	8	0.024		2	Norway	22	2014
Bausbakkelva	Flagstadelva	0	msats	8	0.026		2	Norway	22	2014
Bausbakkelva	Finsalbekken	0	msats	8	0.040		2	Norway	22	2014
Bausbakkelva	Måsabekken	0	msats	8	0.026		2	Norway	22	2014
Bausbakkelva	Måsabekken	0	msats	8	0.031		2	Norway	22	2014
Bausbakkelva	Vikselva	0	msats	8	0.030		2	Norway	22	2014
Bausbakkelva	Vikselva	0	msats	8	0.016		2	Norway	22	2014
Bausbakkelva	Labelva	0	msats	8	0.076		2	Norway	22	2014
Bausbakkelva	Labelva	0	msats	8	0.113		2	Norway	22	2014
Brumunda	Vesleelva			8	0.023		2	Norway	22	2014
Brumunda	Flagstadelva			8	0.019		2	Norway	22	2014

Brumunda	Flagstadelva			8	0.010	2	Norway	22	2014
Brumunda	Flagstadelva			8	0.010	2	Norway	22	2014
Brumunda	Finsalbekken			8	0.015		Norway	22	2014
Brumunda	Måsabekken			8	0.030		Norway	22	2014
Brumunda	Måsabekken			8	0.048		Norway	22	2014
Brumunda	Vikselva			8	0.038		Norway	22	2014
Brumunda	Vikselva			8	0.028		Norway	22	2014
Brumunda	Labelva			8	0.081		Norway	22	2014
Brumunda	Labelva			8	0.116		Norway	22	2014
Vesleelva	Flagstadelva			8	0.021		Norway	22	2014
Vesleelva	Flagstadelva			8	0.016		Norway	22	2014
Vesleelva	Flagstadelva			8	0.009		Norway	22	2014
Vesleelva	Finsalbekken	0	msats	8	0.019	2	Norway	22	2014
Vesleelva	Måsabekken	0	msats	8	0.002	2	Norway	22	2014
Vesleelva	Måsabekken	0	msats	8	0.031	2	Norway	22	2014
Vesleelva	Vikselva	0	msats	8	0.024	2	Norway	22	2014
Vesleelva	Vikselva	0	msats	8	0.007	2	Norway	22	2014
Vesleelva	Labelva	0	msats	8	0.057	2	Norway	22	2014
Vesleelva	Labelva	0	msats	8	0.095	2	Norway	22	2014
Brumunda	Vesleelva	0	msats	8	0.012	2	Norway	22	2014
Brumunda	Flagstadelva	0	msats	8	0.016	2	Norway	22	2014
Brumunda	Flagstadelva	0	msats	8	0.014	2	Norway	22	2014
Brumunda	Flagstadelva	0	msats	8	0.003	2	Norway	22	2014
Brumunda	Finsalbekken	0	msats	8	0.021	2	Norway	22	2014
Brumunda	Måsabekken	0	msats	8	0.014	2	Norway	22	2014
Brumunda	Måsabekken	0	msats	8	0.033	2	Norway	22	2014
Brumunda	Vikselva	0	msats	8	0.030	2	Norway	22	2014

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Brumunda	Vikselva	0	msats	8	0.015		2	Norway	22	2014
Brumunda	Labelva	0	msats	8	0.077		2	Norway	22	2014
Brumunda	Labelva	0	msats	8	0.116		2	Norway	22	2014
Flagstadelva	Finsalbekken	0	msats	8	0.021		2	Norway	22	2014
Flagstadelva	Måsabekken	0	msats	8	0.023		2	Norway	22	2014
Flagstadelva	Måsabekken	0	msats	8	0.046		2	Norway	22	2014
Flagstadelva	Vikselva	0	msats	8	0.041		2	Norway	22	2014
Flagstadelva	Vikselva	0	msats	8	0.026		2	Norway	22	2014
Flagstadelva	Labelva	0	msats	8	0.089		2	Norway	22	2014
Flagstadelva	Labelva	0	msats	8	0.134		2	Norway	22	2014
Flagstadelva	Finsalbekken	0	msats	8	0.019		2	Norway	22	2014
Flagstadelva	Måsabekken	0	msats	8	0.031		2	Norway	22	2014
Flagstadelva	Måsabekken	0	msats	8	0.046		2	Norway	22	2014
Flagstadelva	Vikselva			8	0.029		2	Norway	22	2014
Flagstadelva	Vikselva			8	0.027		2	Norway	22	2014
Flagstadelva	Labelva			8	0.063		2	Norway	22	2014
Flagstadelva	Labelva			8	0.101		2	Norway	22	2014
Flagstadelva	Finsalbekken			8	0.022			Norway	22	2014
Flagstadelva	Måsabekken			8	0.020			Norway	22	2014
Flagstadelva	Måsabekken			8	0.040			Norway	22	2014
Flagstadelva	Vikselva			8	0.031			Norway		2014
Flagstadelva	Vikselva			8	0.020			Norway	22	2014
Flagstadelva	Labelva			8	0.053			Norway	22	2014
Flagstadelva	Labelva			8	0.094			Norway	22	2014
Finsalbekken	Måsabekken			8	0.023			Norway	22	2014
Finsalbekken	Måsabekken			8	0.042			Norway	22	2014

Finsalbekken	Vikselva			8	0.039			Norway	22	2014
Finsalbekken	Vikselva	0	msats	8	0.029		2	Norway	22	2014
Finsalbekken	Labelva	0	msats	8	0.079		2	Norway	22	2014
Finsalbekken	Labelva	0	msats	8	0.107		2	Norway	22	2014
Måsabekken	Vikselva	0	msats	8	0.019		2	Norway	22	2014
Måsabekken	Vikselva	0	msats	8	0.011		2	Norway	22	2014
Måsabekken	Labelva	0	msats	8	0.063		2	Norway	22	2014
Måsabekken	Labelva	0	msats	8	0.098		2	Norway	22	2014
Måsabekken	Vikselva	0	msats	8	0.010		2	Norway	22	2014
Måsabekken	Vikselva	0	msats	8	0.015		2	Norway	22	2014
Måsabekken	Labelva	0	msats	8	0.082		2	Norway	22	2014
Måsabekken	Labelva	0	msats	8	0.114		2	Norway	22	2014
Vikselva	Labelva	0	msats	8	0.048		2	Norway	22	2014
Vikselva	Labelva	0	msats	8	0.081		2	Norway	22	2014
Vikselva	Labelva	0	msats	8	0.038		2	Norway	22	2014
Vikselva	Labelva	0	msats	8	0.081		2	Norway	22	2014
Färsån B	Färsån C	0	msats	5	0.015	1.45	1	Sweden	23	2000
Färsån B	Färsån D	0	msats	5	0.005	2.45	1	Sweden	23	2000
Färsån B	Färsån E	0	msats	5	0.014	6.2	1	Sweden	23	2000
Färsån B	Färsån F	0	msats	5	0.015	8	1	Sweden	23	2000
Färsån B	Färsån G	0	msats	5	0.060	10	1	Sweden	23	2000
Färsån B	Färsån C	0	msats	5	0.029	1.45	1	Sweden	23	2000
Färsån B	Färsån D	0	msats	5	0.000	2.45	1	Sweden	23	2000
Färsån B	Färsån E	0	msats	5	0.033	6.2	1	Sweden	23	2000
Färsån B	Färsån F	0	msats	5	0.018	8	1	Sweden	23	2000
Färsån B	Färsån G	0	msats	5	0.049	10	1	Sweden	23	2000
Färsån C	Färsån D	0	msats	5	0.020	1	1	Sweden	23	2000

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Färsån C	Färsån E	0	msats	5	0.011	4.75	1	Sweden	23	2000
Färsån C	Färsån F	0	msats	5	0.015	6.5	1	Sweden	23	2000
Färsån C	Färsån G			5	0.054	8.5		Sweden	23	2000
Färsån C	Färsån D			5	0.024	1		Sweden	23	2000
Färsån C	Färsån E			5	0.021	4.75		Sweden	23	2000
Färsån C	Färsån F			5	0.012	6.5		Sweden	23	2000
Färsån C	Färsån G			5	0.053	8.5		Sweden	23	2000
Färsån D	Färsån E			5	0.027	3.75		Sweden	23	2000
Färsån D	Färsån F			5	0.017	5.5		Sweden	23	2000
Färsån D	Färsån G			5	0.062	7.5		Sweden		2000
Färsån D	Färsån E			5	0.036	3.75		Sweden	23	2000
Färsån D	Färsån F			5	0.013	5.5		Sweden	23	2000
Färsån D	Färsån G			5	0.035	7.5		Sweden	23	2000
Färsån E	Färsån F			5	0.002	1.75		Sweden	23	2000
Färsån E	Färsån G			5	0.027	3.75		Sweden	23	2000
Färsån E	Färsån F			5	0.000	1.75		Sweden	23	2000
Färsån E	Färsån G	0	msats	5	0.015	3.75	1	Sweden	23	2000
Färsån F	Färsån G	0	msats	5	0.009	2	1	Sweden	23	2000
Färsån F	Färsån G	0	msats	5	0.007	2	1	Sweden	23	2000
Amm Brook, Amm house weir	Ashburn, Belford Hill	1	msats	9	0.050		1	England	24	2009
Amm Brook, Amm house weir	Dury Brook, Dury Farm	0	msats	9	0.021		1	England	24	2009
Amm Brook, Amm house weir	East Dart, Postbridge	0	msats	9	0.016		1	England	24	2009
Amm Brook, Amm house weir	East Webburn, Bagpark Estate	0	msats	9	0.023		1	England	24	2009
Amm Brook, Amm house weir	East Webburn, Dunstone Bridge	0	msats	9	0.025		1	England	24	2009
Amm Brook, Amm house weir	East Webburn, Veton Bridge	0	msats	9	0.021		1	England	24	2009
Amm Brook, Amm house weir	East Webburn, Wooder Manor	0	msats	9	0.023		1	England	24	2009
Amm Brook, Amm house weir	Gatacombe River	1	msats	9	0.050		1	England	24	2009

