Dynamic Models and Control of Biological Systems

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To the sacred memory of my beloved parents

late Smt. Vadrevu Satyavathi
late Sri Vadrevu Seshagiri Rao

——————V. Sree Hari Rao

To nature for continued inspiration

—————P. Raja Sekhara Rao

Preface

Our aim in this monograph is to present an essentially self-contained account of the theory of mathematical model building of microbial populations. The emphases and selection of topics reflect our own involvement in the field over the past 10 years and our intent has been to stress the ideas and methods of analysis besides describing the most general and far-reaching results possible. This monograph includes published work as well as work presented at various seminars and conferences. There has been much ferment in this field during the past 15 years resulting in numerous publications with various methods and theoretical arguments. Much experience has been gained from this research during the past decade by researchers that include mathematicians, biologists, limnologists, and chemical and civil engineers. Now it is time to crystallize these concepts into a simple ready-to-use format to enable the implementation of these models by practicing field scientists. Thus, the first and foremost aim of the authors is to encourage others to consider and apply the results and the tools discussed in this book. Also, it is an attempt by the authors, a mathematician with an enthusiasm for biology and a biologist with an interest in mathematics, to encourage and promote the quintessential aspects of a collaborative dialogue between their respective disciplines. Mathematical models that describe the growth of microorganisms feeding on a nutrient in limited supply in a continuous cultured environment are very popular among researchers in mathematical biology. In this case, the mathematical predictions may be tested in a laboratory using a device known as a chemostat. The models are therefore called chemostat models. Chemostat models are identified as instances where mathematics precedes biology. On the basis of similarities, researchers viewed a chemostat as a replica of a simple, natural lake. But a chemostat is a closed system in which some of the key parameters can be controlled. This is not the case with a lake that is influenced by external factors, mainly seasonal changes. A variety of Lyapunov function(al)s are provided and this forms the main approach for the stability studies in most situations. The construction of Lyapunov function(al)s is described step-by-step. Enough care is taken to see that these results actually contribute to the continuity and completeness of the basic line of thinking that we began with. The book consists of eight chapters. The following is an outline of the book.

The first chapter presents an introduction to basic chemostat models. Global qualitative analysis of the stability of equilibria is carried out and this covers all recent literature. This approach forms a basis for the techniques in later chapters and makes a good starting point for subsequent chapters.

In Chap. 2, attention is drawn toward a lake. The device chemostat is compared with a natural lake. Such a lake has some extra features in addition to those of the closed environment of a chemostat, and the models introduced in Chap. 1 are appropriately modified to suit to a lake. Keeping in view the observations of biologists, time delays are introduced into the models of Chap. 1. Various combinations of time delays, both discrete and distributed, as studied by researchers are explained in this chapter in detail. These models are popularly known as chemostat-like models. A complete analysis of each of these models starting from the existence and uniqueness of solutions to the local and global stability of equilibria (implying the extinction/survival of species) is presented. Imbalances and disturbances are common in nature. Thus, species in lakes are prone to these disturbances caused by environmental conditions and exhibit instability characteristics unlike the models of Chap. 1, which are structurally stable. It is observed that time delays and variations in nutrient supply and its supply rate (due to seasonal changes) influence the dynamics of the system and tend to destabilize it. Unbounded growth or extinction are the characteristics observed. These instability characteristics of the models are discussed in Chap. 3. How to combat such an unstable situation is the content of the next three chapters, identifying the root cause of instability in each case. Having a good grasp of how a season cycle tends to infuse instability in a system, we study the natural response of consumer species (system) in each case. We consider the system in its most possible general form and study the behavior (response) of species.

Chapter 4 introduces the self-regulation of species due to a low supply of the nutrient (during summer months) and lack of support from the environment. This may also be understood as the effect of finite carrying capacity or overcrowding on the system. In Chap. 5 the behavior of species when the inflows and outflows in a lake are very high (during the rainy season) is studied. In this case, the nutrient is freely available to the species but there is always a danger of a species being washed out of the system. How the species survive the high washout is the point of interest here. The concept of wall growth (species finding a safer place in the same environment) is introduced and its influence studied in this chapter.

The survival and growth of microbial populations depends upon the consumption levels of the nutrient and this leads to another interesting phenomenon. We discuss the following prominent situations that have a direct bearing on the modeling perspective of these species. The first represents the natural tendency of a species to maintain the consumption levels at equilibrium values showing a natural inactive state of the consumer species. The second state may be understood as a regulation of the supply of the nutrient during the transition from high supply to low supply and vice versa. These are defined as the zones of no activation for the consumer species. The influence of this zone on the behavior of the system is the content of Chap. 6.

As the stability of equilibria implies the eventual survival of species, sufficient conditions are provided for the stability of the equilibria of the system equations. The tendencies toward instability introduced by the presence of time delays and variations in nutrient supply/consumption are then controlled by the mechanisms henceforth termed as "biocontrol mechanisms." The switch from instability to stability is thus explained and established. A number of examples are provided at each stage that help one understand how each of these mechanisms works on the system.

In the final chapter, we present some of the latest techniques to realize the mathematical results obtained. This forms a direct link between a mathematician and a biologist, which is the main objective of the study of chemostat(-like) models. This is achieved by finding ways to easily estimate the control (key) parameters that influence the dynamics of the system. Dynamic optimization algorithms are employed for this purpose. Such an approach is entirely new to the researchers working in this area.

Research articles that motivated the preparation of the book are cited in the section on "Notes and Remarks" at the end of each chapter. Scope for further research is discussed and gaps in the literature are pointed out. Examples are provided at every stage to illustrate, to compare the results, and to realize the underlying biological situation. It is hoped that this book will serve as a basis for further research for new entrants interested in this interdisciplinary area of research. It is our strong belief that this type of interdisciplinary work will not only be stimulating but will also open up many more new vistas, offering exciting prospects. This book is suitable for a one to two semester course for senior undergraduate and graduate students of mathematics, biology, agriculture, limnology, and chemical and civil engineering. Moreover, the reader feels throughout the reading of this monograph that the basic motif behind chemostat models, that is, "theory(mathematics) precedes experiment(biology)," is always cherished. Writing this book has been both interesting and challenging. Challenging, particularly, because it is not easy for us, as the authors, to judge whether we have succeeded in the aims we set for ourselves. Have we provided an accessible and informative overview of the subject? Have we managed to strike a balance between theory and application? Have we interested the readers enough that they can move on and build new mathematical models? We are honest enough to realize that answers to these and similar questions cannot be an unequivocal yes. We would therefore encourage readers to respond with ideas for further improvements.

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Chapter 1
Basic Models

1.1 Introduction

Quite often students pursuing a course in mathematics face an embarrassing situation when a nonmathematician raises the question of applicability of mathematics to real-world problems. This may be due to the abstractness of mathematical theory that the readers come across. Further, it is generally viewed that mathematical models are built and the theory is developed with an experiment or observations at its back ground. Of course, this approach helps understanding the system under consideration and also in the evolution of better systems from it. This approach, as may be called "theory after experiment", helps the experts in other areas look for mathematical solutions for more complex problems that arise in the development of their experiments/models.

Keeping in view the ability of mathematics to make valid, logically sound predictions, an important question is, can a "mathematical stage" be set where any experiment may it be physical, biological, or economic, etc. is conducted with a mathematically predicted outcome? In other words, can mathematics be tried in a laboratory? If the answer is yes, then this may help make life predictable, of course, within the limitations of mathematical logic. This leads to the development of new theories and opens new worlds of applications.

In this chapter, we present a simple case that gives a definite yes to this "experiment after theory" concept. To understand this we study a simple mathematical model of an ecological problem relating to the survival of populations. Why an ecological problem? Understanding the nature, either to live in harmony with it or to survive all odds posed by it, has been the main concern of the mankind. Thus, modeling a natural system not only evokes curiosity but is also highly important. In such a case what types of systems should we select and formulate mathematical models for them is an important question. There are many factors that influence the growth of populations such as food, environment, competition, and diseases. Assuming that all other conditions are conducive for growth, food has been regarded as the prime factor influencing the growth of populations. In this case, the survival of species depends only on food–consumer interactions.

With this back ground, we select a food (resource or prey) and a consumer species (predator), whatever names we give, and understand their growth interactions. It is

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generally known that "mathematical assumptions for population growth are best met for simple organisms. Especially, the best fit between the model and the data occurs for microorganisms". This motivates us to select a microorganism feeding on an essential nutrient (food) for our study here. The nutrient is "essential" in the sense that in the absence of it the consumer species dies. We then fit a mathematical model to describe their growth. The analysis of the model yields some predictions that are then established by an experiment. Though the mathematical theory described here and the biological experiment look simple, they paved way for a very exciting development of the theory and mathematical models of more complex ecological problems and now a stage has come where one can talk about a mathematical-biological experiment. This revolution is brought about by a simple laboratory device called a chemostat. The name chemostat is associated with a laboratory device used for growing microorganisms in a cultured environment. The description of a simple chemostat and its mechanism is provided at a later part of this chapter.

Before we go in for a discussion on our model and the chemostat, we first recall the classical link between mathematics and biology. Application of mathematics to biological problems is not new; we recall the Malthusian, Lotka–Volterra models in this context. The model,

$$x'(t) = rx(t),$$

where $' = \mathrm{d}/\mathrm{d}t$ and r is the growth rate coefficient, describes the exponential growth of the population x at any time t.

Introduction of carrying capacity of the environment (food, light, space, etc.), which controls the growth of the species, modifies the aforementioned model into a more realistic model of the form

$$x' = rx\left(1 - \frac{x}{k}\right),$$

where k denotes the carrying capacity of the environment. A model of Lotka–Volterra type that describes the competition between two species x and y (predators) for the same food (prey) is given by

$$\begin{aligned} x' &= rx\left(1 - \frac{x}{k_1}\right), \\ y' &= ry\left(1 - \frac{y}{k_2}\right) \quad \text{(without interference).} \end{aligned} \tag{1.1}$$

$$\begin{aligned} x' &= rx\left(1 - \frac{x}{k_1} - \lambda_1 y\right), \\ y' &= ry\left(1 - \frac{y}{k_2} - \lambda_2 x\right) \quad \text{(with interference).} \end{aligned} \tag{1.2}$$

Here, $k_1,\ k_2$ are the carrying capacities and $\lambda_1,\ \lambda_2$ are interference coefficients, all being positive constants.

It is possible to measure the interference coefficients λ_1 and λ_2 that decide the outcome of the competition only when the organisms are grown together, that is, while the experiment is being carried out. This rules out the possibility of predicting the outcome of the experiment before conducting it. This is a drawback of the Lotka–Volterra model. Moreover, there is no representation for the growth of food (resource) on which the populations grow (feed). Inclusion of the growth equation of the resource (prey) allows us to predict the corresponding changes in the growth of the consumer (predator) population. The main strength of chemostat models lies in the inclusion of the growth equation of the resource along with those of the competing organisms. This observation has prompted the researchers to study the chemostat model equations extensively. By analyzing the model equations the outcome of competition in a chemostat is predicted and the predictions are confirmed by the experiment.

We now begin our endeavor toward building a mathematical model. To begin with, we shall state in the following section the biological principles on which our model is formulated.

1.2 Biological Principles

The model consists of a microorganism feeding on a single growth-limiting nutrient. Let us denote by x the growth-limiting nutrient and by y, the microorganism feeding on the nutrient x. The following assumptions are helpful in formulating our model.

- All the nutrients, expect x, are abundantly available so that we can concentrate on the influence of this essential nutrient x on the species y. Also x is so important that addition of more of other nutrients does not compensate the limited supply of x.
- There is an external source of supply from which the microorganisms receive the essential nutrient x along with other nutrients.
- The nutrient is supplied at a constant rate and the supplied nutrient has constant concentration in the growth medium.
- The nutrient is uniformly distributed in the growth medium so that all the microorganisms have equal access to the nutrient available, that is, there is no disparity in distribution.
- There is an outlet to the system from which the excess material, namely nutrients, microorganisms, and some by-products, is continually removed.

The last assumption is reasonable since in any system such as a laboratory device, the volume is fixed. Hence, we should have an outlet when we allow continuous supply of material. Further to keep the volume of the growth medium fixed, we may assume that the rate of input is same as the rate of removal of the contents of the growth medium.

1. The microorganisms consume the nutrient continuously and the rate of consumption is a constant.

2. The consumption has a saturation, that is, unlimited supply of nutrient does not imply unlimited consumption of nutrient by the species.
3. Growth of microorganisms is proportional to their consumption.
4. All the external factors such as temperature, pressure, etc. are conducive for the growth and do not disturb the system.

These assumptions introduce some real parameters and functional relations into the system. We shall list them out here.

- x_0, the input nutrient concentration that is a positive constant. It denotes the quantity of nutrient available with the system at any time.
- D, the rate at which the nutrient is supplied and also the rate at which the contents of the growth medium are removed. It is also a positive constant.
- a, the maximal consumption rate of the nutrient and also the maximum specific growth rate of the microorganisms – a positive constant. This choice implies that the consumption means growth here.
- U, the functional response of the microorganisms describing how the nutrient is consumed by the species.

We now introduce our mathematical model that describes the dynamics of a limited nutrient–consumer system, which we are going to test in a laboratory.

1.3 Formulation of the Mathematical Model

We denote by $x(t)$ and $y(t)$ the concentrations of the nutrient and the microorganisms at any specific time t. We shall first write down the growth equation for the nutrient x. For this, we have the following:

Gain term: Since an amount of x_0 is supplied each time at a constant rate D into the system, the rate of increase of nutrient concentration at time t is Dx_0.

Loss terms:

1. A quantity of $x(t)$ is removed from the system at a constant rate of D. Therefore, the system loses $Dx(t)$ of nutrient concentration at any time t.
2. Each microorganism y consumes $U(x(t))$ of the nutrient. Therefore, $U(x(t))y(t)$ is the nutrient concentration consumed by the species y at a rate a. Thus, the nutrient concentration is reduced by $aU(x(t))y(t)$ as a consumption by y at any time t.

Thus, we have

rate of change of nutrient concentration in the growth medium
= rate of supply of nutrient − rate of removal − rate of consumption.

Mathematically,

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = Dx_0 - Dx(t) - aU(x(t))y(t). \tag{1.3}$$

For the growth of species y we assumed that the consumption of nutrient means the growth of y. Therefore, the rate at which the nutrient is being consumed, i.e., $aU(x(t))y(t)$ is also the rate at which the microorganism y is growing. Also the microorganism is removed from the system at a constant rate D. Thus, $Dy(t)$ denotes the quantity of microorganism removed from the system. Now,

rate of change of microorganism at any time
= growth rate of microorganism − rate of removal of microorganism.

Mathematically,

$$\frac{\mathrm{d}y(t)}{\mathrm{d}t} = aU(x(t))y(t) - Dy(t). \tag{1.4}$$

Equations (1.3) and (1.4) put together describe the limited resource–consumer dynamical system that we are going to try in the chemostat. For a ready reference, we shall write the equations hereunder as a system.

$$\begin{aligned} \frac{\mathrm{d}x(t)}{\mathrm{d}t} &= Dx_0 - Dx(t) - aU(x(t))y(t), \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} &= aU(x(t))y(t) - Dy(t). \end{aligned} \tag{1.5}$$

1.4 Properties of Solutions

We note that the characteristics of system (1.5) are essentially decided by the nonlinear term on the right hand side, that is, $U(x)$. U is known in literature as response function or consumption function or uptake function. There are some basic assumptions on the consumption function $U : [0, \infty), \to [0, \infty)$, which may be stated as follows:

1. $U(0) = 0$, $U(x) > 0$ for $x > 0$.
2. $\lim_{x\to\infty} U(x) = L_1, \quad 0 < L_1 < \infty$.
3. U is continuously differentiable.
4. U is monotone increasing.

Assumptions 1 and 2 are essential for any function to act as a consumption function. Condition 3 is expensive but always ensures the existence of solutions to the system (1.5). Readers who are familiar with the theory of elementary differential equations may recall that a local Lipschitz condition with mere continuity of U is enough to establish the existence of solutions to (1.5). Condition 4 assuming U to be monotone increasing or $\frac{\mathrm{d}U}{\mathrm{d}x} > 0$ (when 3 is satisfied) has a special purpose here. But we shall see a little later that this condition may also be relaxed, in general.

The following prototype functions, which satisfy all the earlier conditions 1−4, are generally regarded as consumption functions while studying biological models such as (1.5).

$U(x) = x$: Lotka–Volterra or Holling type-I consumption function.

$U(x) = \frac{x}{m+x}$: Michaelis–Menten or Holling type-II consumption function.

$U(x) = \frac{x^2}{(p+x)(q+x)}$ $p, q > 0$: Sigmoidal or Holling type-III consumption function.

The consumption function $U(x) = x$ does not satisfy the condition 2. However, it is popular for Lotka–Volterra type models.

Clearly conditions 1 and 2 ensure the existence of positive constant $L > 0$ such that

$$U(x) \leq L \quad \text{for all} \quad x \in [0, \infty). \tag{1.6}$$

Further, the assumption 3 with (1.6) ensures that the system (1.5) has unique solutions which are continuable on their maximal intervals of existence for any set of initial conditions.

We shall now establish that the solutions of system (1.5) are nonnegative owing to nonnegative initial conditions. This is a prerequisite as x and y represent populations and can not go negative in any case.

Theorem 1.1 *All the solutions of system* (1.5) *are nonnegative for all* $t \geq 0$ *corresponding to any nonnegative initial conditions.*

Proof We shall show that once a solution enters the plane

$$\Omega = \{(x, y)/x \geq 0, y \geq 0\},$$

it remains there forever. By continuity of solutions of (1.5) each solution has to take the value 0 before it assumes a negative value. If $y = 0$ for some $t = t_1 > 0$, then from the second equation of (1.5), $y'(t_1) = 0$, and hence, y is nondecreasing at t_1, which means that y is at least nondecreasing at $y = 0$. This rules out the possibility of y taking a negative value. Again when $x = 0$, we have

$$x'(t) = Dx_0 > 0,$$

since $y \geq 0, U(0) = 0$.

Therefore, x is increasing at $x = 0$. When $y = 0$, $x'(t) = Dx_0 - Dx$ and again at $x = 0$, $x'(t) = Dx_0 > 0$ and hence, x is increasing at $x = 0$. Thus, we can conclude that the solutions of (1.5) are non negative for all $t > 0$. □

How are the populations growing under limited supply of nutrient? Can the growth be alarming? We have an answer.

Theorem 1.2 *Any positive solution of* (1.5) *is bounded for nonnegative initial conditions that are not identically zero on any interval.*

Proof Consider

$$V(t) = V(x(t), y(t)) = x(t) + y(t).$$

Clearly,

$$V(0,0) = 0,\ V(x(t), y(t)) \geq 0 \quad \text{for} \quad t \geq 0 \text{ and } V(t) \to \infty$$

as $x(t),\ y(t) \to \infty$.

The time derivative of V along the solutions of (1.5) is

$$\begin{aligned} V'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) + aU(x(t))y(t) - Dy(t) \\ &= Dx_0 - D(x(t) + y(t)) \\ &\leq Dx_0 - DV(t). \end{aligned}$$

Thus, outside the region bounded by the positive coordinate plane and the surface $Dx + Dy = Dx_0$ or $x + y = x_0$, $V'(t)$ is negative definite. Thus, V is the required Lyapunov function.

Now, the conclusion follows from Theorem B.2 (Appendix B) with $W(t, X(t)) = x(t)$, $Q(t, X(t)) = V(t)$, and $\tilde{U} = x_0$. □

Notice that our journey with Lyapunov functions has begun.

1.5 Equilibrium Solutions

The study of existence of equilibria is very important, for an equilibrium state represents a state of lowest energy of the system. If the energy of the system decays from any initial state then it is known that the system remains stable. Thus, if a system approaches the equilibrium solution, the system stays in a stable state.

Equilibria of (1.5) are the points in the xy-plane satisfying $\frac{\mathrm{d}x}{\mathrm{d}t} = 0$ and $\frac{\mathrm{d}y}{\mathrm{d}t} = 0$. Thus, the equilibria of (1.5) are given by the solutions of the algebraic system

$$\begin{aligned} Dx_0 - Dx - aU(x)y &= 0, \\ aU(x)y - Dy &= 0. \end{aligned} \tag{1.7}$$

An immediate solution of this system is $(x_0, 0)$. This is a partially feasible equilibrium solution or axial equilibrium solution. If we are looking for a positive solution say (x^*, y^*) of (1.7) we should solve

$$\begin{aligned} Dx_0 - Dx^* - aU(x^*)y^* &= 0, \\ aU(x^*) - D &= 0. \end{aligned} \tag{1.8}$$

This yields,

$$U(x^*) = \frac{D}{a} \text{ and } x_0 = x^* + y^*. \tag{1.9}$$

From (1.9), we may understand that in order to possess a positive equilibrium state, the consumption level should at least touch the value D/a once. That is, there should exist an $x^* \in (0, \infty)$ such that $U(x^*) = \frac{D}{a}$.

Since $U(x) \leq L$ for all $x \in [0, \infty)$, (1.9) implies that

$$\frac{D}{a} \leq L \tag{1.10}$$

is a necessary condition for the existence of a positive solution for (1.8). If we further assume that

$$x_0 > x^* \tag{1.11}$$

then in view of (1.9), system (1.8) yields a positive solution, and hence, (1.5) possesses a positive equilibrium solution, designated hereafter as (x^*, y^*).

1.6 Stability Analysis

Having obtained the equilibrium solutions, we now study the stability of each of them. We have two different tasks here.

1. The axial equilibrium $(x_0, 0)$ is stable, which means that the microorganisms y become extinct.
2. If we are looking for the survival of the species x and y we have to establish the conditions under which the positive equilibrium (x^*, y^*) is stable.

We discuss both the cases here.

We recall that the equilibrium solution (x^*, y^*) of the system (1.5) is globally asymptotically stable, if every solution $(x(t), y(t))$ of (1.5) corresponding to an arbitrary choice of initial conditions satisfies

$$\lim_{t\to\infty} x(t) = x^* \text{ and } \lim_{t\to\infty} y(t) = y^*.$$

We refer the readers to Appendix C for more details on stability.

The following result states the conditions under which $(x_0, 0)$ is stable.

Theorem 1.3 *The axial equilibrium* $(x_0, 0)$ *is globally asymptotically stable provided* $aL < D$ *holds.*

Proof It is clear from the second equation of (1.5) that $\lim_{t\to\infty} y(t) = 0$ as $t \to \infty$ when $aL < D$ for the system (1.5). It suffices to prove that $x(t) \to x_0$ as $t \to \infty$ when the earlier inequality holds.

Consider

$$V(t) = V(x(t), y(t)) = x(t) + y(t).$$

Clearly,

$$V(0, 0) = 0 \text{ and } V(x(t), y(t)) > 0 \text{ for } x > 0,\ y > 0.$$

Further along the solutions of (1.5),

$$\begin{aligned} V'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) \\ &\quad - Dy(t) + aU(x(t))y(t) \\ &= Dx_0 - D(x(t) + y(t)) \\ &= Dx_0 - DV(t). \end{aligned}$$

That is, $V'(t) = -DV(t) + Dx_0$, from which it follows that

$$V(t) = V(0)e^{-Dt} + x_0.$$

Thus, $\lim_{t\to\infty} V(t) = \lim_{t\to\infty}[x(t) + y(t)] = x_0$. The conclusion follows from the observation that $\lim_{t\to\infty} y(t) = 0$. Hence, the theorem. □

We shall now turn our attention toward the stability of (x^*, y^*). It is natural to expect that the condition $aL > D$ may revert the earlier situation as it is a necessary condition for the existence of a positive equilibrium, and therefore, may have the strength to destabilize the axial equilibrium. The following result establishes that this condition is sufficient also.

Theorem 1.4 *The positive equilibrium* (x^*, y^*) *of* (1.5) *is globally asymptotically stable provided* $aL > D$.

We provide a detailed proof based on Lyapunov theory for Theorem 1.4 at the end of this chapter.

It is not easy to conduct an experiment to verify our "experiment after theory" concept simply by basing on the conclusions of these results, because we should specifically know how the species y consumes the nutrient x and identify at least some key parameters that control the dynamics of the system. It is observed during some experiments on microorganisms in cultured environments that the consumption clearly follows a specific functional response given by

$$U(x) = \frac{x}{m + x},$$

where $m > 0$ is called the half-saturation constant. It denotes the concentration at which the per capita growth rate achieves the half maximum growth rate.

Note that $L = 1$ for this uptake function.

Using this definition of consumption function directly, we write system (1.5) as

$$\begin{aligned} \frac{dx}{dt} &= Dx_0 - Dx - a\frac{x}{m + x}y, \\ \frac{dy}{dt} &= a\frac{x}{m + x}y - Dy. \end{aligned} \tag{1.12}$$

A positive equilibrium solution of (1.12) is given by

$$U(x^*) = \frac{x^*}{m + x^*} = \frac{D}{a}.$$

That is

$$x^* = \frac{mD}{a-D} \quad \text{and} \quad y^* = x_0 - x^*.$$

Then a set of necessary and sufficient conditions for the existence of a positive equilibrium solution for (1.12) is (see (1.10) and (1.11)) as follows:

$$a > D \quad \text{and} \quad \frac{mD}{a-D} < x_0.$$

The second inequality after a rearrangement gives us $a\frac{x_0}{m+x_0} > D$. But $\frac{x_0}{m+x_0} \leq 1$. This implies that a positive equilibrium solution exists if and only if

$$D < a\frac{x_0}{m+x_0}.$$

Now Theorems 1.3 and 1.4 assume the following form.

Theorem 1.5 *If* $a \leq D$ *or* $a > D$ *and* $\frac{mD}{a-D} \geq x_0$ *then* $\lim_{t\to\infty} x(t) = x_0$ *and* $\lim_{t\to\infty} y(t) = 0$.

Proof The proof of this theorem follows from that of Theorem 1.3. □

Note that conditions of Theorem 1.5 imply the non existence of a positive equilibrium also.

Theorem 1.6 *If* $a > D$ *and* $\frac{mD}{a-D} < x_0$ *then* $\lim_{t\to\infty} x(t) = x^* = \frac{mD}{a-D}$ *and* $\lim_{t\to\infty} y(t) = y^* = x_0 - x^*$.

Proof Consider the function

$$V(t) \equiv V(x(t), y(t)) = \frac{1}{2}(x_0 - x - y)^2 + \alpha\Big(y - y^* - y^* \log\frac{y}{y^*}\Big).$$

Clearly $V(x^*, y^*) = 0$, and $V(x, y) > 0$ for $x > x^*,\ y > y^*$ and is fit to be a Lyapunov function.

Then differentiating V along the solutions of (1.12) we have

$$\begin{aligned}
V' &= (x_0 - x - y)(-x' - y') + \alpha(y' - y^*\frac{1}{y}y') \\
&= -(x_0 - x - y)\Big\{Dx_0 - Dx - a\frac{x}{m+x}y + a\frac{x}{m+x}y - Dy\Big\} \\
&\quad + \alpha(y - y^*)\Big(\frac{ax}{m+x} - D\Big) \\
&= -D(x_0 - x - y)^2 + \alpha(y - y^*)\Big(\frac{ax}{m+x} - D\Big) \\
&= -D[(x - x^*) + (y - y^*)]^2 + \alpha\frac{am}{(m+x)(m+x^*)}(x - x^*)(y - y^*)
\end{aligned}$$

$$= -D[(x - x^*) + (y - y^*)]^2 + \alpha \frac{D}{x^*} \frac{m}{m + x}(x - x^*)(y - y^*)$$
$$= -D \left\{ (x - x^*)^2 + (y - y^*)^2 + \left(2 - \frac{\alpha}{x^*} \frac{m}{m + x}\right)(x - x^*)(y - y^*) \right\}.$$

using $x_0 = x^* + y^*$, $D = \frac{ax^*}{m+x^*}$ in the aforementioned fourth line.

The expression in brackets on the right hand side of earlier equation is of the type $AX_1^2 + BX_1Y_1 + CY_1^2$ and the conditions for its positive definiteness are $A > 0$, $B^2 < 4AC$ (see Theorem A.5, Appendix A). Letting $X_1 = x - x^*$, $Y_1 = y - y^*$, $A = C = 1$ and $B = 2 - \frac{\alpha}{x^*} \frac{m}{m+x}$, we have,

$$D \left\{ (x - x^*)^2 + (y - y^*)^2 + \left(2 - \frac{\alpha}{x^*} \frac{m}{m + x}\right)(x - x^*)(y - y^*) \right\}$$

is positive definite provided

$$\left(2 - \frac{\alpha}{x^*} \frac{m}{m + x}\right)^2 < 4.$$

On expansion and simplification, we get $\frac{\alpha}{x^*} \frac{m}{m+x} < 4$. Since $\frac{m}{m+x} \leq 1$ for all x, m, the condition is $\frac{\alpha}{x^*} < 4$; in other words, if $\alpha < 4x^* = 4\frac{mD}{a-D}$ holds the aforementioned expression is positive definite.

Now choosing $0 \leq \alpha < 4\frac{mD}{a-D}$, we have $V' < 0$. Thus, V is the required Lyapunov function, and hence, by Theorem C.9 (Appendix C), the equilibrium (x^*, y^*) is asymptotically stable. □

With the statements of the Theorems 1.5 and 1.6, the model seems ready for a test in the chemostat. Truly the experiment has not been conducted for the model equations (1.12) but for a competition model that is a simple extension of (1.12) with two different microorganisms say y_1 and y_2 competing for the same nutrient x.

Accordingly the model assumes the form

$$\begin{aligned} \frac{dx}{dt} &= Dx_0 - Dx - a_1 \frac{x}{m_1 + x} y_1 - a_2 \frac{x}{m_2 + x} y_2, \\ \frac{dy_1}{dt} &= a_1 \frac{x}{m_1 + x} y_1 - Dy_1, \\ \frac{dy_2}{dt} &= a_2 \frac{x}{m_2 + x} y_2 - Dy_2, \end{aligned} \tag{1.13}$$

with some positive initial conditions.

As in (1.12), the quantities a_1, a_2 represent the maximum specific growth rates as well as consumption rates of y_1, y_2, and m_1, m_2 are the corresponding half-saturation constants of the consumption.

The equilibria of (1.13) are given by the solutions of

$$
\begin{aligned}
Dx_0 - Dx - a_1 \frac{x}{m_1 + x} y_1 - a_2 \frac{x}{m_2 + x} y_2 &= 0, \\
a_1 \frac{x}{m_1 + x} y_1 - D y_1 &= 0, \\
a_2 \frac{x}{m_2 + x} y_2 - D y_2 &= 0.
\end{aligned}
$$

Clearly $(x_0, 0, 0)$ is one immediate solution of this system. As other nontrivial solutions, we have $(x^*, {y_1}^*, 0)$, $(x^*, 0, {y_2}^*)$. For a positive equilibrium solution $(x^*, {y_1}^*, {y_2}^*)$ we should solve

$$
\begin{aligned}
x_0 - x^* - {y_1}^* - {y_2}^* &= 0, \\
a_1 \frac{x^*}{m_1 + x^*} - D &= 0, \\
a_2 \frac{x^*}{m_2 + x^*} - D &= 0.
\end{aligned}
$$

Last two equations yield a solution for x^* provided the parameters satisfy

$$
\frac{m_1 D}{a_1 - D} = \frac{m_2 D}{a_2 - D}.
$$

From the first equation we have ${y_1}^* + {y_2}^* = x_0 - x^*$.

As in the case of (1.12), a positive equilibrium exists if and only if the inequalities

$$
a_1 > D,\ a_2 > D \ \text{ and } \ x_0 > x^* = \frac{m_1 D}{a_1 - D} = \frac{m_2 D}{a_2 - D}
$$

hold. Notice in this case that we are unable to write explicitly what ${y_1}^*$ and ${y_2}^*$ are.

Define the quantities $\lambda_1 = \frac{m_1 D}{a_1 - D}$, and $\lambda_2 = \frac{m_2 D}{a_2 - D}$, called the break-even concentrations. λ_i determines the survival of the species (y_i) at least till the stage of possible competition. More specifically, If λ_i is small, the corresponding y_i will continue to survive till a competition decides its fate and for large λ_i the corresponding y_i may not even see what a competition is. Now we extend Theorems 1.5 and 1.6 for the model (1.13).

Theorem 1.7 *The following results hold:*

1. *If* $a_i \le D$ *for* $i = 1, 2$ *or* $a_i > D,\ i = 1, 2$ *and* $x_0 < \min\{\lambda_1,\ \lambda_2\}$ *then any solution of* (1.13) *satisfies*

$$
\lim_{t\to\infty} x(t) = x_0,\ \lim_{t\to\infty} y_1(t) = 0,\ \text{and} \ \lim_{t\to\infty} y_2(t) = 0.
$$

2. *If* $a_i > D,\ \ i = 1, 2$ *and* $0 < \lambda_1 < \lambda_2 < x_0$ *or* $0 < \lambda_1 < x_0 < \lambda_2$ *then any solution of* (1.13) *with positive initial conditions satisfies*

$$\lim_{t\to\infty} x(t) = \frac{m_1 D}{a_1 - D} \equiv \lambda_1,\ \lim_{t\to\infty} y_1(t) = x_0 - \lambda_1,\ \textit{and}\ \lim_{t\to\infty} y_2(t) = 0.$$

In case $0 < \lambda_2 < \lambda_1 < x_0$ *or* $0 < \lambda_2 < x_0 < \lambda_1$ *then*

$$\lim_{t\to\infty} x(t) = \lambda_2,\ \lim_{t\to\infty} y_1(t) = 0,\ \textit{and}\ \lim_{t\to\infty} y_2(t) = x_0 - \lambda_2.$$

3. *If* $a_i > D,\ \ i = 1, 2$ *and* $\lambda_1 = \lambda_2 = \frac{m_1 D}{a_1 - D}$ *then*

$$\lim_{t\to\infty} x(t) = \lambda_1,\ \lim_{t\to\infty} (y_1(t) + y_2(t)) = x_0 - \lambda_1.$$

Proof Clearly case 1 explains the extinction of both the consumer species. Case 2 supports the competitive exclusion principle that states that "no ecological community in which n species are limited by less than n resources can survive indefinitely". But Case 3 provides conditions for coexistence. The proof of Case 1 is a simple extension of the proof of Theorem 1.3, and hence, omitted.

Proof for case 2 We need to rearrange (1.13) before we proceed.

Observe that for $i = 1, 2$,

$$\begin{aligned} a_i \frac{x}{m_i + x} y_i - D y_i &= a_i \frac{x}{m_i + x} y_i - D \left[\frac{m_i + x}{m_i + x}\right] y_i \\ &= (a_i - D) \frac{x}{m_i + x} y_i - \left[\frac{m_i D}{m_i + x}\right] y_i \\ &= (a_i - D) \frac{x}{m_i + x} y_i - (a_i - D)\lambda_i \frac{y_i}{m_i + x} \\ &= (a_i - D) \frac{(x - \lambda_i)}{m_i + x} y_i. \end{aligned}$$

This enables us to write (1.13) as

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= D x_0 - D x - a_1 \frac{x}{m_1 + x} y_1 - a_2 \frac{x}{m_2 + x} y_2, \\ \frac{\mathrm{d}y_1}{\mathrm{d}t} &= (a_1 - D) \frac{(x - \lambda_1)}{m_1 + x} y_1, \\ \frac{\mathrm{d}y_2}{\mathrm{d}t} &= (a_2 - D) \frac{(x - \lambda_2)}{m_2 + x} y_2. \end{aligned} \tag{1.14}$$

Now consider the Lyapunov function

$$V = x - \lambda_1 - \lambda_1 \log \frac{x}{\lambda_1} + c_1 \left(y_1 - {y_1}^* - {y_1}^* \log \frac{y_1}{{y_1}^*} \right) + c_2 y_2,$$

in which $c_i = \frac{a_i}{a_i - D}$ for $i = 1, 2$ are positive constants.

Then along the solutions of (1.14), we have

$$
\begin{aligned}
V' &= x' - \lambda_1 \frac{1}{x} x' + c_1\Big(y_1' - {y_1}^* \frac{1}{y_1} {y_1}'\Big) + c_2 {y_2}' \\
&= \frac{(x-\lambda_1)}{x}\left[D x_0 - D x - a_1 \frac{x}{m_1+x} y_1 - a_2 \frac{x}{m_2+x} y_2\right] \\
&\quad + c_1 (y_1 - {y_1}^*)(a_1 - D)\frac{(x-\lambda_1)}{m_1+x} + c_2 y_2 (a_2 - D)\frac{(x-\lambda_2)}{m_2+x} \\
&= \frac{(x-\lambda_1)}{x}(D x_0 - D x) - a_1 \frac{x-\lambda_1}{m_1+x} y_1 - a_2 \frac{x-\lambda_1}{m_2+x} y_2 \\
&\quad + a_1 y_1 \frac{(x-\lambda_1)}{m_1+x} - a_1 {y_1}^* \frac{(x-\lambda_1)}{m_1+x} + a_2 \frac{(x-\lambda_2)}{m_2+x} y_2 \\
&= \frac{(x-\lambda_1)}{x}(D x_0 - D x) - a_1 {y_1}^* \frac{(x-\lambda_1)}{m_1+x} + a_2 \frac{(\lambda_1-\lambda_2)}{m_2+x} y_2 \\
&= (x-\lambda_1)\left[\frac{D(x_0-x)}{x} - a_1 \frac{{y_1}^*}{m_1+x}\right] + a_2 \frac{(\lambda_1-\lambda_2)}{m_2+x} y_2 .
\end{aligned}
$$

Now we consider the equilibrium solution $(x^* = \lambda_1, {y_1}^*, 0)$ of (1.14) and we can show that

$$
{y_1}^* = \frac{D(x_0-\lambda_1)(m_1+\lambda_1)}{a_1\lambda_1}. \tag{1.15}
$$

Consider the term

$$
\begin{aligned}
\frac{D(x_0-x)}{x} - a_1 \frac{{y_1}^*}{m_1+x} &= \frac{D(x_0-x)}{x} - \frac{D(x_0-\lambda_1)(m_1+\lambda_1)}{\lambda_1(m_1+x)} \\
&= \frac{D}{\lambda_1 x (m_1+x)}\Big[(x_0-x)\lambda_1(m_1+x) \\
&\qquad - x(x_0-\lambda_1)(m_1+\lambda_1)\Big] \\
&= \frac{D}{\lambda_1 x (m_1+x)}\Big[-m_1 x_0 (x-\lambda_1) \\
&\qquad - \lambda_1 x (x-\lambda_1)\Big] \\
&= -\frac{D(x-\lambda_1)}{\lambda_1 x (m_1+x)}[m_1 x_0 + \lambda_1 x].
\end{aligned}
$$

Using this in V' we get

$$
V' = -\frac{D(x-\lambda_1)^2}{\lambda_1 x (m_1+x)}[m_1 x_0 + \lambda_1 x] + a_2 \frac{(\lambda_1-\lambda_2)}{m_2+x} y_2 \le 0.
$$

Thus, V' is negative semi definite and we need to apply Theorem C.10 (Appendix C). Observing that $M = \{(x^* = \lambda_1, {y_1}^*, 0)\}$ is the largest invariant set in $E = \{(x^* = \lambda_1, y_1, 0) : \ y_1 \geq 0\}$, the conclusion that $(x^*, y_1^*, 0)$ is asymptotically stable follows from Theorem C.10 (Appendix C). The proof of second part follows similarly.

Proof of case 3 Extending the Lyapunov function used in Theorem 1.6, we consider

$$\begin{aligned} V(t) &\equiv V(x(t), y(t)) \\ &= \frac{1}{2}(x_0 - x - y_1 - y_2)^2 + \alpha \sum_{i=1}^{2} \left(y_i - y_i{}^* - y_i{}^* \log \frac{y_i}{y_i{}^*} \right). \end{aligned}$$

Clearly

$$V(x^*, y_1{}^*, y_2{}^*) = 0 \ \text{ and } \ V(x, y_1, y_2) > 0 \ \text{ for } \ x > x^*, \ y_1 > y_1{}^*, \ y_2 > y_2{}^*.$$

Then differentiating V along the solutions of (1.13) and proceeding as in Theorem 1.6, we get

$$\begin{aligned} V' &= -D[(x - x^*) + (y_1 + y_2 - y_1{}^* - y_2{}^*)]^2 \\ &\quad + \alpha \textstyle\sum_{i=1}^{2} \frac{a_i m_i}{(m_i + x)(m_i + x^*)}(x - x^*)(y_i - y_i{}^*) \\ &= -D[(x - x^*) + (y_1 + y_2 - y_1{}^* - y_2{}^*)]^2 \\ &\quad + \tfrac{\alpha D}{x^*} \textstyle\sum_{i=1}^{2} \frac{m_i}{m_i + x}(x - x^*)(y_i - y_i{}^*), \end{aligned} \tag{1.16}$$

using $\frac{a_1}{m_1 + x^*} = \frac{D}{x^*} = \frac{a_2}{m_2 + x^*}$.

Since $\frac{m_i}{m_i + x}$ is monotone in both m_i (increasing) and x (decreasing) and $0 \leq \frac{m_i}{m_i + x} \leq 1$ for all $m_i \geq 0$, $x \geq 0$, we have from (1.16) that

$$\begin{aligned} &-D[(x - x^*) + (y_1 + y_2 - y_1{}^* - y_2{}^*)]^2 \leq V' \\ &\leq -D[(x - x^*) + (y_1 + y_2 - y_1{}^* - y_2{}^*)]^2 \\ &\quad + \frac{\alpha D}{x^*}(x - x^*)(y_1 + y_2 - y_1{}^* - y_2{}^*), \end{aligned} \tag{1.17}$$

or in the reverse order, the inequality $\leq$, replaced by the inequality $\geq$.

Then $V' < 0$ follows from the negative definiteness of

$$-D[(x - x^*) + (y_1 + y_2 - y_1{}^* - y_2{}^*)]^2 + \frac{\alpha D}{x^*}(x - x^*)(y_1 + y_2 - y_1{}^* - y_2{}^*).$$

Expanding and rearranging the terms we get the expression

$$-D\left[(x - x^*)^2 + (y_1 + y_2 - y_1{}^* - y_2{}^*)^2 + \left(2 - \frac{\alpha}{x^*}\right)(x - x^*)(y_1 + y_2 - y_1{}^* - y_2{}^*)\right].$$

In other words, if we can show that

$$(x - x^*)^2 + (y_1 + y_2 - y_1{}^* - y_2{}^*)^2 + \left(2 - \frac{\alpha}{x^*}\right)(x - x^*)(y_1 + y_2 - y_1{}^* - y_2{}^*)$$

is positive definite, we are done. We have already established that for the choice $\alpha \in [0, \frac{4m_1 D}{a_1 - D})$, this expression is positive definite (see proof of Theorem 1.6).

Hence it follows that $V' < 0$ along the solutions of (1.13). By an application of Theorem C.9 (Appendix C) the conclusion follows immediately. The proof is complete. □

We are now in a position to understand the experiment that is conducted to check the authenticity of Theorem 1.7. Before we describe the experiment, we give a detailed description and working mechanism of the chemostat. It is important here to notice that the supply/removal rate D and input concentration of nutrient x_0 are at the control of the experimenter and the consumption rate a and half saturation constant m are measured experimentally. The term $\lambda = \frac{mD}{a-D}$ is called the break-even concentration. Then Theorem 1.7 states that the species y_1 survives if its break-even concentration is less than that of y_2 and leading to the elimination of y_2 and viceversa (case 2). Also, if both the species have the same break-even concentrations by any means, the species coexist (case 3). These conditions will be verified experimentally.

We now describe a simple chemostat (Fig. 1.1). The name chemostat is associated with a laboratory device used for growing microorganisms in a cultured environment. The mechanism of a chemostat is described later. We take up the chemostat in its basic, simplest form, though the actual device may be designed in various forms. It consists of three interconnected vessels. The outlet of first vessel is the inlet for the second vessel and the outlet of the second vessel is the inlet for the third.

The first vessel is called a feed bottle. It contains all the nutrients required for the growth of microorganisms. As mentioned earlier, one of the nutrients in this vessel is a limiting nutrient. The contents of this vessel are pumped into the second vessel at a constant rate. In this "culture vessel", the microorganisms grow feeding on the

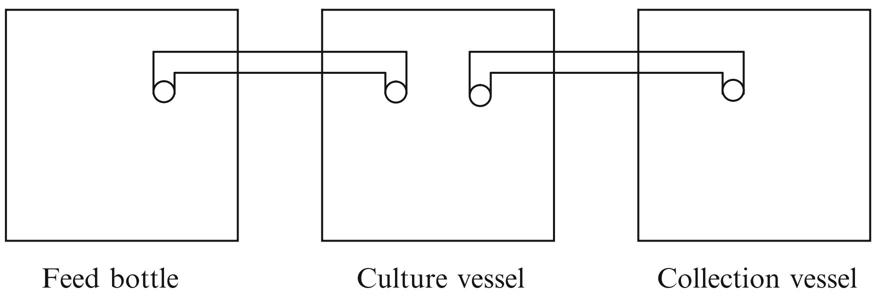

Fig. 1.1 Visualization of a simple chemostat

nutrients supplied from the first vessel. The culture vessel may contain many organisms. It is continuously stirred for the uniform distribution of the nutrient so that all the organisms have equal access to it. All the external factors such as temperature are kept constant as assumed. Since all the other nutrients are abundantly supplied, we are interested only in the study of the effect of limiting nutrient. The contents of this culture vessel are pumped into the third vessel, which is called a overflow vessel or a collection vessel. Naturally it contains nutrients, microorganisms and, of course, the products produced by the microorganisms. The rate at which the contents of the culture vessel are pumped into the third vessel is the same as that of the rate at which the contents of the first vessel are pumped into second vessel, which is our D in (1.5). Measurements are made on the contents of this overflow (collection) vessel without disturbing the contents of the culture vessel.

Further the parameters m, the half-saturation constant and a, the consumption/growth rate of the nutrient can be measured during the experiment (in the absence of a competitor). For the desired results, the following conditions should be met while conducting the experiment.

1. Suitable organisms and nutrient are selected.
2. Washout is fast enough that it does not allow growth on the cell walls and allows no metabolic products.
3. No substances from which the organisms can synthesize the nutrient are available.
4. The organism does not mutate.

Experiment

Three experiments were carried out by Hansen and Hubbell [48]. It should be noted that both x_0 and D are under the control of the experimenter. The nutrient used was tryptophan and the two competing microorganisms are *Escherichia coli* and *Pseudomonas aeruginosa.*

The first experiment was conducted with one organism having larger value of a and smaller value of λ than the second one.

In the second experiment, care was taken to see that one organism has smaller m and larger λ value than the second one.

One may be anxious to state that the organism with a larger consumption/growth rate or smaller half-saturation constant should win the competition. For, in the first case the organism has a better reproductivity and in the second case the organism reaches more of its growth potential at a lower nutrient concentration. But experiments clearly showed that the organism with smaller λ (break-even concentration) always won the competition and survived. Thus, the parameter λ is the predictor. In other words the competing organism whose consumption touches the equilibrium value $U(x^*)$ earlier wins the competition.

The third experiment was conducted with organisms having different a and m values but approximately same λ value. Results are encouraging showing that the organisms do coexist. This completely establishes the mathematical predictions supporting the "theory precedes experiment" concept.

1.7 General Uptake Function

As we have already noted, an uptake function is required to satisfy certain conditions.

(a) It should be nonnegative (takes the values '0' only when its argument vanishes), continuous, bounded and has a saturation limit.
(b) Its nonlinearity should not hold back the system from having unique solutions that are continuable in their maximal interval of existence.