Amm Brook, Amm house weir	Harbourne, Hatcheries Fish Farm	0	msats	9	0.013	1	England	24	2009
Amm Brook, Amm house weir	River Hems	0	msats	9	0.000	1	England	24	2009
Amm Brook, Amm house weir	Holly Brook	0	msats	9	0.014	1	England	24	2009
Amm Brook, Amm house weir	Cherry Brook, Lower Bridge	0	msats	9	0.019	1	England	24	2009
Amm Brook, Amm house weir	Ruddycleave, Bowden Farm	1	msats	9	0.076	1	England	24	2009
Amm Brook, Amm house weir	Ruddycleave, Ruddycleave Cottage	1	msats	9	0.068	1	England	24	2009
Amm Brook, Amm house weir	Ruddycleave, Pudsham Down	1	msats	9	0.092	1	England	24	2009
Amm Brook, Amm house weir	River Swincombe, Wydemeet	0	msats	9	0.016	1	England	24	2009
Amm Brook, Amm house weir	Cherry Brook, Upper Bridge	0	msats	9	0.016	1	England	24	2009
Amm Brook, Amm house weir	West Dart, Cockern Tor	0	msats	9	0.021	1	England	24	2009
Amm Brook, Amm house weir	River Webburn, Mistresses Piece	0	msats	9	0.029	1	England	24	2009
Amm Brook, Amm house weir	West Webburn, Pondsworthy Bridge	0	msats	9	0.021	1	England	24	2009
Amm Brook, Amm house weir	West Webburn, Lower Cator Bridge	0	msats	9	0.021	1	England	24	2009
Ashburn, Belford Hill	Dury Brook, Dury Farm	1	msats	9	0.091	1	England	24	2009
Ashburn, Belford Hill	East Dart, Postbridge	1	msats	9	0.068	1	England	24	2009
Ashburn, Belford Hill	East Webburn, Bagpark Estate	1	msats	9	0.085	1	England	24	2009
Ashburn, Belford Hill	East Webburn, Dunstone Bridge	1	msats	9	0.068	1	England	24	2009
Ashburn, Belford Hill	East Webburn, Veton Bridge	1		24	0.054				
Ashburn, Belford Hill	East Webburn, Wooder Manor	1		24	0.077				
Ashburn, Belford Hill	Gatacombe River	1		24	0.067				
Ashburn, Belford Hill	Harbourne, Hatcheries Fish Farm	1		24	0.068				
Ashburn, Belford Hill	River Hems	1		24	0.041				
Ashburn, Belford Hill	Holly Brook	1		24	0.050				
Ashburn, Belford Hill	Cherry Brook, Lower Bridge	1			0.077				
Ashburn, Belford Hill	Ruddycleave, Bowden Farm	1			0.119				
Ashburn, Belford Hill	Ruddycleave, Ruddycleave Cottage	1			0.122			24	
Ashburn, Belford Hill	Ruddycleave, Pudsham Down	1			0.153			24	
Ashburn, Belford Hill	River Swincombe, Wydemeet	1			0.079			24	

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Ashburn, Belford Hill	Cherry Brook, Upper Bridge	1			0.081				24	
Ashburn, Belford Hill	West Dart, Cockern Tor	1			0.065				24	
Ashburn, Belford Hill	River Webburn, Mistresses Piece	1			0.091				24	
Ashburn, Belford Hill	West Webburn, Pondsworthy Bridge	1	msats	9	0.077		1	England	24	2009
Ashburn, Belford Hill	West Webburn, Lower Cator Bridge	1	msats	9	0.099		1	England	24	2009
Dury Brook, Dury Farm	East Dart, Postbridge	0	msats	9	0.021		1	England	24	2009
Dury Brook, Dury Farm	East Webburn, Bagpark Estate	0	msats	9	0.017		1	England	24	2009
Dury Brook, Dury Farm	East Webburn, Dunstone Bridge	0	msats	9	0.021		1	England	24	2009
Dury Brook, Dury Farm	East Webburn, Veton Bridge	0	msats	9	0.020		1	England	24	2009
Dury Brook, Dury Farm	East Webburn, Wooder Manor	0	msats	9	0.012		1	England	24	2009
Dury Brook, Dury Farm	Gatacombe River	1	msats	9	0.086		1	England	24	2009
Dury Brook, Dury Farm	Harbourne, Hatcheries Fish Farm	0	msats	9	0.042		1	England	24	2009
Dury Brook, Dury Farm	River Hems	0	msats	9	0.021		1	England	24	2009
Dury Brook, Dury Farm	Holly Brook	0	msats	9	0.028		1	England	24	2009
Dury Brook, Dury Farm	Cherry Brook, Lower Bridge	0	msats	9	0.013		1	England	24	2009
Dury Brook, Dury Farm	Ruddycleave, Bowden Farm	1	msats	9	0.056		1	England	24	2009
Dury Brook, Dury Farm	Ruddycleave, Ruddycleave Cottage	1	msats	9	0.056		1	England	24	2009
Dury Brook, Dury Farm	Ruddycleave, Pudsham Down	1	msats	9	0.053		1	England	24	2009
Dury Brook, Dury Farm	River Swincombe, Wydemeet	0	msats	9	0.015		1	England	24	2009
Dury Brook, Dury Farm	Cherry Brook, Upper Bridge	0	msats	9	0.012		1	England	24	2009
Dury Brook, Dury Farm	West Dart, Cockern Tor	0	msats	9	0.024		1	England	24	2009
Dury Brook, Dury Farm	River Webburn, Mistresses Piece	0	msats	9	0.013		1	England	24	2009
Dury Brook, Dury Farm	West Webburn, Pondsworthy Bridge	0	msats	9	0.013		1	England	24	2009
Dury Brook, Dury Farm	West Webburn, Lower Cator Bridge	0	msats	9	0.013		1	England	24	2009
East Dart, Postbridge	East Webburn, Bagpark Estate	0	msats	9	0.023		1	England	24	2009
East Dart, Postbridge	East Webburn, Dunstone Bridge	0	msats	9	0.016		1	England	24	2009

East Dart, Postbridge	East Webburn, Veton Bridge	0	msats	9	0.013	1	England	24	2009
East Dart, Postbridge	East Webburn, Wooder Manor	0	msats	9	0.021	1	England	24	2009
East Dart, Postbridge	Gatacombe River	1	msats	9	0.073	1	England	24	2009
East Dart, Postbridge	Harbourne, Hatcheries Fish Farm	0	msats	9	0.040	1	England	24	2009
East Dart, Postbridge	River Hems	0	msats	9	0.020	1	England	24	2009
East Dart, Postbridge	Holly Brook	0			0.016			24	
East Dart, Postbridge	Cherry Brook, Lower Bridge	0			0.007			24	
East Dart, Postbridge	Ruddycleave, Bowden Farm	1			0.072			24	
East Dart, Postbridge	Ruddycleave, Ruddycleave Cottage	1			0.061			24	
East Dart, Postbridge	Ruddycleave, Pudsham Down	1			0.095			24	
East Dart, Postbridge	River Swincombe, Wydemeet	0			0.013			24	
East Dart, Postbridge	Cherry Brook, Upper Bridge	0			0.008				
East Dart, Postbridge	West Dart, Cockern Tor	0			0.013			24	
East Dart, Postbridge	River Webburn, Mistresses Piece	0			0.023			24	
East Dart, Postbridge	West Webburn, Pondsworthy Bridge	0			0.033			24	
East Dart, Postbridge	West Webburn, Lower Cator Bridge	0			0.026			24	
East Webburn, Bagpark Estate	East Webburn, Dunstone Bridge	0			0.005			24	
East Webburn, Bagpark Estate	East Webburn, Veton Bridge	0			0.007			24	
East Webburn, Bagpark Estate	East Webburn, Wooder Manor	0			0.000			24	
East Webburn, Bagpark Estate	Gatacombe River	1	msats	9	0.087	1	England	24	2009
East Webburn, Bagpark Estate	Harbourne, Hatcheries Fish Farm	0	msats	9	0.040	1	England	24	2009
East Webburn, Bagpark Estate	River Hems	0	msats	9	0.020	1	England	24	2009
East Webburn, Bagpark Estate	Holly Brook	0	msats	9	0.029	1	England	24	2009
East Webburn, Bagpark Estate	Cherry Brook, Lower Bridge	0	msats	9	0.024	1	England	24	2009
East Webburn, Bagpark Estate	Ruddycleave, Bowden Farm	1	msats	9	0.039	1	England	24	2009
East Webburn, Bagpark Estate	Ruddycleave, Ruddycleave Cottage	1	msats	9	0.026	1	England	24	2009
East Webburn, Bagpark Estate	Ruddycleave, Pudsham Down	1	msats	9	0.059	1	England	24	2009

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
East Webburn, Bagpark Estate	River Swincombe, Wydemeet	0	msats	9	0.024		1	England	24	2009
East Webburn, Bagpark Estate	Cherry Brook, Upper Bridge	0	msats	9	0.020		1	England	24	2009
East Webburn, Bagpark Estate	West Dart, Cockern Tor	0	msats	9	0.034		1	England	24	2009
East Webburn, Bagpark Estate	River Webburn, Mistresses Piece	0	msats	9	0.000		1	England	24	2009
East Webburn, Bagpark Estate	West Webburn, Pondsworthy Bridge	0	msats	9	0.011		1	England	24	2009
East Webburn, Bagpark Estate	West Webburn, Lower Cator Bridge	0	msats	9	0.015		1	England	24	2009
East Webburn, Dunstone Bridge	East Webburn, Veton Bridge	0	msats	9	0.007		1	England	24	2009
East Webburn, Dunstone Bridge	East Webburn, Wooder Manor	0	msats	9	0.004		1	England	24	2009
East Webburn, Dunstone Bridge	Gatacombe River	1	msats	9	0.079		1	England	24	2009
East Webburn, Dunstone Bridge	Harbourne, Hatcheries Fish Farm	0	msats	9	0.032		1	England	24	2009
East Webburn, Dunstone Bridge	River Hems	0	msats	9	0.018		1	England	24	2009
East Webburn, Dunstone Bridge	Holly Brook	0	msats	9	0.019		1	England	24	2009
East Webburn, Dunstone Bridge	Cherry Brook, Lower Bridge	0	msats	9	0.019		1	England	24	2009
East Webburn, Dunstone Bridge	Ruddycleave, Bowden Farm	1	msats	9	0.045		1	England	24	2009
East Webburn, Dunstone Bridge	Ruddycleave, Ruddycleave Cottage	1	msats	9	0.027		1	England	24	2009
East Webburn, Dunstone Bridge	Ruddycleave, Pudsham Down	1	msats	9	0.078		1	England	24	2009
East Webburn, Dunstone Bridge	River Swincombe, Wydemeet	0	msats	9	0.021		1	England	24	2009
East Webburn, Dunstone Bridge	Cherry Brook, Upper Bridge	0	msats	9	0.017		1	England	24	2009
East Webburn, Dunstone Bridge	West Dart, Cockern Tor	0	msats	9	0.031		1	England	24	2009
East Webburn, Dunstone Bridge	River Webburn, Mistresses Piece	0	msats	9	0.000		1	England	24	2009
East Webburn, Dunstone Bridge	West Webburn, Pondsworthy Bridge	0			0.012				24	
East Webburn, Dunstone Bridge	West Webburn, Lower Cator Bridge	0			0.009				24	
East Webburn, Veton Bridge	East Webburn, Wooder Manor	0			0.004				24	
East Webburn, Veton Bridge	Gatacombe River	1			0.058				24	
East Webburn, Veton Bridge	Harbourne, Hatcheries Fish Farm	0			0.028				24	
East Webburn, Veton Bridge	River Hems	0			0.018				24	

East Webburn, Veton Bridge	Holly Brook	0			0.005				
East Webburn, Veton Bridge	Cherry Brook, Lower Bridge	0			0.020			24	
East Webburn, Veton Bridge	Ruddycleave, Bowden Farm	1			0.046			24	
East Webburn, Veton Bridge	Ruddycleave, Ruddycleave Cottage	1			0.045			24	
East Webburn, Veton Bridge	Ruddycleave, Pudsham Down	1			0.064			24	
East Webburn, Veton Bridge	River Swincombe, Wydemeet	0			0.026			24	
East Webburn, Veton Bridge	Cherry Brook, Upper Bridge	0			0.021			24	
East Webburn, Veton Bridge	West Dart, Cockern Tor	0			0.023			24	
East Webburn, Veton Bridge	River Webburn, Mistresses Piece	0	msats	9	0.008	1	England	24	2009
East Webburn, Veton Bridge	West Webburn, Pondsworthy Bridge	0	msats	9	0.012	1	England	24	2009
East Webburn, Veton Bridge	West Webburn, Lower Cator Bridge	0	msats	9	0.010	1	England	24	2009
East Webburn, Wooder Manor	Gatacombe River	1	msats	9	0.076	1	England	24	2009
East Webburn, Wooder Manor	Harbourne, Hatcheries Fish Farm	0	msats	9	0.045	1	England	24	2009
East Webburn, Wooder Manor	River Hems	0	msats	9	0.017	1	England	24	2009
East Webburn, Wooder Manor	Holly Brook	0	msats	9	0.020	1	England	24	2009
East Webburn, Wooder Manor	Cherry Brook, Lower Bridge	0	msats	9	0.019	1	England	24	2009
East Webburn, Wooder Manor	Ruddycleave, Bowden Farm	1	msats	9	0.044	1	England	24	2009
East Webburn, Wooder Manor	Ruddycleave, Ruddycleave Cottage	1	msats	9	0.031	1	England	24	2009
East Webburn, Wooder Manor	Ruddycleave, Pudsham Down	1	msats	9	0.063	1	England	24	2009
East Webburn, Wooder Manor	River Swincombe, Wydemeet	0	msats	9	0.029	1	England	24	2009
East Webburn, Wooder Manor	Cherry Brook, Upper Bridge	0	msats	9	0.019	1	England	24	2009
East Webburn, Wooder Manor	West Dart, Cockern Tor	0	msats	9	0.034	1	England	24	2009
East Webburn, Wooder Manor	River Webburn, Mistresses Piece	0	msats	9	0.002	1	England	24	2009
East Webburn, Wooder Manor	West Webburn, Pondsworthy Bridge	0	msats	9	0.011	1	England	24	2009
East Webburn, Wooder Manor	West Webburn, Lower Cator Bridge	0	msats	9	0.013	1	England	24	2009
Gatacombe River	Harbourne, Hatcheries Fish Farm	1	msats	9	0.079	1	England	24	2009
Gatacombe River	River Hems	1	msats	9	0.031	1	England	24	2009

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Gatacombe River	Holly Brook	1	msats	9	0.053		1	England	24	2009
Gatacombe River	Cherry Brook, Lower Bridge	1	msats	9	0.077		1	England	24	2009
Gatacombe River	Ruddycleave, Bowden Farm	1	msats	9	0.140		1	England	24	2009
Gatacombe River	Ruddycleave, Ruddycleave Cottage	1	msats	9	0.129		1	England	24	2009
Gatacombe River	Ruddycleave, Pudsham Down	1	msats	9	0.160		1	England	24	2009
Gatacombe River	River Swincombe, Wydemeet	1	msats	9	0.083		1	England	24	2009
Gatacombe River	Cherry Brook, Upper Bridge	1	msats	9	0.072		1	England	24	2009
Gatacombe River	West Dart, Cockern Tor	1	msats	9	0.075		1	England	24	2009
Gatacombe River	River Webburn, Mistresses Piece	1	msats	9	0.086		1	England	24	2009
Gatacombe River	West Webburn, Pondsworthy Bridge	1			0.081				24	
Gatacombe River	West Webburn, Lower Cator Bridge	1			0.086				24	
Harbourne, Hatcheries Fish Farm	River Hems	0			0.011				24	
Harbourne, Hatcheries Fish Farm	Holly Brook	0			0.018				24	
Harbourne, Hatcheries Fish Farm	Cherry Brook, Lower Bridge	0			0.043				24	
Harbourne, Hatcheries Fish Farm	Ruddycleave, Bowden Farm				0.073				24	
Harbourne, Hatcheries Fish Farm	Ruddycleave, Ruddycleave Cottage				0.067					
Harbourne, Hatcheries Fish Farm	Ruddycleave, Pudsham Down				0.112				24	
Harbourne, Hatcheries Fish Farm	River Swincombe, Wydemeet	0			0.027				24	
Harbourne, Hatcheries Fish Farm	Cherry Brook, Upper Bridge	0			0.036				24	
Harbourne, Hatcheries Fish Farm	West Dart, Cockern Tor	0			0.041				24	
Harbourne, Hatcheries Fish Farm	River Webburn, Mistresses Piece	0			0.036				24	
Harbourne, Hatcheries Fish Farm	West Webburn, Pondsworthy Bridge	0			0.023				24	
Harbourne, Hatcheries Fish Farm	West Webburn, Lower Cator Bridge	0			0.027				24	
River Hems	Holly Brook	0	msats	9	0.007		1	England	24	2009
River Hems	Cherry Brook, Lower Bridge	0	msats	9	0.023		1	England	24	2009
River Hems	Ruddycleave, Bowden Farm	1	msats	9	0.071		1	England	24	2009

River Hems	Ruddycleave, Ruddycleave Cottage	1	msats	9	0.066	1	England	24	2009
River Hems	Ruddycleave, Pudsham Down	1	msats	9	0.090	1	England	24	2009
River Hems	River Swincombe, Wydemeet	0	msats	9	0.018	1	England	24	2009
River Hems	Cherry Brook, Upper Bridge	0	msats	9	0.013	1	England	24	2009
River Hems	West Dart, Cockern Tor	0	msats	9	0.018	1	England	24	2009
River Hems	River Webburn, Mistresses Piece	0	msats	9	0.017	1	England	24	2009
River Hems	West Webburn, Pondsworthy Bridge	0	msats	9	0.019	1	England	24	2009
River Hems	West Webburn, Lower Cator Bridge	0	msats	9	0.016	1	England	24	2009
Cherry Brook, Lower Bridge	Ruddycleave, Bowden Farm	1	msats	9	0.054	1	England	24	2009
Cherry Brook, Lower Bridge	Ruddycleave, Ruddycleave Cottage	1	msats	9	0.048	1	England	24	2009
Cherry Brook, Lower Bridge	Ruddycleave, Pudsham Down	1	msats	9	0.071	1	England	24	2009
Cherry Brook, Lower Bridge	River Swincombe, Wydemeet	0	msats	9	0.011	1	England	24	2009
Cherry Brook, Lower Bridge	Cherry Brook, Upper Bridge	0	msats	9	0.000	1	England	24	2009
Cherry Brook, Lower Bridge	West Dart, Cockern Tor	0	msats	9	0.009	1	England	24	2009
Cherry Brook, Lower Bridge	River Webburn, Mistresses Piece	0	msats	9	0.020	1	England	24	2009
Cherry Brook, Lower Bridge	West Webburn, Pondsworthy Bridge	0	msats	9	0.029	1	England	24	2009
Cherry Brook, Lower Bridge	West Webburn, Lower Cator Bridge	0	msats	9	0.024	1	England	24	2009
Ruddycleave, Bowden Farm	Ruddycleave, Ruddycleave Cottage	0	msats	9	0.021	1	England	24	2009
Ruddycleave, Bowden Farm	Ruddycleave, Pudsham Down	0	msats	9	0.033	1	England	24	2009
Ruddycleave, Bowden Farm	River Swincombe, Wydemeet	1	msats	9	0.060	1	England	24	2009
Ruddycleave, Bowden Farm	Cherry Brook, Upper Bridge	1	msats	9	0.050	1	England	24	2009
Ruddycleave, Bowden Farm	West Dart, Cockern Tor	1	msats	9	0.063	1	England	24	2009
Ruddycleave, Bowden Farm	River Webburn, Mistresses Piece	1	msats	9	0.025	1	England	24	2009
Ruddycleave, Bowden Farm	West Webburn, Pondsworthy Bridge	1	msats	9	0.040	1	England	24	2009
Ruddycleave, Bowden Farm	West Webburn, Lower Cator Bridge	1	msats	9	0.037	1	England	24	2009
Ruddycleave, Ruddycleave Cottage	Ruddycleave, Pudsham Down	0			0.061			24	
Ruddycleave, Ruddycleave Cottage	River Swincombe, Wydemeet				0.050			24	

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Ruddycleave, Ruddycleave Cottage	Cherry Brook, Upper Bridge				0.044				24	
Ruddycleave, Ruddycleave Cottage	West Dart, Cockern Tor				0.076				24	
Ruddycleave, Ruddycleave Cottage	River Webburn, Mistresses Piece				0.018				24	
Ruddycleave, Ruddycleave Cottage	West Webburn, Pondsworthy Bridge				0.039				24	
Ruddycleave, Ruddycleave Cottage	West Webburn, Lower Cator Bridge				0.034					
Ruddycleave, Pudsham Down	River Swincombe, Wydemeet				0.090				24	
Ruddycleave, Pudsham Down	Cherry Brook, Upper Bridge				0.071				24	
Ruddycleave, Pudsham Down	West Dart, Cockern Tor				0.088				24	
Ruddycleave, Pudsham Down	River Webburn, Mistresses Piece				0.050				24	
Ruddycleave, Pudsham Down	West Webburn, Pondsworthy Bridge				0.060				24	
Ruddycleave, Pudsham Down	West Webburn, Lower Cator Bridge				0.063				24	
River Swincombe, Wydemeet	Cherry Brook, Upper Bridge	0			0.006				24	
River Swincombe, Wydemeet	West Dart, Cockern Tor	0	msats	9	0.014		1	England	24	2009
River Swincombe, Wydemeet	River Webburn, Mistresses Piece	0	msats	9	0.021		1	England	24	2009
River Swincombe, Wydemeet	West Webburn, Pondsworthy Bridge	0	msats	9	0.025		1	England	24	2009
River Swincombe, Wydemeet	West Webburn, Lower Cator Bridge	0	msats	9	0.013		1	England	24	2009
Cherry Brook, Upper Bridge	West Dart, Cockern Tor	0	msats	9	0.011		1	England	24	2009
Cherry Brook, Upper Bridge	River Webburn, Mistresses Piece	0	msats	9	0.014		1	England	24	2009
Cherry Brook, Upper Bridge	West Webburn, Pondsworthy Bridge	0	msats	9	0.025		1	England	24	2009
Cherry Brook, Upper Bridge	West Webburn, Lower Cator Bridge	0	msats	9	0.016		1	England	24	2009
West Dart, Cockern Tor	River Webburn, Mistresses Piece	0	msats	9	0.030		1	England	24	2009
West Dart, Cockern Tor	West Webburn, Pondsworthy Bridge	0	msats	9	0.034		1	England	24	2009
West Dart, Cockern Tor	West Webburn, Lower Cator Bridge	0	msats	9	0.025		1	England	24	2009
River Webburn, Mistresses Piece	West Webburn, Pondsworthy Bridge	0	msats	9	0.005		1	England	24	2009
River Webburn, Mistresses Piece	West Webburn, Lower Cator Bridge	0	msats	9	0.000		1	England	24	2009
West Webburn, Pondsworthy Bridge	West Webburn, Lower Cator Bridge	0	msats	9	0.000		1	England	24	2009