Though conditions 1–3 on $U(x)$ of Sect. 1.4 are good enough to formulate the uptake function, the earlier two conditions motivate us to look for a general class of uptake functions that are accepted by both mathematics and biology. Though Monod [66] has suggested the Michaelis–Menten uptake function $U(x) = \frac{x}{m+x}$ as the one suitable for studies in a chemostat, one cannot expect all the microorganisms in the nature to follow the same definition. Some specific forms of uptake functions studied by researchers and that have experimental support are given here.

1. Consider the function $U(x) = \frac{mx^2}{(a_1+x)(b_1+x)}$, in which m, a_1 and b_1 are positive constants. Clearly $U(0) = 0$, $U(x) > 0 \quad \text{for } x > 0$, $\lim_{x\to\infty} U(x) = m < \infty$.

Further $U'(x) = \frac{2abmx+(a+b)mx^2}{(a+x)^2(b+x)^2} > 0 \quad \text{for } x > 0$. Also $U'(x) \to 0$ as $x \to \infty$. Certainly $U(x)$ defined here is of the type expected in Sect. 1.4. Note that $U'(x)$ is continuous and bounded.

2. Another well-known example of uptake function is the following:

$$U(x) = \frac{m}{1 + \frac{b}{x} + \frac{x}{c}}, \qquad m, b, c > 0.$$

We now study the properties of this function. It is easy to see that $U(0) = 0$, $U(x) > 0$ for $x > 0$. But $\lim_{x\to\infty} U(x) = 0$. Further,

$$U'(x) = \frac{-m(x^2 - bc)}{(1 + \frac{b}{x} + \frac{x}{c})^2 x^2}.$$

Clearly, $U'(x) > 0$ for $x^2 < bc$ and $U'(x) < 0$ for $x^2 > bc$. Of course, $U'(x)$ is continuous, bounded and approaches 0 as $x \to \infty$. This is clearly an example of a nonmonotone increasing uptake function.

But the problem in considering such nonmonotone increasing uptake functions is that they may approach low values. When the consumption (availability of nutrient) becomes very low that is beyond a threshold value we can not expect the species to survive. Then one should think of how far this decreasing trend is allowed without a danger of extinction of consumer species y in case of nonmonotone increasing consumption. The following class of uptake functions takes care of this situation. Suppose that

1. $U : \mathbf{R}^+ \to \mathbf{R}^+$, $U(0) = 0$ and U is continuously differentiable and
2. there exist unique, positive extended real numbers λ and μ, $\lambda < \mu$ such that $aU(x) < D$ if x does not belong to $[\lambda, \mu]$ and $aU(x) > D$ if $x \in (\lambda, \mu)$. Further, $U'(\lambda) > 0$ if $\lambda < \infty$ and $U'(\mu) < 0$ if $\mu < \infty$.

Note that U defined earlier is monotone increasing if $\mu = \infty$.

The following result (for proof see [21]) establishes conditions for the stability of positive equilibrium solution of (1.5) for the earlier class of uptake functions.

Theorem 1.8 *The following results hold:*

1. *If $\lambda < x_0 < \mu$ then the equilibrium solution (x^*, y^*) of (1.5) attracts all the solutions with positive initial conditions.*
2. *In case $x_0 < \lambda$ or $x_0 > \mu$ then $(x_0, 0)$ is a global attractor.*

The case $x_0 < \lambda$ signifies the extinction of the consumer species due to insufficient food while $x_0 > \mu$ warns that too much availability of nutrient leads to a washout of all of y.

The results provided so far are concerned with the monotonicity of the uptake function only. Observe that we are still asking for a differentiability condition 3 on $U(x)$ when a local Lipschitz condition is enough to ensure the existence of unique solutions. Further the result we provided (Theorem 1.8) as the one for a general uptake function deals with monotonicity of the uptake function while Theorem 1.4 requires maintenance of a minimum level of consumption, $U(x) \geq U(x^*)$ for $x \geq x^*$. Therefore, results in the direction of removing differentiability assumption on U are welcome for the system (1.5).

Now consider the function

$$U(x) = \frac{x^\alpha}{\omega + x^\beta}, \quad \omega > 0, \quad 0 < \alpha \leq \beta, \tag{1.18}$$

which we designate as the generalized Michaelis–Menten uptake function. Clearly, this function satisfies a Lipschitz condition for $\alpha \geq 1$ and fails to satisfy the condition at $x = 0$ when $0 < \alpha < 1$. Observe also that $x = 0$ is only such point. U satisfies all the other conditions required for an uptake function. Further the behavior of all the functions that are mentioned earlier as experimentally proved uptake functions in a chemostat can be studied from this function.

Several articles are available in the literature on model equations (1.5) and several modifications of it. Yet, the system (1.5) is drawing the attention of mathematicians in the areas of mathematical biology due to its flexibility and applications. We notice that the two aspects,

1. The consumption law ($U(x)$) need not be monotone, differentiable in nature;
2. The stability of positive equilibrium solution of (1.5) for such an uptake function; have ever been the points of discussion for researchers working in this area of mathematics.

We now establish the existence of solutions to system (1.5) under conditions weaker than a Lipschitz condition and also establish conditions for the global asymptotic stability for a nonmonotone, nondifferentiable uptake function. This illustrates the robustness of the chemostat model (1.5). We employ the following notation.

We consider the system of equations given by

$$X'(t) = F(t, X(t))$$

with initial conditions $X(t_0) = X_0$.

Let $S(\rho)$ be an open bounded sphere contained in $\mathbf{R}^{n+1}$ and let $F : S \to \mathbf{R}^n$. For a given $(t_0, X_0) \in S$, a solution of the earlier system is a differentiable function $X(t)$ on an interval J such that

$$X' = F(t, X(t)) \;\text{ for }\; t \in J, t_0 \in J \;\text{ and }\; X(t_0) = X_0.$$

For $X \in \mathbf{R}^n$, we define $\|X\| = \sum_{i=1}^n |X_i|$.

The following lemma is a minor extension of a result of Norris and Driver [71], Theorem C.1 (Appendix C).

Lemma 1.9 *Let $F : S \to \mathbf{R}^n$ be continuous and satisfy the following condition: Each point in S has an open neighbourhood N, an integer $m \geq 0$, functions h_j and ψ_j for $j = 1, 2, \cdots, m$, and nonnegative constants $K_1, K_2, K_1 + K_2 \neq 0$ such that*

$$\|F(t,\xi) - F(t,\eta)\| \leq K_1\|\xi - \eta\| + K_2 \sum_{j=1}^{m} |\psi_j(h_j(t,\xi)) - \psi_j(h_j(t,\eta))|$$

on N where $h_j : N \to \mathbf{R}$ is continuously differentiable with

$$\frac{\partial h_j(t,\xi)}{\partial t} + \sum_{i=1}^{n} \frac{\partial h_j(t,\xi)}{\partial \xi_i} F_i(t,\xi) \neq 0 \quad \text{on } N \quad \text{and}$$

each $\psi_j : \mathbf{R} \to \mathbf{R}$ is continuous and of bounded variation on bounded subintervals. Then the system $X' = F(t, X(t))$ with $X(t_0) = X_0, (t_0, X_0) \in S$ has a unique solution on any interval J.

Observe that the choice of $K_2 = 0$ in the earlier lemma reduces our considerations to a Lipschitz condition. Before proving our next result, we rewrite system (1.5) as

$$X'(t) = F(t, X(t)), \tag{1.19}$$

where

$$X(t) = \begin{pmatrix} x(t) \\ y(t) \end{pmatrix} \text{ and } F(t, X(t)) = \begin{pmatrix} D(x_0 - x(t)) - aU(x(t))y(t) \\ -Dy(t) + aU(x(t))y(t) \end{pmatrix}.$$

We now establish the following theorem.

Theorem 1.10 *The given system of equations* (1.19)*, and hence,* (1.5) *has a unique solution for a given set of initial conditions.*

Proof We shall verify the hypotheses of Lemma 1.9 for the system (1.19).

For $t \geq 0$ and functions $\xi(t) = (\xi_1(t), \xi_2(t))$ and $\eta(t) = (\eta_1(t), \eta_2(t))$, we have

$$\begin{aligned}
&\|F(t,\xi) - F(t,\eta)\| \\
&\leq D|\eta_1(t) - \xi_1(t)| + D|\eta_2(t) - \xi_2(t)| + 2a|U(\eta_1(t))\eta_2(t) - U(\xi_1(t))\xi_2(t)| \\
&\leq K_1\|\xi(t) - \eta(t)\| + K_2 \sum_{j=1}^{2} |\psi_j(h_j(t,\xi)) - \psi_j(h_j(t,\eta))|,
\end{aligned}$$

where $K_1 = D$ and $K_2 = 2a$. Now, if we choose

$$\psi_1(h_1(t,\xi)) = \xi_2(t)U(h_1(t,\xi(t))), \; h_1(t,\xi) = \xi_1(t),$$

$$\psi_2(h_2(t,\xi)) = \xi_2(t)U(h_2(t,\xi(t))), \text{ and } h_2(t,\xi) = \xi_1(t),$$

then, it is easy to see that all the hypotheses of Lemma 1.9 are satisfied, and hence, the conclusion follows. □

Now we employ Theorem 1.10 to establish that the system of equations (1.5) admits a unique equilibrium solution (x^*, y^*).

Theorem 1.11 *The system of equations* (1.8) *has a unique solution yielding a unique nontrivial equilibrium solution for the system* (1.5).

Proof Using (1.8) in (1.5), we get

$$\begin{aligned}
x'(t) &= -D(x(t) - x^*) - a[U(x(t))y(t) - U(x^*)y^*], \\
y'(t) &= ay(t)(U(x(t) - U(x^*)).
\end{aligned}$$

Denoting $x(t) - x^* = x_1(t)$, $y(t) - y^* = y_1(t)$ and $U(x(t)) - U(x^*) = U_1(x_1(t))$, earlier system after a simple rearrangement takes the form

$$\begin{aligned}
x_1'(t) &= -Dx_1(t) - a(y_1(t) + y^*)U_1(x_1(t)) - aU(x^*)y_1(t), \\
y_1'(t) &= a(y_1(t) + y^*)U_1(x_1(t)).
\end{aligned} \tag{1.20}$$

Now choose the initial conditions

$$x_1(t_0) = 0 \text{ and } y_1(t_0) = 0. \tag{1.21}$$

Then by the Theorem 1.10, the initial value problem (1.20), (1.21) admits a unique solution. Clearly, the trivial solution is the only solution of the system (1.20) and (1.21). This implies that

$$x_1(t) \equiv 0 \equiv y_1(t) \quad \text{for } t > 0,$$

which implies that $x(t) = x^*$ and $y(t) = y^*$ is the unique solution satisfying (1.7), and hence, (1.8) guaranteeing the existence of a unique equilibrium solution for the system (1.5). □

We now present a proof for Theorem 1.4 (as Theorem 1.12), which becomes more relevant in view of the earlier discussion on uptake functions. It is assumed here that there exist positive constants β and $\bar{\beta}$ such that the uptake function satisfies

$$\beta \leq \frac{U(x) - U(x^*)}{x - x^*} \leq \bar{\beta}.$$

Theorem 1.12 *The positive equilibrium* (x^*, y^*) *of* (1.5) *is globally asymptotically stable provided* $aL > D$.

Proof We use the same Lyapunov function as in Theorem 1.6, that is,

$$V(t) \equiv V(x(t), y(t)) = \frac{1}{2}(x_0 - x - y)^2 + \alpha\Big(y - y^* - y^* \log \frac{y}{y^*}\Big).$$

α is a nonnegative parameter to be chosen later. Differentiating V along the solutions of (1.5) we have

$$\begin{aligned}
V' &= (x_0 - x - y)(-x' - y') + \alpha(y' - y^* \frac{1}{y} y') \\
&= -(x_0 - x - y)\Big\{Dx_0 - Dx - aU(x)y + aU(x)y - Dy\Big\} \\
&\quad + \alpha(y - y^*)(aU(x) - D) \\
&= -D(x_0 - x - y)^2 + a\alpha(y - y^*)(U(x) - U(x^*)) \\
&= -D(x - x^* + y - y^*)^2 + a\alpha\Big(\frac{U(x) - U(x^*)}{x - x^*}\Big)(x - x^*)(y - y^*) \\
&= -D\Big\{(x - x^*)^2 + (y - y^*)^2 + \Big(2 - \frac{a}{D}\alpha\Big(\frac{U(x) - U(x^*)}{x - x^*}\Big)\Big) \\
&\qquad \times (x - x^*)(y - y^*)\Big\}.
\end{aligned}$$

Let

$$\begin{aligned}
V_1 &= D\Big[(x - x^*)^2 + (y - y^*)^2 + \Big(2 - \frac{a}{D}\alpha\beta\Big)(x - x^*)(y - y^*)\Big], \\
V_2 &= D\Big[(x - x^*)^2 + (y - y^*)^2 + \Big(2 - \frac{a}{D}\alpha\bar{\beta}\Big)(x - x^*)(y - y^*)\Big].
\end{aligned}$$

Using the definitions of β and $\bar{\beta}$, one may notice that either $-V_1 \leq V' \leq -V_2$ or $-V_1 \geq V' \geq -V_2$ holds.

Proceeding as in Theorem 1.6, we may establish that V_1 and V_2 are positive definite for the choice of $0 \leq \alpha < 4\frac{D}{a\bar{\beta}}$.

The negative definiteness of V' follows immediately from the positive definiteness of V_1 and V_2. Hence, the conclusion follows from Theorem C.9 (Appendix C). The proof is complete. □

We now consider the counter part of the competition model (1.13), given by

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= Dx_0 - Dx - a_1U_1(x)y_1 - a_2U_2(x)y_2,\\ \frac{\mathrm{d}y_1}{\mathrm{d}t} &= a_1U_1(x)y_1 - Dy_1,\\ \frac{\mathrm{d}y_2}{\mathrm{d}t} &= a_2U_2(x)y_2 - Dy_2,\end{aligned} \tag{1.22}$$

with appropriate positive initial conditions and uptake functions, $U_i(x),\ i = 1, 2$.

We assume that (1.22) possesses a positive equilibrium solution $(x^*, {y_1}^*, y_2^*)$. We then have

Theorem 1.13 *Assume that there exist positive constants* $\beta_i,\ i = 1, 2$ *such that* $\beta_i < \frac{U_i(x)-U_i(x^*)}{(x-x^*)} < \bar{\beta}_i$. *Then the positive equilibrium solution of* (1.22) *is globally asymptotically stable.*

Proof Utilizing the same Lyapunov function as in case 3 of Theorem 1.7 and proceeding similarly, we get after some simplifications and rearrangements,

$$\begin{aligned}V' \leq &-D[(x - x^*) + (y_1 + y_2 - {y_1}^* - {y_2}^*)]^2\\ &+ \alpha \sum_{i=1}^{2} a_i \frac{U_i(x) - U_i(x^*)}{x - x^*}(x - x^*)(y_i - {y_i}^*).\end{aligned}$$

Similar to (1.17), we have

$$-V_1 \leq V' \leq -V_2,$$

in which

$$\begin{aligned}V_1 = D\Big[&(x - x^*)^2 + (y_1 + y_2 - {y_1}^* - {y_2}^*)^2\\ &+\big(2 - \alpha\frac{k_1}{D}\big)(x - x^*)(y_1 + y_2 - {y_1}^* - {y_2}^*)\Big],\\ V_2 = D\Big[&(x - x^*)^2 + (y_1 + y_2 - {y_1}^* - {y_2}^*)^2\\ &+\big(2 - \alpha\frac{k_2}{D}\big)(x - x^*)(y_1 + y_2 - {y_1}^* - {y_2}^*)\Big],\end{aligned}$$

where $k_1 = a\beta$, $k_2 = \bar{a}\bar{\beta}$, $a = \min\{a_1, a_2\}$, $\bar{a} = \max\{a_1, a_2\}$, $\beta = \min\{\beta_1, \beta_2\}$, $\bar{\beta} = \max\{\bar{\beta}_1, \bar{\beta}_2\}$.

Clearly for the choice, $\alpha = [0, \frac{4D}{k_1}) \bigcap [0, \frac{4D}{k_2})$, V_1, V_2 are positive definite, and hence, V' is negative definite. Hence, the conclusion follows. □

By the assumption on the uptake functions, we have $a_i U_i(x) - D > a_i U_i(x^*) - D = 0$, $i = 1, 2$. Then from the second and third equations of (1.22), we have ${y_i}' > 0$, $i = 1, 2$, implying the survival of both the consumer species y_1 and y_2.

1.8 Discussion

Though the conclusions of the experiments are encouraging, the theory could not completely explain the behavior (growth) of the organisms during the experiment. The Theory predicted that the winner organism should approach the steady state monotonically but experiments showed that damped oscillations are present. Further, the losing competitor always lost faster than predicted. These imply that the model equations (1.3) are only a step toward understanding biological systems and we need to improve our system (1.5) to explain a natural phenomenon such as the one considered here. The development of the model in this direction making it more realistic is the main theme of the succeeding chapters.

1.9 Notes and Remarks

It is observed that the rearrangement (1.15) is not possible in case both y_1^* and y_2^* are positive and we can not explicitly write what the positive equilibrium is in case of more than one consumer. One may verify this case for $i = 2$ when $\lambda_1 = \lambda_2$ holds (see discussion before Theorem 1.7). But the proof provided by Hsu [53] utilizes the earlier rearrangement for a system of n competing species satisfying $\lambda_1 = ... = \lambda_k < \lambda_{k+1} < ... < \lambda_n$, thus, possessing an interior equilibrium solution $(x^*, y_1^*, ...y_k^*, 0, 0...0)$. Hence, we remark that the proof of Hsu [53] is not general in the sense that it is valid only for the case of competitive exclusion (case 2 of Theorem 1.7) but not for the case of co-existence (case 3 of Theorem 1.7).

The examples 1, 2 of general uptake functions provided in Sect. 1.6 are first considered by Armstrong and McGehee [1], Boon and Laudelout [14], respectively. The assumptions on uptake function before Theorem 1.8 are from Butler and Wolkowicz [21]. However, Theorem 1.8 is an appropriate restatement of the result provided by them for a model of n competing species.

Our study in Sect. 1.7 enables us to include uptake functions such as (1.18) also. This increases the choice of uptake functions for our models and may include uptake functions that need not be differentiable. As a result, in what follows we designate a function as an uptake function, if it is a continuous and nonnegative function having a saturation limit and ensures the existence of solutions to (1.5).

For some interesting mathematical models in population biology we refer the readers to Cushing [26], Droop [28], Erbe, Freedman and Sree Hari Rao [32], Fisher and Bellows [33], Freedman [34], Freedman and Sree Hari Rao [37], Freedman, Sree Hari Rao and Jaya Lakshmi [38], Gopalsamy [44], Gopalsamy and Weng [45], Kuang [63], Macdonald [65], Murray [67], Nakajima and De Angelis [68], Nisbet and Gurney [69], Novick and Szilard [72], Svirezhev and Logofet [98] and Waltman [100]. Further details on basic chemostat models and its modifications can be obtained from Smith and Waltman [85] and Sree Hari Rao and Raja Sekhara Rao [88, 90]. For some more details on uptake functions, the readers are referred to Butler and Wolkowicz [21], Bingtuan Li [64] and Wolkowicz and Lu [105]. The Lyapunov functions utilized here are proposed by Gard [43] (Theorem 1.6), Hsu [53] (Case (2) of Theorem 1.7) and Sree Hari Rao and Raja Sekhara Rao [94].

1.10 Exercises

1. Find the values for the washout rate D for which the system

$$\frac{\mathrm{d}x(t)}{\mathrm{d}t} = 5D - Dx(t) - 6\frac{x}{2+x}y(t),$$
$$\frac{\mathrm{d}y(t)}{\mathrm{d}t} = 6\frac{x}{2+x}y(t) - Dy(t).$$

   has a positive equilibrium.
2. Verify whether the system in Problem 1 is stable for the values of D obtained there.
3. Give an example (case 3 of Theorem 1.7) to show that we can not write the equilibrium explicitly even though the break-even concentrations ($\lambda_1 = \lambda_2$) are equal.
4. Extend case 3 of Theorem 1.7 for three species y_1, y_2, and y_3 feeding on a single nutrient x.
5. Compare the conditions on the uptake function $U(x)$ in Theorems 1.8 and 1.12 in case of global stability.
6. Can we extend Theorem 1.12 for a nutrient and three or more consumer species? This problem is still open.
7. Do Theorems 1.8 and 1.12 hold for the uptake function $\frac{x}{(a_1+x)(b_1+x)}$? Do the species in system (1.5) survive in this case?

Chapter 2
Chemostat Versus the Lake

2.1 Introduction

For a biologist, chemostat is a replica of a simple lake. Thus, chemostat models are widely used to represent the growth of species in a lake where the organisms such as algae feed on growth-limiting nutrients such as nitrogen and phosphorus. The analogy between a simple lake and a chemostat becomes clear from the Table 2.1.

Availability of a nutrient in a natural system such as a lake depends on the nutrient input and inflows. The algal communities in a lake are observed to survive even at low (undetectably small) levels of nutrient contrary to the opinion that they perish due to insufficiencies. But there is a growth, of course, oscillatory and low. To represent this phenomenon of oscillatory growth in the model equations of a chemostat, researchers have tried various means.

First of all, a variable input and a variable washout rate ([19,40,47,84]) are introduced into the model, which have been assumed to be fixed so far, because the availability of the nutrient (x_0) and also its supply rate (D) in a lake are season dependent – high during the rainy season and low during the summer. To account for this, researchers have varied D and/or x_0 periodically according to time. This could explain the oscillatory growth (coexistence in case of competitors). But periodicity is too simple to assume because the inflows may vary continuously during a particular season (fall/summer) or they may still be regulated (though at high/low levels), if the supplies are from a known source (reservoir). In other words, the supply concentration (x_0) and its rate of supply (D) may vary over a cycle but may be fixed (constants) or with marginal variation during a specific part of the cycle. Therefore, their influence on the system should be understood for the specific season or period of time only.

Another possibility that the mathematicians are prompted to try is the introduction of another trophic level. In this , the model is modified to include a nutrient, a microorganism feeding on this nutrient, and two competitors feeding on the microorganism ([18,20,22,25,49,59,62,104]). It is also shown that there is an oscillatory existence (coexistence) of all the species by establishing the presence of limit cycles under appropriate conditions on parameters of the system. This makes sense as far as the mathematical models are concerned, but it is not possible to introduce a predator (or another trophic level) in a closed system such as a chemostat when we are studying the growth of a nutrient – a microorganism (or competitors) only.

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Table 2.1 Lake and chemostat compared

Property	Lake	Chemostat
Nutrient	The species in a lake receive nutrient through streams flowing in or by regeneration during spring or fall.	Nutrient is supplied through an inlet.
Death	Species die out as they continually sink out of the well-lit upper layers to the bottom layers of the water column.	Nutrient and the species are washed out of the system through an outlet.
Shortage of the nutrient	During summer there is no supply of nutrient from outside and due to lake overturns, some nutrients such as phosphorus, nitrogen, or vitamin B_{12} become less available.	The supply of one or more nutrients (essential) is controlled by the experimenter.

2.2 Models Involving Time Delays

At this juncture, it is the introduction of a time delay into the model that has satisfactorily explained the oscillatory growth of populations, for a time delay is natural in any biological system. In particular, the following observations are important so far as the chemostat models are concerned for the consideration of time delay. Observing the data obtained from the chemostat experiment with algae, Caperon [23] stated that time delays are essential in his model in order to fit the experimental data. The study of Waltman [101] also suggests that the oscillations may be due to the presence of time delays in the growth response of the organisms to the nutrient. To conclude, it is reasonable to expect that consumption does not immediately imply growth and hence, a time delay may be introduced in the growth response of y.

A chemostat model with time delays was first studied by Caperon [23]. Unfortunately, the model proposed by Caperon created the possibility of negative concentration of the substrate (nutrient). To correct this Bush and Cook [17] have investigated a model of the growth of one microorganism in the chemostat with a delay in the intrinsic growth rate of the organism but with no delay in the nutrient equation and established that oscillations are possible in their model. An important reason for considering a time delay by those studying competition in a chemostat model is the following:

Many competition models of mathematics established the competitive exclusion principle while nature allows the coexistence of competing organisms, and the introduction of time delays into the model produces this coexistence as an unforced periodic solution.

A simple chemostat model with a time delay (say $\tau > 0$) in the growth response of the consumer species may be represented as follows:

$$\begin{aligned} x'(t) &= D(x_0 - x(t)) - aU(x(t))y(t), \\ y'(t) &= -Dy(t) + cU(x(t-\tau))y(t), \end{aligned} \tag{2.1}$$

where $\tau > 0$ is the new parameter that represents the time delay in growth response of y. All the parameters of system (2.1) are same as those of system (1.5). But $0 < c \leq a$ replaces a as the growth rate coefficient of the consumer species.

A primary difference between chemostat and a lake is that the inflow rate and outflow rate in a lake are very low when compared with those of the chemostat. But there are many implications of this low washout rate (inflow/outflow). When the outflow is very low, washout of the nutrient and the organism is very less. This means that the microorganisms stay in the medium for a long time before their turn of washout comes. In the mean time the organism may die naturally (due to ageing, diseases, etc.) and washout is no more the prime factor of death. In this context, we have to modify (2.1) to accommodate the death of microorganisms due to those factors other than washout. If we denote by $\gamma > 0$, the (collective) death rate coefficient of y representing all the aforementioned factors (diseases, ageing, etc.) then γy is now the new death term in the growth equation of y. Introduction of this term modifies (2.1) to

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t), \\ y'(t) &= -Dy(t) - \gamma y(t) + cy(t)U(x(t-\tau)). \end{aligned} \tag{2.2}$$

Again when the washout is small, the dead biomass is not sent out of the system immediately and the lakes have long residence time of nutrient and sediments measured in years. Because of this long stay in the medium, the dead biomass is subject to bacterial decomposition. This decomposition, in turn, leads to regeneration of nutrient, which adds up to the nutrient pool. Also, during summer months, there may be no circulation of nutrient between the surface and the bottom of the water column but during spring and fall nutrient generated by the decomposition process at the bottom can circulate and reach the algal communities living in the upper layers. Effect of such material recycling on the stability of closed systems was studied by Nisbet et al. [70] and Ulanowicz [99]. Taking this phenomenon into consideration, the following model represents a chemostat model with material recycling,

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) + b\gamma y(t), \\ y'(t) &= -Dy(t) - \gamma y(t) + cy(t)U(x(t-\tau)). \end{aligned} \tag{2.3}$$

Note that the recycling is carried out only from the dead material (microorganism) available with the system (not washed out), that is, γy term. Also the nutrient pool is enriched by this recycling. Further we cannot expect 100% recycling of the material but only a fraction. The constant $b \in (0, 1)$ signifies that not all dead biomass is recycled, but a fraction of it.

Powell and Richerson [75] and Nisbet et al. [70] studied closed systems with material recycling and concluded that time delays involved in decomposition process cannot be neglected. Whittaker [102] has suggested that in a natural system a delay is always present in material recycling. He further established that the delay present increases with decreasing temperature. Thus, introducing a discrete time delay into material recycling, we have

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) + b\gamma y(t-\tau), \\ y'(t) &= -Dy(t) - \gamma y(t) + cy(t)U(x(t-\tau)). \end{aligned} \tag{2.4}$$

Nisbet and Gurney [69] and D'Ancona [27] stress the importance of considering a distributed time delay in material recycling in closed systems such as chemostat models. According to Caswell [24], distributed time delays are more realistic than discrete time delays in such biological models (see also Wolkowicz et al. [106]). Thus, in our model (2.4) we include the term $b\gamma \int_{-\infty}^{t} y(s)ds$ to this effect in the growth equation of the nutrient concentration.

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) \\ &\quad + b\gamma \int_{-\infty}^{t} f(s)y(t-s)ds, \\ y'(t) &= -Dy(t) - \gamma y(t) + cy(t)U(x(t-\tau)). \end{aligned} \tag{2.5}$$

Here f is the corresponding delay kernel for material recycling. It signifies the contribution of dead biomass from time immemorial.

Naturally, one is tempted to introduce a distributed delay in growth response also, which appears more appropriate in view of the earlier discussion. Thus, we have

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) \\ &\quad + b\gamma \int_{-\infty}^{t} f(s)y(t-s)ds, \\ y'(t) &= -Dy(t) - \gamma y(t) \\ &\quad + cy(t) \int_{-\infty}^{t} g(s)U(x(t-s))ds. \end{aligned} \tag{2.6}$$

Here, g is the delay kernel representing the time delay in growth response from a long past.

An interesting question now is to see what new dynamics would the time delays introduce besides explaining the oscillatory existence (growth). We see a great deal of contribution from researchers in this exciting area of chemostat models right from the development of the basic model (2.1) to the model (2.6) that can help understand many biological phenomena, establishing at each stage the survival of the species. We shall begin with model (2.1) in the following section.

2.3 Time Delay Models in Growth Response

Consider system (2.1) given by,

$$\begin{aligned}\frac{\mathrm{d}x(t)}{\mathrm{d}t} &= D(x_0 - x(t)) - aU(x(t))y(t),\\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} &= -Dy(t)) + aU(x(t-\tau))y(t),\end{aligned} \tag{2.7}$$

in which $\tau > 0$ represents the time delay in growth response of y.

The presence of time delay forces us to study the basic properties of the system (2.7) beginning with the existence of solutions as (2.7) is a system of *retarded functional differential equations*. We defer this discussion for (2.7) until a little later where these properties are established for a more general system than (2.7). Until such a time we assume that solutions for (2.7) exist uniquely and are nonnegative in their maximal intervals of existence. We refer the readers to Hale [46] for results on existence, uniqueness, and continuability of solutions of retarded functional differential equations.

The first aspect that needs to be attended at once is whether the system is greatly disturbed by the presence of a time delay resulting in the wild growth of any or all of the constituent species. Mathematically this amounts to determining whether the solutions to model equations (2.7) are bounded. Of course, we show later that the time delay we have introduced has no such influence on the boundedness of the solutions of (2.7). Before we establish such a result for (2.7), we shall scale the system.

Let $\bar{x} = \frac{x}{x_0}$, $\bar{y} = \frac{y}{x_0}$, and $\bar{t} = \frac{t}{D}$. Then (2.7) may be written as

$$\begin{aligned}\frac{\mathrm{d}\bar{x}}{\mathrm{d}\bar{t}} &= 1 - \bar{x}(\bar{t}) - \bar{U}(\bar{x}(\bar{t}))\bar{y}(\bar{t}),\\ \frac{\mathrm{d}\bar{y}}{\mathrm{d}\bar{t}} &= -\bar{y}(\bar{t}) + \bar{U}(\bar{x}(\bar{t}-\bar{\tau}))\bar{y}(\bar{t}),\end{aligned}$$

where the new terms are given by $\bar{U}(\bar{x}) = \bar{a}U(x)$, $\bar{a} = \frac{a}{D}$, and $\bar{\tau} = D\tau$.

Redesignating all the terms, we write the aforementioned equations as

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= 1 - x(t) - U(x(t))y(t),\\ \frac{\mathrm{d}y}{\mathrm{d}t} &= -y(t) + U(x(t-\tau))y(t).\end{aligned} \tag{2.8}$$

We assume that $U'(x) > 0$ for all $x \geq 0$. We now have the following theorem.

Theorem 2.1 *The solutions of* (2.8) *are bounded for all positive time.*

Proof If $x(t) > 1$ for all t then $x'(t) < 0$. Therefore, without loss of generality, we can assume that $0 \leq x(t) \leq 1$. Now if $U(1) \leq 1$ then $y'(t) \leq 0$ for all t, and hence, $y(t)$ is bounded. Assume that $U(1) > 1$. Since $U(x)$ is strictly increasing with $U(0) = 0$, there exists a unique x^*, $0 < x^* < 1$ such that $U(x^*) = 1$.

Now from the second equation of (2.8), we have $y'(t) \leq y(t)(U(1) - 1)$. From this we have for every $t_2 \geq t_1 \geq 0$,

$$y(t_2) \leq y(t_1)\ \exp\left[(U(1) - 1)(t_2 - t_1)\right] \tag{2.9}$$

and

$$t_2 - t_1 \geq \frac{1}{(U(1) - 1)}\ log_e\ \frac{y(t_2)}{y(t_1)}. \tag{2.10}$$

Now if for some t, $\ y(t) \geq 1$ then

$$x'(t) \leq 1 - x(t) - U(x(t)). \tag{2.11}$$

Define $\bar{x}$ as the unique positive root of $x + U(x) = 1$. Then $0 < \bar{x} < x^* < 1$.

Suppose (2.11) holds for $t \geq t_0 \geq 0$. Since the solutions of

$$z'(t) = 1 - z(t) - U(z(t)), \quad 0 \leq z(0) \leq 1 \tag{2.12}$$

tend to $\bar{x}$ uniformly as $t \to \infty$, there exists a time $\hat{T} > 0$ independent of t_0 such that $z(t) < x^*$ for $t \geq t_0 + \hat{T}$.

Now suppose that $y(t)$ is unbounded. We consider the following possibilities:

1. There exists $T > 0$ such that $y(t) \geq 1$ for $t \geq T$. Then from (2.11) and (2.12), we have for $t \geq T + \hat{T}$, $x(t) < x^*$ and hence for $t \geq T + \hat{T} + \tau$, $x(t - \tau) < x^*$. Thus, for $t \geq T + \hat{T} + \tau$, $y'(t) < 0$. This contradicts the unboundedness of $y(t)$.
2. Suppose there exist sequences $\{s_n\}$ and $\{t_n\}$ of time t such that $s_n \to \infty, t_n \to \infty$ as $n \to \infty$, $y(s_n) < 1$, $y(t_n) \to \infty$, as $t_n \to \infty$ and $y'(t_n) \geq 0$ and $t_{n-1} < s_n < t_n$ for $n > 1$. Let l_n be such that $s_n < l_n < t_n, y(l_n) = 1$, and $y(t) > 1$ for $l_n < t \leq t_n$.

   Choose subsequences of $\{s_n\}, \{l_n\}, \{t_n\}$ relabeled as $\{s_n\}$, $\{l_n\}$, and $\{t_n\}$ such that $y(t_n) \geq \exp{(U(1) - 1)n}$.

   Then from (2.10),

$$t_n - l_n \geq \frac{1}{U(1) - 1} \ln \frac{y(t_n)}{y(l_n)} \geq \frac{1}{U(1) - 1}\ (U(1) - 1)n = n.$$

   Let $N > \hat{T} + \tau$. Then for $n \geq N$, $t_n \geq l_n + n \geq l_n + \hat{T} + \tau$. Then since $y(t) > 1$ for $l_n < t \leq t_n$ and hence for $l_n + \hat{T} + \tau < t \leq t_n$, we have from (2.11) and (2.12) as argued above $x(t) < x^*$. Then for $l_n + \hat{T} < t-\tau < t_n-\tau,\ x(t-\tau) < x^*$. This implies that $U(x(t-\tau)) < U(x^*) = 1$ and hence $y'(t_n) < 0$. This contradicts the assumption that $y'(t_n) \geq 0$, implying that $y(t)$ is bounded. □

Let $U_m = \min\{U'(x), x \in [0,1]\}$ and $U_M = \max\{U'(x), x \in [0,1]\}$.
The following result estimates the bounds explicitly.

Theorem 2.2 *Let* $U(1) > 1$. *For large* t, $x(t) < 1$ *and* $y_m < y(t) < y_M$ *in which*

$$y_m = \left[\frac{1-x^*}{2U_m x^*}\right] \exp\left\{-\tau - \frac{2x^*}{1+x^*} \quad \ln\left(\frac{2}{1-x^*}\right)\right\},$$
$$y_M = \left[1+\frac{1-x^*}{U_m x^*}\right] \exp\left\{(U(1)-1)\left[\tau + \left(\frac{x^*}{1+U_m x^*}\right) \quad \ln\left(\frac{1+(U_m-1)x^*}{U_m x^{*2}}\right)\right\}.$$

Letting $K = \frac{U_m x^*+1}{x^*}$, we see that $K > Kx^* = U_m x^* + 1 > 1$. This implies that $K > 1$, $Kx^* > 1$, and $K - 1 > Kx^* - 1$.

Thus,

$$\ln\left(\frac{1+(U_m-1)x^*}{U_m x^{*2}}\right) = \ln\left(\frac{K-1}{Kx^*-1}\right)$$

and is positive. Therefore, the bounds in Theorem 2.2 are well defined.

Proof We have already noticed in Theorem 2.1 that $x(t) < 1$, for all t. From the second equation of (2.8) we have for some $t \geq t_0$,

$$-y(t) \leq y'(t) \leq (U(1)-1)y(t). \tag{2.13}$$

This implies that for $t \geq t_0$,

$$y(t_0)\exp\{-(t-t_0)\} \leq y(t) \leq y(t_0)\exp\{(U(1)-1)(t-t_0)\}. \tag{2.14}$$

Define $\tilde{L} = 1 + \frac{(1-x^*)}{(U_m x^*)}$. Then we notice that for large t, $y(t) \leq \tilde{L}$. Otherwise, we have for large t,

$$x'(t) \leq 1 - x(t) - U(x(t))\tilde{L}.$$

Arguing as in Theorem 2.1, we can show that for sufficiently large t, $x(t) < x^*$. Using this in the second equation of (2.8), we obtain $\lim_{t\to\infty} y(t) = 0$ contradicting the assumption that $y(t) \geq \tilde{L}$. We shall now establish that $y(t) < y_M$. Suppose that this is not true. From the discussion before the proof, it is easy to see that $y_M > \tilde{L}$. Therefore, there exist t_1, t_2, $t_1 < t_2$ such that $x(t_1) < 1$, $y(t_1) = \tilde{L}$, $y(t_2) = y_M$, $y'(t_2) \geq 0$, $y(t) \in [\tilde{L}, y_M]$, for $t \in [t_1, t_2]$. But $x(t_1) < 1$ implies that $x(t) < 1$ for $t \geq t_1$. Now from (2.14), we have

$$t_2 - t_1 \geq \frac{\ln(y_M/\tilde{L})}{(U(1)-1)}.$$

From the definition of y_M,

$$t_2 - t_1 - \tau \geq \frac{1}{K} \ln(\frac{K-1}{Kx^* - 1}) > 0. \tag{2.15}$$

Thus, $t_2 - \tau > t_1$. Observe that

$$1 - x(t) - U_M x(t)y(t) \leq x'(t) \leq 1 - x(t) - U_m x(t)y(t). \tag{2.16}$$

Then for $t \in [t_1, t_2]$,

$$x'(t) \leq 1 - x(t) - U_m \tilde{L} x(t),$$

from which we have

$$x(t_2 - \tau) \leq \frac{1}{1 + U_m \tilde{L}} + \left[x(t_1) - \frac{1}{1 + U_m \tilde{L}} \right] \exp\{-(1 + U_m \tilde{L})(t_2 - t_1 - \tau)\}.$$

That is,

$$\begin{aligned} x(t_2 - \tau) &\leq \frac{1}{K} + \left[x(t_1) - \frac{1}{K} \right] \exp\{-K(t_2 - t_1 - \tau)\} \\ &< \frac{1}{K} + \left[1 - \frac{1}{K} \right] \exp\{-K(t_2 - t_1 - \tau)\} \end{aligned}$$

since, $x(t_1) < 1$. Now from (2.15), we have

$$\exp\{-K(t_2 - t_1 - \tau)\} \leq \frac{Kx^* - 1}{K - 1}.$$

Using this in the aforementioned inequality, we have after a rearrangement

$$x(t_2 - \tau) < x^*.$$

This implies that $y'(t_2) < 0$ (see arguments in Theorem 2.1), contradicting the selection of t_2. Thus, we may conclude that $\limsup_{t\to\infty} y(t) \leq y_M$.

Arguing similarly we can establish that $\liminf_{t\to\infty} y(t) \geq y_m$. The proof is complete. □

Along the way, we notice that by employing the estimates $y_m, \ y_M$ in equation (2.16), we obtain the following:

$$x_m \equiv \frac{1}{1 + U_M y_M} \leq \liminf_{t\to\infty} x(t) \leq \limsup_{t\to\infty} x(t) \leq \frac{1}{1 + U_m y_m} \equiv x_M.$$

Since x_m and y_m are positive, we may infer that the system (2.7) is uniformly persistent.

2.3.1 Global Stability

In this section, we establish results on stability of the systems of Sect. 2.2, making use of the results on global and local stability that are presented in Appendix C. We obtain sufficient conditions for the global stability of positive equilibrium solution of (2.8). Here, one may recall the discussion in Sects. 1.5 and 1.7 of Chap. 1, for the existence of a positive equilibrium (x^*, y^*) for system (2.7) as the presence of a delay does not effect the equilibria. The positive equilibrium of (2.8) satisfies $1 - x^* - U(x^*)y^* = 0, \;\; U(x^*) = 1$.

By introducing a suitable Lyapunov functional V, an estimate on the length of the delay for which the positive equilibrium (x^*, y^*) of (2.8) is globally stable will be obtained.

Letting $u = x - x^*, \quad v = y - y^*$, and $g(u) = U(x) - U(x^*)$, we transform (2.8) as

$$\begin{aligned} u' &= -(u+v) - g(u)y, \\ v' &= yg(u(t-\tau)) = y\left[g(u) - \int_{t-\tau}^{t} g'(u)u'(s)ds\right]. \end{aligned} \tag{2.17}$$

We assume that $g(u).u > 0$ for $u \neq 0$. This is, of course, true in case $U(x)$ is increasing.

Consider the function, $V_0 = u + v$. Then

$$\frac{\mathrm{d}V_0}{\mathrm{d}t} = u' + v' = -(u+v) + y\int_{t-\tau}^{t} g'(u(s))\Big[u(s) + v(s) + y(s)g(u(s))\Big]\mathrm{d}s.$$

Hence,

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{V_0^2}{2}\right) &= -(u+v)^2 + (u+v)y\int_{t-\tau}^{t} g'(u(s)) \\ &\quad \times\Big[u(s) + v(s) + y(s)g(u(s))\Big]\mathrm{d}s \\ &\leq -(u+v)^2 + \frac{1}{2}(u+v)^2 y\int_{t-\tau}^{t} g'(u(s))\mathrm{d}s \\ &\quad + \frac{1}{2}y\int_{t-\tau}^{t} g'(u(s))\Big[u(s) + v(s) + y(s)g(u(s))\Big]^2\mathrm{d}s, \\ &\leq -(u+v)^2 + \frac{1}{2}y_M(u+v)^2(U_M\tau) \\ &\quad + \frac{1}{2}y_M U_M\int_{t-\tau}^{t}\Big[u(s) + v(s) + y(s)g(u(s))\Big]^2\mathrm{d}s. \end{aligned}$$

Again let

$$V_1 \equiv \frac{V_0^2}{2} + \frac{1}{2}y_M U_M\int_{t-\tau}^{t}\mathrm{d}z\int_{z}^{t}\Big[u(s) + v(s) + y(s)g(u(s))\Big]^2\mathrm{d}s.$$

Then

$$\begin{aligned}\frac{\mathrm{d}V_1}{\mathrm{d}t} &\leq -(u+v)^2 + \frac{1}{2}y_M U_M \tau (u+v)^2 \\ &\quad + \frac{1}{2}y_M U_M \int_{t-\tau}^{t} \Big[u(s) + v(s) + y(s)g(u(s))\Big]^2 \mathrm{d}s \\ &\quad + \frac{1}{2}y_M U_M \Big[u + v + yg(u)\Big]^2 \tau \\ &\quad - \frac{1}{2}y_M U_M \int_{t-\tau}^{t} \Big[u(s) + v(s) + y(s)g(u(s))\Big]^2 \mathrm{d}s, \\ &\leq -(1 - y_M U_M \tau)(u+v)^2 + \frac{1}{2}y_M^2 U_M g^2(u)\tau \\ &\quad + y_M U_M y g(u)(u+v)\tau.\end{aligned}$$

Let α be a positive constant to be determined later and

$$V_2 = \alpha \int_0^u g(s)\mathrm{d}s.$$

Then

$$\frac{\mathrm{d}V_2}{\mathrm{d}t} = \alpha g(u)u' = -\alpha(u+v)g(u) - \alpha y g^2(u).$$

Now consider the functional $V(t) \equiv V_1 + V_2$. We then have

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &\leq -(1 - y_M U_M \tau)(u+v)^2 + (y_M U_M \tau y - \alpha)g(u)(u+v) \\ &\quad - (\alpha - \frac{1}{2}y_M^2 U_M \tau) y g^2(u).\end{aligned}$$

Then $\frac{\mathrm{d}V}{\mathrm{d}t}$ is negative definite if

$$(y y_M U_M \tau - \alpha)^2 < 4(1 - y_M U_M \tau) y \left(\alpha - \frac{1}{2}y_M^2 U_M \tau\right). \tag{2.18}$$

That is,

$$(Ay - \alpha)^2 < 2(1 - A)(2\alpha - Ay_M)y, \text{ where } A = y_M U_M \tau.$$

Thus

$$A^2 y^2 - 2A\alpha y + a\alpha^2 < 2y y_M A^2 + 4y\alpha - 2Ay y_M - 4A\alpha y,$$

and from this it follows that

$$y(2y_M - y)A^2 - y(2y_M + 2\alpha)A + (4\alpha y - \alpha^2) > 0.$$

Letting $\alpha = 2y_m$, we have

$$y(2y_M - y)A^2 - y(2y_M + 4y_m)A + 8yy_m - 4y_m^2 > 0. \qquad (2.19)$$

Now since $y_m < y < y_M$, we see that (2.19) holds if

$$(2y_M - y_m)A^2 - (2y_M + 4y_m)A + 4y_m > 0$$
$$\text{and}$$
$$y_M A^2 - (2y_M + 4y_m)A + 4y_m > 0.$$

Clearly both these inequalities hold when

$$A < \frac{(y_M + 2y_m) - \sqrt{4y_m^2 + y_M^2}}{y_M}. \qquad (2.20)$$

Also (2.18) requires,

$$1 - y_M U_M \tau > 0, \quad \alpha - \frac{1}{2} y_M^2 U_M \tau > 0, \quad \text{or} \quad 4y_m - y_M^2 U_M \tau > 0, \qquad (2.21)$$

to hold.

We are now in a position to state and prove the following theorem.

Theorem 2.3 *The positive equilibrium solution* (x^*, y^*) *of* (2.8) *is globally asymptotically stable provided the delay parameter satisfies the inequality*

$$\tau < \min\left\{ \frac{1}{y_M U_M}, \frac{4y_m}{y_M^2 U_M}, \frac{2y_m + y_M - \sqrt{4y_m^2 + y_M^2}}{y_M^2 U_M} \right\}.$$

Proof Choosing the Lyapunov functional V defined earlier, the negative definiteness of $\frac{\mathrm{d}V}{\mathrm{d}t}$ follows from (2.20) and (2.21) and the hypotheses.

The conclusion then follows from Theorem C.11 (Appendix C). □

We shall now present the conclusions of a local stability analysis of the system (2.8) (Kato and Pan [58]) to see if any bifurcation is possible. An estimate on τ is to be found beyond which the equilibrium is becoming unstable. This helps one to understand the influence of time delay on the systems (2.7) and (2.8).