Gudbrandsdalslågen below Otta	Gudbrandsdalslågen above Otta	0	msats	10	0.012	1	Norway	26	2014
Gudbrandsdalslågen below Otta	Gudbrandsdalslågen above Rosten	1	msats	10	0.037	1	Norway	26	2014
Gudbrandsdalslågen below Otta	Otta below Eidefoss	0	msats	10	0.005	1	Norway	26	2014
Gudbrandsdalslågen below Otta	Otta above Eidefoss	1	msats	10	0.050	1	Norway	26	2014
Gudbrandsdalslågen above Otta	Gudbrandsdalslågen above Rosten	1	msats	10	0.011	1	Norway	26	2014
Gudbrandsdalslågen above Otta	Otta below Eidefoss	0	msats	10	0.013	1	Norway	26	2014
Gudbrandsdalslågen above Otta	Otta above Eidefoss	1	msats	10	0.089	1	Norway	26	2014
Gudbrandsdalslågen above Rosten	Otta below Eidefoss	1	msats	10	0.044	1	Norway	26	2014
Gudbrandsdalslågen above Rosten	Otta above Eidefoss	1	msats	10	0.110	1	Norway	26	2014
Otta below Eidefoss	Otta above Eidefoss	1	msats	10	0.041	1	Norway	26	2014
Ringedalsvatn	Løyningsvatn	1	msats	11	0.021	2	Norway	29	2007
Ringedalsvatn	Kollsvatn	1	msats	11	0.091	2	Norway	29	2007
Ringedalsvatn	Litlosvatn	1	msats	11	0.100	2	Norway	29	2007
Ringedalsvatn	Kvennsjøen	1	msats	11	0.154	2	Norway	29	2007
Ringedalsvatn	Øvre Krokavatn	1		11	0.168	2	Norway	29	2007
Ringedalsvatn	Midtre Krokavatn			11	0.134	2	Norway	29	2007
Ringedalsvatn	Nedre Krokavatn			11	0.174	2	Norway	29	2007
Ringedalsvatn	Øvre Bjørnavatn			11	0.112	2	Norway	29	2007
Ringedalsvatn	Nedre Bjørnavatn			11	0.118	2	Norway	29	2007
Ringedalsvatn	Dimmedalsvatn			11	0.145	2	Norway	29	2007
Ringedalsvatn	Bessvatn			11	0.117	2	Norway	29	2007
Løyningsvatn	Kollsvatn			11	0.066	2	Norway	29	2007
Løyningsvatn	Litlosvatn			11	0.066	2	Norway	29	2007
Løyningsvatn	Kvennsjøen			11	0.109	2	Norway	29	2007
Løyningsvatn	Øvre Krokavatn			11	0.120	2	Norway	29	2007
Løyningsvatn	Midtre Krokavatn			11	0.097	2	Norway	29	2007
Løyningsvatn	Nedre Krokavatn			11	0.131	2	Norway	29	2007

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Løyningsvatn	Øvre Bjørnavatn	1		11	0.074		2	Norway	29	2007
Løyningsvatn	Nedre Bjørnavatn	1	msats	11	0.073		2	Norway	29	2007
Løyningsvatn	Dimmedalsvatn	1	msats	11	0.126		2	Norway	29	2007
Løyningsvatn	Bessvatn	1	msats	11	0.087		2	Norway	29	2007
Kollsvatn	Litlosvatn	1	msats	11	0.007		2	Norway	29	2007
Kollsvatn	Kvennsjøen	1	msats	11	0.023		2	Norway	29	2007
Kollsvatn	Øvre Krokavatn	1	msats	11	0.063		2	Norway	29	2007
Kollsvatn	Midtre Krokavatn	1	msats	11	0.058		2	Norway	29	2007
Kollsvatn	Nedre Krokavatn	1	msats	11	0.071		2	Norway	29	2007
Kollsvatn	Øvre Bjørnavatn	1	msats	11	0.057		2	Norway	29	2007
Kollsvatn	Nedre Bjørnavatn	1	msats	11	0.070		2	Norway	29	2007
Kollsvatn	Dimmedalsvatn	1	msats	11	0.098		2	Norway	29	2007
Kollsvatn	Bessvatn	1	msats	11	0.053		2	Norway	29	2007
Litlosvatn	Kvennsjøen	1	msats	11	0.014		2	Norway	29	2007
Litlosvatn	Øvre Krokavatn	1	msats	11	0.042		2	Norway	29	2007
Litlosvatn	Midtre Krokavatn	1	msats	11	0.044		2	Norway	29	2007
Litlosvatn	Nedre Krokavatn	1	msats	11	0.060		2	Norway	29	2007
Litlosvatn	Øvre Bjørnavatn	1	msats	11	0.049		2	Norway	29	2007
Litlosvatn	Nedre Bjørnavatn	1	msats	11	0.066		2	Norway	29	2007
Litlosvatn	Dimmedalsvatn	1	msats	11	0.120		2	Norway	29	2007
Litlosvatn	Bessvatn	1	msats	11	0.065		2	Norway	29	2007
Kvennsjøen	Øvre Krokavatn	1	msats	11	0.031		2	Norway	29	2007
Kvennsjøen	Midtre Krokavatn	1	msats	11	0.069		2	Norway	29	2007
Kvennsjøen	Nedre Krokavatn	1	msats	11	0.056		2	Norway	29	2007
Kvennsjøen	Øvre Bjørnavatn	1	msats	11	0.069		2	Norway	29	2007
Kvennsjøen	Nedre Bjørnavatn	1	msats	11	0.079		2	Norway	29	2007

Kvennsjøen	Dimmedalsvatn	1	msats	11	0.157	2	Norway	29	2007
Kvennsjøen	Bessvatn	1	msats	11	0.107	2	Norway	29	2007
Øvre Krokavatn	Midtre Krokavatn	1	msats	11	0.005	2	Norway	29	2007
Øvre Krokavatn	Nedre Krokavatn	1		11	0.008	2	Norway	29	2007
Øvre Krokavatn	Øvre Bjørnavatn			11	0.041	2	Norway	29	2007
Øvre Krokavatn	Nedre Bjørnavatn			11	0.056	2	Norway	29	2007
Øvre Krokavatn	Dimmedalsvatn			11	0.179	2	Norway	29	2007
Øvre Krokavatn	Bessvatn			11	0.120	2	Norway	29	2007
Midtre Krokavatn	Nedre Krokavatn			11	0.008	2	Norway	29	2007
Midtre Krokavatn	Øvre Bjørnavatn			11	0.030	2	Norway	29	2007
Midtre Krokavatn	Nedre Bjørnavatn			11	0.034	2	Norway	29	2007
Midtre Krokavatn	Dimmedalsvatn			11	0.173	2	Norway	29	2007
Midtre Krokavatn	Bessvatn			11	0.116	2	Norway	29	2007
Nedre Krokavatn	Øvre Bjørnavatn			11	0.036	2	Norway	29	2007
Nedre Krokavatn	Nedre Bjørnavatn			11	0.045	2	Norway	29	2007
Nedre Krokavatn	Dimmedalsvatn			11	0.175	2	Norway	29	2007
Nedre Krokavatn	Bessvatn	1		11	0.118	2	Norway	29	2007
Øvre Bjørnavatn	Nedre Bjørnavatn	1	msats	11	0.009	2	Norway	29	2007
Øvre Bjørnavatn	Dimmedalsvatn	1	msats	11	0.122	2	Norway	29	2007
Øvre Bjørnavatn	Bessvatn	1	msats	11	0.069	2	Norway	29	2007
Nedre Bjørnavatn	Dimmedalsvatn	1	msats	11	0.147	2	Norway	29	2007
Nedre Bjørnavatn	Bessvatn	1	msats	11	0.093	2	Norway	29	2007
Dimmedalsvatn	Bessvatn	1	msats	11	0.045	2	Norway	29	2007
Møsvatn	Kvenna	0	msats	8	0.002	1	Norway	37	2002
Møsvatn	Hondle	0	msats	8	0.014	1	Norway	37	2002
Møsvatn	Skinåi	0	msats	8	0.012	1	Norway	37	2002
Møsvatn	Tunhovd	1	msats	8	0.052	2	Norway	37	2002

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Kvenna	Hondle	0	msats	8	0.013		1	Norway	37	2002
Kvenna	Skinåi	0	msats	8	0.039		1	Norway	37	2002
Kvenna	Tunhovd	1	msats	8	0.038		2	Norway	37	2002
Hondle	Skinåi	0	msats	8	0.054		1	Norway	37	2002
Hondle	Tunhovd	1	msats	8	0.058		2	Norway	37	2002
Skinåi	Tunhovd	0	msats	8	0.088		2	Norway	37	2002
Azika	Azika	0	msats	10	0.009	0	1	Russia	38	2009
Azika	Gorodjonka	1	msats	10	0.045	26	1	Russia	38	2009
Azika	Khrevitsa	1	msats	10	0.058	28	1	Russia	38	2009
Azika	Lemovzha	0	msats	10	0.069	96	1	Russia	38	2009
Azika	Lubenka	0	msats	10	0.056	23.5	1	Russia	38	2009
Azika	Solka	0	msats	10	0.015	42.5	1	Russia	38	2009
Azika	Solka	0	msats	10	0.042	42.5	1	Russia	38	2009
Azika	Solka above	1	msats	10	0.037	51.5	1	Russia	38	2009
Azika	Sumka	0	msats	10	0.051	49	1	Russia	38	2009
Azika	Ukhora	0	msats	10	0.037	70	1	Russia	38	2009
Azika	Vidon	0	msats	10	0.041	55	1	Russia	38	2009
Azika	Vruda	0	msats	10	0.027	49	1	Russia	38	2009
Azika	Vruda	0			0.016	49	1			
Azika	Lohijoki				0.122		2			
Azika	Ur’ja				0.170		2			
Azika	Gorodjonka				0.043	26				
Azika	Khrevitsa				0.051	28				
Azika	Lemovzha				0.080	96				
Azika	Lubenka				0.057	23.5				
Azika	Solka	0			0.038	42.5	1			

Azika	Solka	0			0.029	42.5	1			
Azika	Solka above	1			0.039	51.5	1			
Azika	Sumka	0			0.045	49	1			
Azika	Ukhora	0			0.036	70	1			
Azika	Vidon	0			0.023	55	1			
Azika	Vruda	0			0.043	49	1			
Azika	Vruda	0	msats	10	0.012	49	1	Russia	38	2009
Azika	Lohijoki	1	msats	10	0.099		2	Russia	38	2009
Azika	Ur'ja	1	msats	10	0.177		2	Russia	38	2009
Gorodjonka	Khrevitsa	1	msats	10	0.032	15	1	Russia	38	2009
Gorodjonka	Lemovzha	0	msats	10	0.089	95	1	Russia	38	2009
Gorodjonka	Lubenka	0	msats	10	0.044	22.5	1	Russia	38	2009
Gorodjonka	Solka	0	msats	10	0.061	62.5	1	Russia	38	2009
Gorodjonka	Solka	0	msats	10	0.078	62.5	1	Russia	38	2009
Gorodjonka	Solka above	1	msats	10	0.055	71.5	1	Russia	38	2009
Gorodjonka	Sumka	0	msats	10	0.051	48	1	Russia	38	2009
Gorodjonka	Ukhora	0	msats	10	0.042	69	1	Russia	38	2009
Gorodjonka	Vidon	0	msats	10	0.055	54	1	Russia	38	2009
Gorodjonka	Vruda	0	msats	10	0.052	48	1	Russia	38	2009
Gorodjonka	Vruda	0	msats	10	0.015	48	1	Russia	38	2009
Gorodjonka	Lohijoki	1	msats	10	0.126		2	Russia	38	2009
Gorodjonka	Ur'ja	1	msats	10	0.191		2	Russia	38	2009
Khrevitsa	Lemovzha	1	msats	10	0.103	97	1	Russia	38	2009
Khrevitsa	Lubenka	0	msats	10	0.065	24.5	1	Russia	38	2009
Khrevitsa	Solka	0	msats	10	0.056	64.5	1	Russia	38	2009
Khrevitsa	Solka	0	msats	10	0.067	64.5	1	Russia	38	2009
Khrevitsa	Solka above	1	msats	10	0.046	73.5	1	Russia	38	2009

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Khrevitsa	Sumka	0	msats	10	0.066	50	1	Russia	38	2009
Khrevitsa	Ukhora	0	msats	10	0.060	71	1	Russia	38	2009
Khrevitsa	Vidon	0	msats	10	0.064	56	1	Russia	38	2009
Khrevitsa	Vruda	0	msats	10	0.035	50	1	Russia	38	2009
Khrevitsa	Vruda	0	msats	10	0.024	50	1	Russia	38	2009
Khrevitsa	Lohijoki	1	msats	10	0.112		2	Russia	38	2009
Khrevitsa	Ur'ja	1	msats	10	0.168		2	Russia	38	2009
Lemovzha	Lubenka	0			0.142	88.5	1			
Lemovzha	Solka	0			0.063	132.5	1			
Lemovzha	Solka	0			0.106	132.5	1			
Lemovzha	Solka above				0.116	141.5				
Lemovzha	Sumka				0.127	83				
Lemovzha	Ukhora				0.100	104				
Lemovzha	Vidon				0.089	51				
Lemovzha	Vruda	0			0.089	83	1			
Lemovzha	Vruda	0			0.071	83	1			
Lemovzha	Lohijoki	1			0.203		2			
Lemovzha	Ur'ja	1			0.252		2			
Lubenka	Solka	0			0.065	60	1			
Lubenka	Solka	0			0.083	60	1			
Lubenka	Solka above	1			0.037	69	1			
Lubenka	Sumka	0	msats	10	0.043	33.5	1	Russia	38	2009
Lubenka	Ukhora	0	msats	10	0.062	62.5	1	Russia	38	2009
Lubenka	Vidon	0	msats	10	0.036	47.5	1	Russia	38	2009
Lubenka	Vruda	0	msats	10	0.054	41.5	1	Russia	38	2009
Lubenka	Vruda	0	msats	10	0.026	41.5	1	Russia	38	2009
Lubenka	Lohijoki	1	msats	10	0.105		2	Russia	38	2009

Lubenka	Ur'ja	1	msats	10	0.161		2	Russia	38	2009
Solka	Solka	0	msats	10	0.030	0	1	Russia	38	2009
Solka	Solka above	1	msats	10	0.031	9	1	Russia	38	2009
Solka	Sumka	0	msats	10	0.065	85.5	1	Russia	38	2009
Solka	Ukhora	0	msats	10	0.070	106.5	1	Russia	38	2009
Solka	Vidon	0	msats	10	0.052	91.5	1	Russia	38	2009
Solka	Vruda	0	msats	10	0.016	85.5	1	Russia	38	2009
Solka	Vruda	0	msats	10	0.033	85.5	1	Russia	38	2009
Solka	Lohijoki	1	msats	10	0.132		2	Russia	38	2009
Solka	Ur'ja	1	msats	10	0.174		2	Russia	38	2009
Solka	Solka above	1	msats	10	0.016	9	1	Russia	38	2009
Solka	Sumka	0	msats	10	0.050	85.5	1	Russia	38	2009
Solka	Ukhora	0	msats	10	0.062	106.5	1	Russia	38	2009
Solka	Vidon	0	msats	10	0.044	91.5	1	Russia	38	2009
Solka	Vruda	0	msats	10	0.041	85.5	1	Russia	38	2009
Solka	Vruda	0	msats	10	0.054	85.5	1	Russia	38	2009
Solka	Lohijoki	1	msats	10	0.115		2	Russia	38	2009
Solka	Ur'ja	1	msats	10	0.184		2	Russia	38	2009
Solka above	Sumka	1	msats	10	0.030	94.5	1	Russia	38	2009
Solka above	Ukhora	1	msats	10	0.058	115.5	1	Russia	38	2009
Solka above	Vidon	1	msats	10	0.048	100.5	1	Russia	38	2009
Solka above	Vruda	1	msats	10	0.023	64	1	Russia	38	2009
Solka above	Vruda	1			0.035	64	1			
Solka above	Lohijoki	1			0.110		2			
Solka above	Ur'ja	1			0.165		2			
Sumka	Ukhora	0			0.034	23				
Sumka	Vidon				0.052	42				
Sumka	Vruda				0.051	2				
Sumka	Vruda				0.025	2				

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Sumka	Lohijoki				0.113		2			
Sumka	Ur'ja	1			0.181		2			
Ukhora	Vidon	0			0.059	63	1			
Ukhora	Vruda	0			0.063	21	1			
Ukhora	Vruda	0			0.015	21	1			
Ukhora	Lohijoki	1			0.116		2			
Ukhora	Ur'ja	1			0.164		2			
Vidon	Vruda	0	msats	10	0.054	42	1	Russia	38	2009
Vidon	Vruda	0	msats	10	0.023	42	1	Russia	38	2009
Vidon	Lohijoki	1	msats	10	0.129		2	Russia	38	2009
Vidon	Ur'ja	1	msats	10	0.218		2	Russia	38	2009
Vruda	Vruda	0	msats	10	0.018	0	1	Russia	38	2009
Vruda	Lohijoki	1	msats	10	0.143		2	Russia	38	2009
Vruda	Ur'ja	1	msats	10	0.174		2	Russia	38	2009
Vruda	Lohijoki	1	msats	10	0.105		2	Russia	38	2009
Vruda	Ur'ja	1	msats	10	0.136		2	Russia	38	2009
Lohijoki	Ur'ja	1	msats	11	0.178		2	Russia	38	2009
Nordre Finnvikelv Tributary	Nordre Finnvikelv	0	msats	6	0.047		1	Norway	44	1999
Nordre Finnvikelv Tributary	Nordre Finnvikelv	0	msats	6	0.044		1	Norway	44	1999
Nordre Finnvikelv Tributary	Nordre Finnvikelv	0	msats	6	0.063		1	Norway	44	1999
Nordre Finnvikelv Tributary	Nordre Finnvikelv	1	msats	6	0.114		1	Norway	44	1999
Nordre Finnvikelv	Nordre Finnvikelv	0	msats	6	0.000		1	Norway	44	1999
Nordre Finnvikelv	Nordre Finnvikelv	0	msats	6	0.000		1	Norway	44	1999
Nordre Finnvikelv	Nordre Finnvikelv	1	msats	6	0.280		1	Norway	44	1999
Nordre Finnvikelv	Nordre Finnvikelv	0	msats	6	0.000		1	Norway	44	1999
Nordre Finnvikelv	Nordre Finnvikelv	1	msats	6	0.031		1	Norway	44	1999

Nordre Finnvikelv	Nordre Finnvikelv	1	msats	6	0.018	1	Norway	44	1999
Trollsvattnet	Trollsvattnet	0	allozyme	14	0.001	1	Sweden	50	2013
Trollsvattnet	Trollsvattnet	0	msats	7	0.001	1	Sweden	50	2013
Steindalsbekken	Fjelldalselva	0	allozyme	15	0.001	2	Norway	52	2001
Steindalsbekken	Pendalsbekken	0	allozyme	15	0.074	2	Norway	52	2001
Steindalsbekken	Sævelibekken	0	allozyme	15	0.014	2	Norway	52	2001
Steindalsbekken	Allemannsbekken	0	allozyme	15	0.065	2	Norway	52	2001
Steindalsbekken	Songebekken	0	allozyme	15	0.008	2	Norway	52	2001
Steindalsbekken	Mørefjærbekken	0	allozyme	15	0.044	2	Norway	52	2001
Steindalsbekken	Langangsvassdraget	0	allozyme	15	0.044	2	Norway	52	2001
Fjelldalselva	Pendalsbekken	0	allozyme	15	0.080	2	Norway	52	2001
Fjelldalselva	Sævelibekken	0	allozyme	15	0.022	2	Norway	52	2001
Fjelldalselva	Allemannsbekken	0	allozyme	15	0.043	2	Norway	52	2001
Fjelldalselva	Songebekken		allozyme	15	0.012	2	Norway	52	2001
Fjelldalselva	Mørefjærbekken		allozyme	15	0.046	2	Norway	52	2001
Fjelldalselva	Langangsvassdraget		allozyme	15	0.030	2	Norway	52	2001
Pendalsbekken	Sævelibekken	0	allozyme	15	0.136	2	Norway	52	2001
Pendalsbekken	Allemannsbekken	0	allozyme	15	0.150	2	Norway	52	2001
Pendalsbekken	Songebekken	0	allozyme	15	0.093	2	Norway	52	2001
Pendalsbekken	Mørefjærbekken	0	allozyme	15	0.058	2	Norway	52	2001
Pendalsbekken	Langangsvassdraget	0	allozyme	15	0.104	2	Norway	52	2001
Sævelibekken	Allemannsbekken	0	allozyme	15	0.047	2	Norway	52	2001
Sævelibekken	Songebekken	0	allozyme	15	0.024	2	Norway	52	2001
Sævelibekken	Mørefjærbekken	0	allozyme	15	0.077	2	Norway	52	2001
Sævelibekken	Langangsvassdraget	0	allozyme	15	0.075	2	Norway	52	2001
Allemannsbekken	Songebekken	0	allozyme	15	0.072	2	Norway	52	2001
Allemannsbekken	Mørefjærbekken	0	allozyme	15	0.086	2	Norway	52	2001