Linearizing (2.8) around the positive equilibrium (x^*, y^*), we get

$$x' = -(1 + U'(x^*)y^*)x - U(x^*)y,$$
$$y' = U'(x^*)y^* x(t - \tau) + (U(x^*) - 1)y.$$

Using $U(x^*) = 1$ and letting $\beta = U'(x^*)y^*$, the earlier system reduces to

$$x' = -(1 + \beta)x - y,$$
$$y' = \beta x(t - \tau).$$

It is easy to see that the characteristic equation corresponding to this system is as follows:

$$\begin{vmatrix} -(1+\beta)-\lambda & -1 \\ \beta e^{-\lambda\tau} & -\lambda \end{vmatrix} = 0,$$

which on expansion gives the following:

$$\lambda^2 + (1+\beta)\lambda + \beta e^{-\tau\lambda} = 0. \tag{2.22}$$

The change of stability is characterized by the presence of a pure imaginary zero of (2.22). We, therefore, try to locate the pure imaginary zeros of (2.22).

Letting $\lambda = i\omega,\ \omega > 0$ and separating the real and imaginary parts we get after a rearrangement,

$$\omega^2 + \cos\tau\omega - \omega\sin\tau\omega = 0 \tag{2.23}$$

and

$$\beta = \frac{\omega^2}{\cos\tau\omega}. \tag{2.24}$$

The following conclusions may be drawn using the method for local stability analysis.

There exist numbers $0 < \tau_0(\beta) < \tau_1(\beta) < \tau_2(\beta) < \ldots.$ such that:

- The system (2.22) has a pair of pure imaginary roots $i\omega_k, -i\omega_k$ if $\tau = \tau_k(\beta)$.
- The system (2.8) is globally exponentially stable for $\tau \in (0, \tau_0(\beta))$ and unstable for $\tau > \tau_0(\beta)$.
- The system (2.8) has a Hopf bifurcation at $\tau = \tau_k(\beta)$.

Analyzing further it is shown in Kato and Pan [58] that

- Since $\beta > 0$, for each nonnegative integer k, the equation (2.23) has a solution $\omega_k(\tau)$, which is analytic on $(2k\pi + \frac{\pi}{2}, \infty)$ and satisfies $\omega_k(\tau)\tau \in (2k\pi, 2k\pi + \frac{\pi}{2})$.
- The function $\beta_k(\tau)$ defined by (2.24) with $\omega = \omega_k(\tau)$ is analytic on $(2k\pi + \frac{\pi}{2}, \infty)$ and satisfies

$$\lim_{r\to\infty} \beta_k(r) = 0, \lim_{r\to 2k\pi+\frac{\pi}{2}} \beta_k(r) = \infty, \beta_k(r) < \beta_{k+1}(r)$$

  on the common domain. Further, the interior equilibrium (x^*, y^*) is asymptotically stable when $\tau < \frac{\pi}{2}$ or $\beta < \beta_0(\tau)$ and unstable when $\beta > \beta_0(\tau)$ and has a Hopf bifurcation at $\beta = \beta_k(\tau)$, for $\tau \geq 2k\pi + \frac{\pi}{2},\ k \geq 0$.
- For the system (2.7) with $U(x) = \frac{x}{m+x}$, we have

$$x_0 = \frac{amD\beta_k(D\tau) + mD(a-D)}{(a-D)^2} \equiv f_k(D),$$

which is defined on $\left(\frac{4k+1}{2\tau}\pi, a\right)$ satisfying

$$\lim_{D\to a} f_k(D) = \infty, \qquad \lim_{D\to \frac{4k+1}{2\tau}\pi} f_k(D) = \infty, \qquad f_k(D) < f_{k+1}(D)$$

on the common domain.
The interior equilibrium $(x^*, y^*) = \left(\frac{mD}{a-D}, \frac{x_0(a-D)-mD}{a-D}\right)$ exists only when

$$\Sigma : a - D > 0 \text{ and } x_0 > \frac{mD}{a-D}.$$

Then (x^*, y^*) is asymptotically stable when $D < \frac{\pi}{2\tau}$ or $x_0 < f_0(D)$ and is unstable when $x_0 > f_0(D)$ on Σ. Moreover, (2.7) has a Hopf bifurcation at $x_0 = f_k(D)$ for $D \in \left(\frac{4k+1}{2\tau}\pi, a\right)$ for $k \geq 0$. □

The model (2.7) is developed into a competition model given by

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - a_1U_1(x(t))y_1(t) \\ &\quad -a_2U_2(x(t))y_2(t), \\ y_1'(t) &= a_1U_1(x(t-\tau))y_1(t) - Dy_1(t), \\ y_2'(t) &= a_2U_2(x(t-\tau))y_2(t) - Dy_2(t), \end{aligned} \tag{2.25}$$

where y_1 and y_2 are two competing microorganisms and $\tau_1 > 0$ and $\tau_2 > 0$ are the corresponding delays in the growth of microorganisms. Supposing that the periodic solution $(x(t), y(t))$ of (2.7) with finite period $T > 0$ is asymptotically stable, Freedman et al. [36] obtained a critical value a_2^* of the bifurcation parameter a_2 (the specific growth rate of the organisms) and a branch of the periodic orbit of (2.25) with positive y_2 component, bifurcating from the hypothesized orbit for a_2 near a_2^*. This means that the periodic solution of (2.7) develops into a periodic solution (orbit) of (2.25) establishing that coexistence is possible for competing predators.

2.3.2 A Modified Model

Consider the situation in which some of the microorganisms are washed out before they have reproduced during the time delay between consumption and growth (birth). Then the washout of any population $N(t)$ between time $t-\tau$ and t with no reproduction during this time is obtained by solving the equation

$$N'(t) = -DN(t)$$

from $t-\tau$ to t. This gives us $N(t) = N(t-\tau)e^{-D\tau}$.

This has enabled Freedman et al. [35] to derive the model,

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t), \\ y'(t) &= ae^{-D\tau}U(x(t-\tau))y(t-\tau) - Dy(t). \end{aligned} \tag{2.26}$$

As in the case of system (2.7) the stability of interior equilibrium of (2.26) was established for all values of τ for which the equilibrium exists. Basing on these, we may expect the possibility of coexistence of the competing predators in case of a competition, that is, the existence of a periodic solution to the model,

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - a_1U_1(x(t))y_1(t) - a_2U_2(x(t))y_2(t), \\ y_1'(t) &= a_1e^{-D\tau_1}U_1(x(t-\tau_1))y_1(t-\tau_1) - Dy_1(t), \\ y_2'(t) &= a_2e^{-D\tau_2}U_2(x(t-\tau_2))y_2(t-\tau_2) - Dy_2(t). \end{aligned} \tag{2.27}$$

But the study of Freedman et al. [35] reveals that only either $(x^*, 0, y_2{}^*)$ or $(x^*, y_1{}^*, 0)$ is asymptotically stable. The system (2.27) does not give rise to any secondary Hopf bifurcation implying that coexistence may not be possible. A similar model was obtained by Ellermeyer [30] by considering the nutrient stored internally by the consumer population y. Ellermeyer [30] and Hsu et al. [56] established that either $(x^*, 0, y_2{}^*)$ or $(x^*, y_1{}^*, 0)$ is globally stable and the system (2.27) does not exhibit any oscillations. Thus, the principle of competitive exclusion holds and the system (2.27) behaves like a simple chemostat.

The following distributed delay model is considered by Wolkowicz et al. [106].

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - a_1U_1(x(t))y_1(t) - a_2U_2(x(t))y_2(t), \\ y_1'(t) &= -Dy_1(t) + a_1\int_{-\infty}^{t} f_1(t-s)e^{-D(t-s)}U_1(x(s))y_1(s)\mathrm{d}s, \\ y_2'(t) &= -Dy_2(t) + a_2\int_{-\infty}^{t} f_2(t-s)e^{-D(t-s)}U_2(x(s))y_2(s)\mathrm{d}s \end{aligned} \tag{2.28}$$

in which $f_i : \mathbf{R}_+ \to \mathbf{R}_+, \mathbf{R}_+ = [\mathbf{0}, \infty),\ i = 1, 2$ are delay kernels of the type

$$f_i(u) = \frac{\alpha_i{}^{r_i+1}u_i{}^{r_i}}{r_i!}\mathrm{e}^{-\alpha_i u}, \quad i = 1, 2,$$

where $\alpha_i > 0$ are any constants and r_i are nonnegative integers. The mean delay corresponding to the kernel f_i is given by

$$\tau_i = \int_0^\infty sf_i(s)ds = \frac{r_i+1}{\alpha_i}.$$

Let $\lambda_1(\tau_1)$ and $\lambda_2(\tau_2)$ denote the breakeven concentrations of the competing predators y_1 and y_2, respectively, for average delays τ_1 and τ_2. In the absence of any delays it is known from the results of Chap. 1 that if $\lambda_i(0) < \lambda_j(0)$ holds for $i \neq j,\ i, j = 1, 2$ then the species y_i wins the competition. However, when the delays are introduced it is possible by increasing the mean delays $\tau_i, \quad i = 1,2$ to see that $\lambda_i(\tau_i) > \lambda_j(\tau_j)$ holds for $i \neq j,\ i,j = 1,2$. In such a case, it is established that the species y_j wins the competition irrespective of who wins the competition in the absence of delays. Also, numerical simulations have suggested that if the mean delay of winning population is longer than that of losing population, the death rate of loser is slow as observed in experiments and vice versa.

The analysis of models presented in this section may appear to be brief and complicated. However, we shall return to models (2.7) and (2.8) to provide some more details in subsequent chapters as new techniques are introduced and new theory is developed. Specifically, in Example 2.20 and Remark 2.21, we discuss some of these points.

In the following section we consider models involving material recycling. These models enable us to understand the direct influence of material recycling on the stability of the system (2.7), which under the influence of a time delay in growth response exhibits instability tendencies (undergoes a Hopf bifurcation for large values of τ) as seen in this section.

2.4 Material Recycling with and without Time Delays

The first model we consider here is (2.3), given by,

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) + b\gamma y(t), \\ y'(t) &= -(\gamma + D)y(t) + cU(x(t-\tau))y(t). \end{aligned} \tag{2.29}$$

So far as system (2.7) is considered, (2.29) has an additional term $b\gamma y$ that represents the recycling from the dead biomass γy. For details, go back to system (2.3).

For an uptake function satisfying

$$U(0) = 0, \quad U'(x) > 0, \quad \lim_{x\to\infty} U(x) = 1, \tag{2.30}$$

the equilibrium solutions are given by

- $(x_0, 0)$(partially feasible equilibrium) and
- $(x^*, y^*) = \left(U^{-1}\left(\frac{\gamma+D}{c}\right), \frac{D(x_0-x^*)}{aU(x^*)-b\gamma}\right)$.

Clearly (x^*, y^*) is a positive equilibrium if and only if

$$U(x^*) = \frac{\gamma + D}{c} < \min\{1, U(x_0)\}. \tag{2.31}$$

Following the arguments in Sect. 2.3 we can establish the following:

- System (2.29) is dissipative. That is solutions of (2.29) that enter a positive cone will remain in that for all future time.

- If the inequality (2.31) holds, the system (2.29) is uniformly persistent [see Definition C.13 (Appendix C)].
  Thus existence of a positive equilibrium itself implies the long term survival of the species.
- There exists a $\tau_0 > 0$ such that a family of periodic solutions of (2.29) bifurcates from (x^*, y^*) for τ near τ_0.

However, we present sufficient conditions for the global asymptotic stability of the positive equilibrium solution (x^*, y^*) of (2.29).

Theorem 2.4 *Assume that the time delay τ satisfies*

$$\frac{c}{2}\Big[aU(x^*) - b\gamma\Big]\left[\frac{1}{\gamma + D}\Big(1 - e^{-(\gamma+D)\tau}\Big) + \tau e^{-(\gamma+D)\tau}\right] < a.$$

Then the positive equilibrium (x^*, y^*) of (2.29) is globally asymptotically stable.

Proof The proof of this theorem can be obtained as a special case of Theorem 2.15, and hence, the details are omitted. □

The following result is a special case of Theorem 2.17 (below) and the proof is omitted.

Theorem 2.5 *The equilibrium solution (x^*, y^*) of (2.29) is globally asymptotically stable for*

$$0 \le \tau < \tau^* = \min\left\{\frac{D - ck - aky^*}{(D + ay^*)ck}, \frac{a\bar{\alpha} - b\gamma}{(a + b\gamma)ck}\right\},$$

provided $D - ck - aky^* > 0$ and $a\bar{\alpha} - b\gamma > 0$, in which $\bar{\alpha} = \min_{x \ge x^*}\{U(x)\}$ and k is such that $|U(x) - U(x^*)| \le k|x - x^*|$.

Model (2.29) is a special case of forthcoming model (2.67) for which we make a detailed analysis there. An enthusiastic reader may come back from (2.67) to (2.29) to make suitable studied and we intentionally leave the details here.

2.4.1 Finite Delays in Material Recycling

Our next step is to consider a time delay in material recycling only. We first study the influence of a discrete time delay and then proceed to a system with a distributed time delay to include the distant past. The system involving distributed time delay has received much attention as it yields a large region of stability.

Consider the system

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) + b\gamma y(t - \tau), \\ y'(t) &= -(\gamma + D)y(t) + cU(x(t))y(t). \end{aligned} \tag{2.32}$$

The basic properties of solutions of this system such as positivity, boundedness, continuous dependence on initial conditions, etc. may be understood by arguments similar to those given in earlier sections. Further, (2.29) and (2.32) have the same set of equilibrium solutions. Thus, a positive equilibrium solution of (2.32) is given below equation (2.30) assuming that the inequality (2.31) holds. Further, (x^*, y^*) satisfies

$$\begin{aligned} Dx_0 &= Dx^* + aU(x^*)y^* - b\gamma y^*, \\ \gamma + D &= cU(x^*). \end{aligned}$$

We now discuss the global stability of (x^*, y^*) of (2.32). For this we need the following transformation.

$$x_1(t) = x(t) - x^*, \ \ y_1(t) = \log \frac{y(t)}{y^*}, \text{ and } U_1(x_1(t)) = U(x(t)) - U(x^*).$$

Then $y^* e^{y_1} = y(t)$. We further assume that the uptake function U satisfies the condition $x_1 U(x_1) > 0$ for $x_1 \neq 0$ throughout this section.

Using this we rewrite system (2.32) as

$$\begin{aligned} x_1{}'(t) &= -Dx_1 - ay^* e^{y_1} U_1(x_1) - ay^* U(x^*)\Big[e^{y_1} - 1\Big] \\ &\quad + b\gamma y^* \Big[e^{y_1(t-\tau)} - 1\Big], \\ y_1{}'(t) &= cU_1(x_1(t)). \end{aligned} \tag{2.33}$$

Now we construct the required Lyapunov functional step by step verifying at each stage what is required. First define

$$V_1(t) = \int_0^{x_1} U_1(x_1(s))\mathrm{d}s.$$

Then differentiating V_1 with respect to t along the solutions of (2.33), we get

$$\begin{aligned} V_1{}'(t) &= U_1(x_1(t))x_1{}'(t) \\ &= -Dx_1U_1(x_1) - ay^*\mathrm{e}^{y_1}U_1{}^2(x_1) \\ &\quad - ay^*U(x^*)\Big[\mathrm{e}^{y_1} - 1\Big]U_1(x_1) \\ &\quad + b\gamma y^*\Big[\mathrm{e}^{y_1(t-\tau)} - 1\Big]U_1(x_1) \\ &= -Dx_1U_1(x_1) - ay^*\mathrm{e}^{y_1}U_1{}^2(x_1) \\ &\quad - (aU(x^*) - b\gamma)y^*\Big[\mathrm{e}^{y_1} - 1\Big]U_1(x_1) \\ &\quad - b\gamma y^*\Big[\mathrm{e}^{y_1} - \mathrm{e}^{y_1(t-\tau)}\Big]U_1(x_1) \\ &= -Dx_1U_1(x_1) - ay^*\mathrm{e}^{y_1}U_1{}^2(x_1) \\ &\quad - (aU(x^*) - b\gamma)y^*\Big[\mathrm{e}^{y_1} - 1\Big]U_1(x_1) \\ &\quad - b\gamma y^*c\left[\int_{t-\tau}^{t} \mathrm{e}^{y_1(s)}U_1(x_1(s))\mathrm{d}s\right]U_1(x_1(t)), \end{aligned}$$

observing that

$$e^{y_1(t)} - e^{y_1(t-\tau)} = \int_{t-\tau}^{t} e^{y_1(s)} {y_1}'(s)\mathrm{d}s = c\int_{t-\tau}^{t} e^{y_1(s)} U_1(x_1(s))\mathrm{d}s.$$

Utilizing the inequality $ab \leq \frac{a^2+b^2}{2}$ on the last term of the above, we have

$$\begin{aligned} {V_1}'(t) \leq\ & -Dx_1U_1(x_1) - ay^*e^{y_1}{U_1}^2(x_1) \\ & -(aU(x^*) - b\gamma)y^*[e^{y_1} - 1]U_1(x_1) \\ & + \frac{1}{2}b\gamma y^* c\Big(\int_{t-\tau}^{t} e^{y_1(u)}\mathrm{d}u\Big){U_1}^2(x_1(t)) \\ & + \frac{1}{2}b\gamma y^* c\int_{t-\tau}^{t} e^{y_1(u)}{U_1}^2(x_1(u))\mathrm{d}u. \end{aligned} \tag{2.34}$$

Now consider

$$V_2(t) = \frac{1}{2}b\gamma y^* c\int_{t-\tau}^{t}\int_{v}^{t} e^{y_1(u)}{U_1}^2(x_1(u))\mathrm{d}u\mathrm{d}v.$$

Then

$${V_2}' = \frac{1}{2}b\gamma y^* c\left[e^{y_1(t)}{U_1}^2(x_1(t))\tau - \int_{t-\tau}^{t} e^{y_1(u)}{U_1}^2(x_1(u))\mathrm{d}u\right]$$

and

$$\begin{aligned} {V_1}'(t) + {V_2}'(t) \leq\ & -Dx_1U_1(x_1) - ay^*e^{y_1}{U_1}^2(x_1) \\ & -(aU(x^*) - b\gamma)y^*\Big[e^{y_1} - 1\Big]U_1(x_1) \\ & +\frac{1}{2}b\gamma y^* c\left[\int_{t-\tau}^{t} e^{y_1(u)}du + \tau e^{y_1(t)}\right]{U_1}^2(x_1(t)). \end{aligned} \tag{2.35}$$

From the second equation of (2.32), we have

$$y'(t) \geq -(\gamma + D)y(t)$$

from this it follows that

$$y(s) \leq e^{(\gamma+D)(t-s)}y(t),$$

and further, we have

$$\begin{aligned} y^*\int_{t-\tau}^{t} e^{y_1(s)}\mathrm{d}s &= \int_{t-\tau}^{t} y(s)\mathrm{d}s \leq y(t)\int_{t-\tau}^{t} e^{(\gamma+D)(t-s)}\mathrm{d}s \\ &= \frac{1}{\gamma + D}y(t)\Big(e^{(\gamma+D)\tau} - 1\Big). \end{aligned}$$

Using this in (2.35), we get

$$\begin{aligned} V_1'(t) + V_2'(t) \le \; & -Dx_1U_1(x_1) - ay^*\mathrm{e}^{y_1}U_1{}^2(x_1) \\ & -(aU(x^*) - b\gamma)y^*\Big[\mathrm{e}^{y_1} - 1\Big]U_1(x_1) \\ & + \frac{1}{2}b\gamma y^*c\left[\frac{1}{\gamma + D}(e^{(\gamma+D)\tau} - 1) + \tau\right] \times \\ & \times y(t)U_1{}^2(x_1(t)). \end{aligned} \tag{2.36}$$

Define

$$V_3(t) = \int_0^{y_1}\Big[\mathrm{e}^s - 1\Big]\mathrm{d}s.$$

Then

$$V_3(t) = \Big[\mathrm{e}^{y_1} - 1\Big]y_1'(t) = c\Big[\mathrm{e}^{y_1} - 1\Big]U_1(x_1(t)). \tag{2.37}$$

Consider the functional

$$V(t) = V_1(t) + V_2(t) + \alpha V_3(t)$$

and along the solutions of (2.33), we have, using (2.36) and (2.37),

$$\begin{aligned} V'(t) \; \le & - Dx_1U_1(x_1) - ay^*\mathrm{e}^{y_1}U_1{}^2(x_1) \\ & -(aU(x^*) - b\gamma)y^*\Big[\mathrm{e}^{y_1} - 1\Big]U_1(x_1) \\ & + \frac{1}{2}b\gamma y^*c\left[\frac{1}{\gamma + D}\left(e^{(\gamma+D)\tau} - 1\right) + \tau\right] \times \\ & \times y(t)U_1{}^2(x_1(t)) + c\alpha\Big[\mathrm{e}^{y_1} - 1\Big]U_1(x_1(t)) \\ \le & - Dx_1U_1(x_1) - \left[a - \frac{1}{2}b\gamma y^*c\left(\frac{1}{\gamma + D}\left(e^{(\gamma+D)\tau} - 1\right) + \tau\right)\right] \times \\ & \times y(t)U_1{}^2(x_1(t)), \end{aligned} \tag{2.38}$$

choosing $c\alpha = (aU(x^*) - b\gamma)y^*$.

Now we have the following theorem.

Theorem 2.6 *The positive equilibrium* (x^*, y^*) *of* (2.32) *is globally asymptotically stable provided the delay parameter satisfies the condition*

$$b\gamma c\left[\frac{1}{\gamma + D}\left(\mathrm{e}^{(\gamma+D)\tau} - 1\right) + \tau\right] < 2a. \tag{2.39}$$

Proof We may notice that the functional $V(t)$ constructed earlier, is the one required here. The negative definiteness of $V'(t)$ follows from (2.38) using the condition (2.39). The conclusion of the theorem follows from Theorem C.11 (Appendix C). □

Now we consider a variable delay in material recycling in (2.32) in place of a fixed delay. That means, we now consider $\tau \equiv \tau(t)$ in (2.32) where $\tau(t)$ is a continuous function such that $0 \leq \tau(t) \leq T$ for some $T > 0$. In such a case, arguing as in Theorem 2.6, one may establish the following theorem.

Theorem 2.7 *Assume that the delay $\tau(t)$ is such that $0 \leq \tau'(t) \leq 1$. Assume further that the condition*

$$b\gamma c\left[\frac{1}{\gamma + D}\left(e^{(\gamma+D)\tau(t)} - 1\right) + q(t)\right] < 2a$$

holds for all $t > 0$. Then the positive equilibrium (x^*, y^*) of (2.32) is globally asymptotically stable. Here $q(t) = \sigma^{-1}(t) - t$ and $\sigma(t) = t - \tau(t)$.

Note that the functions $q(t)$ and $\sigma(t)$ are well defined following the hypotheses on $\tau(t)$.

2.4.2 Distributed Delays

We consider a further modification of (2.32) by incorporating a distributed time delay in material recycling. That is, we are interested in the model

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) \\ &\quad + b\gamma\int_{-\infty}^{t} f(t-s)y(s), \\ y'(t) &= -(\gamma + D)y(t) + cU(x(t))y(t). \end{aligned} \tag{2.40}$$

System (2.40) may be derived from (2.5) by letting $\tau = 0$ or from (2.6) assuming $g(s) = \delta(s)$, the Dirac delta. Model (2.40) has received much attention keeping in view the importance of distributed time delays in biological models.

The delay kernel f that is nonnegative and a bounded function is assumed to satisfy the following conditions.

$$(I) \qquad \int_0^\infty f(s)\mathrm{d}s = 1, \quad T_f = \int_0^\infty sf(s)\mathrm{d}s < \infty.$$

The quantity T_f denotes the average time delay in material recycling. We assume that these conditions apply throughout the present section unless specified otherwise.

Theorem 2.8 *If $b\gamma c < a(\gamma + D)$ holds then all the solutions of* (2.40) *are bounded.*

Proof To prove this, we consider the functional

$$V(t, x, y) = x(t) + \frac{a}{c}y(t) + b\gamma\int_0^\infty f(s)\int_{t-s}^{t} y(u)\mathrm{d}u\mathrm{d}s.$$

Clearly $V \geq 0$, $V \to \infty$ as $|(x, y)| \to \infty$. Now along the solutions of (2.40),

$$\begin{aligned} V'(t) &= Dx_0 - Dx - aU(x)y + b\gamma \int_0^\infty f(s)y(t-s)\mathrm{d}s \\ &\quad + \frac{a}{c}y\Big[-(\gamma + D) + cU(x)\Big] \\ &\quad + b\gamma \int_0^\infty f(s)\Big[y(t) - y(t-s)\Big]\mathrm{d}s \\ &= Dx_0 - Dx - \Big[\frac{a}{c}(\gamma + D) - b\gamma\Big]y, \end{aligned}$$

employing the condition $\int_0^\infty f(s)\mathrm{d}s = 1$.

Thus, outside the region bounded by the axes and the line

$$y = \frac{D(x_0 - x)}{\frac{a}{c}(\gamma + D) - b\gamma},$$

we have $V'(t) < 0$. The conclusion follows at once from Theorem B.2 (Appendix B). □

It is obvious that the choice $a \geq c$ and $b \in (0, 1)$, the inequality in the earlier Theorem 2.8 above is trivial. Thus, in this case the solutions are automatically bounded.

Now we present a set of sufficient conditions for the local asymptotic stability of positive equilibrium of (2.40). It may be noticed at this stage that due to the normalized nature of the kernel f, the equilibrium solutions of (2.32) and (2.40) are identical. Hence, we assume that the conditions for the existence of a positive equilibrium are satisfied. We now have the following theorem.

Theorem 2.9 *The positive equilibrium solution* (x^*, y^*) *of* (2.40) *is locally asymptotically stable provided the inequality*

$$\gamma \leq \frac{D^2 + a^2\bar{k}^2}{2a\bar{k}},$$

in which $\bar{k} = U'(x^*)y^*$, *holds.*

Proof We first linearize system (2.40) around (x^*, y^*) to get

$$\begin{aligned} x_1{}'(t) &= -(D + ay^*U'(x^*))x_1 - aU(x^*)y_1 \\ &\quad + b\gamma \int_{-\infty}^t f(t-s)y_1(s), \\ y_1{}'(t) &= cy^*U'(x^*)x_1 \end{aligned} \tag{2.41}$$

in which $x_1 = x - x^*$ and $y_1 = y - y^*$.

The characteristic equation of (2.41) is given by

$$\lambda^2 + (D + a\bar{k})\lambda + a(\gamma + D)\bar{k} - b\gamma c\bar{k}F(\lambda) = 0 \tag{2.42}$$

Here $F(\lambda) = \int_0^\infty e^{-\lambda s} f(s)ds$. A change in the stability of the system is indicated by the presence of a pure imaginary zero for (2.42). That is , we have to find $\lambda = i\omega$, $\omega > 0$, satisfying (2.42). Also we notice that since $a(\gamma + D)\bar{k} - b\gamma c\bar{k} > 0$ (condition for boundedness), $\lambda = 0$ is not a root of (2.42). Letting $\lambda = i\omega$ in (2.42), we obtain

$$H(i\omega) = F(i\omega), \tag{2.43}$$

where

$$H(i\omega) = \frac{a(\gamma + D)\bar{k} - \omega^2 + i\omega(D + a\bar{k})}{b\gamma c\bar{k}}.$$

Since

$$F(i\omega) \leq \int_0^\infty f(s)|e^{-i\omega s}|ds = 1,$$

a necessary condition for the existence of a solution to (2.43) is $H(i\omega) \leq 1$.

Now consider

$$R(\omega) = |H(i\omega)|^2 = \frac{\left(a(\gamma + D)\bar{k} - \omega^2\right)^2 + \omega^2(D + a\bar{k})^2}{(b\gamma c\bar{k})^2}. \tag{2.44}$$

Clearly from the condition for boundedness of solutions of (2.40), we get $R(0) = \frac{a^2(\gamma+D)^2}{(b\gamma c)^2} > 1$. Further, $R(\omega) \to \infty$ as $\omega \to \infty$. Moreover,

$$R'(\omega) = \frac{4\omega^3 + 2\omega(D^2 + a^2\bar{k}^2 - 2a\bar{k}\gamma}{(b\gamma c\bar{k})^2}.$$

Then by the hypothesis

$$\gamma \leq \frac{D^2 + a^2\bar{k}^2}{2a\bar{k}}, \quad R'(\omega) > 0.$$

Thus, $R(\omega)$ is an increasing function in ω, and hence, $R(\omega) > R(0) = 1$ for all ω. This implies that $|H(i\omega)| > 1$ for $\omega \in \mathbf{R}_+$, contradicting the assumption that $|H(i\omega)| \leq 1$. This excludes the possibility of a change of stability. This completes the proof. □

Now we study the global stability of the positive equilibrium (x^*, y^*) of (2.40). The following transformation is useful in establishing the first result.

$$x_1(t) = x(t) - x^*, \quad y_1(t) = \log\frac{y(t)}{y^*}, \text{ and } U_1(x_1(t)) = U(x(t)) - U(x^*).$$

This transforms (2.40) into

$$
\begin{aligned}
x_1{}'(t) &= -Dx_1 - ay^* e^{y_1} U_1(x_1) - ay^* U(x^*)\Big[e^{y_1} - 1\Big] \\
&\qquad + b\gamma y^* \int_0^\infty f(s)\Big[e^{y_1(t-s)} - 1\Big] ds, \\
y_1{}'(t) &= cU_1(x_1(t)).
\end{aligned} \tag{2.45}
$$

As in Theorem 2.6, we construct a suitable Lyapunov functional V. We expect that the functional V used earlier may serve the purpose with a suitable modification.

Consider

$$
V_1(t) = \int_0^{x_1} U_1(s) ds.
$$

Differentiating $V_1(t)$ with respect to t along the solutions of (2.45) and proceeding as in Theorem 2.6 we get

$$
\begin{aligned}
V_1{}'(t) \leq\ & -Dx_1 U_1(x_1) - ay^* e^{y_1} U_1{}^2(x_1) \\
& - (aU(x^*) - b\gamma) y^* \Big[e^{y_1} - 1\Big] U_1(x_1) \\
& + \frac{1}{2} b\gamma y^* c \Big(\int_0^\infty f(s) \int_{t-s}^t e^{y_1(u)} du ds\Big) U_1{}^2(x_1(t)) \\
& + \frac{1}{2} b\gamma y^* c \int_0^\infty f(s) \int_{t-s}^t e^{y_1(u)} U_1{}^2(x_1(u)) du ds.
\end{aligned} \tag{2.46}
$$

Now consider

$$
V_2(t) = \frac{1}{2} b\gamma y^* c \int_0^\infty f(s) \int_{t-s}^t \int_v^t e^{y_1(u)} U_1{}^2(x_1(u)) du dv ds.
$$

Then

$$
\begin{aligned}
V_2{}' =\ & \frac{1}{2} b\gamma y^* c e^{y_1(t)} U_1{}^2(x_1(t)) \int_0^\infty s f(s) ds \\
& - \frac{1}{2} b\gamma y^* c \int_0^\infty f(s) \int_{t-s}^t e^{y_1(u)} U_1{}^2(x_1(u)) du ds.
\end{aligned} \tag{2.47}
$$

Now from (2.46) and (2.47)

$$
\begin{aligned}
V_1{}'(t) + V_2{}'(t) \leq\ & -Dx_1 U_1(x_1) - ay^* e^{y_1} U_1{}^2(x_1) \\
& - (aU(x^*) - b\gamma) y^* \Big[e^{y_1} - 1\Big] U_1(x_1) \\
& + \frac{1}{2} b\gamma y^* c \left[\int_0^\infty f(s) \int_{t-s}^t e^{y_1(u)} du ds + T_f e^{y_1(t)}\right] \\
& \times U_1{}^2(x_1(t)),
\end{aligned} \tag{2.48}
$$

where $T_f = \int_0^\infty sf(s)\mathrm{d}s$. Now from the second equation of (2.40),

$$y'(t) \geq -(\gamma + D)y(t),$$

which implies that

$$y(s) \leq e^{(\gamma+D)(t-s)}y(t).$$

Using this we have

$$\begin{aligned} y^* \int_0^\infty f(s) \int_{t-s}^t \mathrm{e}^{y_1(u)}\mathrm{d}u\mathrm{d}s &= \int_0^\infty f(s) \int_{t-s}^t y(u)\mathrm{d}u\mathrm{d}s \\ &\leq y(t) \int_0^\infty f(s) \int_{t-s}^t \mathrm{e}^{(\gamma+D)(t-u)}\mathrm{d}u\mathrm{d}s \\ &= \frac{1}{\gamma + D} y(t) \int_0^\infty f(s)\left(\mathrm{e}^{(\gamma+D)s} - 1\right)\mathrm{d}s. \end{aligned} \tag{2.49}$$

Again consider

$$V_3(t) = \int_0^{y_1} \left(\mathrm{e}^s - 1\right)\mathrm{d}s.$$

Then along the solutions of (2.45),

$$V_3{}'(t) = c\left(\mathrm{e}^{y_1(t)} - 1\right)U_1(x_1(t)). \tag{2.50}$$

We are now in a position to establish the following theorem.

Theorem 2.10 *Assume that the parameters of* (2.40) *satisfy the inequality*

$$b\gamma c[T_f{}^* + T_f] < 2a.$$

Then the positive equilibrium (x^*, y^*) *of* (2.40) *is globally asymptotically stable. Here,*

$$T_f = \int_0^\infty sf(s)\mathrm{d}s < \infty \quad \textit{and} \quad T_f{}^* = \frac{1}{\gamma + D} \int_0^\infty f(s)\left(\mathrm{e}^{(\gamma+D)s} - 1\right)\mathrm{d}s < \infty.$$

Proof We consider the functional

$$V(t) = V_1(t) + V_2(t) + \alpha V_3(t),$$

in which $\alpha = \frac{(aU(x^*)-b\gamma)y^*}{c} > 0$.

Then it follows from (2.48) to (2.50) that along the solutions of (2.45),

$$V'(t) \leq -Dx_1U_1(x_1) - y(t)\left[a - T_f{}^* - T_f\right]U_1{}^2(x_1) < 0,$$

by the hypotheses.

The conclusion of the theorem follows from Theorem C.11, (Appendix C). □

We now present another result on the global asymptotic stability of (x^*, y^*). The proof of this result may be obtained as a special case of Theorem 2.33 of the following section, we provide only a statement.

Theorem 2.11 *The equilibrium solution* (x^*, y^*) *of* (2.40) *is globally asymptotically stable provided* $D - ck + aky^* > 0$ *and* $a\bar{\alpha} - b\gamma > 0$, *in which* $\bar{\alpha} = \min_{x \geq x^*} \{U(x)\}$ *and* k *is such that* $|U(x) - U(x^*)| \leq k|x - x^*|$.

Remark 2.12 It is observed by Ruan [79] that the system (2.40) is uniformly persistent if conditions (2.31) hold. That means, the very existence of a positive equilibrium, implying the instability of $(x_0, 0)$, ensures the eventual survival of the species in case of system (2.40).

We now include some more results on the global asymptotic stability, established for some special case of (2.40). The following result assumes a linear consumption or the Lotka–Volterra coupling term, namely $U(x) = x$. Though the basic assumption of saturation on consumption is obviously violated, the result is of academic interest.

Let

$$x_1(t) = x(t) - x^* \text{ and } y_1(t) = y(t) - y^*.$$

This transforms (2.40) into

$$\begin{aligned} x_1'(t) &= -Dx_1 - a(y_1 + y^*)x_1 - ax^* y_1 \\ &\quad + b\gamma \int_0^\infty f(s) y_1(t-s) \mathrm{d}s, \\ y_1'(t) &= c(y_1 + y^*)x_1. \end{aligned} \tag{2.51}$$

Notice that the positive equilibrium of (2.40) now gets transformed to $(0, 0)$ for (2.51).

Theorem 2.13 *Assume that the average time delay* T_f *satisfies the inequality*

$$T_f < \min\left\{\frac{2}{b\gamma}, \frac{2a(ax^* - b\gamma)}{b\gamma c(D + 2ax^* - 2b\gamma)}\right\} \tag{2.52}$$

in addition to (I) *below equation* (2.40). *Then the equilibrium solution* $(0, 0)$ *of* (2.51) *is globally asymptotically stable.*

Proof Consider the Lyapunov functional

$$\begin{aligned} V(x_t) &= w_1 {x_1}^2 + w_2\Big(y_1 - y^* \ \log(\frac{y_1 + y^*}{y^*})\Big) \\ &\quad + {V_0}^2(x_t) + w_1 b\gamma \int_0^\infty f(s) \int_{t-s}^t {y_1}^2(u) \mathrm{d}u \mathrm{d}s \\ &\quad + b\gamma(D + ax^* - b\gamma) \int_0^\infty f(s) \int_{t-s}^t \mathrm{d}t_1 \int_{t_1}^t {y_1}^2(u) \mathrm{d}u \mathrm{d}s, \end{aligned} \tag{2.53}$$

where $ax^* - b\gamma > 0, \;\; w_1 > 0, \; w_2 > 0$

$$V_0(x_t) = x_1 + \frac{a}{c} y_1 + b\gamma \int_0^\infty f(s) \int_{t-s}^t y_1(u)\mathrm{d}u\mathrm{d}s.$$

Clearly $V(0) = 0$ and

$$V(x_t) \geq w_1 {x_1}^2 + w_2 \left(y_1 - y^* \;\; \log \left(\frac{y_1 + y^*}{y^*} \right) \right)$$

and is positive definite and approaches ∞ as $x_1, \;\; y_1 \to \infty$. Observe further that along the solutions of (2.51)

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t}(w_1 {x_1}^2) \leq w_1 \Big\{ &-2D{x_1}^2 - 2a(y_1 + y^*){x_1}^2 - 2ax^* x_1 y_1 \\ &+ b\gamma {x_1}^2 + b\gamma \int_0^\infty f(s){y_1}^2(t-s)\mathrm{d}s \Big\}, \end{aligned} \tag{2.54}$$

Employing $b\gamma x_1 \int_0^\infty f(s) y_1(t-s) ds \leq b\gamma \frac{x_1^2}{2} + b\gamma \int_0^\infty f(s){y_1}^2(t-s)ds$ for the last two terms ($ab \leq \frac{a^2}{2} + \frac{b^2}{2}$)

$$\frac{\mathrm{d}}{\mathrm{d}t} w_2 \left(y_1 - y^* \;\; \log \left(\frac{y_1 + y^*}{y^*} \right) \right) = w_2 c x_1 y_1, \tag{2.55}$$

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t}{V_0}^2(x_t) \leq &-D(2 - b\gamma T_f){x_1}^2 - 2\left(D\frac{a}{c} + ax^* - b\gamma \right) x_1 y_1 \\ &- \left(2\frac{a}{c} - b\gamma T_f \right)(ax^* - b\gamma){y_1}^2 \\ &+ b\gamma(D + ax^* - b\gamma) \int_0^\infty f(s) \int_{t-s}^t {y_1}^2(u)\mathrm{d}u\mathrm{d}s, \end{aligned} \tag{2.56}$$

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t}\Big\{ w_1 b\gamma \int_0^\infty f(s) \int_{t-s}^t {y_1}^2(u)\mathrm{d}u\mathrm{d}s \Big\} = \\ w_1 b\gamma \Big({y_1}^2 - \int_0^\infty f(s){y_1}^2(t-s)\mathrm{d}s \Big) \end{aligned} \tag{2.57}$$

and

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t}\left\{ b\gamma(D + ax^* - b\gamma) \int_0^\infty f(s) \int_{t-s}^t \mathrm{d}t_1 \int_{t_1}^t {y_1}^2(u)\mathrm{d}u\mathrm{d}s \right\} = \\ b\gamma(D + ax^* - b\gamma) \Big\{ {y_1}^2 T_f - \int_0^\infty f(s) \int_{t-s}^t {y_1}^2(u)\mathrm{d}u\,\mathrm{d}s \Big\}. \end{aligned} \tag{2.58}$$

Now letting $w_2 c = 2aw_1 x^* + 2(D\frac{a}{c} + ax^* - b\gamma) > 0$ for any arbitrary choice of w_1, we have from (2.54) to (2.58), the time derivative of $V(x_t)$ (2.53) along the solutions of (2.51) is given by

$$V'(x_t) \leq -\Big[(2D - b\gamma)w_1 + 2D - Db\gamma T_f\Big]{x_1}^2$$
$$-\Big[2\frac{a}{c}(ax^* - b\gamma) - b\gamma w_1 - b\gamma(D + 2ax^* - 2b\gamma)T_f\Big]{y_1}^2.$$

By the assumption (2.52) on T_f the negative definiteness of $V'(x_t)$ follows. The conclusion is now clear. □

Now let $U(x) = x/(m + x)$ in (2.40). Letting $x_1 = x - x^*$ and $y_1 = y - y^*$ and $U_1(x_1) = U(x) - U(x^*)$ (2.40) is transformed to

$$\begin{aligned} {x_1}'(t) &= -Dx_1 - ayU_1(x_1) - aU(x^*)y_1 \\ &\quad + b\gamma \int_0^\infty f(s)y_1(t-s)\mathrm{d}s, \\ {y_1}'(t) &= cyU_1(x_1). \end{aligned} \tag{2.59}$$

Observe that for the aforementioned definition of U_1, we have

$${U_1}^2(x_1) < \frac{1}{m + x^*}x_1U_1(x_1), \quad \forall x_1. \tag{2.60}$$

It is known that the set of all bounded, continuous functions defined on $[0, \infty)$ forms a complete normed linear space with supremum norm, that is, $\|f\| = \sup_{0 \leq x < \infty} |f(x)|$. Obviously, if f is bounded, there exists a $H > 0$ such that $\|f\| \leq H$.

Thus, we choose initial conditions say $\phi_t = (\phi_{1t}, \phi_{2t})$ from a space of bounded, continuous, nonnegative functions with appropriate norm such that

$$\phi_t(s) = \phi(t + s), \ \ -\eta < s \leq t_0, \quad t_0 \geq 0, \ \ \|\phi\| < H \in (0, \infty),$$

$\eta > 0$ may be an extended real number depending on how far we wish to go into the past. The functions are assumed to be nonnegative because they have to represent populations here.

Theorem 2.14 *If the average time delay T_f satisfies that*

$$T_f < \min\left\{\frac{1}{b\gamma}, \ \frac{2}{b\gamma}\sqrt{\frac{aDx^*}{c^2U(x^*)K}}\right\}, \tag{2.61}$$

then all the solutions of (2.59) *approach* $(0, 0)$ *as* $t \to \infty$.

Here $K = \max\{(1 + b\gamma T_f)H, \ x_0/(1 - b\gamma T_f)\}$, *in which* H *is the bound on the initial conditions.*

Proof Consider the Lyapunov functional

$$\begin{aligned} V(x_t) &= w_1x^* \int_0^{x_1} U_1(v)dv + w_2\left(y_1 - y^* \ \log\left(\frac{y_1 + y^*}{y^*}\right)\right) \\ &\quad + w_3x^* \int_0^\infty f(s) \int_{t-s}^t \int_{t_1}^t y^2(u){U_1}^2(x_1(u))\mathrm{d}u\mathrm{d}s, \end{aligned} \tag{2.62}$$

where $w_i, \ i = 1, 2, 3$ are arbitrary constants.

The time derivative of V along the solutions of (2.59) is given by

$$\begin{aligned}
V'(x_t) &= w_1 x^* U_1(x_1)\Big\{-Dx_1 - ayU_1(x_1) \\
&\qquad - aU(x^*)y_1 + b\gamma\int_0^\infty f(s)y_1(t-s)\mathrm{d}s\Big\} \\
&\quad + w_2 y_1 U_1(x_1) + w_3 x^* y^2 T_f U_1{}^2(x_1) \\
&\quad - w_3 x^* \int_0^\infty f(s)\int_{t-s}^t y^2(u)U_1{}^2(x_1(u))\mathrm{d}u\mathrm{d}s \\
&= -x^* y[w_1 a - w_3 y T_f]U_1{}^2(x_1) + [w_2 c - w_1 x^* aU(x^*)]U_1(x_1)y_1 \\
&\quad - w_1 x^* DU_1(x_1)y_1 - w_3 x^* \int_0^\infty f(s)\int_{t-s}^t y^2(u)U_1{}^2(x_1(u))\mathrm{d}u\mathrm{d}s \\
&\quad + w_1 b\gamma x^* U_1(x_1)\int_0^\infty f(s)y_1(t-s)\mathrm{d}s. \qquad (2.63)
\end{aligned}$$

Observe that

$$\int_0^\infty f(s)\int_{t-s}^t y'_1(u)\mathrm{d}u\mathrm{d}s = y_1 - \int_0^\infty f(s)y_1(t-s)\mathrm{d}s.$$

Using this along with the second equation of (2.59), we obtain

$$\begin{aligned}
w_1 b\gamma x^* U_1(x_1)\int_0^\infty f(s)y_1(t-s)\mathrm{d}s &= w_1 b\gamma x^* U_1(x_1)y_1 \\
- w_1 b\gamma c x^* U_1(x_1)\int_0^\infty f(s)\int_{t-s}^t y(u)U_1(x_1(u))\mathrm{d}u\mathrm{d}s. \qquad (2.64)
\end{aligned}$$

Choosing $w_2 c = w_1 x^*(aU(x^*) - b\gamma)$ and utilizing (2.60) and (2.64) in (2.63), we get

$$\begin{aligned}
V'(x_t) &\le -x^* y[w_1 a - w_3 y T_f]U_1{}^2(x_1) \\
&\quad + [w_2 c - w_1 x^*(aU(x^*) - b\gamma)]U_1(x_1)y_1 \\
&\quad - w_1 x^* D(m + x^*)U_1{}^2(x_1) \\
&\quad - w_1 b\gamma c x^* U_1(x_1)\int_0^\infty f(s)\int_{t-s}^t y(u)U_1(x_1(u))\mathrm{d}u\mathrm{d}s \\
&\quad - w_3 x^* \int_0^\infty f(s)\int_{t-s}^t y^2(u)U_1{}^2(x_1(u))\mathrm{d}u\mathrm{d}s \\
&\le -x^* y[w_1 a - w_3 K T_f]U_1{}^2(x_1) \\
&\quad - x^* \int_0^\infty f(s)\int_{t-s}^t \Big\{\frac{w_1 x^* D}{U(x^*)T_f}U_1{}^2(x_1(t)) \\
&\quad + w_1 b\gamma c y(u)U_1(x_1(t))U_1(x_1(u)) \\
&\quad + w_3 y^2(u)U_1{}^2(x_1(u))\Big\}\mathrm{d}u\mathrm{d}s, \qquad (2.65)
\end{aligned}$$

which may be written as

$$V'(x_t) \leq -x^* y[w_1 a - w_3 K T_f] {U_1}^2(x_1) \\ - x^* \int_0^\infty f(s) \int_{t-s}^t [P(t,u) \times A(u) P(t,u)] \mathrm{d}u \mathrm{d}s, \qquad (2.66)$$

where

$$P(t,u) = \Big(U_1(x_1(t)), U_1(x_1(u))\Big)^T$$

and

$$A(u) = \begin{pmatrix} \frac{w_1 D x^*}{U(x^*) T_f} & \frac{1}{2} w_1 b\gamma c y(u) \\ \frac{1}{2} w_1 b\gamma c y(u) & w_3 y^2(u) \end{pmatrix}.$$

Negative semidefiniteness of V' follows from the positive definiteness of $A(u)$, that is when

$$\frac{a}{K T_f} \frac{w_3}{w_1} > (b\gamma c)^2 T_f \frac{U(x^*)}{4 D x^*}$$

holds. By the hypothesis (2.61), such a choice of w_1 and w_3 is possible. Thus, V' is negative semi definite and conclusion follows from Theorem C.10 (Appendix C), by the observation that the largest invariant set is $M = \{(0,0)\}$. This completes the proof. □

We shall now understand the influence of a discrete delay in growth response in the presence of a distributed time delay in material recycling. The model we consider here is system (2.5), that is,

$$\begin{aligned} x'(t) &= D x_0 - D x(t) - a U(x(t)) y(t) \\ &\quad + b\gamma \int_{-\infty}^t f(t-s) y(s) \mathrm{d}s, \\ y'(t) &= -(\gamma + D) y(t) + c U(x(t-\tau)) y(t). \end{aligned} \qquad (2.67)$$

The basic properties of the solutions of (2.67) may be obtained as in the case of earlier models. We assume tacitly that the solutions of (2.67) exist, are nonnegative, bounded, and continuable on their maximal intervals of existence, consistent with the biology.