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Allemannsbekken	Langangsvassdraget	0	allozyme	15	0.055		2	Norway	52	2001
Songebekken	Mørefjærbekken	0	allozyme	15	0.039		2	Norway	52	2001
Songebekken	Langangsvassdraget	0	allozyme	15	0.048		2	Norway	52	2001
Mørefjærbekken	Langangsvassdraget	0	allozyme	15	0.023		2	Norway	52	2001
Ferox Awe	River Awe	0	msats	5	0.010		1	Scotland	54	2006
Ferox Laggan	River Patack	0	msats	5	0.001		1	Scotland	54	2006
Tjærbæk	Karup River 1993	0	msats	8	0.038		3	Denmark	55	2000
Tjærbæk	Karup River 1996	0	msats	8	0.025		3	Denmark	55	2000
Tjærbæk	Esrum River	0	msats	8	0.025		3	Denmark	55	2000
Karup River 1993	Esrum River	0	msats	8	0.024		3	Denmark	55	2000
Karup River 1996	Esrum River	0	msats	8	0.025		3	Denmark	55	2000
Färsån	Eldsjöbäcken	0	msats	5	0.058		1	Sweden	59	2001
Färsån	Gulån	0	msats	5	0.066		1	Sweden	59	2001
Färsån	Öravatsbäcken	0	msats	5	0.035		1	Sweden	59	2001
Färsån	Borgforsen	0	msats	5	0.166		1	Sweden	59	2001
Färsån	Laxsjöbäcken	0	msats	5	0.350		1	Sweden	59	2001
Färsån	Lycktorpsbäcken	1	msats	5	0.579		1	Sweden	59	2001
Eldsjöbäcken	Gulån	0	msats	5	0.018		1	Sweden	59	2001
Eldsjöbäcken	Öravatsbäcken	0	msats	5	0.095		1	Sweden	59	2001
Eldsjöbäcken	Borgforsen	0	msats	5	0.157		1	Sweden	59	2001
Eldsjöbäcken	Laxsjöbäcken	0	msats	5	0.320		1	Sweden	59	2001
Eldsjöbäcken	Lycktorpsbäcken	1	msats	5	0.574		1	Sweden	59	2001
Gulån	Öravatsbäcken	0	msats	5	0.104		1	Sweden	59	2001
Gulån	Borgforsen	0	msats	5	0.206		1	Sweden	59	2001
Gulån	Laxsjöbäcken	0		5	0.353		1		59	2001

Gulån	Lycktorpsbäcken	1		5	0.613	1		59	2001
Öravatsbäcken	Borgforsen	0		5	0.168	1		59	2001
Öravatsbäcken	Laxsjöbäcken	0		5	0.364	1		59	2001
Öravatsbäcken	Lycktorpsbäcken	1		5	0.562	1		59	2001
Borgforsen	Laxsjöbäcken			5	0.243	1		59	2001
Borgforsen	Lycktorpsbäcken			5	0.538	1		59	2001
Laxsjöbäcken	Lycktorpsbäcken			5	0.648	1		59	2001
Abbert	Baelnabrack	0		12	0.055	1	Irland	60	2010
Abbert	Black	0		12	0.035	1	Irland	60	2010
Abbert	Cong	0		12	0.049	1	Irland	60	2010
Abbert	Cornamona	0		12	0.044	1	Irland	60	2010
Abbert	Cross	0		12	0.032	1	Irland	60	2010
Abbert	Drimneen	0		12	0.066	1	Irland	60	2010
Abbert	Grange	0	msats	12	0.194	1	Irland	60	2010
Abbert	Oughterard	0	msats	12	0.054	1	Irland	60	2010
Baelnabrack	Black	0	msats	12	0.037	1	Irland	60	2010
Baelnabrack	Cong	0	msats	12	0.040	1	Irland	60	2010
Baelnabrack	Cornamona	0	msats	12	0.012	1	Irland	60	2010
Baelnabrack	Cross	0	msats	12	0.037	1	Irland	60	2010
Baelnabrack	Drimneen	0	msats	12	0.021	1	Irland	60	2010
Baelnabrack	Grange	0	msats	12	0.149	1	Irland	60	2010
Baelnabrack	Oughterard	0	msats	12	0.017	1	Irland	60	2010
Black	Cong	0	msats	12	0.043	1	Irland	60	2010
Black	Cornamona	0	msats	12	0.025	1	Irland	60	2010
Black	Cross	0	msats	12	0.000	1	Irland	60	2010
Black	Drimneen	0	msats	12	0.021	1	Irland	60	2010
Black	Grange	0	msats	12	0.146	1	Irland	60	2010

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Black	Oughterard	0	msats	12	0.021		1	Irland	60	2010
Cong	Cornamona	0	msats	12	0.035		1	Irland	60	2010
Cong	Cross	0	msats	12	0.043		1	Irland	60	2010
Cong	Drimneen	0	msats	12	0.047		1	Irland	60	2010
Cong	Grange	0	msats	12	0.161		1	Irland	60	2010
Cong	Oughterard	0	msats	12	0.034		1	Irland	60	2010
Cornamona	Cross	0	msats	12	0.030		1	Irland	60	2010
Cornamona	Drimneen	0	msats	12	0.026		1	Irland	60	2010
Cornamona	Grange	0	msats	12	0.153		1	Irland	60	2010
Cornamona	Oughterard	0	msats	12	0.007		1	Irland	60	2010
Cross	Drimneen	0	msats	12	0.031		1	Irland	60	2010
Cross	Grange	0	msats	12	0.148		1	Irland	60	2010
Cross	Oughterard	0	msats	12	0.027		1	Irland	60	2010
Drimneen	Grange	0	msats	12	0.142		1	Irland	60	2010
Drimneen	Oughterard	0		12	0.017		1	Irland	60	2010
Grange	Oughterard	0		12	0.120		1	Irland	60	2010
Tinnsjøen Måna	Måna 1	0		9	0.033		1	Norway	62	2006
Tinnsjøen Måna	Måna 2	1		9	0.035		1	Norway	62	2006
Tinnsjøen Måna	Måna 3	1		9	0.039		1	Norway	62	2006
Tinnsjøen Måna	Måna 4	1		9	0.019		1	Norway	62	2006
Tinnsjøen Måna	Måna 5			9	0.023		1	Norway	62	2006
Tinnsjøen Måna	Måna 6			9	0.043		1	Norway	62	2006
Tinnsjøen Måna	Møsvatn	1		9	0.021		1	Norway	62	2006
Måna 1	Måna 2	1		9	0.007		1	Norway	62	2006
Måna 1	Måna 3	1		9	0.016		1	Norway	62	2006
Måna 1	Måna 4	1		9	0.020		1	Norway	62	2006

Måna 1	Måna 5	1		9	0.027	1	Norway	62	2006
Måna 1	Måna 6	1		9	0.079	1	Norway	62	2006
Måna 1	Møsvatn	1	msats	9	0.004	1	Norway	62	2006
Måna 2	Måna 3	1	msats	9	0.035	1	Norway	62	2006
Måna 2	Måna 4	1	msats	9	0.019	1	Norway	62	2006
Måna 2	Måna 5	1	msats	9	0.039	1	Norway	62	2006
Måna 2	Måna 6	1	msats	9	0.070	1	Norway	62	2006
Måna 2	Møsvatn	1	msats	9	0.013	1	Norway	62	2006
Måna 3	Måna 4	1	msats	9	0.023	1	Norway	62	2006
Måna 3	Måna 5	1	msats	9	0.047	1	Norway	62	2006
Måna 3	Måna 6	1	msats	9	0.081	1	Norway	62	2006
Måna 3	Møsvatn	1	msats	9	0.023	1	Norway	62	2006
Måna 4	Måna 5	1	msats	9	0.027	1	Norway	62	2006
Måna 4	Måna 6	1	msats	9	0.049	1	Norway	62	2006
Måna 4	Møsvatn	1	msats	9	0.009	1	Norway	62	2006
Måna 5	Måna 6	1	msats	9	0.035	1	Norway	62	2006
Måna 5	Møsvatn	1	msats	9	0.022	1	Norway	62	2006
Måna 6	Møsvatn	1	msats	9	0.059	1	Norway	62	2006
Säverå	Ume-Vindelälven	0	msats	8	0.033	3	Sweden	63	2008
Säverå	Öreälven	0	msats	8	0.026	3	Sweden	63	2008
Ume-Vindelälven	Öreälven	0	msats	8	0.023	3	Sweden	63	2008
Umeälven A	Umeälven B	0	msats	8	0.004	1	Sweden	65	2012
Umeälven A	Laisälven A	0	msats	8	0.025	1	Sweden	65	2012
Umeälven A	Laisälven B	0	msats	8	0.027	1	Sweden	65	2012
Umeälven A	Ammaarnäs	1	msats	8	0.098	1	Sweden	65	2012
Umeälven A	Giertsbäcken	1	msats	8	0.118	1	Sweden	65	2012
Umeälven A	Krokforsen	0	msats	8	0.067	1	Sweden	65	2012

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Umeälven A	Gargån	1	msats	8	0.156		1	Sweden	65	2012
Umeälven A	Krycklan	0	msats	8	0.053		1	Sweden	65	2012
Umeälven A	Matjokkbäcken	0	msats	8	0.031		1	Sweden	65	2012
Umeälven A	Rågobäcken above	1			0.194		1			
Umeälven A	Rågobäcken below	0			0.044		1			
Umeälven A	Renforsen	0			0.012		1			
Umeälven A	Piteälven	0			0.031		3			
Umeälven A	Sikån	0			0.069		3			
Umeälven A	Hundforsen	0			0.119		3			
Umeälven A	Varjisån				0.043		3			
Umeälven A	Stockforsälven				0.077		3			
Umeälven B	Laisälven A	0			0.023		1			
Umeälven B	Laisälven B	0			0.023		1			
Umeälven B	Ammaarnäs	1			0.102		1			
Umeälven B	Giertsbäcken	1			0.119		1			
Umeälven B	Krokforsen	0			0.047		1			
Umeälven B	Gargån	1			0.141		1			
Umeälven B	Krycklan	0	msats	8	0.044		1	Sweden	65	2012
Umeälven B	Matjokkbäcken	0	msats	8	0.022		1	Sweden	65	2012
Umeälven B	Rågobäcken above	1	msats	8	0.165		1	Sweden	65	2012
Umeälven B	Rågobäcken below	0	msats	8	0.030		1	Sweden	65	2012
Umeälven B	Renforsen	0	msats	8	0.006		1	Sweden	65	2012
Umeälven B	Piteälven	0	msats	8	0.020		3	Sweden	65	2012
Umeälven B	Sikån	0	msats	8	0.078		3	Sweden	65	2012
Umeälven B	Hundforsen	0	msats	8	0.095		3	Sweden	65	2012

Umeälven B	Varjisån	1	msats	8	0.042	3	Sweden	65	2012
Umeälven B	Stockforsälven	1	msats	8	0.073	3	Sweden	65	2012
Laisälven A	Laisälven B	0	msats	8	0.006	1	Sweden	65	2012
Laisälven A	Ammaarnäs	1	msats	8	0.066	1	Sweden	65	2012
Laisälven A	Giertsbäcken	1	msats	8	0.094	1	Sweden	65	2012
Laisälven A	Krokforsen	0	msats	8	0.042	1	Sweden	65	2012
Laisälven A	Gargån	1	msats	8	0.183	1	Sweden	65	2012
Laisälven A	Krycklan	0	msats	8	0.043	1	Sweden	65	2012
Laisälven A	Matjokkbäcken	0	msats	8	0.015	1	Sweden	65	2012
Laisälven A	Rågobäcken above	1	msats	8	0.214	1	Sweden	65	2012
Laisälven A	Rågobäcken below	0	msats	8	0.043	1	Sweden	65	2012
Laisälven A	Renforsen	0	msats	8	0.037	1	Sweden	65	2012
Laisälven A	Piteälven	0	msats	8	0.027	3	Sweden	65	2012
Laisälven A	Sikån	0	msats	8	0.096	3	Sweden	65	2012
Laisälven A	Hundforsen	0	msats	8	0.087	3	Sweden	65	2012
Laisälven A	Varjisån	1	msats	8	0.068	3	Sweden	65	2012
Laisälven A	Stockforsälven	1	msats	8	0.078	3	Sweden	65	2012
Laisälven B	Ammaarnäs	1	msats	8	0.095	1	Sweden	65	2012
Laisälven B	Giertsbäcken	1	msats	8	0.093	1	Sweden	65	2012
Laisälven B	Krokforsen	0	msats	8	0.043	1	Sweden	65	2012
Laisälven B	Gargån	1			0.197	1			
Laisälven B	Krycklan	0			0.057	1			
Laisälven B	Matjokkbäcken	0			0.020	1			
Laisälven B	Rågobäcken above	1			0.221	1			
Laisälven B	Rågobäcken below	0			0.048	1			
Laisälven B	Renforsen	0			0.047	1			
Laisälven B	Piteälven	0			0.036	3			

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Laisälven B	Sikån	0			0.088		3			
Laisälven B	Hundforsen	0			0.114		3			
Laisälven B	Varjisån	1			0.073		3			
Laisälven B	Stockforsälven	1			0.064		3			
Ammaarnäs	Giertsbäcken	1			0.190		1			
Ammaarnäs	Krokforsen	1			0.140		1			
Ammaarnäs	Gargån	1			0.234		1			
Ammaarnäs	Krycklan	1	msats	8	0.140		1	Sweden	65	2012
Ammaarnäs	Matjokkbäcken	1	msats	8	0.099		1	Sweden	65	2012
Ammaarnäs	Rågobäcken above	1	msats	8	0.302		1	Sweden	65	2012
Ammaarnäs	Rågobäcken below	1	msats	8	0.138		1	Sweden	65	2012
Ammaarnäs	Renforsen	1	msats	8	0.113		1	Sweden	65	2012
Ammaarnäs	Piteälven	1	msats	8	0.102		3	Sweden	65	2012
Ammaarnäs	Sikån	1	msats	8	0.143		3	Sweden	65	2012
Ammaarnäs	Hundforsen	1	msats	8	0.129		3	Sweden	65	2012
Ammaarnäs	Varjisån	1	msats	8	0.145		3	Sweden	65	2012
Ammaarnäs	Stockforsälven	1	msats	8	0.154		3	Sweden	65	2012
Giertsbäcken	Krokforsen	1	msats	8	0.137		1	Sweden	65	2012
Giertsbäcken	Gargån	1	msats	8	0.268		1	Sweden	65	2012
Giertsbäcken	Krycklan	1	msats	8	0.094		1	Sweden	65	2012
Giertsbäcken	Matjokkbäcken	1	msats	8	0.101		1	Sweden	65	2012
Giertsbäcken	Rågobäcken above	1	msats	8	0.353		1	Sweden	65	2012
Giertsbäcken	Rågobäcken below	1	msats	8	0.159		1	Sweden	65	2012
Giertsbäcken	Renforsen	1	msats	8	0.118		1	Sweden	65	2012
Giertsbäcken	Piteälven	1	msats	8	0.103		3	Sweden	65	2012
Giertsbäcken	Sikån	1	msats	8	0.171		3	Sweden	65	2012

Giertsbäcken	Hundforsen	1	msats	8	0.200	3	Sweden	65	2012
Giertsbäcken	Varjisån	1	msats	8	0.162	3	Sweden	65	2012
Giertsbäcken	Stockforsälven	1	msats	8	0.149	3	Sweden	65	2012
Krokforsen	Gargån	1	msats	8	0.200	1	Sweden	65	2012
Krokforsen	Krycklan	0	msats	8	0.063	1	Sweden	65	2012
Krokforsen	Matjokkbäcken	0	msats	8	0.021	1	Sweden	65	2012
Krokforsen	Rågobäcken above	1	msats	8	0.205	1	Sweden	65	2012
Krokforsen	Rågobäcken below	0	msats	8	0.042	1	Sweden	65	2012
Krokforsen	Renforsen	0	msats	8	0.068	1	Sweden	65	2012
Krokforsen	Piteälven	0			0.049	3			
Krokforsen	Sikån	0			0.159	3			
Krokforsen	Hundforsen	0			0.098	3			
Krokforsen	Varjisån	1			0.085	3			
Krokforsen	Stockforsälven	1			0.092	3			
Gargån	Krycklan	1			0.149	1			
Gargån	Matjokkbäcken	1			0.174	1			
Gargån	Rågobäcken above				0.311	1			
Gargån	Rågobäcken below	1			0.214	1			
Gargån	Renforsen	1			0.141	1			
Gargån	Piteälven	1			0.164	3			
Gargån	Sikån	1			0.206	3			
Gargån	Hundforsen	1			0.265	3			
Gargån	Varjisån	1			0.158	3			
Gargån	Stockforsälven	1	msats	8	0.271	3	Sweden	65	2012
Krycklan	Matjokkbäcken	0	msats	8	0.041	1	Sweden	65	2012
Krycklan	Rågobäcken above	1	msats	8	0.229	1	Sweden	65	2012
Krycklan	Rågobäcken below	0	msats	8	0.075	1	Sweden	65	2012

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Krycklan	Renforsen	0	msats	8	0.016		1	Sweden	65	2012
Krycklan	Piteälven	0	msats	8	0.029		3	Sweden	65	2012
Krycklan	Sikån	0	msats	8	0.113		3	Sweden	65	2012
Krycklan	Hundforsen	0	msats	8	0.123		3	Sweden	65	2012
Krycklan	Varjisån	1	msats	8	0.054		3	Sweden	65	2012
Krycklan	Stockforsälven	1	msats	8	0.074		3	Sweden	65	2012
Matjokkbäcken	Rågobäcken above	1	msats	8	0.167		1	Sweden	65	2012
Matjokkbäcken	Rågobäcken below	0	msats	8	0.032		1	Sweden	65	2012
Matjokkbäcken	Renforsen	0	msats	8	0.031		1	Sweden	65	2012
Matjokkbäcken	Piteälven	0	msats	8	0.012		3	Sweden	65	2012
Matjokkbäcken	Sikån	0	msats	8	0.109		3	Sweden	65	2012
Matjokkbäcken	Hundforsen	0	msats	8	0.081		3	Sweden	65	2012
Matjokkbäcken	Varjisån	1	msats	8	0.045		3	Sweden	65	2012
Matjokkbäcken	Stockforsälven	1	msats	8	0.061		3	Sweden	65	2012
Rågobäcken above	Rågobäcken below	1	msats	8	0.174		1	Sweden	65	2012
Rågobäcken above	Renforsen	1	msats	8	0.167		1	Sweden	65	2012
Rågobäcken above	Piteälven	1	msats	8	0.175		3	Sweden	65	2012
Rågobäcken above	Sikån	1	msats	8	0.266		3	Sweden	65	2012
Rågobäcken above	Hundforsen	1	msats	8	0.260		3	Sweden	65	2012
Rågobäcken above	Varjisån	1	msats	8	0.182		3	Sweden	65	2012
Rågobäcken above	Stockforsälven	1	msats	8	0.252		3	Sweden	65	2012
Rågobäcken below	Renforsen	0	msats	8	0.031		1	Sweden	65	2012
Rågobäcken below	Piteälven	0	msats	8	0.032		3	Sweden	65	2012
Rågobäcken below	Sikån	0	msats	8	0.118		3	Sweden	65	2012
Rågobäcken below	Hundforsen	0			0.134		3			
Rågobäcken below	Varjisån	1			0.045		3			

Rågobäcken below	Stockforsälven	1			0.056	3			
Renforsen	Piteälven	0			0.020	3			
Renforsen	Sikån	0			0.065	3			
Renforsen	Hundforsen	0			0.102	3			
Renforsen	Varjisån	1			0.035	3			
Renforsen	Stockforsälven	1			0.083	3			
Piteälven	Sikån	0			0.068	1			
Piteälven	Hundforsen	0			0.070	1			
Piteälven	Varjisån	1			0.018	1			
Piteälven	Stockforsälven	1			0.040	1			
Sikån	Hundforsen	0			0.187	1			
Sikån	Varjisån	1			0.066	1			
Sikån	Stockforsälven	1	msats	8	0.107	1	Sweden	65	2012
Hundforsen	Varjisån	1	msats	8	0.131	1	Sweden	65	2012
Hundforsen	Stockforsälven	1	msats	8	0.159	1	Sweden	65	2012
Varjisån	Stockforsälven	1	msats	8	0.064	1	Sweden	65	2012
Stannon	Gwills	0	msats	23	0.022	1	England	66	2015
Stannon	Kestle Mill	0	msats	23	0.023	1	England	66	2015
Stannon	Tregony	0	msats	23	0.017	1	England	66	2015
Stannon	Geen Mill	0	msats	23	0.020	1	England	66	2015
Stannon	Tehidy Brook	0	msats	23	0.045	1	England	66	2015
Stannon	Roseworthy Farm	0	msats	23	0.039	1	England	66	2015
Stannon	St Erth	0	msats	23	0.071	1	England	66	2015
Stannon	Porthcocllum	0	msats	23	0.073	1	England	66	2015
Stannon	Drym Farm	0	msats	23	0.057	1	England	66	2015
Stannon	Clowance wood	0	msats	23	0.063	1	England	66	2015
Stannon	Cuccurian	0	msats	23	0.060	1	England	66	2015