Notice that the equilibrium solutions of (2.67) are same as those of the earlier models in this chapter and are given here:

$$\begin{aligned} D x_0 &= D x^* + a U(x^*) y^* - b\gamma y^*. \\ \gamma + D &= c U(x^*). \end{aligned}$$

Now we directly proceed to the global stability of the positive equilibrium (x^*, y^*) of (2.67).

The following transformation will be useful here. Let

$$x_1(t) = x(t) - x^*,\ y_1(t) = \log\frac{y(t)}{y^*},\ \text{ and } U_1(x_1(t)) = U(x(t)) - U(x^*).$$

This transforms (2.67) into

$$\begin{aligned} x_1{}'(t) &= -Dx_1 - ay^*\mathrm{e}^{y_1}U_1(x_1) - ay^*U(x^*)\left[\mathrm{e}^{y_1} - 1\right] \\ &\quad + b\gamma y^*\int_0^\infty f(s)\left[\mathrm{e}^{y_1(t-s)} - 1\right]\mathrm{d}s, \\ y_1{}'(t) &= cU_1(x_1(t-\tau)). \end{aligned} \tag{2.68}$$

As in Theorems 2.6 and 2.10, we construct a suitable Lyapunov functional V. We again modify appropriately the functional V used earlier.

Consider

$$V_1(x_1(t)) = \int_0^{x_1} U_1(x_1(s))\mathrm{d}s.$$

Differentiating $V_1(t)$ with respect to t along the solutions of (2.68) and rearranging we get

$$\begin{aligned} V_1{}'(t) &= -Dx_1U_1(x_1) - ay^*\mathrm{e}^{y_1}U_1{}^2(x_1) - (aU(x^*) - b\gamma)y^*\left[\mathrm{e}^{y_1} - 1\right]U_1(x_1) \\ &\quad + b\gamma y^*cU_1(x_1)\int_0^\infty f(s)\int_{t-s}^t \mathrm{e}^{y_1(u)}y_1{}'(u)\mathrm{d}u\mathrm{d}s. \end{aligned}$$

That is,

$$\begin{aligned} V_1{}'(t) &= -Dx_1U_1(x_1) - ay^*\mathrm{e}^{y_1}U_1{}^2(x_1) \\ &\quad - (aU(x^*) - b\gamma)y^*\left[\mathrm{e}^{y_1(t+\tau)} - 1\right]U_1(x_1) \\ &\quad + (aU(x^*) - b\gamma)y^*\left[\mathrm{e}^{y_1(t+\tau)} - \mathrm{e}^{y_1(t)}\right]U_1(x_1) \\ &\quad + b\gamma y^*cU_1(x_1)\int_0^\infty f(s)\int_{t-s}^t \mathrm{e}^{y_1(u)}U_1(x_1(u-\tau))\mathrm{d}u\mathrm{d}s. \end{aligned} \tag{2.69}$$

Consider

$$V_2(y_1(t)) = \int_0^{y_1} (\mathrm{e}^s - 1)\mathrm{d}s.$$

Then along the solutions of (2.68),

$$V_2{}'(y_1(t+\tau)) = cU_1(x_1)\left[\mathrm{e}^{y_1(t+\tau)} - 1\right].$$

Choose $\alpha = \frac{(aU(x^*)-b\gamma)y^*}{c} > 0$
and let

$$V_3(t) = V_1(x_1(t)) + \alpha V_2(y_1(t+\tau)).$$

We notice from the second equation of (2.67) that

$$e^{y_1(t+\tau)} - e^{y_1(t)} = \int_t^{t+\tau} e^{y_1(u)} y_1'(u)du = c\int_t^{t+\tau} e^{y_1(u)} U_1(x_1(u-\tau))du.$$

It follows that

$$\begin{aligned}
V_3{}'(t) &= -Dx_1U_1(x_1) - ay^*\mathrm{e}^{y_1}U_1{}^2(x_1)\\
&\quad + (aU(x^*) - b\gamma)y^*cU_1(x_1)\int_t^{t+\tau} e^{y_1(u)}U_1(x_1(u-\tau))du\\
&\quad + b\gamma y^*cU_1(x_1)\int_0^\infty f(s)\int_{t-s}^t \mathrm{e}^{y_1(u)}U_1(x_1(u-\tau))\mathrm{d}u\mathrm{d}s\\
&\le -Dx_1U_1(x_1) - ay^*\mathrm{e}^{y_1}U_1{}^2(x_1)\\
&\quad + \frac{1}{2}(aU(x^*) - b\gamma)y^*c\int_t^{t+\tau} \mathrm{e}^{y_1(u)}\left[U_1{}^2(x_1(t)) + U_1{}^2(x_1(u-\tau))\right]\mathrm{d}u\\
&\quad + \frac{1}{2}b\gamma y^*c\int_0^\infty f(s)\int_{t-s}^t \mathrm{e}^{y_1(u)}\left[U_1{}^2(x_1(t)) + U_1{}^2(x_1(u-\tau))\right]\mathrm{d}u\mathrm{d}s.
\end{aligned}$$

Now define

$$V(t) = V_3(t) + V_4(t)$$

in which

$$\begin{aligned}
V_4(t) = &\frac{1}{2}(aU(x^*) - b\gamma)y^*c\int_{t-\tau}^t\int_v^t \mathrm{e}^{y_1(u+\tau)}U_1{}^2(x_1(u))\mathrm{d}v\mathrm{d}u\\
&+ \frac{1}{2}b\gamma y^*c\int_0^\infty f(s)\int_{t-s}^t\int_v^t y(u)U_1{}^2(x_1(u-\tau))\mathrm{d}v\mathrm{d}u\mathrm{d}s.\\
&+ \frac{1}{2}b\gamma y^*c\int_{t-\tau}^t y(s+\tau)U_1{}^2(x_1(s))\mathrm{d}s.
\end{aligned}$$

Then we have

$$\begin{aligned}
V'(t) \le &-Dx_1U_1(x_1) - ayU_1{}^2(x_1)\\
&+ \frac{1}{2}(aU(x^*) - b\gamma)y^*c\left[\int_t^{t+\tau} \mathrm{e}^{y_1(u)}\mathrm{d}u + \tau\mathrm{e}^{y_1(t+\tau)}\right]U_1{}^2(x_1)\\
&+ \frac{1}{2}b\gamma cU_1{}^2(x_1)\int_0^\infty f(s)\int_{t-s}^t y(u)\mathrm{d}u\mathrm{d}s\\
&+ \frac{1}{2}b\gamma cU_1{}^2(x_1)T_f y(t+\tau).
\end{aligned} \tag{2.70}$$

From the second equation of (2.67), we have

$$y'(t) \ge -(\gamma + D)y(t)$$

and hence,

$$y(s) \leq y(t)\mathrm{e}^{(\gamma+D)(t-s)}. \tag{2.71}$$

It follows from (2.71) that

$$\begin{aligned} y^* \left[\int_t^{t+\tau} \mathrm{e}^{y_1(s)} \mathrm{d}s + \tau \mathrm{e}^{y_1(t+\tau)} \right] &= \int_t^{t+\tau} y(s)\mathrm{d}s + \tau y(t+\tau) \\ &\leq y(t) \int_t^{t+\tau} \mathrm{e}^{(\gamma+D)(t-s)} \mathrm{d}s \\ &\quad + y(t)\tau \mathrm{e}^{-(\gamma+D)\tau} \\ &= \Big[\frac{1}{\gamma+D} \left(1 - \mathrm{e}^{-(\gamma+D)\tau}\right) \\ &\quad + \tau \mathrm{e}^{-(\gamma+D)\tau} \Big] y(t). \end{aligned} \tag{2.72}$$

Also

$$\begin{aligned} y^* \int_0^\infty f(s) \int_{t-s}^t \mathrm{e}^{y_1(u)} \mathrm{d}u\mathrm{d}s &= \int_0^\infty f(s) \int_{t-s}^t y(u)\mathrm{d}u\mathrm{d}s \\ &\leq y(t) \int_0^\infty f(s) \int_{t-s}^t \mathrm{e}^{(\gamma+D)(t-u)} \mathrm{d}u\mathrm{d}s \\ &= \frac{1}{\gamma+D} y(t) \int_0^\infty f(s) \Big(\mathrm{e}^{(\gamma+D)s} - 1 \Big) \mathrm{d}s. \end{aligned} \tag{2.73}$$

From (2.70), (2.72) and (2.73), we get

$$\begin{aligned} V'(t) &\leq -Dx_1 U_1(x_1) - ayU_1{}^2(x_1) \\ &\quad + y(t)U_1{}^2(x_1)\frac{1}{2}(aU(x^*) - b\gamma)c \\ &\quad \times \left[\frac{1}{\gamma+D} \left(1 - e^{-(\gamma+D)\tau}\right) + \tau e^{-(\gamma+D)\tau} \right] \\ &\quad + \frac{1}{2} b\gamma c \Big[\tilde{T_f} + T_f e^{-(\gamma+D)\tau} \Big] y(t) U_1{}^2(x_1). \end{aligned} \tag{2.74}$$

Clearly $V'(t) < 0$ provided

$$T_\tau + T_{\tau,f} < a, \tag{2.75}$$

where

$$\begin{aligned} T_\tau &= \frac{1}{2}(aU(x^*) - b\gamma)c \left[\frac{1}{\gamma+D} \left(1 - \mathrm{e}^{-(\gamma+D)\tau}\right) + \tau \mathrm{e}^{-(\gamma+D)\tau} \right], \\ T_{\tau,f} &= \frac{1}{2} b\gamma c \Big[\tilde{T_f} + T_f \mathrm{e}^{-(\gamma+D)\tau} \Big], \\ \tilde{T_f} &= \frac{1}{\gamma+D} \int_0^\infty f(s) \Big(\mathrm{e}^{(\gamma+D)s} - 1 \Big) \mathrm{d}s. \end{aligned}$$

We record these observations in the following theorem.

Theorem 2.15 *Assume that the delay kernel in addition to* (I) *satisfies* $\tilde{T_f} < \infty$ *and the delay parameter* τ *is such that* (2.75) *holds. Then the positive equilibrium* (x^*, y^*) *of* (2.67) *is globally asymptotically stable.*

Notice that when material recycling is instantaneous, Theorem 2.15 reduces to Theorem 2.4. For this, we let $f(s) = \delta(s)$, the Dirac delta function, and observe that $T_{\tau,f}$ will disappear. The sufficient condition on the parameters (2.75) now reduces to $T_\tau < a$.

Remark 2.16 From the second equation of (2.67), we have

$$y'(t) \leq [c - (\gamma + D)]y(t) = \gamma_1 y(t),$$

where $\gamma_1 = c - (\gamma + D) > 0$. Therefore,

$$y(s) \leq y(t)\mathrm{e}^{\gamma_1(s-t)}.$$

Using this in (2.73) we obtain the sufficient condition (2.75)

$$T_\tau + T_{\tau,f} < a$$

for the negative definiteness of $V'(t)$, in which the condition on the delay kernel gets modified to

$$\tilde{T_f} = \min\left\{\frac{1}{\gamma + D}\int_0^\infty f(s)\left(\mathrm{e}^{(\gamma+D)s} - 1\right)\mathrm{d}s,\ \frac{1}{\gamma_1}\int_0^\infty f(s)\left(1 - \mathrm{e}^{-\gamma_1 s}\right)\mathrm{d}s\right\}.$$

Now we present another global stability result.

For this we need

(a) by the transformation $x_1(t) = x(t) - x^*$, $y_1(t) = y(t) - y^*$ and $U_1(x_1(t)) = U(x(t)) - U(x^*)$ (2.67) may be written as

$$\begin{aligned} {x_1}'(t) &= -Dx_1 - aU(x)y_1 - ay^*U_1(x_1) + b\gamma\int_0^\infty f(s)y_1(t-s)ds \\ {y_1}'(t) &= c(y_1 + y^*)U_1(x_1(t-\tau)); \end{aligned}$$

(b) there exists a $k > 0$ such that $|U(x_1)| \leq k|x_1|$ (a Lipschitz constant for U).

Theorem 2.17 *The equilibrium solution* (x^*, y^*) *of* (2.67) *is globally asymptotically stable for*

$$0 \leq \tau < \tau^* = \min\left\{\frac{D - ck - aky^*}{(D + ay^*)ck}, \frac{a\bar{\alpha} - b\gamma}{(aL + b\gamma)ck}\right\},$$

provided $D - ck - aky^* > 0$ *and* $a\bar{\alpha} - b\gamma > 0$, *in which* $\bar{\alpha} = \min_{x \geq x^*} \{U(x)\}$, *k is the Lipschitz constant, and L is the bound defined on* $U(x)$.

Proof We consider the functional, $V(t) = V_1(t) + V_2(t)$ where

$$V_1(t) = |x_1(t)| + |\log\left(\frac{y_1(t) + y^*}{y^*}\right)| + b\gamma \int_0^\infty f(s) \int_{t-s}^t |y(u)|\mathrm{d}u\mathrm{d}s$$

and

$$\begin{aligned} V_2(t) = ck\Big[D \int_{t-\tau}^t \mathrm{d}s \int_s^t |x_1(u)|\mathrm{d}u + aL \int_{t-\tau}^t \mathrm{d}s \int_s^t |y_1(u)|\mathrm{d}u \\ + ay^* \int_{t-\tau}^t \mathrm{d}s \int_s^t |U_1(x_1(u))|\mathrm{d}u \\ + b\gamma \int_{t-\tau}^t \mathrm{d}s \int_0^\infty f(z) \int_{s-z}^t |y_1(u)|\mathrm{d}u\mathrm{d}z\Big]. \end{aligned}$$

We have

$$\begin{aligned} D^+V_1(t) \leq -D|x_1(t)| - aU(x(t))|y_1(t)| - ay^*|U_1(x_1(t))| \\ + c|U_1(x_1(t-\tau))| + b\gamma|y_1(t)|. \end{aligned}$$

Now,

$$\begin{aligned} |U_1(x_1(t-\tau))| &\leq k|x_1(t-\tau)| = k|x_1(t) - \int_{t-\tau}^t x_1'(s)\mathrm{d}s| \\ &= k|x_1(t) - \int_{t-\tau}^t \Big[-Dx_1(s) - aU(x(s))y_1(s) \\ &\quad - ay^*U_1(x_1(s)) + b\gamma \int_0^\infty f(z)y_1(s-z)\mathrm{d}z\Big]\mathrm{d}s| \\ &\leq k|x_1(t)| + k\Big[D \int_{t-\tau}^t |x_1(s)|\mathrm{d}s + aL \int_{t-\tau}^t |y_1(s)|\mathrm{d}s \\ &\quad + ay^* \int_{t-\tau}^t |U_1(x_1(s))|\mathrm{d}s + b\gamma \int_{t-\tau}^t \int_0^\infty f(z)|y_1(s-z)|\mathrm{d}z\mathrm{d}s\Big]. \end{aligned}$$

Thus,

$$\begin{aligned} D^+V_1(t) \leq -(D - ck - aky^*)|x_1(t)| - (aU(x) - b\gamma)|y_1(t)| \\ + ck\Big[D \int_{t-\tau}^t |x_1(s)|\mathrm{d}s + aL \int_{t-\tau}^t |y_1(s)|\mathrm{d}s \\ + ay^* \int_{t-\tau}^t |U_1(x_1(s))|\mathrm{d}s + b\gamma \int_{t-\tau}^t \int_0^\infty f(z)|y_1(s-z)|\mathrm{d}z\mathrm{d}s\Big]. \end{aligned} \tag{2.76}$$

Now,

$$D^+V_2(t) \le ck\Big[D|x_1(t)|\tau + aL|y_1(t)|\tau + ay^*|U_1(x_1(t))|\tau + b\gamma|y_1(t)|\tau\Big]$$
$$-ck\left[D\int_{t-\tau}^{t}|x_1(s)|\mathrm{d}s + aL\int_{t-\tau}^{t}|y_1(s)|\mathrm{d}s\right.$$
$$\left.+ay^*\int_{t-\tau}^{t}|U_1(x_1(s))|\mathrm{d}s + b\gamma\int_{t-\tau}^{t}\int_0^\infty f(z)|y_1(s-z)|\mathrm{d}z\mathrm{d}s\right]. \tag{2.77}$$

Using (2.76) and (2.77) we have after some simplifications,

$$\begin{aligned} D^+V(t) &\le -(D - ck - aky^*)|x_1(t)| - (aU(x) - b\gamma)|y_1(t)| \\ &\quad + ck(D + aky^*)\tau|x_1(t)| + ck(aL + b\gamma)\tau|y_1(t)| \\ &= -\Big(D - ck - aky^* - ck(D + aky^*)\tau\Big)|x_1(t)| \\ &\quad - \Big(aU(x) - b\gamma - ck(aL + b\gamma)\tau\Big)|y_1(t)| \\ &< 0, \quad \text{by the hypotheses.} \end{aligned}$$

The remainder of the proof may be completed employing standard arguments (see Theorem C.11 (Appendix C)). □

The following example compares the lengths of delay parameter estimated by Theorems 2.15 and 2.17.

Example 2.18 Consider the system,

$$\begin{aligned} x'(t) &= 8(x_0 - x(t)) - 22U(x(t))y(t) + \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s, \\ y'(t) &= -10y(t) + 20U(x(t-\tau)), \end{aligned}$$

in which $D = 8,\ \gamma = 2,\ b = 0.5$, $x_0 = 11$, and $U(x) = x/(10 + x)$.

Then $(x^*, y^*) = (10, 0.8)$ and $U(x^*) = 0.5$ with $k = 1/10$.

For these parametric values, the length of the delay given by Theorem 2.17 for which the system is globally asymptotically stable is $\tau^* = 0.2172$ while Theorem 2.15 estimates the delay to be $\tau^* = 0.162$.

Example 2.19 Consider the system,

$$\begin{aligned} x'(t) &= 2(14 - x(t)) - 14U(x(t))y(t) + \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s, \\ y'(t) &= -6y(t) + 8U(x(t-\tau)), \end{aligned}$$

in which $\gamma = 4,\ b = 0.25$, and $U(x) = x/(4 + x)$ with $f(s) = 4\mathrm{e}^{-4s}$.

Then $(x^*, y^*) = (12, 8/15)$ and $U(x^*) = 0.75$ with $k = 1/8$.

Clearly all the conditions of Theorem 2.17 are satisfied yielding $\tau^* = 0.00704$. Therefore, Theorem 2.17 ensures the global asymptotic stability of $(12, 8/15)$ for $0 \leq \tau < \tau^* = 0.00704$. At the same time, as $\int_0^\infty f(s)[\exp^{(\gamma+D)s} - 1]ds \to \infty$, Theorem 2.15 cannot be applied here.

Now we compare some results in Sect. 2.1 with regard to the estimation of the length of delay. Consider the case when the death of the species is attributed only to the washout. That is, the washout is fast enough that the natural death is insignificant ($\gamma = 0$). In such a case (2.67) reduces to (2.7). The following example compares Theorem 2.17 when $\gamma = 0$ with Theorem 2.3.

Example 2.20 Consider the system,

$$x'(t) = 3(x_0 - x(t)) - 5U(x(t))y(t),$$
$$y'(t) = -3y(t) + 5U(x(t - \tau))y(t),$$

in which $D = 3, a = 5 = c, x_0 = 5.5$, and $U(x) = x/(3 + x)$.

Then $(x^*, y^*) = (4.5, 1)$ with $k = 2/15$ and $\bar{\alpha} = 3/5$. Now from Theorem 2.17, we have after some calculations, $\tau^* = 5/16$. This further implies (x^*, y^*) is globally asymptotically stable for $0 \leq \tau \leq 5/16$ by virtue of Theorem 2.17.

By appropriate scaling we obtain $(\frac{9}{11}, \frac{2}{11})$ as the corresponding equilibrium solution of system (2.8). The length of the delay for which this equilibrium is stable is estimated to be $\tau^* = 0.002115$ employing Theorem 2.3.

It is clear that the estimate on the length of delay parameter given by Theorem 2.17 here is much larger than the one given by Theorem 2.3 . Further, we may notice that the procedure for the estimation of τ^* in Theorem 2.3 is tedious as it involves number of calculations. Moreover, length of the delay parameter given by Theorem 2.3 depends on the bounds on the solutions of the system which, in turn, depend on the delay parameter itself, which is not the case with the earlier Theorem 2.17.

Remark 2.21 Noting that the equilibrium solution (x^*, y^*) of (2.8) satisfies $1-x^*-y^* = 0$ and $U(x^*) = 1$, the length of the delay τ^* in this case is given by

$$\tau^* = \min\left\{\frac{1 - kx^*}{(1 + y^*)k}, \frac{1}{Lk}\right\},$$

using Theorem 2.17. Thus, if we can find k (Lipschitz constant defined for U) such that $kx^* < 1$, then for $0 \leq \tau < \tau^*$, the system (2.8) is globally asymptotically stable. It may be seen that this estimate on τ^* is different from the one obtained in Theorem 2.3.

Also observe that Theorem 2.17 reduces to Theorem 2.5 in the special case $f(s) = \delta(s)$ and $L = 1$.

Viewing persistence as another way of establishing the survival of species, we shall prove a result on uniform persistence of solutions of (2.67). For a definition of uniform persistence(see Definition C.13 (Appendix C)).

Theorem 2.22 *The system (2.67) is uniformly persistent if inequality (2.31) for the existence of a positive equilibrium holds.*

Proof We set $f(s) = \alpha e^{-\alpha s},\ \alpha > 0$ and let,

$$z(t) = \int_{-\infty}^{t} \alpha \mathrm{e}^{-\alpha(t-s)} y(s)\mathrm{d}s.$$

This transforms system (2.67) into

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) + b\gamma z(t), \\ y'(t) &= -(\gamma + D)y(t) + cU(x(t-\tau))y(t), \\ z'(t) &= \alpha y(t) - \alpha z(t). \end{aligned} \tag{2.78}$$

Linearizing (2.78) around (x^*, y^*, z^*), where $z^* = y^*$ and $x^*,\ y^*$ are given by

$$Dx_0 = Dx^* + aU(x^*)y^* - b\gamma y^*.$$

$$\gamma + D = cU(x^*),$$

we have

$$\begin{aligned} x_1{}'(t) &= -(D + ay^*U'(x^*))x_1(t) \\ &\quad - aU(x^*)y_1(t) + b\gamma z_1(t), \\ y_1{}'(t) &= cy^*U'(x^*)x_1(t-\tau), \\ z_1{}'(t) &= \alpha y_1(t) - \alpha z_1(t), \end{aligned} \tag{2.79}$$

where $x_1(t) = x(t) - x^*$, $y_1(t) = y(t) - y^*$, and $z_1(t) = z(t) - z^*$.

Corresponding to the equilibrium $E_0(x_0, 0, 0)$ the characteristic equation of (2.79) is

$$(\lambda + D)(\lambda + \alpha)\Big[\lambda - \Big(cU(x_0) - (b\gamma + D)\Big)\Big] = 0. \tag{2.80}$$

If a positive equilibrium exists, that is if the condition (2.31) holds then the eigen value $\lambda = cU(x_0) - (b\gamma + D) > 0$, the other two being negative. Also in a sufficiently small half-disc neighbourhood of E_0, $dy/dt > 0$ holds from the second equation of (2.78). Therefore, no trajectory approaches E_0 from y direction and thus, E_0 is stable in x, z direction while unstable in y direction (i.e., E_0 is a saddle point). Solutions starting on X-axis approach E_0 and the stable set of E_0 does not intersect the positive cone. Thus, E_0 is compact invariant only on the boundary and there are no cycles in the boundary. Thus, the conclusion follows. □

2.5 A More Realistic Model

We now consider the following system of integro-differential equations to describe the limited nutrient–consumer dynamics (see (2.6)).

$$x'(t) = D(x_0 - x(t)) - aU(x(t))y(t) + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s,$$
$$y'(t) = -(\gamma + D)y(t) + cy(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s. \tag{2.81}$$

All the terms of (2.81) are as explained in earlier models. The characteristics of (2.81) are quite interesting and this model is going to be the starting point of the development of the theory in subsequent chapters as well. f and g are the delay kernels for the nutrient recycling and the growth of the biomass, respectively. The kernel f describes the contribution of the dead biomass from the past to the nutrient recycled at time t whereas g indicates that the growth is not immediate to consumption and there is a time delay (e.g. due to gestation).

We recall that the growth rate is no more than the consumption, that is, $c \le a$.

We recall the assumptions on the uptake function U earlier.

(A_1) $U(x)$ is continuous real-valued function defined on $\mathbf{R}_+ = [0, \infty)$ such that

$$U(0) = 0, U(x) > 0 \quad \text{for } x > 0 \text{ and } \lim_{x\to\infty} U(x) = L_1 < \infty.$$

These conditions imply that $|U(x)| \le L$ for all] x, for some $L > 0$.

Some times we may require a Lipschitz condition on U, such as,

(A_2) there exists a constant $k > 0$ such that for all $x_1,\ x_2 \in \mathbf{R}_+$,

$$|U(x_1) - U(x_2)| \le k|x_1 - x_2|. \tag{2.82}$$

Mathematical imposition on the delay kernels requires that they are nonnegative and satisfy,

$$\int_0^\infty f(s)\mathrm{d}s = 1, \quad \int_0^\infty g(s)\mathrm{d}s = 1, \tag{2.83}$$

$$\int_0^\infty sf(s)\mathrm{d}s < \infty, \quad \int_0^\infty sg(s)\mathrm{d}s < \infty. \tag{2.84}$$

Some examples of such normalized kernels with finite first order positive moments are given later.

1. $f^{(k)}(s) = \dfrac{\alpha^k}{(k-1)!}s^{k-1}\mathrm{e}^{-\alpha s}, \quad g^{(k)}(s) = \dfrac{\beta^k}{(k-1)!}s^{k-1}\mathrm{e}^{-\beta s},$

$s \ge 0,\ \ \alpha > 0,\ \ \beta > 0$ (Gamma distribution).

2. $f(s) = \alpha\mathrm{e}^{-\alpha s}, \quad g(s) = \beta\mathrm{e}^{-\beta s}$ (Exponential).

The quantities $T_f = \int_0^\infty sf(s)\mathrm{d}s < \infty$, $T_g = \int_0^\infty sg(s)\mathrm{d}s < \infty$ represent the average time delays in the recycling process and the growth of biomass, respectively.

We assume the following initial conditions on system (2.81).

$$x(s) = \phi_1(s), \quad y(s) = \phi_2(s) \quad -\infty < s \le t_0, \quad t_0 \in \mathbf{R}_+. \tag{2.85}$$

Owing to the biological description of the model, these functions are assumed to be nonnegative, bounded, and continuous on $(-\infty, t_0]$.

In the next section we shall discuss various basic properties of the solutions of the system (2.81) subject to the initial conditions (2.85).

2.5.1 Qualitative Properties of Solutions

In this section, we obtain conditions for the existence and uniqueness of solutions, equilibria and establish that the solutions are nonnegative and bounded, which is an important requirement.

In view of the Lipschitz condition (A_2) on U, it is easy to establish the local existence, uniqueness, and continuous dependence on the initial conditions (2.85) of the solutions of (2.81) for all $t \in J = [t_0, t_0 + T)$, for some $T > 0$ (see Theorem B.1 (Appendix B)). But we shall establish the existence and uniqueness of solutions of the system (2.81), (2.85) for the uptake function U under conditions weaker than a Lipschitz condition (remember Theorem 1.10?). Before proving the theorem, we rewrite system (2.81) as

$$X'(t) = F(t, X_t) \text{ where } X(t) = \begin{pmatrix} x(t) \\ y(t) \end{pmatrix} \text{ and}$$

$$F(t, X_t) = \begin{pmatrix} D(x_0 - x(t)) - aU(x(t))y(t) + b\gamma \int_0^\infty f(s)y(t-s)\mathrm{d}s \\ -(\gamma + D)y(t) + cy(t)\int_0^\infty g(s)U(x(t-s))\mathrm{d}s \end{pmatrix}.$$

Now we consider the system of equations given by $X'(t) = F(t, X_t)$ with initial conditions $X(t_0) = X_0$.

Let $S(\rho)$ be an open bounded sphere contained in $\mathbf{R}^{n+1}$ and let $F : S \to \mathbf{R}^n$. For a given $(t_0, X_0) \in S$, a solution of the aforementioned system is a differentiable function $X(t)$ on an interval J such that

$$X' = F(t, X_t) \text{ for } t \in J, t_o \in J \text{ and } X(t_0) = X_0.$$

For $X \in \mathbf{R}^n$, we define $\|X\| = \sum_{i=1}^n |X_i|$.

Lemma 2.23 *Let $F : S \to \mathbf{R}^n$ be continuous and satisfy the following condition: Each point in S has an open neighbourhood N, an integer $m \ge 0$, functions h_j and ψ_j for $j = 1, 2, \cdots, m$, and nonnegative constants $K_1, K_2, K_1 + K_2 \ne 0$ such that*

$$(A_3) \quad \|F(t,\xi) - F(t,\eta)\| \le K_1\|\xi - \eta\| + K_2 \sum_{j=1}^m |\psi_j(h_j(t,\xi)) - \psi_j(h_j(t,\eta))|$$

on N where $h_j : N \to \mathbf{R}$ is continuously differentiable with

$$\frac{\partial h_j(t,\xi)}{\partial t} + \sum_{i=1}^{n} \frac{\partial h_j(t,\xi)}{\partial \xi_i} F_i(t,\xi) \neq 0 \ \text{ on } \ N \ \text{ and}$$

each $\psi_j : \mathbf{R} \to \mathbf{R}$ is continuous and of bounded variation on bounded subintervals. Then the system $X' = F(t, X_t)$ with $X(t_0) = X_0, (t_0, X_0) \in S$ has a unique solution on any interval J.

Now we establish the following theorem.

Theorem 2.24 *The given system of equations (2.81) has a unique solution for a given set of initial conditions.*

Proof We shall verify the hypotheses of Lemma 2.23 for the system (2.81).

For $t \geq 0$ and functions $\xi(t) = (\xi_1(t), \xi_2(t))$ and $\eta(t) = (\eta_1(t), \eta_2(t))$, we have

$$\begin{aligned}
&\|F(t,\xi) - F(t,\eta)\| \\
&\leq D|\eta_1(t) - \xi_1(t)| + b\gamma \int_{-\infty}^{t} f(t-s)|\xi_2(s) - \eta_2(s)|\mathrm{d}s \\
&\quad +(\gamma + D)|\eta_2(t) - \xi_2(t)| + a|U(\eta_1(t))\eta_2(t) - U(\xi_1(t))\xi_2(t)| \\
&\quad +c|\xi_2(t) \int_{-\infty}^{t} g(t-s)U(\xi_1(s)\mathrm{d}s - \eta_2(t) \int_{-\infty}^{t} g(t-s)U(\eta_1(s)\mathrm{d}s| \\
&\leq K_1\|\xi(t) - \eta(t)\| \\
&\quad +K_2 \sum_{j=1}^{2} |\psi_j(h_j(t,\xi)) - \psi_j(h_j(t,\eta))|,
\end{aligned}$$

where $K_1 = b\gamma + D + \gamma + D$ and $K_2 = a$.

Now, if we choose,

$$\begin{gathered}
h_1(t,\xi) = \xi_1(t), \ \ \psi_1(h_1(t,\xi)) = \xi_2(t) \int_{-\infty}^{t} g(t-s)U(h_1(s,\xi(s)))\mathrm{d}s, \\
h_2(t,\xi) = \xi_1(t), \ \text{ and } \ \psi_2(h_2(t,\xi)) = \xi_2(t)U(h_2(t,\xi(t))),
\end{gathered}$$

then it is easy to see that all the hypotheses of Lemma 2.23 are satisfied, and hence, the conclusion follows. □

Observe that the choice of $K_2 = 0$ in the earlier lemma reduces our considerations to a Lipschitz condition.

We shall now find out the equilibrium solutions of (2.81). Clearly, equilibria of (2.81) are the solutions of the algebraic system,

$$\begin{aligned}
Dx_0 - Du - aU(u)v + b\gamma v &= 0, \\
(-(\gamma + D) + cU(u))v &= 0.
\end{aligned} \tag{2.86}$$

Obviously, $(x_0, 0)$ is a solution of (2.86), which is a partially feasible equilibrium of (2.81).

Any nontrivial solution of (2.86) must satisfy the equations,

$$\begin{aligned} Dx_0 - Dx^* - aU(x^*)y^* + b\gamma y^* &= 0, \\ -(\gamma + D) + cU(x^*) &= 0. \end{aligned} \tag{2.87}$$

From this we have $U(x^*) = (\gamma + D)/c$ and $y^* = [D(x_0 - x^*)]/[aU(x^*) - b\gamma]$.

Since $c \leq a$ and $b \in (0, 1)$, we have $U(x^*) = (\gamma + D)/c > (b\gamma)/a$, which implies that $aU(x^*) > b\gamma$. Therefore, for a positive y^* we must have $x_0 > x^*$. Since U is continuous and $U(x) \leq L$ for all x, a necessary and sufficient condition for the existence of a positive x^* is $0 < (\gamma + D)/c < L$. Thus, the aforementioned inequalities yield a set of necessary and sufficient conditions for the existence of a positive equilibrium solution (x^*, y^*) for (2.81).

Now we employ Theorem 2.24 to establish that the system of equations (2.81) admits a unique equilibrium solution (x^*, y^*).

Theorem 2.25 *The system of equations* (2.87) *has a unique solution yielding a unique nontrivial equilibrium solution for the system* (2.81).

Proof Using (2.87) in (2.81), we get

$$\begin{aligned} x'(t) &= -D(x(t) - x^*) - a[U(x)y(t) - U(x^*)y^*] \\ &\quad + b\gamma \int_{-\infty}^{t} f(t - s)(y(s) - y^*)\mathrm{d}s, \\ y'(t) &= cy(t) \int_{-\infty}^{t} g(t - s)(U(x(t) - U(x^*))\mathrm{d}s. \end{aligned}$$

Denoting $x(t) - x^* = x_1(t)$, $y(t) - y^* = y_1(t)$, and $U(x(t)) - U(x^*) = U_1(x_1(t))$, the earlier system after a simple rearrangement takes the form

$$\begin{aligned} x_1'(t) &= -Dx_1(t) - a(y_1(t) + y^*)U_1(x_1(t)) - aU(x^*)y_1(t) \\ &\quad + b\gamma \int_{-\infty}^{t} f(t - s)y_1(s)\mathrm{d}s \\ y_1'(t) &= c(y_1(t) + y^*) \int_{-\infty}^{t} g(t - s)U_1(x_1(s))\mathrm{d}s. \end{aligned} \tag{2.88}$$

Choose the initial functions

$$x_1(t) \equiv 0 \quad \text{and} \quad y_1(t) \equiv 0 \quad \text{for} \quad t \in (-\infty, 0]. \tag{2.89}$$

Then by Theorem 2.24, the initial value problem (2.88) and (2.89) admits a unique solution. Clearly, the trivial solution is the only solution of the system (2.88) and (2.89). This implies that

$$x_1(t) \equiv 0 \equiv y_1(t) \quad \text{for} \quad t > 0, \tag{2.90}$$

which in turn implies that $x(t) = x^*$ and $y(t) = y^*$ is the unique solution satisfying (2.87) and hence (2.86). This guarantees the existence of a unique equilibrium solution for the system (2.81). □

The following theorem establishes that the solutions of (2.81) are nonnegative.

Theorem 2.26 *All the solutions of system* (2.81) *are nonnegative for all* $t \geq 0$ *corresponding to the initial conditions* (2.85).

Proof We shall show that once a solution enters the plane

$$\Omega = \{(x, y)/x \geq 0, y \geq 0\},$$

then it remains there forever. By continuity of solutions of (2.71) each solution has to take the value 0 before it assumes a negative value. If $y = 0$ for some $t = t_1 > 0$, then from the second equation of (2.81), $y'(t_1) = 0$, and hence, y is nondecreasing at t_1, which means that y is at least nondecreasing at $y = 0$. This rules out the possibility of y taking a negative value. Again when $x = 0$, we have

$$x'(t) = Dx_0 + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s > 0,$$

since $y \geq 0$.

Clearly, x is increasing at $x = 0$. When $y = 0$, $x'(t) = Dx_0 - Dx$ and again at $x = 0$, $x'(t) = Dx_0 > 0$ and hence, x is increasing at $x = 0$. Thus, we can conclude that the solutions of (2.81) are nonnegative for all $t > 0$. □

Theorem 2.27 *Let* $\phi_j \geq 0, \quad j = 1, 2$ *and not identically zero on any interval. All the solutions of* (2.81) *are bounded provided*

$$\delta \equiv \min_{x>0}\{aU(x(t)) + \gamma + D - b\gamma - cL\} > 0$$

holds.

Proof Consider

$$V(t) = V(x(t), y(t)) = x(t) + y(t) + \int_0^{\infty} f(s) \int_{t-s}^{t} y(u)\mathrm{d}u.$$

Clearly,

$$V(0,0) = 0, \; V(x(t), y(t)) > 0 \; \text{for} \quad x, y > 0 \; \text{and} \; V(t) \to \infty$$

as $x(t), \quad y(t) \to \infty$.

The time derivative of V along the solutions of (2.81) is

$$\begin{aligned} V'(t) = &\ Dx_0 - Dx(t) - aU(x(t))y(t) + b\gamma \int_0^\infty f(s)y(t-s)\mathrm{d}s \\ &- (\gamma + D)y(t) + cy(t)\int_0^\infty g(s)U(x(t-s))\mathrm{d}s \\ &+ b\gamma y(t) - b\gamma \int_0^\infty f(s)y(t-s)\mathrm{d}s \\ = &\ Dx_0 - Dx(t) - (aU(x(t)) + \gamma + D - b\gamma)y(t) \\ &+ cy(t)\int_0^\infty g(s)U(x(t-s))\mathrm{d}s \\ \le &\ Dx_0 - Dx(t) - (aU(x(t)) + \gamma + D - b\gamma - cL)y(t), \end{aligned}$$

utilizing the conditions, $U(x) \le L$ for all x and $\int_0^\infty g(s)ds = 1 = \int_0^\infty f(s)\mathrm{d}s$.

Thus, outside the region bounded by the positive coordinate plane and the surface $Dx + \delta y = Dx_0$, $V'(t)$ is negative.

The conclusion follows from Theorem B.2 (Appendix B) with $W(t, X(t)) = x(t)$, $Q(t, X(t)) = V(t)$, and $\tilde{U} = x_0$. □

We shall now present another result.

Theorem 2.28 *The solutions of* (2.81) *are uniformly bounded provided the delay kernels satisfy either of the following conditions.*

1. $T_g = \int_0^\infty sg(s) < \dfrac{a - bc}{acL}, \quad T_f = \int_0^\infty sf(s) < \dfrac{1}{\gamma},$
2. $T_g = \int_0^\infty sg(s) < \dfrac{a - c}{acL}, \quad T_f = \int_0^\infty sf(s) < \dfrac{1}{b\gamma}.$

Proof First, we shall provide a proof for case 1. Consider the functional

$$\begin{aligned} V(t) \equiv &\ V(x, y) \\ &= x(t) + by(t) + b\gamma \int_0^\infty f(s) \int_{t-s}^t y(u)\,\mathrm{d}u\mathrm{d}s \\ &\quad + ay(t)\int_0^\infty g(s)\int_{t-s}^t U(x(u))\,\mathrm{d}u\mathrm{d}s. \end{aligned}$$

The time derivative of V along the solutions of (2.81) after some rearrangements becomes

$$\begin{aligned} \frac{\mathrm{d}V}{\mathrm{d}t} = &\ Dx_0 - Dx(t) - aU(x(t))y(t) + b\gamma \int_0^\infty f(s)y(t-s)\mathrm{d}s \\ &- b(\gamma + D)y(t) + bcy(t)\int_0^\infty g(s)U(x(t-s)\mathrm{d}s \end{aligned}$$

$$
\begin{aligned}
&+ b\gamma y(t) - b\gamma \int_0^\infty f(s) y(t-s)\mathrm{d}s \\
&+ a\Big\{-(\gamma + D) y(t) + c y(t) \int_0^\infty g(s) U(x(t-s))\mathrm{d}s\Big\} \\
&\times \int_0^\infty g(s) \int_{t-s}^t U(x(u))\,\mathrm{d}u\mathrm{d}s \\
&+ a y(t)\Big\{U(x) - \int_0^\infty g(s) U(x(t-s))\mathrm{d}s\Big\}.
\end{aligned}
$$

That is,

$$
\begin{aligned}
\frac{\mathrm{d}V}{\mathrm{d}t} \le\ & D x_0 - D x(t) - b D y(t) \\
& - a(\gamma + D) y(t) \int_0^\infty g(s) \int_{t-s}^t U(x(u))\,\mathrm{d}u\mathrm{d}s \\
& - \Big[a - bc - ac \int_0^\infty g(s) \int_{t-s}^t U(x(u))\,\mathrm{d}u\mathrm{d}s\Big] \\
& \times y(t) \int_0^\infty g(s)\ U(x(t-s))\,\mathrm{d}s,
\end{aligned}
$$

ignoring the third term and invoking (2.83) on f.

Now using $U(x) \le L$ for all x and observing that

$$
\int_0^\infty g(s) \int_{t-s}^t U(x(u))\,\mathrm{d}u\mathrm{d}s \le L \int_0^\infty s g(s)\mathrm{d}s = L T_g,
$$

we have

$$
\begin{aligned}
\frac{\mathrm{d}V}{\mathrm{d}t} \le\ & D x_0 - D x(t) - b D y(t) \\
& - (a - bc - acLT_g) y(t) \int_0^\infty g(s)\ U(x(t-s))\,\mathrm{d}s \\
\le\ & D x_0 - D x(t) - b D y(t),
\end{aligned}
$$

invoking the hypothesis on T_g.

Now define $\omega = \{(x, y) \in \mathbf{R}_+^2 : Dx + bDy \le Dx_0\}$. Consider $\mathbf{R}_+^2 - \omega$. If a trajectory starts from $t_0 > 0$ in $\mathbf{R}_+^2 - \omega$, then the functional $V(x, y)$ along a trajectory starting from this point would be decreasing for all times $t \ge t_0$ such that $(x, y) \in \mathbf{R}_+^2 - \omega$.

Clearly $V(t) \ge bx(t) + by(t) = b||X(t)||$, since $0 < b < 1$. Using the initial conditions (2.85), we have

$$\begin{aligned} V &\leq \phi_1 + b\phi_2 + b\gamma T_f \phi_2 + aLT_g\phi_2 \\ &\leq 3\eta||\Phi|| \end{aligned}$$

where $\eta = \max\{1, b + b\gamma T_f + aLT_g\}$ and $||\Phi|| = \sup_{t\in(-\infty,0)}\{|\phi_1|, |\phi_2|\}$. Let $\beta = 3\eta||\Phi||$. Then we have $b||X(t)|| \leq V(x, y) \leq \beta$, which implies the uniform boundedness of the solutions of (2.81) here.

Case 1-(a). If $(x, y) \in \omega$ for all t then by definition of ω, all the solutions are uniformly bounded.

Case 1-(b). Suppose that a trajectory enters the plane ω at t_0 and leaves ω at t_1. Then for all $t \in (t_0, t_1)$,

$$\begin{aligned} V(x, y) &\leq x_0 + \frac{ax_0}{b}\int_0^\infty g(s)\int_{t-s}^t U(x(u))\,\mathrm{d}u\mathrm{d}s \\ &\quad + b\gamma\int_0^\infty f(s)\int_{t-s}^t y(u)\mathrm{d}u\mathrm{d}s \\ &\leq x_0 + \frac{aLx_0}{b}T_g + b\gamma\int_0^\infty f(s)\int_{t-s}^t y(u)\mathrm{d}u\mathrm{d}s. \end{aligned}$$

Since

$$y(u) \leq \frac{1}{b}V(x, y) \leq \frac{\beta}{b} \ \text{ for } \ u \in (-\infty, t_0)$$

and

$$y \leq \frac{x_0}{b} \ \text{ for } \ u \in (t_0, t_1),$$

we have for $t \in (t_0, t_1)$,

$$\begin{aligned} V(x, y) &\leq x_0\left(1 + \frac{aL}{b}T_g\right) \\ &\quad + \gamma T_f \max\{\beta, x_0\} = \beta_1, \quad \text{(say)}. \end{aligned}$$

Suppose the trajectory that leaves ω at $t = t_1$ reenters ω at $t = t_2$ and leaves again at $t = t_3$ and so on. Continuing the earlier process for the interval (t_n, t_{n+1}), we can show that

$$\begin{aligned} V(x, y) &\leq x_0\left(1 + \frac{aL}{b}T_g\right) \\ &\quad + \gamma T_f \max\left\{\beta, \frac{bDx_0}{\alpha_1}, \beta_1, \beta_2, .., \beta_n\right\} = \beta_{n+1}, \quad \text{(say)}. \end{aligned}$$

It is easy to see that

$$\beta_n \leq \max\left\{\beta, \frac{x_0}{1 - \gamma T_f}\left(1 + \frac{aL}{b}T_g\right)\right\}$$

and moreover $\beta_i \leq \beta_{i+1}$ for $i = 1, 2, ...$ By the hypothesis that $T_f < 1/\gamma$ we have $\{\beta_n\}$ is bounded and thus for $t \geq t_0$,

$$b||X(t)|| < V(x, y) \leq \max\left\{\beta, \frac{x_0}{1-\gamma T_f}\left(1 + \frac{aL}{b}T_g\right)\right\}.$$

The proof of case 1 is complete.

The argument for case 2 is similar with the Lyapunov functional

$$\begin{aligned} V(t) &\equiv V(x, y) \\ &= x(t) + y(t) + b\gamma \int_0^\infty f(s) \int_{t-s}^t y(u)\, \mathrm{d}u\mathrm{d}s \\ &\quad + ay(t) \int_0^\infty g(s) \int_{t-s}^t U(x(u))\, \mathrm{d}u\mathrm{d}s. \end{aligned}$$

□

In the reminder of this chapter we shall tacitly assume that (2.81) has a unique positive equilibrium (x^*, y^*), and all its solutions are nonnegative and bounded.

2.5.2 Local Stability

We rewrite equations (2.81) around the positive equilibrium as

$$\begin{aligned} x'(t) &= -D(x - x^*) - ay\Big(U(x) - U(x^*)\Big) - aU(x^*)(y - y^*) \\ &\quad + b\gamma \int_0^\infty f(s)(y(t-s) - y^*)\mathrm{d}s, \\ y'(t) &= c\int_0^\infty g(s)\Big(U(x(t-s)) - U(x^*)\Big)\mathrm{d}s. \end{aligned} \tag{2.91}$$

Denoting $x_1(t) = x(t) - x^*$, $y_1(t) = y(t) - y^*$, and $U_1(x_1) = U(x) - U(x^*)$ and rearranging, (2.91) may be written as

$$\begin{aligned} x_1'(t) &= -Dx_1(t) - aU_1(x_1(t))(y_1(t) + y^*) - aU(x^*)y_1(t) \\ &\quad + b\gamma \int_0^\infty f(s)y_1(t-s)\mathrm{d}s, \\ y_1'(t) &= c(y_1(t) + y^*) \int_0^\infty g(s)U_1(x_1(t-s))\mathrm{d}s. \end{aligned} \tag{2.92}$$

Note that $(0, 0)$ is the equilibrium solution of (2.92) corresponding to (x^*, y^*) of (2.91).

Assume that $U'(x)$ exists.

Linearizing (2.92) around $(0, 0)$, taking $U_1(x_1) \approx U'(x^*)x_1$, we obtain after some rearrangements,

$$\begin{aligned} x_1'(t) &= -(D + ay^*U'(x^*))x_1(t) - aU(x^*)y_1(t) \\ &\quad + b\gamma \int_0^\infty f(s)y_1(t-s)\mathrm{d}s, \\ y_1'(t) &= cy^*U'(x^*) \int_0^\infty g(s)x_1(t-s)\mathrm{d}s, \end{aligned} \tag{2.93}$$

which may be written as

$$X'(t) = RX(t) + \int_0^\infty k(s)X(t-s)\mathrm{d}s, \tag{2.94}$$

where $X(t) = (x_1(t),\ y_1(t))^T$,

$$R = \begin{pmatrix} -D - ay^*U'(x^*) & -aU(x^*) \\ 0 & 0 \end{pmatrix}; \quad k(s) = \begin{pmatrix} 0 & b\gamma f(s) \\ cy^*U'(x^*)g(s) & 0 \end{pmatrix}.$$

The characteristic equation of (2.94) is given by

$$P(\lambda) = |\lambda I - R - \int_0^\infty k(s)\mathrm{e}^{-\lambda s}\mathrm{d}s| = 0, \tag{2.95}$$

which may be written as

$$P(\lambda) = \lambda^2 + A\lambda + G(\lambda)[B - CF(\lambda)] = 0, \tag{2.96}$$

where

$$\begin{aligned} A &= D + ay^*U'(x^*), \\ B &= acy^*U(x^*)U'(x^*), \\ \text{and} \quad C &= b\gamma cy^*U'(x^*) \\ F(\lambda) &= \int_0^\infty f(s)\mathrm{e}^{-\lambda s}\mathrm{d}s \\ G(\lambda) &= \int_0^\infty g(s)e^{-\lambda s}\mathrm{d}s. \end{aligned} \tag{2.97}$$

Choose nonnegative parameters δ and ϵ such that

$$\delta + \epsilon = A. \tag{2.98}$$

Then we observe that

$$P(\lambda) = \begin{vmatrix} \lambda + \delta & G(\lambda)(CF(\lambda) - B) + \delta\epsilon \\ 1 & \lambda + \epsilon \end{vmatrix} \tag{2.99}$$

yields the same characteristic equation as (2.96). We also notice that characteristic equation (2.99), and hence, (2.96) corresponds to the integro-differential system

$$\begin{aligned} v' &= -\delta v + \delta\epsilon u - \int_0^\infty f_1(s)u(t-s)\mathrm{d}s \\ &\quad + \int_0^\infty f_2(s)u(t-s)\mathrm{d}s, \\ u' &= v - \epsilon u, \end{aligned} \tag{2.100}$$

where $f_1(s) = Bg(s)$ and $f_2(s) = c\int_0^s g(s-\nu)f(\nu)\mathrm{d}\nu, \quad s \in [0,\infty)$.

We are now in a position to establish the following theorem.

Theorem 2.29 *The positive equilibrium of* (2.91) *is locally asymptotically stable provided*

$$\alpha_1 + \beta_1 < A.$$

Here

$$\alpha_1 = \int_0^\infty sf_2(s)ds, \;\; \beta_1 = \int_0^\infty sf_1(s)ds, \;\; \textit{and} \;\; A = D + ay^*U'(x^*)$$

in which f_1 *and* f_2 *are as defined earlier.*

Proof We consider the Lyapunov functional

$$\begin{aligned} V(X_t) &= v^2 + w_0u^2 + V_0^2(X_t) \\ &\quad + \int_0^\infty \Big[f_1(s) + f_2(s)\Big]\int_{t-s}^t \mathrm{d}t_1 \\ &\quad \times \int_{t_1}^t \Big[v^2(z) + (\epsilon + \beta_0 - \alpha_0)u^2(z)\Big]\mathrm{d}z\mathrm{d}s, \end{aligned}$$

in which

$$\alpha_0 = \int_0^\infty f_2(s)\mathrm{d}s < \infty, \;\; \beta_0 = \int_0^\infty f_1(s)\mathrm{d}s < \infty$$

and

$$V_0(X_t) = v + \delta u - \int_0^\infty f_1(s)\int_{t-s}^t u(t_1)\mathrm{d}t_1\mathrm{d}s + \int_0^\infty f_2(s)\int_{t-s}^t u(t_1)\mathrm{d}t_1\mathrm{d}s$$

and w_0 is a positive constant to be chosen in the due course. Clearly

$$V(0) = 0, \;\; V(X_t) \geq \eta(v^2 + u^2),$$

where $\eta = \min\{1, w_0\}$.

Now along the solutions of (2.100), we have

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}(v^2) &= 2v\left\{-\delta v + \delta\epsilon u - \int_0^\infty f_1(s)u(t-s)\mathrm{d}s + \int_0^\infty f_2(s)u(t-s)\mathrm{d}s\right\}\\ &\le -2\delta v^2 + 2\delta\epsilon uv - 2(\beta_0-\alpha_0)uv + (1+\epsilon)(\alpha_1+\beta_1)v^2\\ &\quad + \int_0^\infty \Big[f_1(s)+f_2(s)\Big]\int_{t-s}^t \Big[v^2(z)+\epsilon u^2(z)\Big]\mathrm{d}z\,\mathrm{d}s. \qquad (2.101)\end{aligned}$$

Now

$$\begin{aligned}&\frac{\mathrm{d}}{\mathrm{d}t}\left\{\int_0^\infty \Big[f_1(s)+f_2(s)\Big]\int_{t-s}^t \mathrm{d}t_1\int_{t_1}^t \Big[v^2(z)+(\epsilon+\beta_0-\alpha_0)u^2(z)\Big]\mathrm{d}z\,\mathrm{d}s\right\}\\ &= (\alpha_1+\beta_1)\Big[v^2(z)+(\epsilon+\beta_0-\alpha_0)u^2(z)\Big]\\ &- \int_0^\infty \Big[f_1(s)+f_2(s)\Big]\int_{t-s}^t \Big[v^2(z)+(\epsilon+\beta_0-\alpha_0)u^2(z)\Big]\mathrm{d}z\,\mathrm{d}s \qquad (2.102)\end{aligned}$$

and

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}(V_0^2) &= 2V_0\Big[v' + \delta u' - (\beta_0-\alpha_0)u\\ &\quad + \int_0^\infty f_1(s)u(t-s)\mathrm{d}s - \int_0^\infty f_2(s)u(t-s)\mathrm{d}s\Big]\\ &= -2(\beta_0-\alpha_0)uV_0\\ &\le -2(\beta_0-\alpha_0)uv - 2(\beta_0-\alpha_0)\delta u^2 + (\beta_0-\alpha_0)(\beta_1-\alpha_1)u^2\\ &\quad +(\beta_0-\alpha_0)\int_0^\infty \Big[f_1(s)+f_2(s)\Big]\int_{t-s}^t u^2(t_1)\mathrm{d}t_1\mathrm{d}s. \qquad (2.103)\end{aligned}$$

Using (2.101) – (2.103) we obtain after some simplifications and rearrangement,

$$\begin{aligned}V'(X_t) &\le -\Big[2(\beta_0-\alpha_0)\delta + 2w_0\epsilon - (2(\beta_0-\alpha_0)+\epsilon)(\beta_1-\alpha_1)\Big]u^2\\ &\quad +2\Big[w_0 - 2(\beta_0-\alpha_0) + \delta\epsilon\Big]uv\\ &\quad -\Big[2\delta - (2+\epsilon)(\beta_1-\alpha_1)\Big]v^2. \qquad (2.104)\end{aligned}$$

Using the definitions of α_0 and β_0 we may show that $\beta_0 > \alpha_0$.
Now letting $\epsilon = 0,\quad \delta = A$, and $w_0 = 2(\beta_0-\alpha_0)$, we have

$$V' \le -2(\beta_0-\alpha_0)\Big[A-(\beta_1-\alpha_1)\Big]u^2 - 2\Big[A-(\beta_1-\alpha_1)\Big]v^2,$$

which is clearly negative definite by the hypotheses that $A > \alpha_1+\beta_1$. The conclusion now follows from Theorem C.11 (Appendix C). The proof is complete. □

We present another local stability result. For this we need to represent system (2.93) as

$$x_1'(t) = -Ax_1(t) - \frac{B}{C}y_1(t) + b\gamma \int_0^\infty f(s)y_1(t-s)\mathrm{d}s,$$
$$y_1'(t) = \frac{C}{b\gamma}\int_0^\infty g(s)x_1(t-s)\mathrm{d}s, \tag{2.105}$$

in which A, B, and C are as defined in (2.97).

From the discussion following equation (2.87), for the existence of a positive equilibrium, we must have $aU(x^*) > b\gamma$ and hence, it follows that $B > C$.

Consider

$$V_{11}(t) = {x_1}^2(t).$$

Then along the solutions of (2.105),

$$\begin{aligned}
V_{11}'(t) &= 2x_1x_1' \\
&= -2A{x_1}^2 - 2b\gamma\frac{B}{C}x_1y_1 - 2b\gamma x_1y_1 \\
&\quad -2b\gamma x_1\int_0^t f(s)\int_{t-s}^t {y'}_1(z)\mathrm{d}z\mathrm{d}s + I(t) \\
&= -2A{x_1}^2 - 2b\gamma(\frac{B}{C}-1)x_1y_1 + I(t) \\
&\quad -2Cx_1\int_0^t f(s)\int_{t-s}^t\int_0^\infty g(w)x_1(z-w)\mathrm{d}w\mathrm{d}z\mathrm{d}s \\
&\le -2A{x_1}^2 - 2b\gamma(\frac{B}{C}-1)x_1y_1 + I(t) \\
&\quad +C\int_0^\infty f(s)\int_{t-s}^t\int_0^\infty g(w)({x_1}^2(t) + {x_1}^2(z-w))\mathrm{d}w\mathrm{d}z\mathrm{d}s \\
&= -2A{x_1}^2 - 2b\gamma(\frac{B}{C}-1)x_1y_1 + CT_f{x_1}^2 + I(t) \\
&\quad +C\int_0^\infty f(s)\int_{t-s}^t\int_0^\infty g(w){x_1}^2(z-w)\mathrm{d}w\mathrm{d}z\mathrm{d}s.
\end{aligned} \tag{2.106}$$

Here

$$T_f = \int_0^\infty sf(s)\mathrm{d}s$$

and

$$I(t) = -2b\gamma x_1\int_t^\infty f(s)(y_1(t) - y_1(t-s))\mathrm{d}s. \tag{2.107}$$

Now consider

$$V_{12} = C\int_0^\infty f(s)\int_{t-s}^t\int_r^t\int_0^\infty g(w){x_1}^2(z-w)\mathrm{d}w\mathrm{d}z\mathrm{d}r\mathrm{d}s.$$

Then from (2.106), we have

$$
\begin{aligned}
V_{11}'(t) + V_{12}'(t) &\le -2Ax_1{}^2 - 2b\gamma(\frac{B}{C} - 1)x_1y_1 + CT_f x_1{}^2 + I(t) \\
&\quad + C\int_0^{\infty} f(s)\int_{t-s}^{t}\int_0^{\infty} g(w)x_1{}^2(t-w)\mathrm{d}w\mathrm{d}z\mathrm{d}s \\
&\le -2Ax_1{}^2 - 2b\gamma(\frac{B}{C} - 1)x_1y_1 + CT_f x_1{}^2 + I(t) \\
&\quad + CT_f\int_0^{\infty} g(s)x_1{}^2(t-s)\mathrm{d}s.
\end{aligned} \tag{2.108}
$$

Now we consider the function

$$V_1(t) = V_{11}(t) + V_{12}(t) + CT_f\int_0^{\infty} g(s)\int_{t-s}^{t} x_1{}^2(u)\mathrm{d}u\mathrm{d}s.$$

Then from (2.108),

$$V_1'(t) \le -2(A - CT_f)x_1{}^2 - 2b\gamma(\frac{B}{C} - 1)x_1y_1 + I(t). \tag{2.109}$$

From the second equation of (2.105), we have

$$\frac{\mathrm{d}}{\mathrm{d}t}\left[y_1 + \frac{C}{b\gamma}\int_0^{\infty} g(s)\int_{t-s}^{t} x_1(u)\mathrm{d}u\mathrm{d}s\right] = \frac{C}{b\gamma}x_1(t).$$

Define

$$
\begin{aligned}
V_2(t) = &\left[y_1 + \frac{C}{b\gamma}\int_0^{\infty} g(s)\int_{t-s}^{t} x_1(u)\mathrm{d}u\mathrm{d}s\right]^2 \\
&+\Big(\frac{C}{b\gamma}\Big)^2\int_0^{\infty} g(s)\int_{t-s}^{t}\int_v^{t} x_1{}^2(u)\mathrm{d}u\mathrm{d}v\mathrm{d}s.
\end{aligned}
$$

After some simplifications, we can show that

$$V_2'(t) = \frac{2C}{b\gamma}x_1y_1 + 2\Big(\frac{C}{b\gamma}\Big)^2 T_g x_1{}^2, \tag{2.110}$$

in which

$$T_g = \int_0^{\infty} sg(s)ds.$$

Now define

$$V(t) = V_1(t) + \frac{(b\gamma)^2}{C}\left[\int_t^{\infty} f(s)ds + \frac{B}{C} - 1\right]V_2(t).$$

From (2.107), (2.109), and (2.110), we have

$$\begin{aligned}
V'(t) &\le -2\left[A - CT_f - \left(c\int_t^\infty f(s)\mathrm{d}s + B - C\right)T_g\right]{x_1}^2 \\
&\quad + 2b\gamma x_1 y_1 \int_t^\infty f(s)\mathrm{d}s + I(t) \\
&= -2\left[A - CT_f - \left(c\int_t^\infty f(s)\mathrm{d}s + B - C\right)T_g\right]{x_1}^2 \\
&\quad + 2b\gamma x_1 \int_t^\infty f(s)y_1(t-s)\mathrm{d}s, \quad \text{using (2.107)} \\
&\le -2\left[A - CT_f - \left(c\int_t^\infty f(s)\mathrm{d}s + B - C\right)T_g\right]{x_1}^2 \\
&\quad + 2b\gamma x_1 \|\phi_2\| \int_t^\infty f(s)\mathrm{d}s \\
&\le -2\left[A - CT_f - \left(c\int_t^\infty f(s)\mathrm{d}s + B - C\right)T_g\right]{x_1}^2 \\
&\quad + b\gamma {x_1}^2 \int_t^\infty f(s)\mathrm{d}s + b\gamma\|\phi_2\|^2 \int_t^\infty f(s)ds \\
&= -2\left[A - CT_f - (B-C)T_g\right]{x_1}^2 \\
&\quad + [2cT_g + b\gamma]{x_1}^2 \int_t^\infty f(s)\mathrm{d}s + b\gamma\|\phi_2\|^2 \int_t^\infty f(s)\mathrm{d}s. \qquad (2.111)
\end{aligned}$$

Here $\phi_2 \in (-\infty, 0)$ is the initial condition for y_1.

We are now in a position to state and prove the following theorem.

Theorem 2.30 *Assume that the delay kernels satisfy the conditions*

$$\int_0^\infty s^2 f(s)\mathrm{d}s < \infty, \qquad \int_0^\infty s^2 g(s)\mathrm{d}s < \infty,$$

in addition to (2.83) *and* (2.84). *Then the positive equilibrium solution* (x^*, y^*) *of* (2.105) *is locally asymptotically stable provided the following inequality holds*

$$CT_f + (B-C)T_g < A. \qquad (2.112)$$

Proof If (2.112) holds, then there exists an $\epsilon > 0$ such that

$$Q(\epsilon) \equiv CT_f + (B-C)T_g + \left(cT_g + \frac{b\gamma}{2}\right)\epsilon < A.$$

Let $T = T(\epsilon) > 0$ be such that $\int_t^\infty f(s)ds < \epsilon$ for $t \ge T$.

Then from (2.111), we have for $t \ge T$,

$$V'(t) \le -2(A - Q(\epsilon)){x_1}^2 + b\gamma\|\phi_2\|^2 \int_t^\infty f(s)\mathrm{d}s.$$

Integrating from T to t, we have

$$V(t) - V(T) \leq -2(A - Q(\epsilon)) \int_T^t {x_1}^2(s)\mathrm{d}s + b\gamma\|\phi_2\|^2 \int_T^t \int_s^\infty f(u)\mathrm{d}u\,\mathrm{d}s.$$

That is,

$$V(t) + 2(A - Q(\epsilon)) \int_T^t {x_1}^2(s)\mathrm{d}s \leq V(T) + b\gamma\|\phi_2\|^2 \int_0^\infty s f(s)\mathrm{d}s.$$

This implies that x_1 and y_1 are bounded and ${x_1}^2 \in L_1[0, \infty)$. It follows from (2.105) and the Mean value theorem that x_1, x_1', y_1, and y_1' are uniformly continuous on $[0, \infty)$. Applying Barb$\bar{a}$lat lemma (Lemma B.4 (Appendix B)), we can conclude that $x_1 \to 0$ and $x_1' \to 0$ as $t \to \infty$.

Then from the first equation of (2.105),

$$\lim_{t\to\infty} \left[-\frac{B}{C} y_1 + \int_0^\infty f(s) y_1(t-s)\mathrm{d}s \right] = 0. \tag{2.113}$$

If $\liminf_{t\to\infty} y_1(t) = \alpha$ $\limsup_{t\to\infty} y_1(t) = \beta$ then for any sequence $\{t_m\} \uparrow \infty$ such that $y_1(t_m) \to \beta$ as $t_m \to \infty$ then from (2.113),

$$\frac{B}{C}\beta = \lim_{m\to\infty} \int_0^\infty f(s) y_1(t_m - s) ds \leq \beta \int_0^\infty f(s) ds = \beta.$$

Since $B > C$, it follows that $\beta \leq 0$. Similarly, we can show that $\alpha \geq 0$. But $\alpha \leq \beta$. Thus, $\alpha = \beta = 0$ implying that $y_1 \to 0$ as $t \to \infty$. The conclusion of the theorem follows. □

In Beretta and Takeuchi [10], it is shown that a sufficient condition for the local asymptotic stability of (2.105) is

$$CT_f + (B + C)T_g < A,$$

by arguments similar to those given in earlier Theorem 2.29. Comparing the terms, the condition (2.112) of Theorem 2.30 appears to be an improvement of the aforementioned condition. We, therefore, understand that the system may have a larger region of stability than these conditions actually estimate. This observation is not just a conclusion drawn from the earlier results but has enough support as we shall see in the next subsection.

Before we go in for global stability of equilibria of the system (2.81) we first obtain conditions for the local stability of the axial equilibrium $(x_0, 0)$ of (2.81).

Linearizing (2.81) around $(x_0, 0)$ and letting

$$x_1 = x_0, \quad y_1 = y, \quad \text{and} \quad U(x) \approx U(x_0) + U'(x_0)x_1,$$

we get

$$x_1{}' = -Dx_1 - aU(x_0)y_1 + b\gamma \int_0^\infty f(s)y_1(t-s)\mathrm{d}s,$$
$$y_1{}' = -(\gamma + D - cU(x_0))y_1.$$

The characteristic equation corresponding to the earlier system is

$$P(\lambda) = \begin{vmatrix} \lambda + D & aU(x_0) - b\gamma F(\lambda) \\ 0 & \lambda + (\gamma + D - cU(x_0)) \end{vmatrix} = 0.$$

That is,

$$(\lambda + D)(\lambda + (\gamma + D - cU(x_0)) = 0.$$

The two roots are $\lambda_1 = -D < 0$ and $\lambda_2 = -(\gamma + D - cU(x_0))$. Clearly, the second root is negative if $cU(x_0) < \gamma + D$. Thus, we have the following theorem.

Theorem 2.31 *The equilibrium* $(x_0, 0)$ *is locally asymptotically stable provided the inequality*

$$U(x_0) < \frac{\gamma + D}{c}$$

holds.

Notice that this inequality excludes the possibility of the existence of a positive equilibrium for (2.81) (see also discussion before Theorem 2.25).

2.5.3 Global Asymptotic Stability Results

In this section, we obtain sufficient conditions for the global asymptotic stability of the equilibria of the system (2.81). Our first result deals with the global asymptotic stability of the axial equilibrium $(x_0, 0)$. The next three results give sufficient conditions for the global asymptotic stability of the positive equilibrium (x^*, y^*). Also, we provide some examples to verify that they are independent of each other.

Theorem 2.32 *The partially feasible equilibrium* $(x_0, 0)$ *of* (2.81) *is globally asymptotically stable if* $L_1 < \gamma + D/c$.

Proof It is clear from the second equation of (2.81) that $\lim_{t\to\infty} y(t) = 0$ as $t \to \infty$ when $L_1 < \gamma + D/c$ for the system (2.81). It suffices to prove that $x(t) \to x_0$ as $t \to \infty$ when the aforementioned inequality holds.

Consider

$$V(t) = V(x(t), y(t)) = x(t) + y(t).$$

Clearly,

$$V(0,0) = 0 \quad \text{and} \quad V(x(t), y(t)) \geq 0 \quad \text{for } t \geq 0.$$

Further,

$$\begin{aligned}
V'(t) = &\, Dx_0 - Dx(t) - aU(x(t))y(t) + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s \\
&- (\gamma + D)y(t) + cy(t) \int_{-\infty}^{t} g(t-s)U(x(s)\mathrm{d}s \\
= &\, Dx_0 - D(x(t) + y(t)) \\
&- aU(x(t))y(t) + cy(t) \int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s \\
&- \gamma y(t) + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s.
\end{aligned}$$

Now observing that $c \le a$, $b\gamma < \gamma$, and $y(t) \to 0$ as $t \to \infty$, the behavior of the right hand side is decided by the term $Dx_0 - D(x(t) + y(t)) = Dx_0 - DV(t)$.

Thus, we have, $V'(t) \le -DV(t) + Dx_0$, from which it follows that

$$V(t) = V(x(t), y(t)) \le V(0)e^{-Dt} + x_0.$$

Accordingly, $\lim_{t\to\infty} V(t) = x_0 = \lim_{t\to\infty} \Big[x(t) + y(t)\Big]$.

The conclusion follows from the fact that $\lim_{t\to\infty} y(t) = 0$. Hence, the theorem. □

Since, we are interested in the survival of species we concentrate our study on the global asymptotic stability of the positive equilibrium (x^*, y^*).

Using (2.87) in (2.81) we rewrite (2.81) as

$$\begin{aligned}
x'(t) &= -D(x(t) - x^*) - aU(x(t))(y(t) - y^*) - ay^*(U(x(t)) - U(x^*)) \\
&\quad + b\gamma \int_0^\infty f(s)(y(t-s) - y^*)\mathrm{d}s, \\
y'(t) &= cy(t) \int_0^\infty g(s)(U(x(t-s)) - U(x^*))\mathrm{d}s.
\end{aligned} \tag{2.114}$$

The constant $k > 0$ that appears in the next result is the Lipschitz constant for U defined in (A_2). We state and prove the following result.

Theorem 2.33 *Assume that the uptake function $U(x)$ satisfies (A_1) and (A_2) and the delay kernels satisfy* (2.83) *and* (2.84)*. The equilibrium solution (x^*, y^*) of* (2.81) *is globally asymptotically stable provided,*

$$D - (c - ay^*)k > 0 \quad \textit{and} \quad \Delta \equiv \min_{x \ge x^*}\{aU(x) - b\gamma\} > 0.$$

Proof We consider the functional,

$$V(t) \equiv V(x(t), y(t)) = |x(t) - x^*| + |\log (y(t)) - \log y^*| + b\gamma \int_0^\infty f(s) \int_{t-s}^t |y(u) - y^*| \mathrm{d}u \mathrm{d}s + c \int_0^\infty g(s) \int_{t-s}^t |U(x(u)) - U(x^*)| \mathrm{d}u \mathrm{d}s.$$

Clearly, $V(x^*, y^*) = 0$ and

$$V(x(t), y(t)) \geq |x(t) - x^*| + |\log (y(t)) - \log y^*| > 0.$$

The upper Dini derivative of V along the solutions of (2.81) using (2.114) is given by,

$$\begin{aligned} D^+V \leq & -D|x(t) - x^*| - aU(x(t))|y(t) - y^*| - ay^*|U(x(t) - U(x^*)| \\ & + b\gamma \int_0^\infty f(s)|y(t-s) - y^*|\mathrm{d}s \\ & + c \int_0^\infty g(s)|U(x(t-s) - U(x^*)|\mathrm{d}s \\ & + b\gamma|y(t) - y^*| - b\gamma \int_0^\infty f(s)|y(t-s) - y^*|\mathrm{d}s \\ & + c|U(x(t)) - U(x^*)| - c \int_0^\infty g(s)|U(x(t-s) - U(x^*)|\mathrm{d}s, \\ \leq & -D|x(t) - x^*| - aU(x(t))|y(t) - y^*| - ay^*|U(x(t)) - U(x^*)| \\ & + b\gamma|y(t) - y^*| + c|(Ux(t)) - U(x^*)| \\ = & -D|x(t) - x^*| + (c - ay^*)|U(x) - U(x^*)| \\ & - (aU(x) - b\gamma)|y(t) - y^*|. \end{aligned}$$

If $c \leq ay^*$, then the condition $\min_{x \geq x^*}\{aU(x) - b\gamma\} > 0$ is alone sufficient to ensure the negative definiteness of D^+V. Hence, we assume that $c > ay^*$. Then we have,

$$\begin{aligned} D^+V \leq & -D|x(t) - x^*| + (c - ay^*)|U(x) - U(x^*)| \\ & -(aU(x) - b\gamma)|y(t) - y^*| \\ < & -(D + aky^* - ck)|x(t) - x^*| - \Delta|y(t) - y^*| \quad < 0, \end{aligned}$$

invoking the hypotheses and using (A_2). Thus,

$$D^+V < -(D + aky^* - ck)|x(t) - x^*| - \frac{\Delta}{k_1}|\log y(t) - \log y^*| \quad < 0, \quad (2.115)$$

where $k_1 > 0$ is such that $|\log y(t) - \log y^*| \leq k_1|y(t) - y^*|$.

Now integrating (2.115) with respect to t from 0 to t, we get

$$V(t) + (D - ck + ay^*k)\int_0^t |x(s) - x^*|\mathrm{d}s + \frac{\Delta}{k_1}\int_0^t |\log\, y(s) - \log\, y^*|\mathrm{d}s \le V(0).$$

Therefore, $V(t) \equiv V(x(t), y(t))$ is bounded on $[0, \infty)$ and since $x(t), y(t)$ are bounded on $[0, \infty)$, $|x(t) - x^*|$ and $|\log\, y(t) - \log\, y^*|$ are bounded on $[0, \infty)$ and these imply the boundedness of their derivatives on $[0, \infty)$.

Now the conclusion follows from Theorem B.3 (Appendix B) with $G(z) = z$ and letting $z = |x - x^*| + |\log\, y - \log\, y^*|$. □

We now rewrite (2.114) as

$$\begin{aligned} x'(t) &= -D(x(t) - x^*) - aU(x^*))(y(t) - y^*) - ay(t)(U(x(t)) - U(x^*)) \\ &\quad + b\gamma \int_0^\infty f(s)(y(t-s) - y^*)\mathrm{d}s \\ y'(t) &= cy(t)\int_0^\infty g(s)(U(x(t-s)) - U(x^*))\mathrm{d}s. \end{aligned}$$

We state and prove our next result.

Theorem 2.34 *Assume that the uptake function $U(x)$ satisfies (A_1) and (A_2) and the delay kernels satisfy (2.83) and (2.84). The equilibrium solution (x^*, y^*) of (2.81) is globally asymptotically stable provided,*

$$D - ck > 0 \quad \textit{and} \quad aU(x^*) - b\gamma > 0.$$

Proof We again consider the functional,

$$\begin{aligned} V(t) \equiv V(x(t), y(t)) &= |x(t) - x^*| + |\log\,(y(t)) - \log\, y^*| \\ &\quad + b\gamma \int_0^\infty f(s)\int_{t-s}^t |y(u) - y^*|\mathrm{d}u\mathrm{d}s \\ &\quad + c\int_0^\infty g(s)\int_{t-s}^t |U(x(u)) - U(x^*)|\mathrm{d}u\mathrm{d}s. \end{aligned}$$

Then the upper right derivative of V along the solutions of (2.81), as in Theorem 2.33, using the earlier system, becomes after some simplifications,

$$\begin{aligned} D^+V &\le -D|x(t) - x^*| - ay|U(x(t)) - U(x^*)| - aU(x^*)|y(t) - y^*| \\ &\quad + c|U(x(t)) - U(x^*)| + b\gamma|y(t) - y^*| \\ &\le -(D - ck)|x(t) - x^*| - (aU(x^*) - b\gamma)|y(t) - y^*| \\ &< 0, \end{aligned}$$

by hypotheses.

The rest of the argument is similar to that of Theorem 2.33, and hence omitted. □

Note that the condition $aU(x^*) > b\gamma$ is necessary for the existence of a positive equilibrium.

We can observe that Theorem 2.33 is a stronger result (in terms of parametric conditions) than Theorem 2.34 in case of monotone increasing uptake functions and for other uptake functions (e.g., bell shaped) so long as $aU(x) \geq b\gamma$, other conditions being same. Theorem 2.34 comes into play when $aU(x) < b\gamma$ for $x > x^*$.

In the next result we relax the condition (2.84) on the delay kernels. But we observe that this results in restricting the parameters of the system more.

Theorem 2.35 *Assume that the uptake function satisfies* (A_1) *and* (A_2) *and the delay kernels satisfy* (2.83). *The positive equilibrium* (x^*, y^*) *of* (2.81) *is globally asymptotically stable provided,*

$$b\gamma + ck < \beta \equiv \min\{D - aky^*, \min_{x \geq x^*}\{aU(x)\}\}. \tag{2.116}$$

Proof We consider the following functional

$$V(t) \equiv V(x(t), y(t)) = |x(t) - x^*| + |\log y(t) - \log y^*|.$$

Clearly, $V(x^*, y^*) = 0$ and $V(t) \geq 0$.

The upper Dini derivative of V along the solutions of (2.81), using (2.114) is given by,

$$\begin{aligned} D^+V &\leq -D|x(t) - x^*| - aU(x(t))|y(t) - y^*| - ay^*|U(x(t)) - U(x^*)| \\ &\quad + b\gamma \int_0^\infty f(s)|y(t-s) - y^*| \\ &\quad + c\int_0^\infty g(s)|U(x(t-s)) - U(x^*)|\mathrm{d}s \\ &\leq -(D - aky^*)|x(t) - x^*| + ck\int_0^\infty g(s)|x(t-s) - x^*|\mathrm{d}s \\ &\quad - aU(x(t))|y(t) - y^*| + b\gamma\int_0^\infty f(s)|y(t-s) - y^*|\mathrm{d}s \\ &\leq -(D - aky^*)|x(t) - x^*| + ck\int_0^\infty g(s)|x(t-s) - x^*|\mathrm{d}s \\ &\quad - aU(x(t))|\log y(t) - \log y^*| + b\gamma\int_0^\infty f(s)|\log y(t) - \log y^*|\mathrm{d}s \\ &\leq -\beta V(t) + ck\int_0^\infty g(s)V(t-s)\mathrm{d}s \\ &\quad + b\gamma\int_0^\infty f(s)V(t-s)\mathrm{d}s. \end{aligned} \tag{2.117}$$

Now we prove that $V(t)$ is bounded. For $-\infty < t \leq 0$, we have

$$V(t) = |x(t) - x^*| + |\log\left[\frac{y(t)}{y^*}\right]| = |\phi_1(t) - x^*| + |\log\left[\frac{\phi_2(t)}{y^*}\right]|$$
$$= \sup_{-\infty<t\leq 0}\left\{|\phi_1(t) - x^*| + |log\left[\frac{\phi_2(t)}{y^*}\right]|\right\} = M \text{ (say)}.$$

We claim that $V(t) \leq M$ for all $t > 0$. If not, we can find a $t_1 > 0$ such that $V(t_1) = M$ and $V(t) < M$ for $-\infty < t < t_1$.

Then clearly, $D^+V(t_1) \geq 0$. But from (2.117),

$$D^+V(t_1) \leq -\beta M + b\gamma \int_0^\infty f(s)M\,\mathrm{d}s + ck\int_0^\infty g(s)M\,\mathrm{d}s$$
$$= -(\beta - b\gamma - ck)M < 0.$$

This contradiction proves that $V(t) \leq M$ for all $t > 0$.

Now, let $\limsup_{t\to\infty} V(t) = \bar{\sigma}$ and $\liminf_{t\to\infty} V(t) = \underline{\sigma}$. We shall prove that $\bar{\sigma} = 0$. Assume that $\bar{\sigma} > 0$ and choose $\epsilon > 0$ such that

$$\epsilon < \frac{1}{2}\left[\frac{\beta - b\gamma - ck}{\beta + (1+M)(b\gamma + ck)}\right]\bar{\sigma}.$$

Since, $\int_0^\infty f(s)\mathrm{d}s = 1$ and $\int_0^\infty g(s)\mathrm{d}s = 1$, there exists a $T > 0$ such that $\int_T^\infty f(s)\mathrm{d}s < \epsilon$ and $\int_T^\infty g(s)\mathrm{d}s < \epsilon$.

Corresponding to this $\epsilon > 0$, we can find $t_2 > 0$ and $t_3 > 0$ such that

$$V(t) \leq \bar{\sigma} + \epsilon \quad \text{for} \quad t > t_2$$

and

$$V(t-\tau) \leq \bar{\sigma} + \epsilon \quad \text{for} \quad t > t_3, \tau > 0.$$

We shall first prove that $\bar{\sigma} = \underline{\sigma}$.

Suppose $\bar{\sigma} > \underline{\sigma}$. Then $V(t)$ is nondecreasing on infinite number of intervals. Thus, we can find $t_5 > t_4 \geq \max\{t_2 + T, t_3 + T\}$ such that on (t_4, t_5), $V(t) > \bar{\sigma} - \epsilon$ and is nondecreasing.

Then from (2.117) for $t \in (t_4, t_5)$,

$$\begin{aligned} D^+V(t) &\leq -\beta V(t) + ck[\int_T^\infty g(s)M\,\mathrm{d}s + \int_0^T g(s)(\bar{\sigma}+\epsilon)\mathrm{d}s] \\ &\quad + b\gamma[\int_T^\infty f(s)M\,\mathrm{d}s + \int_0^T f(s)(\bar{\sigma}+\epsilon)\mathrm{d}s] \\ &\leq -\beta(\bar{\sigma}-\epsilon) + (b\gamma + ck)M\epsilon + (b\gamma+ck)(\bar{\sigma}+\epsilon) \\ &< -[\beta - (b\gamma + ck)]\bar{\sigma}/2 \\ &< 0, \end{aligned} \tag{2.118}$$

by the choice of $\epsilon > 0$.

This contradicts the assumption that $V(t)$ is nondecreasing on (t_4, t_5), proving that $\bar{\sigma} = \underline{\sigma}$. Since, $\bar{\sigma} = \underline{\sigma}$ there exists $t_6 = \max\{t_2, t_3\}$ such that for $t \geq t_6$, $\bar{\sigma} - \epsilon < V(t) < \bar{\sigma} + \epsilon$.

The mean value theorem suggests that there exists a $\xi \in [0, \infty)$ such that for $t \geq t_6$,

$$V(t) - V(t_6) = V'(\xi)(t - t_6).$$

Now from (2.118),

$$V(t) = V(t_6) + (t - t_6)V'(\xi) \leq V(t_6) - (\beta - b\gamma - ck)\frac{\bar{\sigma}}{2}(t - t_6).$$

The right hand side of this inequality approaches "$-\infty$" as $t \to \infty$, since $V(t_6) \leq M$ is finite. But by definition, $V(t) \geq 0$. This contradiction proves that the assumption $\bar{\sigma} > 0$ is wrong. Therefore, $\bar{\sigma} = 0$, which means that $-\epsilon < V(t) < \epsilon$ for $t \geq t_6$. Thus, in the limiting case, $V(t) \to 0$.

Thus, $\lim_{t\to\infty}[|x(t) - x^*| + |\log(y(t)/y^*)|] = 0$, which implies the global asymptotic stability of (x^*, y^*). Hence, the theorem. □

The procedure followed in establishing Theorem 2.30 may motivate us to try for a global stability result. But the road to global stability is much more difficult as compared to the one for local stability. The proof is not only quite lengthy, but involves number of calculations and adjustments also. We shall not go into the details of the proof for this reason. However, for the sake of an interested reader we shall provide the Lyapunov functionals used in establishing the following result.

Theorem 2.36 *Assume that the delay kernels in addition to* (2.83) *and* (2.84) *satisfy*

$$T_f{}^* = \frac{1}{\gamma + D}\int_0^\infty f(s)\Big(e^{[\gamma+D]s} - 1\Big)ds < \infty \quad \textit{and}$$
$$T_g{}^* = \frac{1}{c - \gamma - D}\int_0^\infty g(s)\Big(e^{[c-\gamma-D]s} - 1\Big)ds < \infty.$$

Further let

$$b\gamma c\Big(T_f{}^* + T_f + (c - \gamma - D)T_f T_g{}^*\Big) + c(aU(x^*) - b\gamma)e^{cT_g}(T_g + T_g{}^*) < 2a.$$

Then the positive equilibrium (x^*, y^*) *of* (2.81) *is globally asymptotically stable.*

Proof We employ the functional,

$$V(t) = V_1(t) + \frac{y^*}{c}\left(b\gamma\int_t^\infty f(s)ds + aU(x^*) - b\gamma\right)V_2(t).$$

Here

$$V_1(t) = \int_0^{x_1(t)} U_1(u)\mathrm{d}u + \frac{1}{2}b\gamma c \int_0^{\infty} f(s) \int_{t-s}^{t} \int_w^t P(u) \int_0^{\infty} g(v)\mathrm{d}v\mathrm{d}u\mathrm{d}w\mathrm{d}s + \frac{1}{2}b\gamma c T_f \int_0^{\infty} g(s) \int_{t-s}^{t} P(u+s){U_1}^2(x_1(u))\mathrm{d}u\mathrm{d}s,$$

in which

$$P(t) = y^* \mathrm{e}^{y_1(t)}$$

and

$$V_2(t) = \int_0^{z(t)} (\mathrm{e}^s - 1)\mathrm{d}s + \frac{1}{2}c^2 \mathrm{e}^{cT_g} \int_0^{\infty} g(s) \int_{t-s}^{t} \mathrm{e}^{y_1(v+s)} \int_v^t {U_1}^2(x_1(u))\mathrm{d}u\mathrm{d}v\mathrm{d}s,$$

where

$$z(t) = y_1(t) + c\int_0^{\infty} g(s) \int_{t-s}^{t} U_1(x_1(u))\mathrm{d}u\mathrm{d}s.$$

After evaluating V' along the solutions of (2.92), the proof is quite is similar to that of Theorem 2.30. For more details, one may refer to Theorems 2.10 and 2.15 of Sect. 2.4. □

Following examples compare Theorems 2.33 and 2.36, qualitatively.

Example 2.37 For the system (2.81) choose, $a = 14, c = 8, D = 2, \gamma = 4, b = 3/4, x_0 = 14$ and let $U(x) = x/4 + x$. Then $U(x^*) = (\gamma + D)/c = 3/4$ and therefore, $x^* = 12, y^* = 8/15$, and $k = 1/8$. Further let $f(s) = 4\mathrm{e}^{-4s}$ and $g(s) = \delta(s)$, the Dirac delta.

Then all the hypotheses of Theorem 2.33 are satisfied and hence, $(x^*, y^*) = (12, 8/15)$ is globally asymptotic stable by virtue of Theorem 2.33. Further since $T_f^* \to \infty$, Theorem 2.36 does not hold here.

Example 2.38 For system (2.81), let $a = 12, c = 10, D = 1, \gamma = 4, b = 1/8, x_0 = 4.5$, and $U(x) = x/(4 + x)$. Then $U(x^*) = 1/2$ and $x^* = 4, y^* = 1/11$ with $k = 1/8$.

Since $D + aky^* < ck$, Theorem 2.33 cannot be applied here.

Now let $f(s) = 10\mathrm{e}^{-10s} = g(s)$. Then $T_f = T_g = 1/10$ and $T_f^* = T_g^* = 0$. Then the condition on the parameters of (2.81) in Theorem 2.36 reduces to

$$bc\gamma T_f + c(aU(x^*) - b\gamma)\exp(cT_g)T_g < 2a$$

is clearly valid, and hence, (x^*, y^*) is globally asymptotically stable.

Thus, from the earlier two examples we can conclude that Theorem 2.33 is independent of Theorem 2.36.

The following examples illustrate the results in this section.

Example 2.39 Consider the following model

$$x'(t) = 8(x_0 - x(t)) - 22\, U(x(t))y(t) + \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s,$$
$$y'(t) = -10y(t) + 20y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s,$$

in which $U(x) = x/10 + x, b = 0.5, \gamma = 2, D = 8$, and $x_0 = 11$.

The equilibrium solutions are $x^* = 10$ and $y^* = 0.8$ with $U(x^*) = 1/2$, $k = 1/10$.

It is easy to see that all the hypotheses of Theorems 2.33 and 2.36 are satisfied, and hence, the equilibrium (10, 0.8) is globally asymptotically stable by virtue of these theorems.

Further, with $\beta = 6.22$, Theorem 2.35 also ensures the global asymptotic stability of (10,0.8).

Example 2.40 Consider the following model,

$$x'(t) = 2(x_0 - x(t)) - 20\, U(x(t))y(t) + (0.5)\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s$$
$$y'(t) = -3y(t) + 19y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s,$$

in which

$$U(x) = \begin{cases} \frac{x}{10+x^2}, & 0 \le x < 40 \\ \frac{4}{161}, & \text{otherwise} \end{cases}$$

Clearly $U(x)$ is the generalized Michaelis–Menten uptake function defined in (1.18) for the choice of $\tilde{\alpha} = 1, \tilde{\beta} = 2$, and $\omega = 10$.

Also in the earlier system, it is chosen that $b = 0.5, \gamma = 1$, and $D = 2$. Then the equilibrium solutions are $x^* = 3$, $y^* = 0.1505$, $U(x^*) = \frac{3}{19}$, $k = 1/10$ with $x_0 = 3.2$.

It is easy to check that all the hypotheses of Theorem 2.34 are satisfied here and hence, $(x^*, y^*) = (3, 0.1505)$ is globally asymptotically stable.

Since $aU(x) < b\gamma$ for $x \ge 40$, we cannot apply Theorem 2.33 here.

Example 2.41 Consider the system,

$$x'(t) = 3(x_0 - x(t)) - 18\, U(x(t))y(t) + \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s,$$
$$y'(t) = -5y(t) + 16y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s,$$

in which $U(x) = x/4 + x, b = 0.5, \gamma = 2, D = 3$, and $x_0 = 2.5$.

The equilibrium solutions are $x^* = 20/11$ and $y^* = 0.24766$ with $U(x^*) = 5/16$, $k = 1/4$. Clearly, all the hypotheses of Theorem 2.33 are satisfied. Hence, (x^*, y^*) is globally asymptotically stable by virtue of Theorem 2.33.

Observe that $D - ck < 0$, and hence, Theorem 2.34 is not applicable here.

From Examples 2.40 and 2.41, it follows that Theorems 2.33 and 2.34 are independent of each other.

The following example illustrates a case where none of the Theorems 2.33–2.35 is applicable.

Example 2.42 Consider the model,

$$x'(t) = 1.7(x_0 - x(t)) - 20\, U(x(t))y(t) + (0.78)\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s$$

$$y'(t) = -3y(t) + 19y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s,$$

in which

$$U(x) = \begin{cases} \frac{x}{10+x^2}, & 0 \le x < 30 \\ \frac{3}{91}, & \text{otherwise} \end{cases}$$

Here we have chosen that $b = 0.6$, $\gamma = 1.3$, $D = 1.7$, and $x_0 = 3.2$.

Then the equilibrium solutions are $x^* = 3$, $y^* = 0.14298$, $U(x^*) = \frac{3}{19}$, $k = 1/10$.

It is easy to check that since, $aU(x) < b\gamma$ for $x \ge 25.25$, Theorem 2.33 and Theorem 2.35 are not applicable here. At the same time, as $D - ck < 0$, Theorem 2.34 is also not applicable.

2.6 Discussion

We have observed throughout that in the absence of any delays the existence of a positive equilibrium implies its stability. In the presence of time delay in material recycling, may it be discrete or distributed, the positive equilibrium continues to be locally stable, independent of time lag. It is also shown numerically in Beretta et al. [7] that the stability region of the positive equilibrium of (2.40) is large but trajectories approach the equilibrium through oscillations when time lags are considered. In case of instantaneous material recycling and no delay in growth response, arguments indicate that the recycling has a stabilizing effect on the system (Ruan [79]). Bischi [13] considered the effect of the delay in material recycling on the resilience, that is, the rate at which the system returns to a stable state following a perturbation. It has been shown that when the system is characterized by oscillatory behavior an increase in time delay can have a stabilizing effect.

As a final remark we conclude from all the local and global results that when the time delays in material recycling and growth response are sufficiently small, the system remains stable.

2.7 Notes and Remarks

From the earlier discussion it is evident that the time delay in growth response of the consumer species is the key so far as the instability due to time delays is concerned. It is observed in Beretta and Takeuchi [12] that for a system with smaller average time delay in growth T_g, the parameter region of global stability of positive equilibrium is wider than the one with larger T_g.

In Theorems 2.33 and 2.35, we require the condition $aU(x) > b\gamma$ for $x \geq x^*$ on the uptake function, which means that there is a threshold level of consumption (supply) for the consumer species to survive. Clearly, these theorems do not provide any clue about the stability of the positive equilibrium when $aU(x) < b\gamma$ for all $x \geq \overline{x}$ for some $\overline{x} > x^*$ (see Example 2.42). There are no supporting terms in the model (2.81) that avert this situation or explain the stability of the system, in such a case. Moreover, one may observe that (2.81) is not complete in its form to explain the limited nutrient–consumer dynamics of a natural system like a lake and there may still be many biological (natural) factors that can influence the growth of the species.

These two observations mean that system (2.81) has a tendency of being disturbed by variations in nutrient supply/consumption and time delays. This is the starting point of our discussion in the following chapter where we explore further the instability characteristics of models of this section.

Results of this chapter are the outcomes of efforts of many researchers. Results of Sect. 2.3 are contributions of Freedman, et al. [35, 36] at the early stages of the development of the time models. The lone global stability result of this section and the estimation on bounds (Theorems 2.2 and 2.3) are taken from the work of Beretta and Kuang [9]. Models (2.27) and (2.28) are the choice of Ellermeyer [30], Hsu [54], Wlokowicz et al. [106], and these models behave like a simple chemostat that follows the principle of competitive exclusion. Readers interested in these models may refer the aforementioned articles for further exploration.