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Stannon	Trythogga	0	msats	23	0.036		1	England	66	2015
Stannon	Noongallas	0	msats	23	0.059		1	England	66	2015
Gwills	Kestle Mill	0	msats	23	0.007		1	England	66	2015
Gwills	Tregony	0	msats	23	0.027		1	England	66	2015
Gwills	Geen Mill	0	msats	23	0.024		1	England	66	2015
Gwills	Tehidy Brook	0	msats	23	0.046		1	England	66	2015
Gwills	Roseworthy Farm	0	msats	23	0.040		1	England	66	2015
Gwills	St Erth	0	msats	23	0.073		1	England	66	2015
Gwills	Porthcocllum	0	msats	23	0.073		1	England	66	2015
Gwills	Drym Farm	0	msats	23	0.055		1	England	66	2015
Gwills	Clowance wood	0	msats	23	0.061		1	England	66	2015
Gwills	Cuccurian	0	msats	23	0.071		1	England	66	2015
Gwills	Trythogga	0	msats	23	0.040		1	England	66	2015
Gwills	Noongallas			23	0.058		1	England	66	
Kestle Mill	Tregony			23	0.031		1	England	66	
Kestle Mill	Geen Mill			23	0.028		1	England	66	
Kestle Mill	Tehidy Brook			23	0.047		1	England	66	
Kestle Mill	Roseworthy Farm			23	0.038		1	England	66	
Kestle Mill	St Erth			23	0.071		1	England	66	
Kestle Mill	Porthcocllum			23	0.073		1	England	66	
Kestle Mill	Drym Farm			23	0.057		1	England	66	
Kestle Mill	Clowance wood			23	0.062		1	England	66	
Kestle Mill	Cuccurian			23	0.066		1	England	66	
Kestle Mill	Trythogga	0		23	0.039		1	England	66	2015
Kestle Mill	Noongallas	0		23	0.058		1	England	66	2015
Tregony	Geen Mill	0		23	0.014		1	England	66	2015

Tregony	Tehidy Brook	0		23	0.050	1	England	66	2015
Tregony	Roseworthy Farm	0	msats	23	0.043	1	England	66	2015
Tregony	St Erth	0	msats	23	0.077	1	England	66	2015
Tregony	Porthcocllum	0	msats	23	0.081	1	England	66	2015
Tregony	Drym Farm	0	msats	23	0.060	1	England	66	2015
Tregony	Clowance wood	0	msats	23	0.069	1	England	66	2015
Tregony	Cuccurian	0	msats	23	0.063	1	England	66	2015
Tregony	Trythogga	0	msats	23	0.038	1	England	66	2015
Tregony	Noongallas	0	msats	23	0.060	1	England	66	2015
Geen Mill	Tehidy Brook	0	msats	23	0.045	1	England	66	2015
Geen Mill	Roseworthy Farm	0	msats	23	0.045	1	England	66	2015
Geen Mill	St Erth	0	msats	23	0.081	1	England	66	2015
Geen Mill	Porthcocllum	0	msats	23	0.084	1	England	66	2015
Geen Mill	Drym Farm	0	msats	23	0.060	1	England	66	2015
Geen Mill	Clowance wood	0	msats	23	0.066	1	England	66	2015
Geen Mill	Cuccurian	0	msats	23	0.063	1	England	66	2015
Geen Mill	Trythogga	0	msats	23	0.037	1	England	66	2015
Geen Mill	Noongallas	0	msats	23	0.056	1	England	66	2015
Tehidy Brook	Roseworthy Farm	0	msats	23	0.030	1	England	66	2015
Tehidy Brook	St Erth	0	msats	23	0.093	1	England	66	2015
Tehidy Brook	Porthcocllum	0	msats	23	0.093	1	England	66	2015
Tehidy Brook	Drym Farm	0	msats	23	0.071	1	England	66	2015
Tehidy Brook	Clowance wood	0	msats	23	0.076	1	England	66	2015
Tehidy Brook	Cuccurian	0	msats	23	0.073	1	England	66	2015
Tehidy Brook	Trythogga	0	msats	23	0.055	1	England	66	2015
Tehidy Brook	Noongallas	0	msats	23	0.069	1	England	66	2015
Roseworthy Farm	St Erth	0	msats	23	0.073	1	England	66	2015

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Roseworthy Farm	Porthcocllum	0	msats	23	0.075		1	England	66	2015
Roseworthy Farm	Drym Farm	0	msats	23	0.058		1	England	66	2015
Roseworthy Farm	Clowance wood			23	0.063		1	England	66	
Roseworthy Farm	Cuccurian			23	0.060		1	England	66	
Roseworthy Farm	Trythogga			23	0.047		1	England	66	
Roseworthy Farm	Noongallas			23	0.068		1	England	66	
St Erth	Porthcocllum			23	0.006		1	England	66	
St Erth	Drym Farm			23	0.024		1	England	66	
St Erth	Clowance wood			23	0.027		1	England	66	
St Erth	Cuccurian			23	0.103		1	England	66	
St Erth	Trythogga			23	0.082		1	England	66	
St Erth	Noongallas			23	0.099		1	England	66	
Porthcocllum	Drym Farm	0		23	0.026		1	England	66	2015
Porthcocllum	Clowance wood	0		23	0.029		1	England	66	2015
Porthcocllum	Cuccurian	0		23	0.106		1	England	66	2015
Porthcocllum	Trythogga	0		23	0.086		1	England	66	2015
Porthcocllum	Noongallas	0	msats	23	0.101		1	England	66	2015
Drym Farm	Clowance wood	0	msats	23	0.012		1	England	66	2015
Drym Farm	Cuccurian	0	msats	23	0.084		1	England	66	2015
Drym Farm	Trythogga	0	msats	23	0.062		1	England	66	2015
Drym Farm	Noongallas	0	msats	23	0.077		1	England	66	2015
Clowance wood	Cuccurian	0	msats	23	0.074		1	England	66	2015
Clowance wood	Trythogga	0	msats	23	0.069		1	England	66	2015
Clowance wood	Noongallas	0	msats	23	0.080		1	England	66	2015
Cuccurian	Trythogga	0	msats	23	0.048		1	England	66	2015
Cuccurian	Noongallas	0	msats	23	0.063		1	England	66	2015

Trythogga	Noongallas	0	msats	23	0.022	1	England	66	2015
Drym Farm	Binnerton	0	msats	7	0.070	1	England	67	2011
Drym Farm	Relubbus	0	msats	7	0.044	1	England	67	2011
Drym Farm	St Erth	0	msats	7	0.060	1	England	67	2011
Drym Farm	Tehidy Brook	0	msats	7	0.079	1	England	67	2011
Binnerton	Relubbus	0	msats	7	0.022	1	England	67	2011
Binnerton	St Erth	0	msats	7	0.019	1	England	67	2011
Binnerton	Tehidy Brook	0	msats	7	0.079	1	England	67	2011
Relubbus	St Erth	0	msats	7	0.002	1	England	67	2011
Relubbus	Tehidy Brook	0	msats	7	0.042	1	England	67	2011
St Erth	Tehidy Brook	0	msats	7	0.045	1	England	67	2011
Torneälven	Kalixälven	0	msats	10	0.031	2	Sweden	73	2015
Torneälven	Piteälven	0	msats	10	0.037	2	Sweden	73	2015
Torneälven	Byskeälven	0	msats	10	0.037	2	Sweden	73	2015
Torneälven	Sävarån	0	msats	10	0.090	2	Sweden	73	2015
Torneälven	Öreälven	0	msats	10	0.058	2	Sweden	73	2015
Torneälven	Bråviken	0	msats	10	0.097	2	Sweden	73	2015
Torneälven	Emån	0	msats	10	0.101	2	Sweden	73	2015
Torneälven	Mörrumsån			10	0.122	2	Sweden	73	
Kalixälven	Piteälven			10	0.063	2	Sweden	73	
Kalixälven	Byskeälven			10	0.064	2	Sweden	73	
Kalixälven	Sävarån			10	0.060	2	Sweden	73	
Kalixälven	Öreälven			10	0.079	2	Sweden	73	
Kalixälven	Bråviken			10	0.107	2	Sweden	73	
Kalixälven	Emån			10	0.115	2	Sweden	73	
Kalixälven	Mörrumsån			10	0.128	2	Sweden	73	
Piteälven	Byskeälven			10	0.017	2	Sweden	73	

(*Continued*)

Location 1	Location 2	Barrier	Marker type	Marker no.	Fst	Distance (km)	Scale	Country	Reference	Publ year
Piteälven	Sävarån			10	0.039		2	Sweden	73	
Piteälven	Öreälven	0	msats	10	0.047		2	Sweden	73	2015
Piteälven	Bråviken	0	msats	10	0.041		2	Sweden	73	2015
Piteälven	Emån	0	msats	10	0.065		2	Sweden	73	2015
Piteälven	Mörrumsån	0	msats	10	0.077		2	Sweden	73	2015
Byskeälven	Sävarån	0	msats	10	0.035		2	Sweden	73	2015
Byskeälven	Öreälven	0	msats	10	0.043		2	Sweden	73	2015
Byskeälven	Bråviken	0	msats	10	0.049		2	Sweden	73	2015
Byskeälven	Emån	0	msats	10	0.056		2	Sweden	73	2015
Byskeälven	Mörrumsån	0	msats	10	0.067		2	Sweden	73	2015
Sävarån	Öreälven	0	msats	10	0.044		2	Sweden	73	2015
Sävarån	Bråviken	0	msats	10	0.069		2	Sweden	73	2015
Sävarån	Emån	0	msats	10	0.073		2	Sweden	73	2015
Sävarån	Mörrumsån	0	msats	10	0.072		2	Sweden	73	2015
Öreälven	Bråviken	0	msats	10	0.055		2	Sweden	73	2015
Öreälven	Emån	0	msats	10	0.080		2	Sweden	73	2015
Öreälven	Mörrumsån	0	msats	10	0.080		2	Sweden	73	2015
Bråviken	Emån	0	msats	10	0.056		2	Sweden	73	2015
Bråviken	Mörrumsån	0	msats	10	0.032		2	Sweden	73	2015
Emån	Mörrumsån	0	msats	10	0.041		2	Sweden	73	2015

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