Contents of Sect. 2.4 are mostly taken from the articles by He and Ruan [50], Ruan [79], Ruan and He [80], and Beretta and Takeuchi [10, 11]. Some of the delay-dependent stability results of this section are provided by Sree Hari Rao and Raja Sekhara Rao [92]. The study in Sect. 2.5 is the culmination of the efforts of Beretta and Bischi [10], He and Ruan [50], Ruan [79], Ruan and He [80], and Beretta and Takeuchi [10, 12], Kolmanovskii et al. [61], Freedman and Xu [39], and Sree Hari Rao and Raja Sekhara Rao [86–90, 92]. Some interesting results are available in Owaidy and Ismail [29], He, Ruan and Xia [51], Sanling and Maoan [81], Sanling, Maoan and Zhein [82], and Sanling, Song and Maoan [83]. Lemma 2.23 is a modified version to functional differential equations of a result by Norris and Driver [71] established for ordinary differential equations. The lemma can be applied to all models of Sect. 2.2 to establish the existence of unique solutions. This obviously provides conditions weaker than Lipschitz condition. Thus, our statements in Sect. 1.7 of Chap. 1 are applicable here also.

Finally, we have used the words "standard arguments" to imply the application of Theorem C.10 or Theorem C.11 of Appendix C as the case may be, in order to obtain local/global stability results.

2.8 Exercises

1. Rewrite Theorem 2.3 for the system (2.7) (that is the one before scaling) to understand the influence of the parameters.
2. Establish that system (2.29) is dissipative and bounded.
3. Obtain conditions for the uniform persistence of (2.29).
4. Perform a bifurcation analysis for (2.29) as in Sect. 2.3 with the delay τ as a bifurcation parameter.
5. Derive the special cases of Theorems 2.4 and 2.5 for system (2.7). Can we let $\gamma = 0$ in the parametric conditions of Theorems 2.4 and 2.5?
6. Examples 2.18 and 2.19 uphold Theorem 2.17 over Theorem 2.15 in terms of the lengths of the delay parameters and conditions on the delay kernel. Give an example where Theorem 2.17 fails and Theorem 2.15 holds ? (see Sect. 2.5).
7. Obtain local stability conditions for the systems (2.29) and (2.32).
8. Study the occurrence of bifurcation phenomenon for model (2.32).
9. Can one conclude that the system (2.32) is unstable for large delays in recycling? Construct an example.
10. The condition in Theorem 2.9 for local asymptotic stability does not depend on the delay kernel of (2.40). What does it mean?
11. Explain how material recycling is going to contribute to the stability of the system (2.40)?
12. Perform a bifurcation analysis of system (2.67). How is it different from those for systems (2.32) and (2.40)? Explain what conclusions can be drawn from this study?
13. Establish local stability results for system (2.67).
14. Theorems 2.15 and 2.17 are delay dependent. Obtain global asymptotic stability results that are delay independent.
15. Utilizing Lemma 2.23 establish the existence of a unique solution to models (2.7), (2.29), (2.32), (2.40), and (2.67).
16. Consider the system with instantaneous material recycling and no delay in growth response,

$$
\begin{aligned}
x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) + b\gamma y(t), \\
y'(t) &= -(\gamma + D)y(t) + cU(x(t)y(t).
\end{aligned}
$$

This model may be seen as a special case of every model we have discussed in this chapter by letting $\tau = 0$ in case of a discrete delay and $f(s) = g(s) = \delta(s)$ (Dirac delta) in the case the delays are continuous.

Apply methods of Chap. 1 to establish (a) existence and uniqueness of solutions, (b) boundedness and positivity, and (c) uniform persistence (see Definition C.13, Appendix C) and modify Theorems 2.6 and 1.12 to establish (d) asymptotic stability of positive equilibrium.

Can the stability of this system be derived from the results of Sect. 2.4 and 2.5? The answer is yes. Deduce all possible results. Can we say that "in the absence of time delays, the very existence of a positive equilibrium itself implies its stability?" Do the earlier results support the statement of Sect. 2.6 that material recycling has a stabilizing effect? This question should be studied in the light of case 2 of Theorem 1.8 that warns against too much of nutrient input, which may lead to washout of species y.

17. Construct a Lyapunov functional as in Theorem 2.15 to prove Theorem 2.4 directly.
18. Modify the Lyapunov functional in Theorem 2.17 appropriately to prove Theorem 2.5.

Chapter 3
Instability Tendencies

3.1 Introduction

The main theme of this chapter is to study the instability characteristics of the model equations induced by time delays. We have established in Chap. 1 that the basic model (1.5) is structurally stable. Also when the average time delays are sufficiently small, results are obtained for the boundedness of solutions, and local and global stability of equilibria of the models of Chap. 2 by restricting the other parameters of these systems. But we have noticed in Sect. 2.3 that in the presence of a time delay in growth response, the system tends to lose its stability leading to Hopf bifurcation. We have not discussed this aspect in case of other models such as (2.29).

Though four independent sets of sufficient conditions (Theorems 2.33 – 2.36) for the global asymptotic stability of the positive equilibrium solution of (2.81) are available, none of them could explain the situation in Example 2.42. Further the independence of these results asserts that they represent different portions of the stability region of system (2.81), which may be large. But Example 2.42, however, escapes these portions. Does this represent a vulnerability of system represented by (2.81)? May be true. Especially, when our model equations represent a natural system it is prone to external disturbances that tend to destabilize the system. Example 2.42 provides one such situation where a low nutrient consumption affects the stability. One may notice that the behavior of a food-consumer system depends chiefly on

- Supply of nutrient and its supply rate;
- Time delays in growth process and material recycling.

The effect of time delay on growth response has already been discussed for the system represented by (2.7). As a continuation of this, the study in the present chapter is devoted to this aspect of instability characteristics that are introduced by the changes in nutrient supply, its supply rate, and the presence of time delays on biological systems represented by the models of the earlier chapter. In this direction we first take up model (2.67) for a discussion.

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3.2 Instability Tendencies

Consider the model (2.67) given by

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) \\ &\quad + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s, \\ y'(t) &= -(\gamma + D)y(t) + cU(x(t-\tau))y(t), \end{aligned} \tag{3.1}$$

in which $\tau > 0$ is a fixed delay parameter. We assume that $f(s) = \alpha \mathrm{e}^{-\alpha s}$, $\alpha > 0$, and transform the system (3.1) by linear chain trick. For this we let,

$$z(t) = \int_{-\infty}^{t} \alpha \mathrm{e}^{-\alpha(t-s)} y(s)\mathrm{d}s.$$

This transforms system (3.1) into

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t) + b\gamma z(t), \\ y'(t) &= -(\gamma + D)y(t) + cU(x(t-\tau))y(t), \\ z'(t) &= \alpha y(t) - \alpha z(t). \end{aligned} \tag{3.2}$$

The equilibria corresponding to (3.2) are $E_0(x_0, 0, 0)$ and $E^*(x^*, y^*, z^*)$ where $z^* = y^*$ and x^*, y^* are given by (2.8) of Chap. 2. Linearizing (3.2) around the positive equilibrium (x^*, y^*, z^*), we have

$$\begin{aligned} x_1'(t) &= -(D + ay^*U'(x^*))x_1(t), \\ &\quad - aU(x^*)y_1(t) + b\gamma z_1(t), \\ y_1'(t) &= cy^*U'(x^*)x_1(t-\tau), \\ z_1'(t) &= \alpha y_1(t) - \alpha z_1(t), \end{aligned} \tag{3.3}$$

where $x_1(t) = x(t) - x^*$, $y_1(t) = y(t) - y^*$, and $z_1(t) = z(t) - z^*$.

The characteristic equation corresponding to (3.3) is

$$\lambda^3 + \rho\lambda^2 + \beta\lambda = \delta e^{-\lambda\tau} + \eta\lambda \mathrm{e}^{-\lambda\tau}, \tag{3.4}$$

in which

$$\rho = \alpha + D + ay^*U'(x^*) > 0,\ \beta = \alpha(D + ay^*U'(x^*)) > 0,$$

$$\delta = -\alpha cy^*U'(x^*)[aU(x^*) - b\gamma] < 0,\ \eta = -acy^*U(x^*)U'(x^*) < 0.$$

Now let $\lambda = \mu + i\nu$ where $\lambda = \lambda(\tau)$, $\mu = \mu(\tau)$, and $\nu = \nu(\tau)$. Using this in (3.4)and rearranging, we get

$$\mu^3 - 3\mu\nu^2 + \rho(\mu^2 - \nu^2) + \beta\mu = \Big[(\delta + \eta\mu)\cos\tau\nu + \eta\nu\sin\tau\nu\Big]e^{-\tau\mu},$$

$$-\nu^3 + 3\mu^2\nu + 2\rho\mu\nu + \beta\nu = \Big[\eta\nu\cos\tau\nu - (\delta + \eta\mu)\sin\tau\nu\Big]e^{-\tau\mu}. \quad (3.5)$$

For a change of stability, we require a pure imaginary root of (3.5), $\lambda = i\nu$. Thus, letting $\mu(\hat{\tau}) = 0$ for some $\tau = \hat{\tau}$ in (3.5), we have

$$-\rho\hat{\nu}^2 = \delta\cos\hat{\tau}\hat{\nu} + \eta\hat{\nu}\sin\hat{\tau}\hat{\nu},$$

$$-\hat{\nu}^3 + \beta\hat{\nu} = \eta\hat{\nu}\cos\hat{\tau}\hat{\nu} - \delta\sin\hat{\tau}\hat{\nu}, \quad (3.6)$$

where $\hat{\nu} = \nu(\hat{\tau})$. Squaring and adding equations (3.6), we have

$$\phi(\hat{\nu}^2) \equiv \hat{\nu}^6 + (\rho^2 - 2\beta)\hat{\nu}^4 + (\beta^2 - \eta^2)\hat{\nu}^2 - \delta^2 = 0. \quad (3.7)$$

Observe that $\phi(0) < 0$ and $\phi(\widehat{\nu^2}) > 0$ for sufficiently large values of $\hat{\nu}$. Therefore, the cubic equation (3.7) in ν^2 has at least one real root $\hat{\nu}^2$.

From (3.6), we have corresponding to this $\hat{\nu}$,

$$\hat{\tau_n} = \frac{1}{\hat{\nu}}\arcsin\left(\frac{\hat{\nu}^3(\delta - \rho\eta) - \hat{\nu}\beta\delta}{\eta^2\hat{\nu}^2 + \delta^2}\right) + \frac{2n\pi}{\hat{\nu}}, \quad n = 0, 1, 2, ... \quad (3.8)$$

Now differentiating both the equations of (3.5) with respect to τ and letting $\tau = \hat{\tau}$, $\nu = \hat{\nu}$, and $\mu = 0$ and solving for $d\mu/d\tau$ and $d\nu/d\tau$, we get

$$\frac{d\mu(\hat{\tau})}{d\tau} = \frac{AC - BD}{A^2 + B^2}, \quad (3.9)$$

in which

$$A = 3\nu^2 - \beta - \eta\hat{\tau}\hat{\nu}\sin\hat{\tau}\hat{\nu} + (\eta - \delta\hat{\tau})\cos\hat{\tau}\hat{\nu},$$
$$B = 2\rho\hat{\nu} + (\eta - \delta\hat{\tau})\sin\hat{\tau}\hat{\nu} + \eta\hat{\tau}\hat{\nu}\cos\hat{\tau}\hat{\nu},$$
$$C = \delta\hat{\tau}\sin\hat{\tau}\hat{\nu} - \eta\nu^2\cos\hat{\tau}\hat{\nu},$$

and

$$D = \eta\nu^2\sin\hat{\tau}\hat{\nu} + \delta\hat{\tau}\cos\hat{\tau}\hat{\nu}.$$

Using (3.6), we have

$$AC - BD = \hat{\nu}^2\Big[3\hat{\nu}^4 + 2(\rho^2 - 2\beta)\hat{\nu}^2 + (\beta^2 - \eta^2)\Big] = \hat{\nu}^2\frac{d\phi}{d\hat{\nu}^2}.$$

Thus, if $\hat{\nu}_0$ is the first root of (3.7), we have

$$\frac{\mathrm{d}\mu(\hat{\tau}_0)}{\mathrm{d}\tau} = \frac{\hat{\nu}_0{}^2}{A^2 + B^2} \frac{\mathrm{d}\phi}{\mathrm{d}\hat{\nu}^2}(\hat{\nu}_0{}^2) > 0,$$

where

$$\hat{\tau}_0 = \frac{1}{\hat{\nu}_0} \arcsin \frac{\hat{\nu}_0{}^3(\delta - \rho\eta) - \hat{\nu}_0\beta\delta}{\eta^2\hat{\nu}_0{}^2 + \delta^2}.$$

The following result is a conclusion of the earlier discussion.

Theorem 3.1 *Hopf-bifurcation from* (x^*, y^*) *of* (3.1) *occurs for* τ *near* $\hat{\tau}_0$.

The following example illustrates this result.

Example 3.2 Consider the system

$$\begin{aligned} x'(t) &= 0.1(20 - x) - 10\frac{x}{6 + x}y \\ &\quad + (3.2)\int_{-\infty}^{t} (0.2)\mathrm{e}^{-0.2(t-s)}y(s)\mathrm{d}s, \\ y'(t) &= -(4.1)y + 9\frac{x(t - \tau)}{6 + x(t - \tau)}y. \end{aligned}$$

For $\tau = 0$ it is shown in Beretta et al. [8] that the system is globally stable. We can use some of the results of Sect. 2.4, Chap. 2 to verify this. However, for $\tau > 0$, Theorem 3.1 shows that at $\hat{\tau}_0 = 0.39$ the system undergoes a Hopf-bifurcation and hence, loses its stability. Further a family of small-amplitude periodic solutions bifurcate from it as τ passes through $\hat{\tau}_0 = 0.39$.

Now consider the following model

$$\begin{aligned} x'(t) &= R - aU(x(t))y(t) + b\gamma \int_{-\infty}^{t} f(t - s)y(s)\mathrm{d}s, \\ y'(t) &= -\gamma y(t) + cy(t) \int_{-\infty}^{t} g(t - s)U(x(s))\mathrm{d}s, \end{aligned} \tag{3.10}$$

which is a special case of (2.81). The model represents the growth in a lake when the washout is negligible. Thus, the corresponding terms $-Dx$ and $-Dy$ are of no significance now in (2.81). Further the new parameter $R > 0$ in place of Dx_0 represents the nutrient available in the system at any time.

We assume that the uptake function is a monotone increasing function. Then a nontrivial equilibrium solution of (3.10) is given by

$$(x^*, y^*) = (U^{-1}(\frac{\gamma}{c}), \frac{R}{\gamma(a/c - b)}).$$

Clearly, (x^*, y^*) is positive provided $\gamma < c$ and $a > bc$ hold.

Linearizing the system (3.10) around the positive equilibrium and with the change of variables $x_1(t) = x(t) - x^*$, $y_1(t) = y(t) - y^*$, and approximating $U(x) = U(x^*) + U'(x^*)x_1$ we get

$$\begin{aligned} x_1{}'(t) &= -aU'(x^*)y^*x_1 - \frac{a\gamma}{c}y_1 \\ &\quad + b\gamma \int_{-\infty}^{t} f(t-s)y_1(s)\mathrm{d}s, \\ y_1{}'(t) &= cy^*U'(x^*)\int_{-\infty}^{t} g(t-s)x_1(s)\mathrm{d}s. \end{aligned} \tag{3.11}$$

The characteristic equation corresponding to (3.11) is

$$\lambda^2 + aU'(x^*)y^*\lambda + cU'(x^*)y^*G(\lambda)\Big[\frac{a\gamma}{c} - b\gamma F(\lambda)\Big], \tag{3.12}$$

where $F(\lambda) = \int_0^\infty f(s)\mathrm{e}^{-\lambda s}\mathrm{d}s$ and $G(\lambda) = \int_0^\infty g(s)\mathrm{e}^{-\lambda s}\mathrm{d}s$.

Let

$$u = aU'(x^*)y^* = \frac{a}{N}U'(x^*)R,$$

where

$$N = \frac{a\gamma}{c} - b\gamma > 0.$$

Then the aforementioned characteristic equation becomes

$$\lambda^2 + u\lambda + u\gamma G(\lambda) - \frac{b\gamma c}{a}uG(\lambda)F(\lambda) = 0. \tag{3.13}$$

Now using

$$f(s) = \alpha\mathrm{e}^{-\alpha s}, \quad g(s) = \beta\mathrm{e}^{-\beta s}, \quad \alpha > 0,\ \beta > 0, \quad s \in [0,\infty)$$

we have

$$F(\lambda) = \frac{\alpha}{\lambda + \alpha},\ G(\lambda) = \frac{\beta}{\lambda + \beta}.$$

Using these in (3.13) and rearranging, we get

$$P(\lambda) \equiv \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0 \tag{3.14}$$

with $a_1 = \alpha + \beta + u$, $a_2 = \alpha\beta + (\alpha + \beta)u$, $a_3 = \beta(\alpha + \gamma)u$, and

$$a_4 = \alpha\beta\Big(1 - \frac{b\gamma}{a}\Big)u.$$

Consider the Routh–Hurwitz polynomial (Theorem C.5, Appendix C)

$$\Phi(R) \equiv a_1a_2a_3 - a_3{}^2 - a_4a_1{}^2.$$

Then the occurrence of Hopf bifurcation at $u = u_0$ is ensured by the following assumptions.

The spectrum $\sigma(u) = \{\lambda / P(\lambda) = 0\}$ of the characteristic equation is such that

- there exists $u_0 \in (0, \infty)$ at which a pair of complex simple eigen values $\lambda_1(u_0) = \bar{\lambda}_2(u_0) \in \sigma(u)$ such that $Re\lambda(u_0) = 0$, $Im\lambda(u_0) = w_0 > 0$ and $\left(\frac{\mathrm{d}}{\mathrm{d}u}(Re\lambda(u))\right)_{u_0} \neq 0$;
- all other elements of $\lambda(u)$ have negative real parts.

These criteria may be recorded here.

Theorem 3.3 *A Hopf bifurcation of the equilibrium* (x^*, y^*) *of* (3.10) *occurs at* $u = u_0 \in (0, \infty)$ *if and only if*

$$\Phi(u_0) = 0, \ \left(\frac{\mathrm{d}\Phi}{\mathrm{d}u}\right)_{u_0} \neq 0.$$

Now define,

$$A = \alpha + \beta + \frac{cN\alpha}{a(\alpha + \gamma)}, \quad B = (\alpha + \beta)^2 - \frac{2cN\alpha(\alpha + \beta)}{a(\alpha + \gamma)}$$

and

$$C = (\alpha + \beta)\left(\alpha\beta - \frac{cN\alpha(\alpha + \beta)}{a(\alpha + \gamma)}\right). \tag{3.15}$$

Then

$$\Phi(u) = \beta(\alpha + \gamma)uh(u), \tag{3.16}$$

in which

$$h(u) = Au^2 + Bu + C.$$

Then (3.16) implies that

$$\text{sgn}\ \Phi(u) = \text{sgn}\ h(u) \tag{3.17}$$

and if $h(u_0) = 0$ then

$$\text{sgn}\ \frac{\mathrm{d}\Phi}{\mathrm{d}u}(u_0) = \text{sgn}\ h'(u_0). \tag{3.18}$$

As the coefficients A, B, C are independent of the uptake function U, we discuss the influence of the delay parameters on the sign of $h(u)$. Also notice that $A > 0$. Then we can observe that $\alpha\beta$-plane is divided into three regions depending on the signs of B, C, and $B^2 - 4AC$. In these regions $h(u)$ will have a unique, two or no positive roots.

From Theorem 3.3 and (3.17), if u_0 is a zero of $h(u)$ then using the definition of u, we have

$$R_0 = \frac{N}{aU'(x^*)}u_0,$$

is a bifurcation value of the parameter R, the nutrient supply. We now have

Theorem 3.4 *The following conclusions hold:*

1. *If $C < 0$ then a unique Hopf bifurcation value $R_0 \in R_+$ exists such that for all $R \in (R_0, \infty)$, (x^*, y^*) is locally asymptotically stable.*
2. *In case $C > 0$, $B < 0$, and $B^2 - 4AC > 0$, two values $R_{01}, R_{02} \in R_+$ exist at each of which a Hopf bifurcation occurs. The equilibrium (x^*, y^*) is locally asymptotically stable for all $R \in R_+ - [R_{01}, R_{02}]$.*
3. *In case $C > 0$, $B > 0$ or $C > 0$, $B < 0$, and $B^2 - 4AC < 0$, (x^*, y^*) is locally asymptotically stable for all $R \in R_+$.*

Notice that in the second case $\beta > \alpha$. This explains the case where the recycling is a slower process than the growth process.

Exploring further the following conclusions are arrived at by Beretta et al. [7] and Beretta and Bischi [6].

Conclusions

1. If the delay in the growth process is neglected, no Hopf bifurcation occurs.
2. A time delay in material recycling gives rise to the possibility of one or two Hopf bifurcations as given in Theorem 3.4.
3. In the absence of a delay in recycling, there is at the most one Hopf bifurcation for $\beta < \bar{\beta} = [\gamma(a - bc)]/c$ and no bifurcation for $\beta > \bar{\beta}$.
4. In case of two Hopf bifurcations R_{01}, R_{02}, we have stability for $R \in R_+ - [R_{01}, R_{02}]$. R_{02} is almost as the one without recycling and R_{01} is due to recycling with delay.
5. Computer simulations show that the bifurcating closed orbits are asymptotically stable near the bifurcation points. As R varies through R_{01} to R_{02}, there exists a family of periodic orbits with amplitude increasing, reaching a maximum and then decreasing. Further, as R increases the biotic species y undergoes a transition from a low stable equilibrium state to a high stable equilibrium through stable oscillations.

To conclude, when the average time lag in the growth process is bigger than the time of decay of the species $(1/\gamma)$ and the time lag due to nutrient recycling is sufficiently large, two Hopf bifurcations occur as nutrient supply R varies. The equilibrium is stable for low values and high values of R and is unstable for intermediate values of R with periodic orbits around it. The time delay in growth process destabilizes the equilibrium for low values of R, while the presence of time delay in recycling stabilizes it for low values of R, giving the possibility of having a lower bifurcation value.

3.3 Instability Characteristics of Model (2.81)

Motivated by the above study, we shall now make a detailed analysis of model equations (2.81) with regard to its instability characteristics. System (2.81) is

$$\begin{aligned} x'(t) &= D(x_0 - x(t)) - aU(x(t))y(t) \\ &\quad + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s, \\ y'(t) &= -(\gamma + D)y(t) + cy(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s. \end{aligned} \tag{3.19}$$

We may expect system (3.19) to fall into one of the following possible situations of instability.

1. System (3.19) may have an unbounded solution and all other solutions approach this unbounded solution asymptotically.
2. Solutions may approach, as $t \to \infty$, the axial equilibrium $(x_0, 0)$ of (3.19) (whose existence is always guaranteed) driving the species y to extinction.
3. System (3.19) may not have a positive equilibrium lying in the interior of the first quadrant. In case system (3.19) admits a positive equilibrium it may be unstable.

We take up each of these possibilities in that order. We shall first obtain sufficient conditions for an unlimited (unbounded) growth of populations. To make matters simple and to obtain explicit conditions we let the delay kernels to be

$$f(s) = \mathrm{e}^{-ps}, \quad g(s) = \mathrm{e}^{-qs}, \quad p > 0, \;\; q > 0, \;\; s \in [0, \infty). \tag{3.20}$$

The following result provides conditions for the existence of a solution of the type
$x(t) \equiv x_0 + Ae^{\alpha t}, \;\; y(t) \equiv Be^{\beta t}, \alpha, \beta \in \mathbf{R}$ to system (3.19) where $A, \;\; B$ are nonnegative real numbers.

Theorem 3.5 *Let the delay kernels be as defined in* (3.20). *Then we have the following:*

Case 1 Let $U(x) = \frac{x}{m+x}$. Then system (3.19) has a solution of the type $(x_0 + A\mathrm{e}^{\alpha t}, B\mathrm{e}^{-\alpha t})$ provided the average delays satisfy either of the conditions,

$$\begin{aligned} &(a) \quad p < \gamma + D + \frac{ABb\gamma}{(\gamma + 2D)x_0^2}, \quad \gamma + D - p < \frac{c}{q} < \gamma + 2D, \\ &(b) \quad p > \gamma + D + \frac{ABb\gamma}{(\gamma + 2D)x_0^2}, \quad \frac{c}{q} > \gamma + 2D. \end{aligned} \tag{3.21}$$

Case 2 System (3.19) admits a solution of the type $(x_0 + Ae^{\alpha t}, Be^{\alpha t})$ provided

$$p < \frac{Bb\gamma}{AD} \quad \text{and} \quad q < \frac{c}{Bpa(\gamma + D)}[Bb\gamma - ApD] \tag{3.22}$$

holds where α is given by

$$\alpha = \frac{-M + \sqrt{M^2 - 4N(Ac + Baq)}}{2(Ac + Baq)} \tag{3.23}$$

in which $M = [Ac(p + D) + Baq(p + \gamma + D)]$, and $N = Bapq(\gamma + D) + AcpD - Bb\gamma c$.

Proof Assuming that $x(t) \equiv x_0 + Ae^{\alpha t}$ and $y(t) \equiv Be^{\beta t}$ satisfy (3.19), we get after a substitution and rearrangement,

$$(\alpha + D)Ae^{\alpha t} = -BaU(x_0 + Ae^{\alpha t})e^{\beta t} + \frac{Bb\gamma}{p + \beta}e^{\beta t} \tag{3.24}$$

and

$$\beta + \gamma + D = c\int_{-\infty}^{t} e^{-q(t-s)}U(x_0 + Ae^{\alpha s})ds. \tag{3.25}$$

Equation (3.25) upon differentiation with reference to t yields

$$U(x_0 + Ae^{\alpha t}) = \frac{q}{c}(\beta + \gamma + D). \tag{3.26}$$

Now from (3.24), we have

$$Ae^{\alpha t} = \frac{B}{\alpha + D}\left[\frac{b\gamma}{p + \beta} - \frac{aq}{c}(\beta + \gamma + D)\right]e^{\beta t}. \tag{3.27}$$

We now explore some possibilities of finding out α and β satisfying (3.26) and (3.27).

Case 1 Let $\alpha + \beta = 0$ and $U(x) = x/(m + x), m > 0$.
In this case (3.26) yields after some simplifications

$$Ae^{\alpha t} = \frac{mq(\gamma + D - \alpha)}{c - q(\gamma + D - \alpha)} - x_0$$

and (3.27) becomes

$$A(\alpha + D)e^{2\alpha t} = B\left[\frac{b\gamma}{p - \alpha} - \frac{aq}{c}(\gamma + D - \alpha)\right].$$

Eliminating $e^{\alpha t}$ from these two equations, and simplifying we get

$$\begin{aligned} &c(\alpha + D)[mq(\gamma + D - \alpha) - x_0(c - q(\gamma + D - \alpha)]^2(p - \alpha) \\ &= AB[b\gamma c - aq(\gamma + D - \alpha)(p - \alpha)][c - p(\gamma + D - \alpha)]^2. \end{aligned}$$

Now consider the polynomial

$$\begin{aligned}H(\alpha) \equiv c(\alpha + D)[mq(\gamma + D - \alpha) - x_0(c - q(\gamma + D - \alpha)]^2(p - \alpha)\\ -AB[b\gamma c - aq(\gamma + D - \alpha)(p - \alpha)][c - p(\gamma + D - \alpha)]^2.\end{aligned}$$

Clearly,

$$H(\gamma + D) = \Big[(\gamma + 2D)x_0^2(p - \gamma - D) - ABb\gamma\Big]c^3$$

and

$$H\left(\gamma + D - \frac{c}{q}\right) = c^3m^2\left(\gamma + 2D - \frac{c}{q}\right)\left(\frac{c}{q} + p - \gamma + D\right).$$

Clearly by the hypotheses (a) of (3.21) we have $H(\gamma + D) < 0$ and $H(\gamma + D - c/q) > 0$, and by (b) of (3.21), we have $H(\gamma + D) > 0$ and $H(\gamma + D - c/q) < 0$. In either case we can always find $\alpha^* \in (\gamma + D - c/q, \gamma + D)$ such that $H(\alpha^*) = 0$, since $H(\alpha)$ being a polynomial in α is continuous in α. Clearly $\alpha = \alpha^*$ is the required solution.

Now consider

Case 2 Let $\alpha = \beta$ in (3.26) and (3.27).

Then from (3.27) we get

$$\begin{aligned}(Ac + Baq)\alpha^2 + [Ac(p + D) + Baq(p + \gamma + D)]\alpha\\ +Bapq(\gamma + D) + AcpD - Bb\gamma c = 0.\end{aligned}$$

This equation certainly has a positive root $\alpha = \alpha^+$ if

$$Bapq(\gamma + D) + AcpD - Bb\gamma c < 0 \tag{3.28}$$

and is given by

$$\alpha^+ = \frac{-M + \sqrt{M^2 - 4N(Ac + Baq)}}{2(Ac + Baq)}, \tag{3.29}$$

where $M = [Ac(p+D)+Baq(p+\gamma+D)]$, $N = Bapq(\gamma+D)+AcpD-Bb\gamma c$. Note that hypotheses (3.22) imply that (3.29) holds. □

The following result is an immediate consequence of Theorem 3.5.

Corollary 3.6 *Assume that the conditions of Theorem 3.5 hold. Then system (3.19) has an unbounded solution.*

Proof Assume that the conditions (3.21) of case 1 of Theorem 3.5 holds. Then the existence of a solution $(x_0 + e^{\alpha t}, e^{-\alpha t})$ implies that either the nutrient or the consumer becomes unlimited as $t \to \infty$ according as $\alpha > 0$ or $\alpha < 0$.

If the conditions of case 2 hold then both the nutrient and consumer tend to ∞ as $t \to \infty$ as the existence of $\alpha = \alpha^+ > 0$ is ensured by (3.22) and (3.23). The proof is complete. □

The following examples illustrate Theorem 3.5.

Example 3.7 Consider the system (3.19) given by

$$x'(t) = 2(3-x) - 10\left(\frac{x}{4+x}\right)y + \frac{1}{2}\int_0^\infty \mathrm{e}^{-\frac{6}{7}s} y(t-s)\mathrm{d}s.$$

$$y'(t) = -6y + 6y\int_0^\infty \mathrm{e}^{-\frac{6}{7}s} U(x(t-s))\mathrm{d}s.$$

Here $\gamma = 4, D = 2, b = \frac{1}{8}, x_0 = 3$, and $U(x) = x/(4+x)$ and $p = 6/7 = q$. Clearly $\gamma + D > p$ and $\gamma + D - p < c/q < \gamma + 2D$ hold, satisfying conditions (a) of case 1 Theorem 3.5. Then by (3.21) we have $-1 < \alpha^* < 7$ such that $H(\alpha^*) = 0$ (see proof of Theorem 3.5) and by case 1 of Theorem 3.5, $x \equiv 3 + A\mathrm{e}^{\alpha^* t}$ and $y \equiv B\mathrm{e}^{-\alpha^* t}$ is a solution of the earlier system for any nonnegative real numbers A, B.

Example 3.8 Consider the system

$$x'(t) = 2(6-x) - 10\left(\frac{x}{4+x}\right)y + \frac{1}{2}\int_0^\infty \mathrm{e}^{-\frac{1}{11}s}\ y(t-s)\mathrm{d}s$$

$$y'(t) = -6y + 6y\int_0^\infty \mathrm{e}^{-\frac{1}{2}s}\ U(x(t-s))\mathrm{d}s$$

with $D = 2, a = 10, c = 6, b = \frac{1}{8}, \gamma = 4, and x_0 = 6$. Clearly, $p = 1/11$ and $q = 1/2$. For the choice, $A = 0.2,\ B = 1$, we observe that

$$\frac{1}{11} = p < \frac{Bb\gamma}{AD} = 1.25 \quad \text{and} \quad \frac{1}{2} = q < \frac{c}{Bpa(\gamma + D)}[Bb\gamma - ApD] = 0.51.$$

Now $M = [Ac(p + D) + Baq(p + \gamma + D)] = 32.96$ and $N = Bapq(\gamma + D) + AcpD - Bb\gamma c = -0.05454$. Using (3.29), we have $\alpha = 0.001484$ (approx.).

Therefore, by case 2 of Theorem 3.5, $x(t) = 3 + (0.2)\mathrm{e}^{0.001484t}$, $y(t) = \mathrm{e}^{0.001484t}$ is a solution of the earlier system.

The following conclusions may be drawn from the earlier results and examples.

From conditions (a) of (3.21) we can understand that when the total death rate $\gamma + D$ is small, a small delay in material recycling in combination with a large delay in growth response of y gives rise to unbounded solutions. This is clearly the case where the nutrient concentration x grows unlimited while the species y becomes extinct eventually.

Again when the death rate $\gamma + D$ is high, conditions (b) of (3.21) imply that the system cannot tolerate a large delay in material recycling when the delay in growth response is small. Obviously in this case the nutrient concentration decreases while the consumer species population grows exponentially.

Finally, we can expect unlimited growth both in nutrient concentration and consumer species population in case the delays in material recycling and growth response are sufficiently small as required by conditions (3.22).

Remark 3.9 Though we have not explicitly shown that the conditions on the parameters in Theorem 3.5 and the conditions 1 and 2 below Theorem 2.28 are complementary, Examples 3.7 and 3.8 show that the conditions for uniform boundedness are violated here. We also note that by dropping the condition $T_f = \int_0^\infty sf(s)\mathrm{d}s < \infty$, it is shown in Beretta and Takeuchi [10] that if (3.19) admits an unbounded solution, it oscillates about $\frac{x_0}{b}$. But Theorem 3.5 explicitly describes the circumstances under which an unbounded solution exists.

We now modify slightly the consumption of the nutrient by the biotic species and see how it influences the unbounded nature of the solutions.

Let $W(x) \equiv U(x) + h(x)$, where $h(x)$ is continuous and bounded on $[0, \infty)$ such that $|h(x)| \to 0$ as $x \to \infty$, represent the new consumption law.

Now consider the system

$$x'(t) = Dx_0 - Dx(t) - aW(x(t))y(t) + b\gamma \int_0^\infty f(s)y(t-s)\mathrm{d}s,$$
$$y'(t) = -(\gamma + D)y(t) + cy(t)\int_0^\infty g(s)W(x(t-s))\mathrm{d}s \tag{3.30}$$

Assuming a local Lipschitz condition on $W(x)$, we may establish that the solutions of (3.30) exist, are unique, and continuable on their maximal intervals of existence. Our aim here is to obtain conditions under which the solutions of (3.30) approach the unbounded solution $(u, v) = (x_0 + \mathrm{e}^{\alpha t}, \mathrm{e}^{\beta t})$ of (3.10) obtained under the hypotheses of Corollary 3.6.

For this, we consider $f(s) = \mathrm{e}^{-ps}, \quad g(s) = \mathrm{e}^{-qs}$, $p, q > 0$ as in (3.20) and $U(x) = x/m + x,\ m > 0$, the Michaelis–Menten uptake function.

Letting $x = x_0 + \mathrm{e}^{\alpha t}$, $\alpha > 0$ and $y = \mathrm{e}^{\beta t}$ in (3.19), we obtain

$$\alpha \mathrm{e}^{\alpha t} = -D\mathrm{e}^{\alpha t} - aU(x_0 + \mathrm{e}^{\alpha t})\mathrm{e}^{\beta t} + b\gamma \int_0^\infty f(s)\mathrm{e}^{-\beta(t-s)},$$
$$\beta = -(\gamma + D) + c\int_0^\infty g(s)U(x_0 + \mathrm{e}^{\alpha(t-s)})\mathrm{d}s. \tag{3.31}$$

Using (3.31) in (3.30) and rearranging, we get

$$\begin{aligned} x' - \alpha\mathrm{e}^{\alpha t} &= -D(x - x_0 - \mathrm{e}^{\alpha t}) - ay[U(x) - U(x_0 + \mathrm{e}^{\alpha t})] \\ &\quad - aU(x_0 + \mathrm{e}^{\alpha t})(y - \mathrm{e}^{\beta t}) \\ &\quad + b\gamma \int_0^\infty f(s)[y(t-s) - \mathrm{e}^{-\beta(t-s)}]\mathrm{d}s - ah(x)y, \\ y'(t) &= \beta y + cy\int_0^\infty g(s)[U(x(t-s)) - U(x_0 + \mathrm{e}^{\alpha(t-s)})]\mathrm{d}s \\ &\quad + cy\int_0^\infty g(s)h(x(t-s))\mathrm{d}s. \end{aligned} \tag{3.32}$$

We now state

Theorem 3.10 *Assume that the conditions of Theorem 3.5 hold. Assume further that* $\int_0^\infty |h(x(s))|\mathrm{d}s < \infty$*. Then the solutions of (3.30) are asymptotic to* $(x_0 + \mathrm{e}^{\alpha t}, \mathrm{e}^{\beta t})$ *provided*

$$q > \frac{ck}{D}, \quad p > \frac{b\gamma D}{ak(\beta + \gamma + D)},$$

where k *is the Lipschitz constant defined on* U *in (2.82).*

Proof For $t \geq 0$ define

$$\begin{aligned} V(t) = &|x - (x_0 + \mathrm{e}^{\alpha t)}| + |\log y(t) - \log \mathrm{e}^{\beta t}| \\ &+ B\gamma \int_0^\infty f(s) \int_{t-s}^t |y(z) - \mathrm{e}^{\beta z}|\mathrm{d}z\mathrm{d}s \\ &+ c \int_0^\infty g(s) \int_{t-s}^t |U(x(z)) - U(x_0 + \mathrm{e}^{\alpha z})|\mathrm{d}z\mathrm{d}s \\ &+ c \int_0^\infty g(s) \int_{t-s}^t |h(x(z))|\mathrm{d}z\mathrm{d}s. \end{aligned}$$

Clearly $V(t) \geq 0$ and

$$V(x_0 + \mathrm{e}^{\alpha t}, \mathrm{e}^{\beta t}) = c \int_0^\infty g(s) \int_{t-s}^t |h(x_0 + \mathrm{e}^{\alpha z}|\mathrm{d}z\mathrm{d}s.$$

Now for sufficiently large t, and positive α, $x_0 + \mathrm{e}^{\alpha t} \to \infty$ implying that $h(x_0 + \mathrm{e}^{\alpha t}) \to 0$, by the assumption on h. That is, we can find $T > 0$ sufficiently large so that $t \geq T$ implies $V(x_0 + \mathrm{e}^{\alpha t}, \mathrm{e}^{\beta t}) \to 0$.
Now for $t \geq T$, the upper right derivative of V along the solutions of (3.32) is given by

$$\begin{aligned} D^+V \leq &- D|x - (x_0 + \mathrm{e}^{\alpha t})| - ay|U(x) - U(x_0 + \mathrm{e}^{\alpha t})| \\ &- aU(x_0 + \mathrm{e}^{\alpha t})|y - \mathrm{e}^{\beta t}| - ay|h(x)| \\ &- c|U(x) - U(x_0 + \mathrm{e}^{\alpha t})| \int_0^\infty g(s)\mathrm{d}s + c|h(x)| \int_0^\infty g(s)\mathrm{d}s \\ &+ b\gamma|y - \mathrm{e}^{\beta t}| \int_0^\infty f(s)\mathrm{d}s \\ \leq &- \left(D - \frac{ck}{q}\right)|x - (x_0 + \mathrm{e}^{\alpha t})| - \left(aU(x_0 + \mathrm{e}^{\alpha t}) - b\gamma\frac{1}{p}\right) \\ &\times |y - \mathrm{e}^{\beta t}| - ay|U(x) - U(x_0 + \mathrm{e}^{\alpha t})| + c\frac{1}{q}|h(x)|. \end{aligned}$$

Now from the second equation of (3.31) (see equation (3.26)), we have

$$U(x_0 + \mathrm{e}^{\alpha t}) = \frac{q}{c}(\beta + \gamma + D)$$

Thus, we have

$$D^+V \le -\left(D - \frac{ck}{q}\right)|x - (x_0 + \mathrm{e}^{\alpha t})| \\ - \left(\frac{aq}{c}(\beta + \gamma + D) - \frac{b\gamma}{p}\right)|y - \mathrm{e}^{\beta t}| + \frac{c}{q}|h(x)|.$$

Now the negative definiteness of D^+V follows from the hypotheses and the remainder of the proof can be completed as we have done in the earlier global stability results. □

Remark 3.11 If $h(x) \equiv 0$, Theorem 3.10 provides conditions under which all the solutions of (3.19) when $f(s) = \mathrm{e}^{-ps}$, $g(s) = \mathrm{e}^{-qs}$, and $U(x) = x/(m + x)$ are asymptotic to the unbounded solutions $(x_0 + \mathrm{e}^{\alpha t}, \mathrm{e}^{\beta t})$.

3.4 Equilibria and Instability

Let $F_1 = \int_0^\infty f(s)ds < \infty$ and $G_1 = \int_0^\infty g(s)ds < \infty$. That is, f, g need not be normalized kernels. The equilibrium solutions of (3.19) are the solutions of the system

$$\begin{aligned} Dx_0 - Du - aU(u)v + b\gamma F_1 v &= 0, \\ -(\gamma + D)v + cvU(u)G_1 &= 0. \end{aligned} \tag{3.33}$$

Clearly $(u, v) = (x_0, 0)$ always satisfies (3.33) and is the partially feasible equilibrium solution of (3.19).

For any nontrivial solution (x^*, y^*) of (3.33), we must have

$$\begin{aligned} Dx_0 - Dx^* - aU(x^*)y^* + b\gamma F_1 y^* &= 0, \\ -(\gamma + D) + cG_1U(x^*) &= 0, \end{aligned} \tag{3.34}$$

which yields

$$U(x^*) = \frac{\gamma + D}{cG_1} \quad \text{and} \quad y^* = \frac{D(x_0 - x^*)}{aU(x^*) - b\gamma F_1}. \tag{3.35}$$

We have the following conclusions.

1. If $(\gamma + D)/(cG_1) > L$, then there exists no x^* satisfying the relation $U(x^*) = (\gamma + D)/(cG_1)$ since $U(x) \le L$, $\forall\ x \in [0, \infty)$.
   Then (3.34) cannot have a positive solution and hence, (3.19) possesses no positive equilibrium solution if $(\gamma + D)/(cG_1) > L$.
2. In case $(\gamma + D)/(cG_1) < L$, by the continuity of U, we can always find $x^* > 0$ satisfying $U(x^*) = (\gamma + D)/(cG_1)$.
   (a) Yet the system (3.34) cannot have a positive solution if $(x_0 - x^*)(aU(x^*) - b\gamma F_1) < 0$.

(b) Finally a positive solution to (3.34) exists and is a positive equilibrium solution of (3.19) if

$$\left.\begin{aligned}(x_0 - x^*)(aU(x^*) - b\gamma F_1) &> 0\\ \text{and} \qquad \frac{\gamma+D}{cG_1} &< L\end{aligned}\right\} \tag{3.36}$$

We study the following cases now:

1. the global asymptotic stability of $(x_0, 0)$ leading to the extinction of species y;
2. conditions under which the positive equilibrium (x^*, y^*) of (3.19) (when it exists) is unstable.

The next theorem provides conditions under which the axial equilibrium $(x_0, 0)$ is globally asymptotically stable. Since the proof of this theorem is quite similar to that of Theorem 2.32, we omit the details.

Theorem 3.12 *Assume that the delay kernels satisfy* (2.84)*. The equilibrium solution* $(x_0, 0)$ *of* (3.19) *is globally asymptotically stable provided* $(\gamma + D)/(cG_1) > L$.

Since $(\gamma + D)/(cG_1) > L$ here, we may conclude that the global asymptotic stability of $(x_0, 0)$ excludes the possibility of the existence of a positive equilibrium to (3.19) (see conditions 3.36).

Now we consider the second possible case for instability of the system, namely, the instability of a positive equilibrium solution. In the remainder of the section, we assume that the conditions (3.36) hold so that a positive equilibrium solution (x^*, y^*) to (3.19) exists. We then linearize system (3.19) around this positive equilibrium (x^*, y^*) and obtain conditions for the instability of (x^*, y^*). One way of establishing this is to show that the characteristic equation corresponding to the linearized system admits at least a root with positive real part under the conditions specified. Such an approach is followed in earlier section for system (3.10) employing Routh–Hurwitz criterion (see Theorem C.5 (Appendix C)). In this section, we shall follow a geometrical approach to find a root with positive real part.

Denoting $x_1(t) = x(t) - x^*$, $y_1(t) = y(t) - y^*$ and $U_1(x_1) = U(x) - U(x^*)$ and rearranging, (3.19) may be written as

$$\begin{aligned}x_1'(t) &= -Dx_1(t) - aU_1(x_1(t))(y_1(t) + y^*) - aU(x^*)y_1(t)\\ &\qquad + b\gamma \int_0^\infty f(s)y_1(t-s)\mathrm{d}s\\ y_1'(t) &= c(y_1(t) + y^*)\int_0^\infty g(s)U_1(x_1(t-s))\mathrm{d}s\end{aligned} \tag{3.37}$$

Note that $(0, 0)$ is the equilibrium solution of (3.37) corresponding to (x^*, y^*) of (3.19).

Assume that $U'(x)$ exists. Now linearizing (3.37) around $(0, 0)$, taking $U_1(x_1) \approx U'(x^*)x_1$, we obtain after some rearrangements,

$$\begin{aligned} x_1'(t) &= -(D + ay^*U'(x^*))x_1(t) - aU(x^*)y_1(t) \\ &\quad + b\gamma \int_0^\infty f(s)y_1(t-s)\mathrm{d}s, \\ y_1'(t) &= cy^*U'(x^*)\int_0^\infty g(s)x_1(t-s)\mathrm{d}s, \end{aligned} \tag{3.38}$$

which can be written as

$$X'(t) = RX(t) + \int_o^\infty k(s)X(t-s)\mathrm{d}s, \tag{3.39}$$

where $X(t) = (x_1(t),\ y_1(t))^T$,

$$R = \begin{pmatrix} -D - ay^*U'(x^*) & -aU(x^*) \\ 0 & 0 \end{pmatrix},$$

$$k(s) = \begin{pmatrix} 0 & b\gamma f(s) \\ cy^*U'(x^*)g(s) & 0 \end{pmatrix}.$$

The characteristic equation of (3.39) is given by

$$P(l) = |lI - R - \int_0^\infty k(s)\mathrm{e}^{-ls}\mathrm{d}s| = 0,$$

which can be written as

$$P(l) = l^2 + Al + G(l)[B - CF(l)] = 0 \tag{3.40}$$

where

$$\begin{aligned} A &= D + ay^*U'(x^*), \\ B &= acy^*U(x^*)U'(x^*) \\ &\text{and} \\ C &= b\gamma cy^*U'(x^*), \\ F(l) &= \int_0^\infty f(s)\mathrm{e}^{-ls}\mathrm{d}s, \\ G(l) &= \int_0^\infty g(s)\mathrm{e}^{-ls}\bar{\mathrm{d}}s. \end{aligned} \tag{3.41}$$

We are now in a position to state the main result of this section.

Theorem 3.13 *The characteristic equation* (3.40) *of system* (3.38) *admits at least one root with positive real part if either of the following conditions holds.*

(a) $0 < U'(x^*)$ *and* $aU(x^*) - b\gamma F_1 < 0$,

(b) $-\frac{D}{ay^*} < U'(x^*) < 0$ *and* $aU(x^*) - b\gamma F_1 > 0$.

Proof We write the characteristic equation (3.40) as $Q(l) = S(l)$, in which

$$Q(l) = l^2 + Al \quad \text{and} \quad S(l) = G(l)[CF(l) - B].$$

Observe that $Q(0) = 0$, $Q(\infty) = \infty$ and

$$Q'(l) = 2l + A > 0 \quad \text{for } l > -\frac{A}{2}.$$

Now

$$\begin{aligned} S(0) &= G(0)(CF(0) - B) \\ &= G_1(CF_1 - B) = G_1[b\gamma F_1 - aU(x^*)]cy^*U'(x^*), \end{aligned}$$

where $G_1 = \int_0^\infty g(s)\mathrm{d}s$ and $F_1 = \int_0^\infty f(s)\mathrm{d}s$.

Clearly $S(0) > 0$ by either of the hypotheses (a) and (b).

Also $S(l) \to 0$ as $l \to \infty$.

Therefore, when (a) or (b) holds, we can always find a $l^* > 0$ such that

$$Q(l^*) = S(l^*).$$

Clearly, $l = l^*$ is the desired positive real root of (3.40). □

The geometrical ideas involved in the proof of Theorem 3.13 are highlighted in Fig. 3.1.

The following result needs no proof.

Corollary 3.14 *Assume that the hypotheses of Theorem 3.13 hold. Then* (x^*, y^*) *of system* (3.19) *is unstable.*

A Special Case

Now consider a special case of (3.19) in which $f(s) = \mathrm{e}^{-ps}$ and $g(s) = \mathrm{e}^{-qs}$, p, q are positive, real and obtain specific conditions on the parameters of the system for instability.

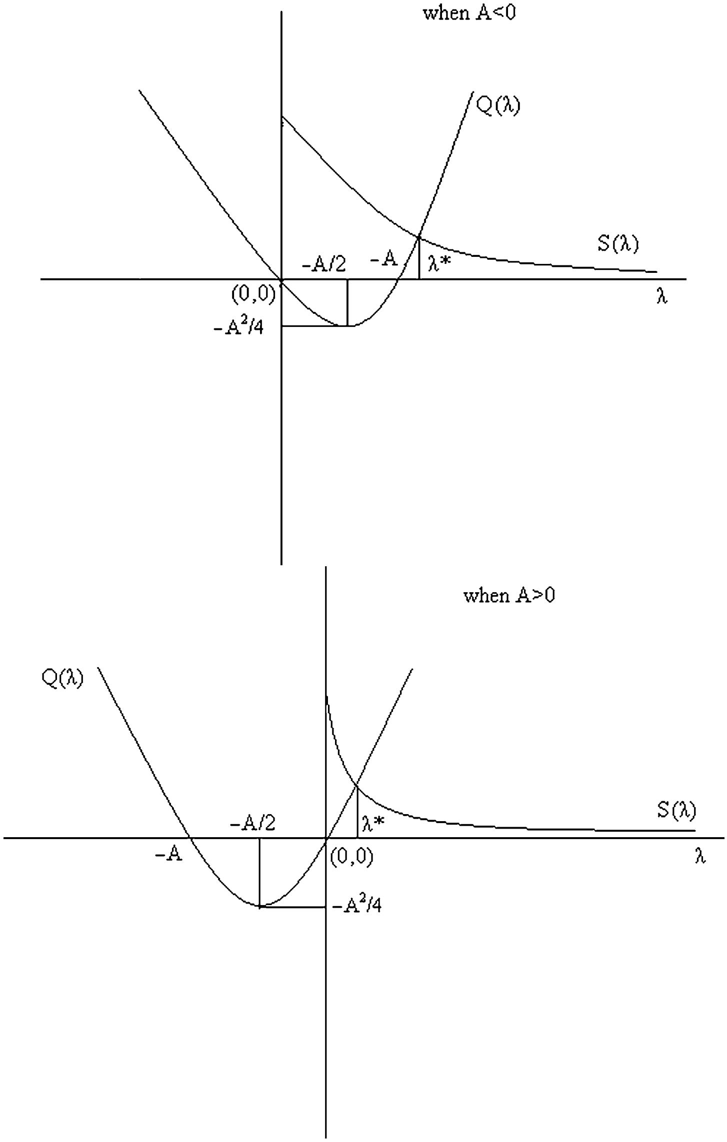

Fig. 3.1 Geometrical explanation

Clearly,

$$F(l) = \int_0^\infty f(s)\mathrm{e}^{-ls}\mathrm{d}s = \frac{1}{l+p}$$

and

$$G(l) = \int_0^\infty g(s)\mathrm{e}^{-ls}\mathrm{d}s = \frac{1}{l+q}.$$

Using these in (3.40) and rearranging we get

$$l^4 + (A + p + q)l^3 + [A(p + q) + pq]l^2 + (Apq + B)l + Bp - C = 0. \quad (3.42)$$

Now we consider

$$\begin{aligned} Bp - C &= acy^* U(x^*)U'(x^*)p - b\gamma c y^* U'(x^*) \\ &= pcy^*[aU(x^*) - \frac{b\gamma}{p}]U'(x^*). \end{aligned}$$

Since p, c, y^* are all positive, $Bp - C$ is negative if and only if

$$\left[aU(x^*) - \frac{b\gamma}{p}\right]U'(x^*) < 0.$$

Since $F_1 = \int_0^\infty f(s)\mathrm{d}s = 1/p$ in this case, we can observe that (3.28) possesses a root with positive real part if $(aU(x^*) - b\gamma F_1)U'(x^*) < 0$, which is exactly the condition required by Theorem 3.13 for the instability of (x^*, y^*). Let us explore for a further possibility of instability of (x^*, y^*). Let us consider the second-order Routh–Hurwitz determinant D_2 corresponding to equation (3.42),

$$\begin{aligned} D_2 &= \begin{vmatrix} A + p + q & Apq + B \\ 1 & A(p + q) + pq \end{vmatrix} \\ &= (A + p + q)(A(p + q) + pq) - (Apq + B) \\ &= (p + q)(A + p)(A + q) - B \quad \text{(after some rearrangements).} \end{aligned}$$

If $D_2 < 0$, there is a change of sign in (3.42) indicating the existence of a root with positive real part, for which we require

$$(p + q)(A + p)(A + q) < B.$$

We record these observations as

Theorem 3.15 *Assume that the delay kernels f and g are given by $f(s) = \mathrm{e}^{-ps}$ and $g(s) = \mathrm{e}^{-qs}$, $p, q > 0$. The positive equilibrium (x^*, y^*) of (3.19) is unstable if*

$$(p + q)(A + p)(A + q) < B, \quad (3.43)$$

in which A and B are as defined in (3.41).

The following example illustrates Theorem 3.15.

Example 3.16 Consider the model

$$\begin{aligned} x'(t) &= (0.25)(6 - x(t)) - 10\, U(x)y(t) + \frac{1}{4}\int_0^\infty \mathrm{e}^{-\frac{1}{4}s} y(t - s)\mathrm{d}s, \\ y'(t) &= -10y(t) + 5y(t)\int_0^\infty \mathrm{e}^{-\frac{1}{4}s}\, U(x(t - s))\mathrm{d}s \end{aligned}$$

in which $\gamma = 9.75$, $b = \frac{1}{39}$, $U(x) = \frac{x}{4+x}$, and $f(s) = \mathrm{e}^{-\frac{1}{4}s} = g(s)$.

Clearly $F_1 = 4 = G_1$. The equilibrium values are $U(x^*) = (\gamma + D)/(cG_1) = 1/2,\ x^* = 4$, and $y^* = 1/8$. Also $U'(x^*) = 1/16$.

Clearly $U'(x^*)(aU(x^*) - b\gamma F_1) > 0$. Therefore, instability expressed by Theorem 3.13 does not arise.

Now with $p = q$, condition (3.43) becomes

$$2p(A + p)^2 - B < 0\ .$$

Here $p = 1/4$, $A = D + ay^*U'(x^*) = 21/64$ and $B = acy^*U(x^*)U'(x^*) = 25/2$, clearly satisfy (3.43). Therefore, $(4, \frac{1}{8})$ is unstable by virtue of Theorem 3.15.

The following example illustrates a case where system (3.19) does not possess a positive equilibrium.

Example 3.17 Consider the system

$$x'(t) = 2(6 - x(t)) - 10\ U(x)y(t) + \frac{1}{2}\int_0^\infty e^{-\frac{1}{11}s}\ y(t - s)\mathrm{d}s$$

$$y'(t) = -6y(t) + 6y(t)\int_0^\infty e^{-\frac{1}{2}s}\ U(x(t - s))\mathrm{d}s$$

in which $\gamma = 4, b = 1/8$, and $U(x) = x/(4 + x)$.

Clearly $F_1 = 11$ and $G_1 = 2$. The equilibrium values are

$$U(x^*) = \frac{1}{2},\ x^* = 4, \quad \text{and} \quad y^* = -8.$$

Since $x_0 = 6 > x^* = 4$ and $aU(x^*) - b\gamma F_1 = -1/2 < 0$, the earlier system does not have a positive equilibrium.

3.5 Biocontrol Mechanisms

We have observed the possibilities of extinction of species in some cases and unlimited growth of species in some other cases. Assuming that all other conditions are conducive for growth, we have regarded so far food (aided by the time delays in the growth process of the consumer and in regeneration of material from the dead) as the prime factors influencing the growth of populations. In this case, the survival of the species depends only on food–consumer interactions. If the populations are either wise enough to store food for future like ants, human beings, etc. or can produce food like human beings do in accordance with the rise in populations, survival may not be a difficult problem in these cases. But most of the species in nature do not possess either of these two qualities and this seems to be one of the important reasons that forces extinction of species.

Yet there are many species still surviving despite the fact that they can neither produce food nor store it for future consumption, maintaining food–consumer balance remarkably. We may understand from this that nature provides some control mechanisms to balance food–consumer equations. This naturally calls for the influence of other factors for growth such as environmental conditions (space, temperature, light, etc.), diseases, and competition among populations. When the basic system has such an in-built mechanism that keeps the system stable, it evokes little interest.

It is going to be important in Nature's view point and challenging in researcher's (naturalist's) view point to find/design some control mechanisms that drive a species from extinction and regulate the unlimited growth of some other species. This balancing act may be viewed as stabilizing a system that tends to exhibit instability characteristics. For such a study identification of key (growth influencing) parameters and mechanisms that can regulate the growth making the system disturbance-tolerant is important. The following are some important observations in this direction.

Nothing is permanent in nature. Especially food supplies are season-dependent. For example, during summer the inflows are very low resulting in a scarcity of food. In such a situation, the species compete for food and only the winners survive eventually. In some cases the species try to settle down at places where food is available and the species may die of suffocation due to overcrowding in these locations. In any case low nutrient levels lead to death of some of the species until such stage that the available nutrient sufficiently feeds the remaining species. In this case survival of species continues in low numbers until the situation improves. The study of this phenomenon leading to a self-regulation of the species will be the content of our next chapter.

During the rainy season the inflows are usually high. Thus, nutrient levels naturally go up. But there is always a danger of high outflows resulting in the washout of nutrient as well as consumer species. To survive this the species may move to a safer place where the washout is low but nutrient is readily available. One such place could be the bank of a lake or canal or walls of the container in case of a chemostat. This type of movement by a portion of the species to a region in the growth medium may help improve the possibility of survival. We shall make this a point of discussion at a later part of this book.

It would be interesting to know what happens in between these two seasons. We suppose a regulated, reasonably good supply of nutrient. That is, the supplies may be fixed in good numbers for a given length of time. Some times it may happen that the total food consumption remains unaltered irrespective of the consumer population size and supply of food. This is a calm-down situation for the consumer species and there is no pressure on the supply/availability of nutrient. We may expect in such a case that the state of the system remains unaltered for a particular length of time. We shall see that this phenomenon is also going to play an important role in our study on the instability of the systems we have considered.

In all the aforementioned situations we notice that the nature has a tendency to regulate the growth accordingly. How to incorporate these phenomena into our model equations and study their characteristics in terms of our mathematics will be the point of contention of the next three chapters.

3.6 Discussion

In this chapter we have understood that the systems represented by the models in the earlier chapter have the tendency of being disturbed by the presence of time delays in growth response and material recycling and also by variations in food supply. Observing the situation more closely, we have recorded various natural reasons for the disturbances and also remedies posed by nature. As already noted the main question before us is to handle these situations in terms of mathematics. Researchers have provided enough clues to this task. Confining our attention to model equations (2.81), we incorporate each of the phenomena noticed in Sect. 3.4 and study its influence on the system. That means we try to understand how the consumer species change their course of reaction to suit the seasonal changes and their needs. In the next chapter we begin with a study of the first situation described in Sect. 3.4 to understand the self-regulation of populations when low supply of nutrient limits their growth.

3.7 Notes and Remarks

To establish the instability of the systems under consideration, we have resorted to a local stability analysis by linearizing the model equations around the equilibria. The readers might have noticed that all the stability analysis whether it is local or global is via Lyapunov function(al)s. To our knowledge there exist no instability results as far as many of the models of Chap. 2 are concerned. Establishing instability using Lyapunov functionals is not new and there are many useful functionals and examples available in the literature (see, e.g., the books by Kolmanovskii and Nosov [60] and by Burton [15]). An attempt in this direction will be very useful and is worthwhile trying. Because the basic model in the absence of time delays, that is (1.3), is structurally stable the very existence of a positive equilibrium solution implies its stability. This may help decide whether the instability is just local or complete. The books by Hirsch, Smale and Devaney [52], Perko [73] and Stepan [97] provide methods on bifurcation analysis for a good understanding of the stability or instability characteristics dynamical systems.

Also for most of the models results on uniform persistence are not available. Since persistence also implies an eventual survival such results could be of interest in the context of instability discussed here.

The analysis of system (3.1) and Example 3.2 presented in the chapter are provided by Ruan [79]. It is noticed by Beretta et al. [7] that for $\tau = 0$, the system in Example 3.2 is stable. Therefore, one may understand that the time delay in growth response is playing a major role in disturbing the stability of the system. See also Remark 3.9 in this context. We refer the readers to the articles by Beretta and Bischi [6] and Beretta et al. [7] for more details on the influence of time delays on stability of these systems in the opinion that a finite mean delay in material recycling contributes to the stability while a delay in growth response destabilizes the system. The remaining results are from Sree Hari Rao and Raja Sekhara Rao [93].

3.8 Exercises

1. Study the instability of (3.1) regarding the supply rate D, as a bifurcation parameter as in Theorem 3.4.
2. Derive instability result for (2.4) when the delays in material recycling and growth response are fixed constants.
3. Study (2.4) with different delays τ_1 in material recycling and τ_2 in growth response. What happens when (a) $\tau_1 << \tau_2$ (b) $\tau_2 << \tau_1$?
4. Obtain results similar to Theorem 3.5 for fixed time delays τ_1 in material recycling and τ_2 in growth response.
5. Check whether the conditions on parameters in Theorem 3.5 and conditions below Theorem 2.28 are complementary. (they define different parameter regions).
6. Can we derive a global instability result for the equilibrium (x^*, y^*)? We notice that for system (3.1) a complete instability region of parameters is difficult to achieve when a positive equilibrium exists. Is this true because the corresponding system without delays is stable?
7. Study the case where material recycling is instantaneous and the delay in growth response in distributed. Analyze the comments in section 3.7 in this case.

Chapter 4
Self-Regulation

4.1 Introduction

Nature generally checks the unlimited growth of populations through many ways. One of the important factors that influence the growth of populations is the "finite carrying capacity" of the environment in which the species grow. The term carrying capacity is a parameter representing the resources, e.g., food, space, sunlight, etc. on which the species grow. If the initial size of the population is small, the population grows approaching the carrying capacity of the environment and if, the population is initially very large, it decreases approaching the carrying capacity asymptotically as $t \to \infty$. A simple differential equation which represents the growth of population with a carrying capacity $\tilde{k}$ is

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{\tilde{k}}\right),$$

where r is any real constant. The solution of the above ordinary differential equation is given by

$$x = \frac{\tilde{k}\tilde{x_0}\mathrm{e}^{rt}}{\tilde{k} - \tilde{x_0} + \tilde{x_0}\mathrm{e}^{rt}},$$

where $\tilde{x_0}$ is the size of the population at $t = 0$.

Clearly when $\tilde{x_0} < \tilde{k}$, the population grows approaching $\tilde{k}$ asymptotically as $t \to \infty$. If $\tilde{x_0} > \tilde{k}$, the population decreases again approaching $\tilde{k}$ asymptotically as $t \to \infty$. If $\tilde{x_0} = \tilde{k}$, the population remains constant in time at $x = \tilde{k}$. A graphical representation of the solution of the above ordinary differential equation is given in Fig. 4.1. The growth of populations is generally confined to the specific region where the nutrient is readily available. For example, in a chemostat the growth of the consumer species is confined to the culture vessel whose volume is finite and in lakes, the growth is more likely in the area where the nutrient levels are rich. Such an environment (nutrient-rich region) can support only a finite group of consumer species. Thus, while modeling population growth, one has to take into account the carrying capacity of the environment.

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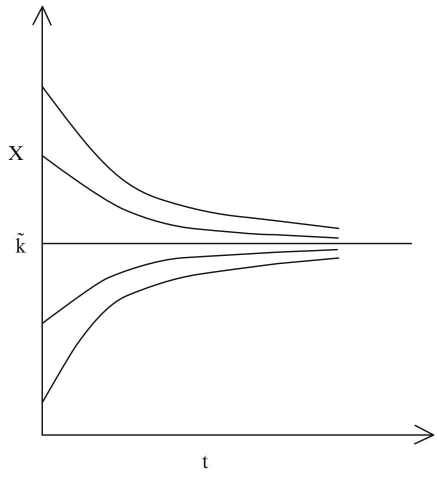

Fig. 4.1 Solution of the system involving carrying capacity

Growing large populations in a small region leads to death of species due to suffocation, diseases, etc. (overcrowding effect). When food supply is limited, large populations compete for food resulting in death of some of the species. Our aim in this chapter is to study the growth of microorganisms with limited nutrient supply under the influence of these factors. We propose the following system of equations modifying the model (2.81) to include the finite carrying capacity of the environment.

$$\begin{aligned} x'(t) &= D(x_0 - x(t)) - aU(x(t))y(t) + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s, \\ y'(t) &= -(\gamma + D)y(t) + cy(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - dy^2(t). \end{aligned} \tag{4.1}$$

All the terms in (4.1) have the same meaning and definition as in (2.81), except for the term "$-dy^2$" which represents the death of the species y due to the finite carrying capacity of the environment or due to the intraspecies competition among the species. The positive constant d is such that $1/d$ is the carrying capacity of the environment. We study the impact of this term $-dy^2$ on the stability properties of the equilibrium solutions of (4.1). We observe that the parametric conditions in Theorems 2.33–2.36 of Sect. 2.5, Chap. 2 do not provide any information about the stability of the positive equilibrium when $aU(x) < b\gamma$ for $x > x^*$ (that is, at low levels of nutrient supply or consumption). Thus, our interest here is to study the survival of species at these low levels of nutrient consumption (supply).

We assume the following initial conditions for the system (4.1).

$$x(s) = \phi_1(s),\ \ y(s) = \phi_2(s), \quad -\infty < s \le 0, \tag{4.2}$$

where ϕ_j for $j = 1, 2$ are bounded, continuous, nonnegative functions on $(-\infty, 0]$. This chapter is organized as follows.

In Sect. 4.2, we study the basic properties of solutions of (4.1) and establish the existence of equilibria. Results relating to the nonnegativity and boundedness of the solutions of (4.1) are presented in this section. Persistence of solutions is given in Sect. 4.3. The global asymptotic stability of equilibria is discussed in Sect. 4.4. Existence of periodic solutions to our model equations is discussed in Sect. 4.5. Influence of self-regulatory mechanism when the delay in growth response is finite is studied in Sect. 4.6. With a discussion in Sect. 4.7 followed by some introspection in Sect. 4.8, we conclude this chapter.

4.2 Qualitative Properties of Solutions

In this section, we present results on the basic properties of solutions of the model equations, such as existence, uniqueness, nonnegativity, and boundedness. We assume that the hypotheses (A_1) and (A_2) on the consumption function $U(x)$ in Sect. 2.5 hold throughout this chapter. Specifically we assume
(A_1). $U(x)$ is a continuous real-valued function defined on $\mathbf{R}_+ = [0, \infty)$ such that

$$U(0) = 0,\ U(x) > 0 \quad \text{for } x > 0 \text{ and } \lim_{x\to\infty} U(x) = L_1 < \infty.$$

and $|U(x)| \leq L$ for all x, for some $L > 0$.
(A_2). There exists a constant $k > 0$ such that for all $x_1,\ x_2 \in \mathbf{R}_+$,

$$|U(x_1) - U(x_2)| \leq k|x_1 - x_2|.$$

In addition, as in the earlier chapters, we assume that the delay kernels are nonnegative and satisfy,

$$(H_1). \qquad \int_0^\infty f(s)\mathrm{d}s = 1,\ \int_0^\infty g(s)\mathrm{d}s = 1,$$

$$(H_2). \qquad \int_0^\infty sf(s)\mathrm{d}s < \infty,\ \int_0^\infty sg(s)\mathrm{d}s < \infty.$$

We shall prove that the systems (4.1) and (4.2) have a unique pair of solutions under conditions weaker than a Lipschitz condition.

Before proving the theorem, we rewrite system (4.1) as

$$X'(t) = F(t, X_t), \quad \text{where} \quad X(t) = \begin{pmatrix} x(t) \\ y(t) \end{pmatrix} \text{ and}$$

$$F(t, X_t) = \begin{pmatrix} D(x_0 - x(t)) - aU(x(t))y(t) + b\gamma \int_0^\infty f(s)y(t-s)\mathrm{d}s \\ -(\gamma + D)y(t) + cy(t)\int_0^\infty g(s)U(x(t-s)\mathrm{d}s - dy^2 \end{pmatrix}.$$

We now consider the system of equations given by $X'(t) = F(t, X_t)$ with initial conditions $X(t_0) = X_0$.

Let $S(\rho)$ be an open bounded sphere contained in R^{n+1} and let $F : S \to R^n$. For a given $(t_0, X_0) \in S$, a solution of the above system is a differentiable function $X(t)$ on an interval J such that

$$X' = F(t, X_t) \quad \text{for } t \in J,\ t_o \in J,\ \text{and } X(t_0) = X_0.$$

For $X \in R^n$, we define $\|X\| = \sum_{i=1}^{n} |X_i|$.

We now state and prove Theorem 4.1.

Theorem 4.1 *The given system of equations* (4.1) *has a unique solution for a given set of initial conditions.*

Proof We shall verify the hypotheses of Lemma 2.23 for the system (4.1).

Now for $t \geq 0$ and functions $\xi(t) = (\xi_1(t), \xi_2(t))$ and $\eta(t) = (\eta_1(t), \eta_2(t))$, we have

$$\begin{aligned}
&\|F(t,\xi) - F(t,\eta)\| \\
&\leq D|\eta_1(t) - \xi_1(t)| + b\gamma \int_{-\infty}^{t} f(t-s)|\xi_2(s) - \eta_2(s)|\mathrm{d}s \\
&\quad + (\gamma + D)|\eta_2(t) - \xi_2(t)| + d|\eta_2(t)^2 - \xi_2(t)^2| \\
&\quad + a|U(\eta_1(t))\eta_2(t) - U(\xi_1(t))\xi_2(t)| \\
&\quad + c|\xi_2(t) \int_{-\infty}^{t} g(t-s)U(\xi_1(s)\mathrm{d}s - \eta_2(t) \int_{-\infty}^{t} g(t-s)U(\eta_1(s)\mathrm{d}s| \\
&\leq K_1\|\xi(t) - \eta(t)\| \\
&\quad + K_2 \sum_{j=1}^{2} |\psi_j(h_j(t,\xi)) - \psi_j(h_j(t,\eta))|,
\end{aligned}$$

where $K_1 = b\gamma + D + \gamma + D + 2d\rho$ and $K_2 = a$.

Now, if we choose,

$$h_1(t,\xi) = \xi_1(t), \quad \psi_1(h_1(t,\xi)) = \xi_2(t) \int_{-\infty}^{t} g(t-s)U(h_1(s,\xi(s)))\mathrm{d}s,$$

$$h_2(t,\xi) = \xi_1(t), \quad \text{and} \quad \psi_2(h_2(t,\xi)) = \xi_2(t)U(h_2(t,\xi(t))),$$

then it is easy to see that all the hypotheses of Lemma 2.33 are satisfied, and hence, the conclusion follows. □

The following discussion yields a set of necessary and sufficient conditions for the existence of a unique positive equilibrium solution of (4.1).

The equilibria of (4.1) are the solutions of

$$\begin{aligned} Dx_0 - Dx - aU(x)y + b\gamma y &= 0, \\ (cU(x) - (\gamma + D) - dy)y &= 0. \end{aligned} \tag{4.3}$$

Observe that $(x_0, 0)$ is a solution of (4.3) which is a partially feasible equilibrium of (4.1). For a nonzero solution (x^*, y^*), the second equation of (4.3) implies

$$y^* = \frac{cU(x^*) - (\gamma + D)}{d}. \tag{4.4}$$

Using (4.4) in the first equation of (4.3) we get

$$x^* = x_0 - \frac{[aU(x^*) - b\gamma][cU(x^*) - (\gamma + D)]}{dD}. \tag{4.5}$$

Then from (4.4) and (4.5)

$$\begin{aligned} &y^* > 0 \text{ if } U(x^*) > (\gamma + D)/c \text{ and} \\ &x^* > 0 \text{ if } [aU(x^*) - b\gamma][cU(x^*) - (\gamma + D)] < x_0\, dD. \end{aligned} \tag{4.6}$$

That is, $acU^2(x^*) - (a(\gamma + D) + b\gamma c)U(x^*) + (\gamma + D)b\gamma - x_0\, dD < 0$.

Consider $acU^2 - [a(\gamma + D) + b\gamma c]U + (\gamma + D)b\gamma - x_0\, dD = 0$ in which $U = U(x^*)$.

Solving for U, we obtain

$$\begin{aligned} U &= \frac{a(\gamma + D) + b\gamma c}{2ac} \\ &\quad \pm \frac{\sqrt{(a(\gamma + D) + b\gamma c)^2 - 4((\gamma + D)b\gamma - x_0\, dD)ac}}{2ac} \\ &= \frac{1}{2}\left\{\left(\frac{\gamma + D}{c} + \frac{b\gamma}{a}\right) \pm \sqrt{\left(\frac{\gamma + D}{c} - \frac{b\gamma}{a}\right)^2 + 4\frac{x_0\, dD}{ac}}\right\}. \end{aligned}$$

Let

$$U_1 = \frac{1}{2}\left\{\left(\frac{\gamma + D}{c} + \frac{b\gamma}{a}\right) + \sqrt{\left(\frac{\gamma + D}{c} - \frac{b\gamma}{a}\right)^2 + 4\frac{x_0\, dD}{ac}}\right\}$$

and

$$U_2 = \frac{1}{2}\left\{\left(\frac{\gamma + D}{c} + \frac{b\gamma}{a}\right) - \sqrt{\left(\frac{\gamma + D}{c} - \frac{b\gamma}{a}\right)^2 + 4\frac{x_0\, dD}{ac}}\right\}.$$

In order to have a positive equilibrium (x^*, y^*) of (4.1), $U(x^*)$ has to satisfy the following inequalities

$$U(x^*) > \frac{\gamma + D}{c} \text{ and } U_1 > U(x^*) > U_2. \tag{4.7}$$

Now observe that

$$\begin{aligned}\frac{\gamma + D}{c} - U_2 &= \frac{\gamma + D}{c}\\ &\quad -\frac{1}{2}\left\{\frac{\gamma + D}{c} + \frac{b\gamma}{a} - \sqrt{\left(\frac{\gamma + D}{c} - \frac{b\gamma}{a}\right)^2 + 4\frac{x_0\, dD}{ac}}\right\}\\ &= \frac{1}{2}\left\{\left[\frac{\gamma + D}{c} - \frac{b\gamma}{a}\right] + \sqrt{\left(\frac{\gamma + D}{c} - \frac{b\gamma}{a}\right)^2 + 4\frac{dDx_0}{ac}}\right\}\\ &> 0.\end{aligned}$$

Thus, it follows that (x^*, y^*) exists and is positive, if the inequality

$$\frac{\gamma + D}{c} < U(x^*) < U_1, \tag{4.8}$$

where

$$U_1 = \frac{1}{2}\left\{\frac{\gamma + D}{c} + \frac{b\gamma}{a} + \sqrt{\left(\frac{\gamma + D}{c} - \frac{b\gamma}{a}\right)^2 + \frac{4dD}{ac}x_0}\right\}$$

holds.

Thus, we have,

Theorem 4.2 *A necessary and sufficient condition that* (4.1) *has a positive equilibrium* (x^*, y^*) *is that* $U(x^*)$ *satisfies the inequality* (4.8)*.*

We remark that U_2 may or may not be positive. If U_2 is nonpositive, the lower estimate for $U(x^*)$ in (4.7) is superfluous. However, $U_2 > 0$ if $x_0 < ((\gamma + D)b\gamma)/dD$.

We now consider the system of equations (4.3) and establish that this system admits a unique equilibrium solution (x^*, y^*) to (4.1), by making use of Theorem 4.1.

Theorem 4.3 *The system of equations* (4.3) *has a unique solution yielding a unique nontrivial equilibrium solution for the system* (4.1)*.*

Proof Any nontrivial solution of (4.3) must satisfy the equations,

$$\begin{aligned}Dx_0 - Dx^* - aU(x^*)y^* + b\gamma y^* &= 0,\\ -(\gamma + D) + cU(x^*) - dy^* &= 0.\end{aligned} \tag{4.9}$$

Using (4.9) in (4.1), we get

$$
\begin{aligned}
x'(t) &= -D(x(t) - x^*) - a[U(x)y(t) - U(x^*)y^*] + \\
&\quad + b\gamma \int_{-\infty}^{t} f(t-s)(y(s) - y^*)\mathrm{d}s, \\
y'(t) &= y(t)\left[c \int_{-\infty}^{t} g(t-s)(U(x(t) - U(x^*))\mathrm{d}s \right. \\
&\quad \left. -d(y(t) - y^*)\right].
\end{aligned}
\tag{4.10}
$$

Denoting $x - x^* = x_1$, $y - y^* = y_1$, and $U(x) - U(x^*) = U_1(x_1)$ the system (4.10) after a simple rearrangement takes the form,

$$
\begin{aligned}
x_1'(t) &= -Dx_1(t) - a(y_1(t) + y^*)U_1(x_1(t)) - aU(x^*)y_1(t) \\
&\quad + b\gamma \int_{-\infty}^{t} f(t-s)y_1(s)\mathrm{d}s \\
y_1'(t) &= (y_1(t) + y^*)\left[c \int_{-\infty}^{t} g(t-s)U_1(x_1(t))\mathrm{d}s - dy_1(t)\right].
\end{aligned}
\tag{4.11}
$$

Now choose the initial functions

$$x_1(t) \equiv 0 \text{ and } y_1(t) \equiv 0 \quad \text{for } t \in (-\infty, 0]. \tag{4.12}$$

Then by Theorem 4.1, the initial value problems (4.11) and (4.12) admit a unique solution. Clearly, the trivial solution is the only solution of the system (4.11) and (4.12). This implies that

$$x_1(t) \equiv 0 \equiv y_1(t) \quad \text{for } t > 0. \tag{4.13}$$

Now, it is easy to see from (4.13) that $x(t) = x^*$ and $y(t) = y^*$ is the unique solution satisfying (4.9) and thus (4.3) guarantees the existence of a unique equilibrium solution for the system (4.1). □

Throughout the reminder of the chapter we tacitly assume that system (4.1) has solutions satisfying the initial conditions (4.2) which are locally unique and continuable on their maximal interval of existence.

We now discuss the problem of boundedness and nonnegativity of solutions for our model equations (4.1).

Theorem 4.4 *All the solutions of system* (4.1) *are nonnegative for all* $t \geq 0$ *corresponding to the initial conditions* (4.2).

Proof We shall show that once a solution enters the plane

$$\Omega = \{(x, y)/x \geq 0, y \geq 0\},$$

it remains there forever. By continuity of solutions of (4.1) each solution has to take the value 0 before it assumes a negative value. If $y = 0$ for some $t = t_1 > 0$, then from the second equation of (4.1) $y'(t_1) = 0$, and hence, y is nondecreasing at t_1, which means that y is at least nondecreasing at $y = 0$. This rules out the possibility of y taking a negative value. Again when $x = 0$, we have

$$x'(t) = Dx_0 + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s > 0,$$

since $y \geq 0$. Therefore, x is increasing at $x = 0$. When $y = 0$, $x'(t) = Dx_0 - Dx$ and again at $x = 0$, $x'(t) = Dx_0 > 0$ and hence, x is increasing at $x = 0$. Thus, we can conclude that the solutions of (4.1) are nonnegative for all $t > 0$. □

The following result ensures conditions for boundedness of solutions of (4.1).

Theorem 4.5 *Let $\phi_j(t) \geq 0$ and not identically zero on any interval. Then*

$$x(t) \leq \max\left\{x_0 + \frac{b\gamma c L}{Dd}, \sup_{-\infty<t\leq 0}\{\phi_1(t)\}\right\} \text{ and}$$
$$y(t) \leq \max\left\{\frac{cL}{d}, \sup_{-\infty<t\leq 0}\{\phi_2(t)\}\right\},$$

for all t.

Proof First, we note that if $x' \leq 0$ and $y' \leq 0$ then $x(t) \leq \sup_{-\infty<t\leq 0} \phi_1(t)$ and $y(t) \leq \sup_{-\infty<t\leq 0} \phi_2(t)$, respectively.

Suppose $y' > 0$ for $t > 0$. Then from the second of the equations (4.1), we have $dy(t) < -(\gamma + D) + c\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s$ and from this it follows that $y(t) \leq Lc/d$ since, $U(x) \leq L$.

Similarly, from the first equation of (4.1), if $x' > 0$, then $0 < x' = D(x_0 - x) - aU(x)y + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s$ and from this we have $x(t) \leq x_0 + Lb\gamma c/Dd$ invoking the estimate on y.

That is the solution $(x(t), y(t))$ of (4.1) is bounded and depends on the initial conditions. □

The conditions (i) and (ii) of Theorem 2.28 for uniform boundedness also hold good here.

$$(i) \quad T_{\mathrm{g}} < \frac{a-bc}{acL} \text{ and } T_{\mathrm{f}} < \frac{1}{\gamma}.$$

$$(ii) \quad T_{\mathrm{g}} < \frac{a-c}{acL} \text{ and } T_{\mathrm{f}} < \frac{1}{b\gamma}.$$

4.3 Persistence of Solutions

In this section, we develop persistence and extinction criteria for the competing populations. We use the following definition of persistence (see Definition C.13 of Appendix C).

Definition 4.6 A component $u(t)$ of a given system is said to persist if for any $u(0) > 0$ it follows that $u(t) > 0 \quad \text{for} \quad t > 0$ and $\liminf_{t\to\infty} u(t) > 0$.

Further, if there exists $\delta > 0$ such that $u(t)$ persists and $\liminf_{t\to\infty} u(t) \geq \delta$ independent of $\phi(t) > 0, -\infty < t \leq 0$, where $\phi(t)$ is an initial condition, then $u(t)$ is said to uniformly persist. A system uniformly persists if each component does.

We rewrite the system (4.1) as

$$\begin{aligned} x'(t) &= D(x_0 - x(t)) - aU(x(t))y(t) \\ &\quad + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s, \\ z'(t) &= -\left[c\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - (\gamma + D)\right] z(t) + d, \end{aligned} \tag{4.14}$$

which $z(t) = 1/y(t) \quad \text{for} \quad t > 0$.

Since $U(x) \leq L$for all x, it follows that

$$c\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - (\gamma + D) \leq cL - (\gamma + D) = M \quad \text{(say)}.$$

Now, it is easy to show that the solution $z(t)$ of the second equation in (4.14) satisfies the inequality

$$z(t) \leq \frac{d}{M}(1 - \mathrm{e}^{-Mt}) + z(0)\mathrm{e}^{-Mt},$$

which upon further simplification yields

$$y(t) \leq \frac{y(0)}{\mathrm{e}^{-Mt} + \frac{d}{M}y(0)(1 - \mathrm{e}^{-Mt})} \to \frac{M}{d} \quad \text{as} \ t \to \infty.$$

Accordingly, there exists a $T > 0$ such that

$$y(t) \leq \frac{M+1}{d} \quad \text{for all} \ t \geq T.$$

For our subsequent considerations we let

$$\tilde{y} = \frac{M+1}{d} \ \text{and} \ \tilde{x} = \frac{Dx_0 - [aL + \gamma + D + d\tilde{y}]\tilde{y}}{D}. \tag{4.15}$$

The following theorem establishes the persistence and extinction criteria.

Theorem 4.7 *Assume that the inequalities (4.7) hold.*

Case (i) The solutions of the system (4.1) with the initial conditions, $x(0) > 0$ and $y(s) = \phi_2(s) > 0, s \in (-\infty, 0]$ are uniformly persistent provided, $\tilde{x} > 0$ and $(\gamma + D)/c < L_1$.

Case (ii) If $L_1 < (\gamma + D)/c$ holds, then the species $y(t)$ goes extinct.

Proof Case (i) In the light of the above discussion, we have for each solution $(x(t), y(t))$ with positive initial conditions, there exists a $T > 0$ satisfying

$$y(t) \leq \tilde{y} = \frac{M+1}{d} \quad \text{for all } \ t \geq T.$$

We define the functional

$$V(t) \equiv V(x(t), y(t)) = x(t) + y(t) \quad \text{for } \ t \geq 0.$$

Clearly, $V(0,0) = 0$ and $V(x, y) > 0$ for $x(t) > 0, y(t) > 0$. Now differentiating V along the solutions of (4.1) we have,

$$\begin{aligned} V'(x(t), y(t)) =& V'(t) = x'(t) + y'(t) \\ =& D(x_0 - x(t)) - aU(x(t))y(t) \\ &+ b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s - (\gamma + D)y(t) \\ &+ cy(t) \int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - dy^2(t) \\ \geq& -DV(t) + Dx_0 - (aU(x(t)) + \gamma + dy(t))y(t) \\ \geq& -DV(t) + Dx_0 - (aL + \gamma + d\tilde{y})\tilde{y}. \end{aligned}$$

That is,

$$V'(t) + DV(t) \geq Dx_0 - (aL + \gamma + d\tilde{y})\tilde{y},$$

and thus,

$$V(t) \geq \frac{Dx_0 - (aL + \gamma + d\tilde{y})\tilde{y}}{D} + c_1 \mathrm{e}^{-D(t-T)}.$$

That is,

$$x(t) + y(t) \geq \frac{Dx_0 - (aL + \gamma + d\tilde{y})\tilde{y}}{D} + c_1 \mathrm{e}^{-D(t-T)}$$

From this it follows that

$$\begin{aligned} x(t) &\geq \frac{Dx_0 - (aL + \gamma + d\tilde{y})\tilde{y}}{D} + c_1 \mathrm{e}^{-D(t-T)} - y(t) \\ &\geq \frac{Dx_0 - (aL + \gamma + D + d\tilde{y})\tilde{y}}{D} + c_1 \mathrm{e}^{-D(t-T)}. \end{aligned}$$

That is,

$$x(t) \geq \tilde{x} + c_1 e^{-D(t-T)} > 0 \quad \text{for all } t \geq T.$$

Finally, we have

$$\lim_{t\to\infty} x(t) \geq \tilde{x} > 0. \tag{4.16}$$

Now, since $(\gamma + D)/c < L_1$, we can find $\eta > 0$ such that $(\gamma + D)/c < L_1 - 2\eta$. For this $\eta > 0$, there exists x_M such that for $x \geq x_M$,

$$L_1 - \eta < U(x) < L_1 + \eta, \text{ since } \lim_{x\to\infty} U(x) = L_1.$$

In view of (4.16), we can choose $T > 0$ large enough so that

$$x(t) \geq \max\{\tilde{x}, x_M\} \quad \text{for } t \geq T.$$

Then for $t \geq T$ and $x(t) \geq \max\{\tilde{x}, x_M\}$, we have

$$\frac{\gamma + D}{c} + \eta < L_1 - \eta < U(x) < L_1 + \eta,$$

from which it follows that $U(x) > (\gamma + D)/c + \eta$.

Then from the second equation of (4.1) upon rearranging the terms and solving for y as before, we get for $t \geq T$,

$$\begin{aligned}
y(t) &= y(T)\Big[\exp\Big(\int_T^t (\gamma + D - c\int_{-\infty}^t g(\tau - s)U(x(s)\mathrm{d}s)\mathrm{d}\tau\Big) \\
&\quad + dy(T)\int_T^t \exp\Big(\int_{\tau_1}^t (\gamma + D - c\int_{-\infty}^{\tau} g(\tau - s)U(x(s))\mathrm{d}s)\mathrm{d}\tau\Big)\mathrm{d}\tau_1\Big]^{-1} \\
&\geq y(T)\Big[\exp(-\eta(t - T)) + dy(T)\int_T^t \exp(-\eta(t - \tau_1)\mathrm{d}\tau_1\Big]^{-1} \\
&= y(T)\Big[e^{-\eta(t-T)} + \frac{d}{\eta}y(T)(1 - e^{-\eta(t-T)})\Big]^{-1}
\end{aligned}$$

and thus, we have $\liminf_{t\to\infty} y(t) \geq (\eta/d) > 0$. □

Proof Case (ii): If $L_1 < (\gamma + D)/c$, by arguing as in Case (i), we can find $T_1 > 0$, $\eta_1 > 0$, and x_{M_1} such that for $t \geq T_1$ and $x \geq \max\{\tilde{x}, x_{M_1}\}$.

$$U(x) < L_1 + \eta_1 < \frac{\gamma + D}{c}.$$

Then from the second equation of (4.1) we have $y'(t) < 0$ for $t \geq T_1$ and hence, $\lim_{t\to\infty} y(t) = 0$. Thus the conclusion follows. □

4.4 Global Asymptotic Stability Results

We note that the system (4.1) has a partially feasible equilibrium $(x_0, 0)$ which lies on the axis and Theorems 4.2 and 4.3 ensure the existence of a unique interior equilibrium solution (x^*, y^*) under fairly general circumstances. The first result in this section establishes the global asymptotic stability of the axial equilibrium $(x_0, 0)$ and is a replica of Theorem 2.32 of Chap. 2 and hence, the details are omitted.

Theorem 4.8 *The partially feasible equilibrium* $(x_0, 0)$ *of* (4.1) *is globally asymptotically stable if* $L_1 < (\gamma + D)/c$.

It is interesting to note that if $L_1 > (\gamma + D)/c$, solutions are uniformly persistent and if the above inequality is reversed, we have global stability which corresponds to the extinction of $y(t)$.

In the reminder of this section, we present several easily verifiable independent sets of sufficient conditions for the global asymptotic stability of (x^*, y^*).

We now rewrite (4.10) as

$$\begin{aligned} x'(t) &= -D(x(t) - x^*) - aU(x(t))(y(t) - y^*) \\ &\quad -ay^*(U(x(t)) - U(x^*)) + b\gamma \int_0^\infty f(s)(y(t-s) - y^*)\mathrm{d}s, \quad (4.17) \\ y'(t) &= y(t)\Big[c\int_0^\infty g(s)(U(x(t-s)) - U(x^*))\mathrm{d}s - d(y(t) - y^*)\Big]. \end{aligned}$$

We now state and prove our next result.

Theorem 4.9 *Assume that the uptake function* $U(x)$ *satisfies* (A_1) *and* (A_2) *and the delay kernels satisfy* (H_1) *and* (H_2)*. The equilibrium solution* (x^*, y^*) *of* (4.1) *is globally asymptotically stable provided,*

$$D - (c - ay^*)k > 0 \text{ and } \Delta \equiv \min_{x \geq x^*}\{d + aU(x) - b\gamma\} > 0.$$

Proof We consider the functional

$$\begin{aligned} V(t) \equiv V(x(t), y(t)) &= |x(t) - x^*| + |\log\,(y(t)) - \log\, y^*| \\ &\quad + b\gamma \int_0^\infty f(s) \int_{t-s}^t |y(u) - y^*| \mathrm{d}u\, \mathrm{d}s \\ &\quad + c\int_0^\infty g(s) \int_{t-s}^t |U(x(u)) - U(x^*)| \mathrm{d}u\, \mathrm{d}s. \end{aligned}$$

Clearly, $V(x^*, y^*) = 0$ and

$$V(x(t), y(t)) \geq |x(t) - x^*| + |\log\,(y(t)) - \log\, y^*| > 0.$$

The upper Dini derivative of V along the solutions of (4.1), using (4.17) is given by

$$\begin{aligned}D^+V \le & -D|x(t)-x^*| - aU(x(t))|y(t)-y^*| - ay^*|U(x(t))-U(x^*)| \\ & + b\gamma\int_0^\infty f(s)|y(t-s)-y^*|\mathrm{d}s \\ & + cy(t)\int_0^\infty g(s)|U(x(t-s))-U(x^*)|\mathrm{d}s - d|y(t)-y^*| \\ & + b\gamma|y(t)-y^*| - b\gamma\int_0^\infty f(s)|y(t-s)-y^*|\mathrm{d}s \\ & + c|(Ux(t))-U(x^*)| - cy(t)\int_0^\infty g(s)|U(x(t-s))-U(x^*)|\mathrm{d}s,\end{aligned}$$

invoking (H_1) on the delay kernels. Now,

$$\begin{aligned}D^+V \le & -D|x(t)-x^*| - aU(x(t))|y(t)-y^*| - ay^*|U(x(t))-U(x^*)| \\ & + b\gamma|y(t)-y^*| + c|(Ux(t))-U(x^*)| - d|y(t)-y^*| \\ = & -D|x(t)-x^*| + (c-ay^*)|U(x)-U(x^*)| \\ & -(d+aU(x)-b\gamma)|y(t)-y^*|.\end{aligned}$$

If $c \le ay^*$, then the condition $\min_{x \ge x^*}\{d+aU(x)-b\gamma\} > 0$ is alone sufficient to ensure the negative definiteness of D^+V. Hence, we assume that $c > ay^*$. Then we have,

$$\begin{aligned}D^+V \le & -D|x(t)-x^*| + (c-ay^*)|U(x)-U(x^*)| \\ & -(d+aU(x)-b\gamma)|y(t)-y^*| \\ < & -(D+aky^*-ck)|x(t)-x^*| - \Delta|y(t)-y^*| < 0,\end{aligned}$$

invoking the hypotheses.

Thus,

$$D^+V < -(D+aky^*-ck)|x(t)-x^*| - \frac{\Delta}{k_3}|\log\ y(t) - \log\ y^*| < 0, \quad (4.18)$$

where $k_3 > 0$ is such that $|\log\ y(t) - \log\ y^*| \le k_3|y(t)-y^*|$.

Now integrating (4.18) with respect to t from 0 to t, we get

$$V(t) + (D-ck+ay^*k)\int_0^t |x(s)-x^*|\mathrm{d}s + \frac{\Delta}{k_3}\int_0^t |\log\ y(s) - \log\ y^*|\mathrm{d}s \le V(0).$$

Therefore, $V(t) \equiv V(x(t),y(t))$ is bounded on $[0,\infty)$ and since $x(t), y(t)$ are bounded on $[0,\infty)$, $|x(t)-x^*|$ and $|\log\ y(t) - \log\ y^*|$ are bounded on $[0,\infty)$ and these imply the boundedness of their derivatives on $[0,\infty)$.

Now the conclusion follows from Theorem C.11 of Appendix C as discussed in Theorem 2.35. □

We now state and prove our next result in which we replace the condition (A_2) on U by a gradient type condition.

We need the following inequality.

Lemma 4.10 *For all real a, b, and $\eta > 0$, we have*

$$ab \leq \frac{1}{4\eta}a^2 + \eta b^2.$$

Proof The proof is obvious from the observation that for all a, b and $\eta > 0$,

$$0 \leq \left(\frac{a}{2\sqrt{\eta}} - b\sqrt{\eta}\right)^2 = \frac{1}{4\eta}a^2 + \eta b^2 - ab.$$

□

Theorem 4.11 *Assume that the delay kernels satisfy (H_1) and (H_2) and the uptake function $U(x)$ satisfies (A_1). Further, assume that $(x - x^*)[U(x) - U(x^*)] > 0$ and $U(x) = U(x^*)$ if and only if $x = x^*$. The positive equilibrium point (x^*, y^*) is global asymptotically stable provided there exist positive constants η_1 and η_2 such that*

$$4D\eta_1 - b\gamma > 0, \;\; 4d\eta_2 - c > 0 \quad \textit{and}$$
$$(4d\eta_2 - c)\sqrt{4D\eta_1 - b\gamma} \quad \delta y^* \geq 8cL\eta_1\eta_2^2\sqrt{b\gamma}$$

in which $\delta = \min_{x\geq 0}\{\frac{x-x^*}{U(x)-U(x^*)}\} > 0$

Proof We consider the functional

$$\begin{aligned} V(t) \equiv V(x(t), y(t)) = \frac{W_1}{2}(x(t) - x^*)^2 + W_2 \int_0^{y(t)-y^*} \frac{z}{z + y^*}\mathrm{d}z \\ +W_3 \int_0^\infty g(s) \int_{t-s}^t [U(x(t_1)) - U(x^*)]^2 \mathrm{d}t_1\, \mathrm{d}s \\ +W_4 \int_0^\infty f(s) \int_{t-s}^t [y(t_1) - y^*]^2 \mathrm{d}t_1, \mathrm{d}s, \end{aligned}$$

where W_1, W_2, W_3, and W_4 are positive constants which will be determined in due course.

Clearly, $V(x^*, y^*) = 0$ and

$$V(x(t), y(t)) \geq \frac{W_1}{2}(x(t) - x^*)^2 + W_2 \int_0^{y(t)-y^*} \frac{z}{z + y^*}\mathrm{d}z > 0.$$

Now the time derivative of V along the solutions of (4.1) is given by

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= W_1(x(t)-x^*)\Big\{Dx_0 - Dx(t) - aU(x(t))y(t)\\ &\quad + b\gamma\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s\Big\} + W_2(y(t)-y^*)\Big\{-(\gamma+D)\\ &\quad + c\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - \mathrm{d}y(t)\Big\} + W_3[U(x(t))-U(x^*)]^2\\ &\quad - W_3\int_0^\infty g(s)[U(x(t-s))-U(x^*)]^2\mathrm{d}s + W_4[y(t)-y^*]^2\\ &\quad - W_4\int_0^\infty f(s)[y(t-s)-y^*]^2\mathrm{d}s.\end{aligned}$$

Using (4.9) in this we obtain,

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= W_1(x(t)-x^*)\Big\{-D(x(t)-x^*) - aU(x(t))(y(t)-y^*)\\ &\quad - ay^*(U(x(t)-U(x^*)) + b\gamma\int_0^\infty f(s)(y(t-s)-y^*)\mathrm{d}s\Big\}\\ &\quad + W_2(y(t)-y^*)\Big\{c\int_0^\infty g(s)[U(x(t-s))-U(x^*)]\mathrm{d}s - d(y(t)-y^*)\Big\}\\ &\quad + W_3[U(x(t))-U(x^*)]^2 - W_3\int_0^\infty g(s)[U(x(t-s))-U(x^*)]^2\mathrm{d}s\\ &\quad + W_4[y(t)-y^*]^2 - W_4\int_0^\infty f(s)[y(t-s)-y^*]^2\mathrm{d}s\\ &\le \Big\{-W_1D(x(t)-x^*)^2 - W_1aU(x(t))(x(t)-x^*)(y(t)-y^*)\\ &\quad - W_1ay^*(x(t)-x^*)(U(x(t))-U(x^*))\\ &\quad + W_1\frac{b\gamma}{4\eta_1}[x(t)-x^*]^2 + W_1b\gamma\eta_1\int_0^\infty f(s)[y(t-s)-y^*]^2\mathrm{d}s\Big\}\\ &\quad + \Big\{W_2\frac{c}{4\eta_2}[y(t)-y^*]^2 + W_2c\eta_2\int_0^\infty g(s)[U(x(t-s))-U(x^*)]^2\mathrm{d}s\\ &\quad - W_2\mathrm{d}[y(t)-y^*]^2\Big\}\\ &\quad + W_3[U(x(t))-U(x^*)]^2 - W_3\int_0^\infty g(s)[U(x(t-s))-U(x^*)]^2\mathrm{d}s\\ &\quad + W_4[y(t)-y^*]^2 - W_4\int_0^\infty f(s)[y(t-s)-y^*]^2\mathrm{d}s,\end{aligned}$$

utilizing the Lemma 4.10 for arbitrary $\eta_1 > 0$ and $\eta_2 > 0$ in the fourth, fifth terms of the above equality. Then,

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} \leq & -W_1 a y^*(x(t)-x^*)(U(x(t)-U(x^*)) + W_3(U(x(t))-U(x^*))^2 \\ & -\Big\{W_1\left(D-\frac{b\gamma}{4\eta_1}\right)(x(t)-x^*)^2 + W_1 a U(x)(x(t)-x^*)(y(t)-y^*) \\ & +\left[W_2\left(d-\frac{c}{4\eta_2}\right)-W_4\right](y(t)-y^*)^2\Big\} \\ & -(W_3-W_2 c\eta_2)\int_0^\infty g(s)[U(x(t-s))-U(x^*)]^2\mathrm{d}s \\ & -(W_4-W_1 b\gamma\eta_1)\int_0^\infty f(s)[y(t-s)-y^*]^2\mathrm{d}s.\end{aligned}$$

Thus, $\mathrm{d}V/\mathrm{d}t < 0$ if

$$\begin{aligned}&\text{(i)} \quad W_4 \geq W_1 b\gamma\eta_1,\\ &\text{(ii)} \quad W_3 \geq W_2 c\eta_2,\\ &\text{(iii)} \quad W_1 a y^*\delta > W_3,\end{aligned}$$

and

$$\text{(iv)} \quad D-\frac{b\gamma}{4\eta_1} > 0, \quad W_2\left(d-\frac{c}{4\eta_2}\right) > W_4$$

and

$$[W_1 a U(x)]^2 < 4W_1\left(D-\frac{b\gamma}{4\eta_1}\right)\left[W_2\left(d-\frac{c}{4\eta_2}\right)-W_4\right].$$

These four conditions imply that $\frac{\mathrm{d}V}{\mathrm{d}t}$ is negative definite if,

$$a^2L^2 < 4\left(D-\frac{b\gamma}{4\eta_1}\right)\left[\frac{ay^*\delta}{c\eta_2}\left(d-\frac{c}{4\eta_2}\right)-b\gamma\eta_1\right]. \tag{4.19}$$

Now consider

$$a^2L^2 = 4\left(D-\frac{b\gamma}{4\eta_1}\right)\left[\frac{ay^*\delta}{c\eta_2}\left(d-\frac{c}{4\eta_2}\right)-b\gamma\eta_1\right].$$

This, after some simplification, becomes

$$4c\eta_1\eta_2^2L^2a^2-(4D\eta_1-b\gamma)(4d\eta_2-c)\delta y^*a + 4b\gamma c(4D\eta_1-b\gamma)\eta_1\eta_2^2 = 0. \tag{4.20}$$

Solving for "a", we get

$$a = \frac{(4D\eta_1 - b\gamma)(4d\eta_2 - c)\delta y^*}{8cL^2\eta_1\eta_2^2} \pm \frac{\sqrt{(4D\eta_1 - b\gamma)^2(4d\eta_2 - c)^2\delta^2 y^{*2} - 64b\gamma c^2 L^2(4D\eta_1 - b\gamma)\eta_1^2\eta_2^4}}{8cL^2\eta_1\eta_2^2}.$$

By the hypotheses, $4D\eta_1 - b\gamma > 0, 4d\eta_2 - c > 0$, and hence, "$a$" exists and is a positive root of (4.20) provided

$$(4D\eta_1 - b\gamma)^2(4d\eta_2 - c)^2\delta^2 y^{*2} \geq 64b\gamma c^2 L^2(4D\eta_1 - b\gamma)\eta_1^2\eta_2^4.$$

That is,

$$(4d\eta_2 - c)\delta y^* \sqrt{4D\eta_1 - b\gamma} \geq 8cL\eta_1\eta_2^2\sqrt{b\gamma}. \tag{4.21}$$

For this value of "a", the inequality (4.19) is clearly satisfied, and hence, the conclusion of the theorem follows. □

Theorem 4.12 *Assume that the delay kernels satisfy the conditions* (H_1) *and* (H_2) *and the uptake function satisfies* (A_1). *The equilibrium solution* (x^*, y^*) *of* (4.1) *is globally asymptotically stable provided there exist constants* $\eta_1 > 0$ *and* $\eta_2 > 0$ *such that*

$$D - \frac{b\gamma}{4\eta_1} + A > 0, \quad d - \frac{c}{4\eta_2} - b\gamma\eta_1 > 0$$

$$\textit{and} \quad a^2L^2 < 4\left\{D - \frac{b\gamma}{4\eta_1} + A\right\}\left[d - \frac{c}{4\eta_2} - b\gamma\eta_1\right] \quad \textit{in which}$$

$$A = \min_{x\geq 0}\left\{ay^*\left(\frac{U(x) - U(x^*)}{x - x^*}\right) - c\eta_2\left(\frac{U(x) - U(x^*)}{x - x^*}\right)^2\right\}.$$

Proof We consider the functional

$$V(t) \equiv V(x(t), y(t)) = \frac{1}{2}(x(t) - x^*)^2 + \int_0^{y(t)-y^*} \frac{z}{z + y^*}\mathrm{d}z$$
$$+ c\eta_2 \int_0^\infty g(s) \int_{t-s}^t [U(x(t_1)) - U(x^*)]^2 \mathrm{d}t_1 \mathrm{d}s$$
$$+ b\gamma\eta_1 \int_0^\infty f(s) \int_{t-s}^t [y(t_1) - y^*]^2 \mathrm{d}t_1 \mathrm{d}s.$$

Clearly, $V(x^*, y^*) = 0$ and

$$V(x(t), y(t)) \geq \frac{1}{2}(x(t) - x^*)^2 + \int_0^{y(t)-y^*} \frac{z}{z + y^*}\mathrm{d}z > 0.$$

Now the time derivative of V along the solutions of (4.1) is given by

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= (x(t)-x^*)x'(t) + \frac{(y(t)-y^*)}{y(t)}y'(t)\\ &+ c\eta_2[U(x(t))-U(x^*)]^2 - c\eta_2\int_0^\infty g(s)[U(x(t-s))-U(x^*)]^2\mathrm{d}s\\ &+ b\gamma\eta_1[y(t)-y^*]^2 - b\gamma\eta_1\int_0^\infty f(s)[y(t-s)-y^*]^2\mathrm{d}s.\end{aligned}$$

Using (4.9) in this we obtain,

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= (x(t)-x^*)\Big\{-D(x(t)-x^*) - aU(x(t))(y(t)-y^*)\\ &- ay^*(U(x(t)-U(x^*)) + b\gamma\int_0^\infty f(s)(y(t-s)-y^*)\mathrm{d}s\Big\}\\ &+ (y(t)-y^*)\Big\{c\int_0^\infty g(s)[U(x(t-s))-U(x^*)]\mathrm{d}s - d(y(t)-y^*)\Big\}\\ &+ c\eta_2[U(x(t))-U(x^*)]^2 - c\eta_2\int_0^\infty g(s)[U(x(t-s))-U(x^*)]^2\mathrm{d}s\\ &+ b\gamma\eta_1[y(t)-y^*]^2 - b\gamma\eta_1\int_0^\infty f(s)[y(t-s)-y^*]^2\mathrm{d}s.\end{aligned}$$

Utilizing the Lemma for arbitrary $\eta_1 > 0$ and $\eta_2 > 0$ in the fourth and fifth terms on the right-hand side of the above equation and invoking (H_1) on the delay kernels and simplifying, we get

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &\le \Big\{-D(x(t)-x^*)^2 - aU(x(t))(x(t)-x^*)(y(t)-y^*)\\ &- ay^*(x(t)-x^*)(U(x(t))-U(x^*))\\ &+ \frac{b\gamma}{4\eta_1}[x(t)-x^*]^2 + b\gamma\eta_1\int_0^\infty f(s)[y(t-s)-y^*]^2\mathrm{d}s\Big\}\\ &+ \Big\{\frac{c}{4\eta_2}[y(t)-y^*]^2 + c\eta_2\int_0^\infty g(s)[U(x(t-s))-U(x^*)]^2\mathrm{d}s\\ &- d[y(t)-y^*]^2\Big\}\\ &+ c\eta_2[U(x(t))-U(x^*)]^2 - c\eta_2\int_0^\infty g(s)[U(x(t-s))-U(x^*)]^2\mathrm{d}s\\ &+ b\gamma\eta_1[y(t)-y^*]^2 - b\gamma\eta_1\int_0^\infty f(s)[y(t-s)-y^*]^2\mathrm{d}s\\ &= -ay^*(x(t)-x^*)(U(x(t)-U(x^*)) + c\eta_2(U(x(t))-U(x^*))^2\\ &- \Big\{\left(D-\frac{b\gamma}{4\eta_1}\right)(x(t)-x^*)^2 + aU(x)(x(t)-x^*)(y(t)-y^*)\\ &+ \left[\left(d-\frac{c}{4\eta_2}\right) - b\gamma\eta_1\right](y(t)-y^*)^2\Big\}\end{aligned}$$

$$= -\left\{\left[D - \frac{b\gamma}{4\eta_1} + ay^* \frac{(U(x(t) - U(x^*))}{(x(t) - x^*)}\right.\right.$$
$$\left. - c\eta_2 \left(\frac{(U(x(t)) - U(x^*)}{(x(t) - x^*)}\right)^2\right] (x(t) - x^*)^2$$
$$\left. + aU(x)(x(t) - x^*)(y(t) - y^*) + \left[\left(d - \frac{c}{4\eta_2}\right) - b\gamma\eta_1\right] (y(t) - y^*)^2\right\}$$
$$= -\left\{\left(D - \frac{b\gamma}{4\eta_1} + A\right)(x(t) - x^*)^2 + aU(x)(x(t) - x^*)(y(t) - y^*)\right.$$
$$\left. + \left[\left(d - \frac{c}{4\eta_2}\right) - b\gamma\eta_1\right](y(t) - y^*)^2\right\}.$$

Then $\mathrm{d}V/\mathrm{d}t < 0$ provided

$$(aU(x))^2 < 4\left[D - \frac{b\gamma}{4\eta_1} + A\right]\left[\left(d - \frac{c}{4\eta_2}\right) - b\gamma\eta_1\right].$$

Since $U(x) \le L$ for all x, $\mathrm{d}V/\mathrm{d}t < 0$ if,

$$a^2L^2 < 4\left[D - \frac{b\gamma}{4\eta_1} + A\right]\left[\left(d - \frac{c}{4\eta_2}\right) - b\gamma\eta_1\right].$$

Now let $Q(t) = (x(t) - x^*, y(t) - y^*)^{\mathrm{T}}$,

$$P = \begin{pmatrix} D - \frac{b\gamma}{4\eta_1} + A & \frac{aL}{2} \\ \frac{aL}{2} & d - \frac{c}{4\eta_2} - b\gamma\eta_1 \end{pmatrix}.$$

Then we have

$$\frac{\mathrm{d}V}{\mathrm{d}t} \le -Q(t)^{\mathrm{T}} P Q(t) \le -\bar{\lambda}((x(t) - x^*)^2 + (y(t) - y^*)^2),$$

for some $\bar{\lambda} > 0$, implying the negative definiteness of dV/dt. Now the conclusion follows from standard arguments. The proof is complete. □

In the following result we relax the condition (H_2) on the delay kernels as in Theorem 2.35 at the expense of placing more restrictions on the parameters of the system.

Theorem 4.13 *Assume that the delay kernels satisfy the condition* (H_1). *Further, assume that the uptake function* $U(x)$ *satisfies* (A_1) *and* (A_2). *The equilibrium solution* (x^*, y^*) *of* (4.1) *is globally asymptotically stable provided,*

$$b\gamma + ck < \min\left\{D - aky^*, \min_{x \ge x^*}\{d + aU(x)\}\right\} = \beta \text{ (say)}. \tag{4.22}$$

Proof We consider the following functional

$$V(x(t), y(t)) = |x(t) - x^*| + |\log\ y(t) - \log\ y^*|.$$

The upper Dini derivative of V along the solutions of (4.1), using (4.10) is given by,

$$\begin{aligned}
D^+V &= -D|x(t) - x^*| - a|U(x(t))y(t) - U(x^*)y^*| \\
&\quad + b\gamma \int_0^\infty f(s)|y(t-s) - y^*|\mathrm{d}s \\
&\quad + c\int_0^\infty g(s)|U(x(t-s)) - U(x^*)|\mathrm{d}s - d|y(t) - y^*| \\
&\le -D|x(t) - x^*| - aU(x(t))|y(t) - y^*| + ay^*|U(x(t)) - U(x^*)| \\
&\quad + b\gamma \int_0^\infty f(s)|y(t-s) - y^*| \\
&\quad + c\int_0^\infty g(s)|U(x(t-s)) - U(x^*)|\mathrm{d}s - d|y(t) - y^*| \\
&\le -(D - aky^*)|x(t) - x^*| + ck\int_0^\infty g(s)|x(t-s) - x^*|\mathrm{d}s \\
&\quad - (d + aU(x(t))|y(t) - y^*| + b\gamma\int_0^\infty f(s)|y(t-s) - y^*|\mathrm{d}s \\
&\le -(D - aky^*)|x(t) - x^*| + ck\int_0^\infty g(s)|x(t-s) - x^*|\mathrm{d}s \\
&\quad - (d + aU(x(t)))|\log\ y(t) - \log\ y^*| \\
&\quad + b\gamma\int_0^\infty f(s)|\log\ y(t) - \log\ y^*|\mathrm{d}s \\
&\le -\beta V(t) + ck\int_0^\infty g(s)V(t-s)\mathrm{d}s \\
&\quad + b\gamma\int_0^\infty f(s)V(t-s)\mathrm{d}s.
\end{aligned} \tag{4.23}$$

Since $x(t)$ and $y(t)$ are bounded, $V(t)$ is bounded. Further, for $-\infty < t \le 0$, we have

$$\begin{aligned}
V(t) &= |x(t) - x^*| + \left|\log\left[\frac{y(t)}{y^*}\right]\right| = |\phi_1(t) - x^*| + \left|\log\left[\frac{\phi_2(t)}{y^*}\right]\right| \\
&= \sup_{-\infty<t\le 0}\left\{|\phi_1(t) - x^*| + \left|\log\left[\frac{\phi_2(t)}{y^*}\right]\right|\right\} = M_2 \quad \text{(say)}
\end{aligned}$$

We claim that $V(t) \leq M_2$ for all $t > 0$. Otherwise, we can find $t_1 > 0$ such that $V(t_1) = M_2$ and $V(t) < M_2$ for $-\infty < t < t_1$.

But from (4.23),

$$D^+V(t_1) \leq -\beta M_2 + b\gamma \int_0^\infty f(s)M_2 \mathrm{d}s + ck \int_0^\infty g(s)M_2 \mathrm{d}s$$

$$= -(\beta - b\gamma - ck)M_2 < 0.$$

This contradiction proves that $V(t) \leq M_2$ for all $t > 0$.

Now, let $\limsup_{t\to\infty} V(t) = \bar{\sigma}$ and $\liminf_{t\to\infty} V(t) = \underline{\sigma}$.

We shall prove that $\bar{\sigma} = 0$. Assume that $\bar{\sigma} > 0$ and choose $\epsilon > 0$ such that

$$\epsilon < \frac{1}{2}\left[\frac{\beta - b\gamma - ck}{\beta + (1 + M_2)(b\gamma + ck)}\right]\bar{\sigma}.$$

Since, $\int_0^\infty f(s)\mathrm{d}s = 1$ and $\int_0^\infty g(s)\mathrm{d}s = 1$, there exists a $T > 0$ such that $\int_T^\infty f(s)\mathrm{d}s < \epsilon$ and $\int_T^\infty g(s)\mathrm{d}s < \epsilon$.

Arguing as in Theorem 2.35, we can show that corresponding to this $\epsilon > 0$, we can find a $t_1 > 0$ such that

$$\bar{\sigma} - \epsilon \leq V(t - \tau) \leq \bar{\sigma} + \epsilon \quad \text{for } t > t_1,\ \tau > 0.$$

Then from (4.23) for $t > t_1 + T = t_2$,

$$D^+V(t) \leq -\beta V(t) + ck\left[\int_T^\infty g(s)M_2 \mathrm{d}s + \int_0^T g(s)(\bar{\sigma} + \epsilon)\mathrm{d}s\right]$$

$$+ b\gamma\left[\int_T^\infty f(s)M_2 \mathrm{d}s + \int_0^T f(s)(\bar{\sigma} + \epsilon)\mathrm{d}s\right]$$

$$\leq -\beta(\bar{\sigma} - \epsilon) + (b\gamma + ck)M_2\epsilon + (b\gamma + ck)(\bar{\sigma} + \epsilon)$$

$$< -[\beta - (b\gamma + ck)]\bar{\sigma}/2$$

by choice of $\epsilon > 0$. The Mean Value Theorem suggests that there exists a $\xi \in [0, \infty)$ such that for $t_3 \geq t_2,\ t \geq t_3$,

$$V(t) - V(t_3) = V'(\xi)(t - t_3).$$

That is,

$$V(t) = V(t_3) + (t - t_3)V'(\xi) \leq V(t_3) - (\beta - b\gamma - ck)\frac{\bar{\sigma}}{2}(t - t_3).$$

The right-hand side of this inequality approaches "$-\infty$" as $t \to \infty$ (for, $V(t)$ is bounded). But by definition, $V(t) \geq 0$.

This contradiction proves that the assumption $\bar{\sigma} > 0$ is wrong. Therefore, $\bar{\sigma} = 0$, which means that $-\epsilon < V(t) < \epsilon$ for $t \geq t_3$. Thus, in the limiting case, $V(t) \to 0$.

Thus, $\lim_{t\to\infty}[|x(t) - x^*| + |\log(y(t)/y^*)|] = 0$. Hence, the theorem. □

The following examples establish that the global asymptotic stability criteria obtained in Theorems 4.10 and 4.11 are independent.

Example 4.14 Consider the following model

$$x'(t) = 2(x_0 - x(t)) - 18U(x(t))y(t) + (0.25)\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s$$

$$y'(t) = -3y(t) + 16y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - 10y^2(t)$$

in which $U(x) = x/(4+x), b = 0.25, \gamma = 1, D = 2$, and $x_0 = 3.85$ approximately.

The equilibrium solutions are $x^* = 8/3$ and $y^* = 0.34$ with $U(x^*) = 2/5$ and $\delta = 20/3$.

Since $D - (ck - aky^*) < 0$, Theorem 4.10 cannot be applied here.

Now with $\eta_1 = \eta_2 = 1/2$, it is easy to see that all the hypotheses of Theorem 4.11 are satisfied and the equilibrium $(8/3, 0.34)$ is globally asymptotically stable by virtue of Theorem 4.11.

Example 4.15 Consider the following model,

$$x'(t) = 2(x_0 - x(t)) - 20U(x(t))y(t) + (0.5)\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s$$

$$y'(t) = -3y(t) + 19y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - 2y^2(t)$$

in which

$$U(x) = \begin{cases} \frac{x}{10+x^2} & , 0 \leq x < 4 \\ \frac{2}{13} & , \text{otherwise} \end{cases}.$$

Clearly $U(x)$ is the generalized Michaelis–Menten uptake function defined in (3.1) for the choice of $\tilde{\alpha} = 1, \tilde{\beta} = 2$, and $\omega = 10$.

Also in the above system, it is chosen that $b = 0.5, \gamma = 1$, and $D = 2$. Then the equilibrium solutions are $x^* = \sqrt{10}$, $y^* = 0.00195$, $U(x^*) = 0.1581$ (approximately), $k = \frac{1}{10}, \delta = 20$ with $x_0 = 3.16487$ approximately.

It is easy to check that all the hypotheses of Theorem 4.10 are satisfied here and hence, $(x^*, y^*) = (\sqrt{10}, 0.00195)$ is globally asymptotically stable.

A straightforward computation yields that the inequality (4.20) in Theorem 4.11 is violated for any choice of η_1 and η_2.

Hence, Theorem 4.11 cannot establish the global asymptotic stability of $(x^*, y^*) = (\sqrt{10}, 0.00195)$.

From Examples 4.14 and 4.15 it follows that Theorems 4.10 and 4.11 are independent of each other.

The following example illustrates Theorem 4.13.

Example 4.16 Consider the following model

$$x'(t) = 9(x_0 - x(t)) - 20U(x(t))y(t) + (1/3)\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s,$$
$$y'(t) = -10y(t) + 16y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - 2y^2(t)$$

in which $U(x) = x/(5+x), b = 1/3, \gamma = 1, D = 9$, and $x_0 = 10.481$ approximately.

The equilibrium solutions are $x^* = 10$ and $y^* = 8/3$ with $U(x^*) = 2/3$.

Clearly, all the hypotheses of Theorem 4.13 are satisfied with $\beta = 9$. Hence, $(10, 1/3)$ is globally asymptotically stable by virtue of Theorem 4.13.

We now provide two more sets of sufficient conditions for the global stability of the positive equilibrium of (4.1).

The following notation is used here.

$x_1 = x - x^*$, $y_1 = y - y^*$, and $U_1(x_1) = U(x) - U(x^*)$.

This transforms (4.1) to

$$\begin{aligned} x_1{}'(t) &= -Dx_1(t)) - aU_1(x_1(t))(y_1(t) + y^*) + aU(x^*)y_1 \\ &\quad + b\gamma\int_0^{\infty} f(s)y_1(t-s)\mathrm{d}s, \end{aligned} \tag{4.24}$$

$$y_1{}'(t) = (y_1(t) + y^*)\Big[c\int_0^{\infty} g(s)U_1(x(t-s))\mathrm{d}s, -dy_1(t)\Big].$$

Theorem 4.17 *Assume that the delay kernels satisfy* (H_1) *and* (H_2) *and the uptake function, in addition to* (A_1) *and* (A_2), *satisfies*

$$x_1U_1(x_1) \geq 0, \quad U_1(x_1) \neq 0 \quad \textit{for} \;\; x_1 \neq 0 \; .$$

The equilibrium solution $(0, 0)$ *of* (4.24) *is globally asymptotically stable provided*

$$d > \frac{(b\gamma c)^2\left[\sqrt{1 + \frac{a^2}{(b\gamma)^2}} + \frac{a}{b\gamma}\right]^2}{4aD\alpha(cU(x^*) - \gamma - D)} \tag{4.25}$$

in which

$$\alpha = \min_{x \geq x^*}\left\{\frac{x_1}{U_1(x_1)}\right\} > 0$$

.

Proof Consider the functional,

$$V(t) = W_1 \int_0^{x_1} U_1(u)\mathrm{d}u + W_2 \left[y_1 - y^* \log\left(\frac{y_1 + y^*}{y^*} \right) \right]$$
$$+ W_3 \int_0^{\infty} g(s) \int_{t-s}^{t} U_1^2(x_1(u))\mathrm{d}u\, \mathrm{d}s$$
$$+ W_4 \int_0^{\infty} f(s) \int_{t-s}^{t} y_1^2(u)\mathrm{d}u\, \mathrm{d}s.$$

The parameters $W_i > 0,\ \ i = 1, 2, 3, 4$ are determined in the due course. Differentiating V with reference to t along the solutions of (4.24), we have

$$V'(t) = W_1 U_1(x_1)x_1' + W_2 y_1 y_1' + W_3\Big[U_1^2(x_1) - \int_0^{\infty} g(s)U_1^2(x_1(t-s))\mathrm{d}s\Big]$$
$$+W_4 y_1^2 - W_4 \int_0^{\infty} f(s)y_1^2(t-s)\mathrm{d}s.$$

After some simplifications and a rearrangement, we obtain

$$V'(t) = -W_1 D U_1(x_1)x_1 + W_3 U_1^2(x_1)$$
$$-\Big\{\epsilon W_1 a y^* {U_1}^2(x_1) + W_1 a(U_1(x_1) + U(x^*))U_1(x_1)y_1$$
$$+\nu(W_2 a - W_4)y_1^2\Big\} - \int_0^{\infty} f(s)\left[(1-\epsilon)W_1 a y^* U_1^2(x_1)\right.$$
$$\left.-W_1 b\gamma U_1(x_1)y_1(t-s) + W_4 y_1^2(t-s)\right]\mathrm{d}s$$
$$-\int_0^{\infty} g(s)\left[(1-\nu)(W_2 d - W_4)y_1^2 - W_2 c y_1 U_1(x_1(t-s))\right.$$
$$\left.+W_3 U_1^2(x_1(t-s))\right]\mathrm{d}s,$$

where $0 < \epsilon, \nu < 1$.

Now $V'(t) < 0$ provided,

(i) $W_3 < W_1 D\tilde{\alpha}$,

(ii) $[W_1 a(U_1(x_1)) + U(x^*))]^2 < 4\epsilon W_1 a y^* \nu(W_2 d - W_4)$,

(iii) $(W_1 b\gamma)^2 < 4(1-\epsilon)W_1 a y^* W_4$, *and*

(iv) $W_4(W_2 d - W_4) > \left[\dfrac{W_2 c}{4(1-\nu)}\right]^2$.

Let $W_2 d = 2W_4$. Then, we get after eliminating $W_i,\ i = 1, 2, 3, 4$ from (i), (ii), (iii), and (iv),

$$D\tilde{\alpha} > \frac{c^2}{2d(1-\mu)} \frac{1}{2dy^*a} \max\left\{\frac{c\nu}{a^2L}, \frac{(b\gamma)^2}{(1-\epsilon)}\right\},$$

which on further rearrangement gives

$$d > \frac{(b\gamma c)^2}{4D\tilde{\alpha}(cU(x^*)-\gamma-D)} \left[\sqrt{1+\frac{a^2L}{(b\gamma)^2}} + \frac{a\sqrt{L}}{b\gamma}\right]^2$$

as a sufficient condition for the negative definiteness of $\mathrm{d}V/\mathrm{d}t$ and the conclusion follows form standard arguments. □

Let us rewrite (4.1) as

$$\begin{aligned} {x_1}'(t) &= D(x_0 - x_1(t) - x^*) - a(U_1(x_1(t)) + U(x^*))(y_1(t) + y^*) \\ &\quad + b\gamma \int_0^\infty f(s)(y_1(t-s) + y^*)\mathrm{d}s, \\ {y_1}'(t) &= (y_1(t) + y^*)\Big[c\int_0^\infty g(s)U_1(x(t-s))\mathrm{d}s - dy_1(t)\Big]. \end{aligned} \tag{4.26}$$

This allows us to prove Theorem 4.18

Theorem 4.18 *Let the delay kernels and the uptake function be as in Theorem 4.17. Then equilibrium solution (x^*, y^*) of (4.26) is globally asymptotically stable provided*

$$d > \frac{(b\gamma c)^2\left[\sqrt{1+\left(aU(x^*)/b\gamma\right)^2} + aU(x^*)/b\gamma\right]^2}{4(aU(x^*)-b\gamma)D\tilde{\alpha}(cU(x^*)-\gamma-D)}$$

holds. Here

$$\tilde{\alpha} = \min_{x \geq x^*}\left\{\frac{x_1}{U(x)U_1(x_1)}\right\} > 0.$$

Proof Employing the functional

$$V(t) = W_1\int_0^{x_1} \frac{U_1(u)}{U_1(u)+U(x^*)}\mathrm{d}u + W_2\left[y_1 - y^*\log\left(\frac{(y_1+y^*)}{y^*}\right)\right]$$

$$+ W_3\int_0^\infty g(s)\int_{t-s}^t U_1^2(x_1(u))\mathrm{d}u\,\mathrm{d}s + W_4\int_0^\infty f(s)\int_{t-s}^t y_1^2(u)\mathrm{d}u\,\mathrm{d}s$$

and proceeding as in Theorem 4.17, we may complete the proof. □

We shall now compare Theorem 4.10 with Theorems 4.17 and 4.18 and establish their independence.

Example 4.19 Consider the following model

$$x'(t) = \frac{7}{6}(x_0 - x(t)) - 4U(x(t))y(t) + (1/3)\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s,$$

$$y'(t) = -(13/6)y(t) + 3y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - (1/21)y^2(t)$$

in which $U(x) = x/(4+x), b = 1/3, \gamma = 1, D = 7/6$, and $x_0 = 16$ approximately.

The equilibrium solutions are $x^* = 12$ and $y^* = 7/4$ with $U(x^*) = 3/4$ and $k = 1/4$.

Clearly all the hypotheses of Theorem 4.10 are satisfied and hence, $(12, 17/6)$ is globally asymptotically stable by virtue of Theorem 4.10. Further, as neither of the parametric conditions on d in Theorems 4.17 and 4.18 are satisfied they are not applicable here.

Example 4.20 Consider the following model

$$x'(t) = 2(x_0 - x(t)) - 25U(x(t))y(t) + 3\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s,$$

$$y'(t) = -8y(t) + 20y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - 315y^2(t)$$

in which $U(x) = x/(4+x), b = 1/2, \gamma = 6, D = 2$, and $x_0 = 4.030$ approximately.

The equilibrium solutions are $x^* = 4$ and $y^* = 0.00635$ with $U(x^*) = 1/2$ and $k = 1/4$.

Clearly, all the hypotheses of Theorems 4.17 and 4.18 are satisfied, and hence $(4, 0.00635)$ is globally asymptotically stable by virtue of these theorems. Observe that since $D - ck + aky^* < 0$, Theorem 4.10 cannot be applied here.

We shall now get back to Example 2.42 and see that the introduction of self-regulatory control mechanism, in fact, helps stabilizing the system under consideration.

Example 4.21 Consider the model,

$$x'(t) = 1.7(x_0 - x(t)) - 20U(x(t))y(t) + (0.78)\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s,$$

$$y'(t) = -3y(t) + 19y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - (0.1546)y^2(t)$$

in which

$$U(x) = \begin{cases} \frac{x}{10+x^2}, & 0 \le x < 30 \\ \frac{3}{91}, & \text{otherwise} \end{cases}$$

In the above system, it is chosen that $b = 0.6, \gamma = 1.3,$ and $D = 1.7$. Then the equilibrium solutions are $x^* = \sqrt{10}$, $y^* = 0.02523$, $U(x^*) = 0.1581$ (approximately), $k = \frac{1}{10}$, with $x_0 = 3.2$.

It is easy to check that all the hypotheses of Theorem 4.10 are satisfied here and hence $(x^*, y^*) = (\sqrt{10}, 0.02523)$ is globally asymptotically stable.

4.5 Oscillations and the Self-regulation

It is generally known in dynamical systems that a transition from stability to instability or vice versa is not an instantaneous process but usually followed by oscillations. Quite often these oscillations may acquire some periodic nature and accordingly, the corresponding dynamical equations admit periodic solutions. As mentioned in Sect. 4.1, we want to consider (4.1) and try to examine the question whether or not the self-regulatory control mechanism would induce any sustainable oscillations.

We note that in model (4.1), input concentration function $x_0(t) \equiv x_0$ and the washout rate function $D(t) \equiv D$ for all t, though periodic functions are trivially periodic in nature and these considerations do not induce any new dynamics into the model equations. It is, therefore, necessary to modify (4.1) incorporating nontrivial input concentration $(x_0(t))$ and washout rate $(D(t))$ as well, and examine the issue of existence of nontrivial periodic solutions of the resulting equations. The motivation for this stems from following observations. Consider the plankton growth in lakes where the limiting nutrients like Silica and Phosphate are supplied from streams draining the water shed. The inflows vary according to the seasons, for example, high during rainy season while they are low during summer.

When we consider the growth of plants, the essential nutrient (fertilizer) is supplied periodically and at various concentrations depending on the nature of the soil. In case of a chemostat, the supply of the nutrient changes, even unexpectedly, if the pump's efficiency changes with fluctuations in the line voltage. Thus, both the input nutrient concentration and its supply rate are time dependent but not mere constants as we have assumed so far.

Although the functions $D(t)$ and $x_0(t)$ be viewed as periodic functions of different periods, to make matters lie under control, we restrict our considerations to the case in which both the functions are periodic with the same period. The modified model equations assume the form,

$$\begin{aligned} x'(t) &= D(t)(x_0(t) - x(t)) - aU(x(t))y(t) + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s, \\ y'(t) &= -(\gamma + D(t))y(t) + cy(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - dy^2(t), \end{aligned} \tag{4.27}$$

The following initial conditions are assumed for the equations (4.27),

$$x(s) = p(s),\ y(s) = q(s) \quad -\infty < s \le 0, \tag{4.28}$$

where p and q are continuous, bounded, nonnegative functions.

In the special case when $x_0(t) \equiv x_0$ and $D(t) \equiv D$ both are positive constants, model (4.27) reduces to (4.1).

4.5.1 Properties of Solutions

In this section, we discuss the basic properties of the solutions of the system, namely, their existence, uniqueness, nonnegativity, and boundedness. Before going for the discussion, we make the following assumption.

(I). $D(t)$ and $x_0(t)$ are bounded besides being positive and continuous for $t \geq 0$.

Under the assumptions (I), (A_1), (A_2), of Sect. (4.2) and (H_1), it is easy to establish the local existence, uniqueness, and continuous dependence on initial conditions of the solutions of (4.27) and (4.28) for all $t \in [t_0, t_0 + \alpha)$ for some $\alpha > 0$ and any initial assigned time t_0. We shall now establish the existence and uniqueness of solutions of (4.27) under fairly general conditions as in Theorem 4.1, in the sense that the nonlinear uptake function need not necessarily satisfy a Lipschitz condition (A_2) always.

We now write the system (4.27) as

$$X' = F(t, X_t) \quad \text{where} \quad X = \begin{pmatrix} x \\ y \end{pmatrix} \quad \text{and}$$

$$F(t, X_t) = \begin{pmatrix} D(t)(x_0(t) - x(t)) - aU(x(t))y(t) + b\gamma \int_0^\infty f(s)y(t-s)\mathrm{d}s \\ -(\gamma + D(t))y(t) + cy(t)\int_0^\infty g(s)U(x(t-s))\mathrm{d}s - dy^2(t) \end{pmatrix}.$$

Similar to Theorem 4.10, we have

Theorem 4.22 *The given system of equations* (4.27) *has a unique solution for a given set of initial conditions.*

Proof We shall verify the hypotheses of Lemma 2.23 for the system (4.27).

Now for $t \geq 0$ and functions $\xi(t) = (\xi_1(t), \xi_2(t))$ and $\eta(t) = (\eta_1(t), \eta_2(t))$, we have

$$\begin{aligned}
&\|F(t,\xi) - F(t,\eta)\| \\
&\quad \leq |D(t)||\eta_1(t) - \xi_1(t)| + b\gamma \int_{-\infty}^t f(t-s)|\xi_2(s) - \eta_2(s)|\mathrm{d}s \\
&\qquad + |\gamma + D(t)||\eta_2(t) - \xi_2(t)| \\
&\qquad + d|{\eta_2}^2(t) - {\xi_2}^2(t)| + a|U(\eta_1(t))\eta_2(t) - U(\xi_1(t))\xi_2(t)| \\
&\qquad + c\left|\xi_2(t)\int_{-\infty}^t g(t-s)U(\xi_1(s)\mathrm{d}s - \eta_2(t)\int_{-\infty}^t g(t-s)U(\eta_1(s)\mathrm{d}s\right| \\
&\quad \leq K_1\|\xi(t) - \eta(t)\| + K_2\sum_{j=1}^{2}|\psi_j(h_j(t,\xi)) - \psi_j(h_j(t,\eta))|,
\end{aligned}$$

where $K_1 = b\gamma + l_\rho + \gamma + 2d\rho$ and $K_2 = a$, $l_\rho > 0$ is such that $D(t) \leq l_\rho$ for all $t \in J$.

Now, if we choose,

$$h_1(t,\xi) = \xi_1(t),\ \psi_1(h_1(t,\xi)) = \xi_2(t)\int_{-\infty}^{t} g(t-s)U(h_1(s,\xi(s)))\mathrm{d}s,$$

$$h_2(t,\xi) = \xi_1(t),\ \text{and}\ \psi_2(h_2(t,\xi)) = \xi_2(t)U(h_2(t,\xi(t))),$$

then it is easy to see that all the hypotheses of Lemma 2.23 are satisfied and hence the conclusion follows. □

We shall now show that the solutions of (4.27) are nonnegative.

Theorem 4.23 *All the solutions of system* (4.27) *are nonnegative in their maximal intervals of existence under non negative initial conditions.*

Proof Let $(x(t), y(t))$ denote a solution of (4.27). By continuity, $x(t), y(t)$ must take 0 before assuming negative values. Let $t = t^*$ be the first value of t for which $y(t^*) = 0$ and let $x(t^*) = \tilde{x}$. Now consider the solution $(\tilde{x}(t), \tilde{y}(t))$ of (4.2) corresponding to the initial condition $(\tilde{x}, 0)$. It follows that $x(t) = \tilde{x}(t)$ and $y(t) = \tilde{y}(t) = 0$, for all t is also a solution of (4.27). Further, this $(x(t), y(t))$ assumes the value $(\tilde{x}, 0)$ at t^*. Therefore, by the uniqueness of solutions of (4.27) we have $y(t) = 0$ for all $t \geq t^*$. Also from the second equation of (4.27), $y'(t^*) = 0$. From this it follows that $y \equiv 0$ or $y > 0$ for all $t > t^*$. Now if, $x(t^*) = 0$ for some $t = t^*$, then, since $y(t) \geq 0$ for all $t \geq 0$, we have $x'(t^*) = D(t^*)x_0(t^*) + b\gamma\int_0^\infty f(s)y(t^*-s)\mathrm{d}s > 0$, which means that x is increasing at t^*. It follows that $x(t) \geq 0$ for $t > t^*$. Hence the theorem. □

We shall now assume that there exist positive constants l_1, l_2, m_1, and m_2 such that $l_1 \leq D(t) \leq l_2$ and $m_1 \leq x_0(t) \leq m_2$ for all t.

The following result establishes the boundedness of the solutions of (4.27).

Theorem 4.24 *Let* $p(t) \geq 0, q(t) \geq 0$ *and not identically zero on any interval. Then for any solution* $(x(t), y(t))$ *of* (4.27)*,*

$$x(t) \leq \max\left\{\frac{l_2 m_2 + b\gamma M_y}{l_1},\quad sup_{-\infty<t\leq 0}\quad \{p(t)\}\right\},$$

$$y(t) \leq \max\left\{\frac{cL}{d},\quad sup_{-\infty<t\leq 0}\quad \{q(t)\}\right\} = M_y\ \text{(say)},$$

for all t.

Proof First we note that if $x' \leq 0$ and $y' \leq 0$ for all $t > 0$ then $x(t) \leq \sup_{-\infty<t\leq 0} p(t)$ and $y(t) \leq \sup_{-\infty<t\leq 0} q(t)$, respectively.

Suppose $y'(t) > 0$ for some $t > 0$. Then from the second of the equations (4.27), we have $dy(t) < -(\gamma + D(t)) + c\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s$ and from this it follows that $y(t) \leq Lc/d$ since, $U(x) \leq L$.

Similarly, from the first equation of (4.27), if $x'(t) > 0$, then $0 < x'(t) = D(t)(x_0(t) - x(t)) - aU(x(t))y(t) + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s$ and from this we have $D(t)x(t) \le D(t)x_0(t) + b\gamma M_y$ invoking the estimate on y. From this we have, $x \le \frac{(l_2 m_2 + b\gamma M_y)}{l_1}$.

Therefore, the solution $(x(t), y(t))$ of (4.27) is bounded and depends on the initial conditions. □

4.5.2 Existence of Periodic Solutions

In this section, we consider an important special case of (4.27) in which the nutrient input and its supply rate (washout rate) are periodic functions and obtain conditions for the existence of a unique periodic solution in this case. That is, we assume that $D(t)$ and $x_0(t)$ are periodic functions of the same period T for some finite $T > 0$, besides being positive and continuous. Consequently, we define the constants l_1, l_2, m_1, and m_2 as $l_1 = \inf\{D(t), 0 \le t \le T\}$, $l_2 = \sup\{D(t), 0 \le t \le T\}$, $m_1 = \inf\{x_0(t), 0 \le t \le T\}$, and $m_2 = \sup\{x_0(t), 0 \le t \le T\}$.

We now write (4.27) as

$$\begin{pmatrix} x'(t) \\ y'(t) \end{pmatrix} = \begin{pmatrix} F_1(t, x_t, y_t) \\ F_2(t, x_t, y_t) \end{pmatrix}$$

or as

$$X'(t) = F(t, X_t). \tag{4.29}$$

The following definitions and notations are used in our subsequent work. Let $P_T = (P_T, ||.||)$ denote the Banach space of all continuous T-periodic functions, $\varphi : \mathbf{R} \to \mathbf{R^n}$ with supremum norm and define

$$P_T^0 = \left\{ \varphi \in P_T : \int_0^T \varphi(t)\mathrm{d}t = 0 \right\}.$$

The following result of Burton and Bo Zhang [16] will be utilized subsequently.

Lemma 4.25 *Consider the system $X'(t) = F(t, X_t)$ in which $F : \mathbf{R} \times \mathbf{BC} \to \mathbf{R^n}$ is continuous and T-periodic in t and for each $t \in \mathbf{R}$, $\mathbf{X}_t$ is defined by $X_t(s) = X(t+s)$ for $s \le 0$. Suppose the following conditions hold.*

(1) *For each $\varphi \in P_T^0$, there is a constant $K_\varphi \in R$ such that $\int_0^T F(t, \Phi_t)\mathrm{d}t = 0$, where $\Phi(t) = K_\varphi + \int_0^t \varphi(s)\mathrm{d}s$ for each $t \in \mathbf{R}$.*
(2) *$E : P_T^0 \to P_T$ defined by $E(\varphi(t)) = \Phi(t)$ in (i) is continuous and for each $\alpha > 0$, there exists a constant $L_\alpha > 0$ such that $|K_\varphi| \le L_\alpha$ whenever $\|\varphi\| \le \alpha$.*
(3) *$F : \mathbf{R} \times P_T \to \mathbf{R}^n$ maps bounded sets into bounded sets.*

(4) *There exists constant $M > 0$ such that $\|X\| \leq M$ whenever $X = X(t)$ is a T-periodic solution of $X'(t) = \lambda F(t, X_t), \lambda \in (0, 1)$.*
Then $X'(t) = F(t, X_t)$ has a T-periodic solution.

Now for our autonomous two-dimensional system (4.29), we define

$$\varphi(t) = \begin{pmatrix} \varphi_1(t) \\ \varphi_2(t) \end{pmatrix}$$

and

$$\Phi(t) = k_\varphi + \int_0^t \varphi(s)\mathrm{d}s = \begin{pmatrix} k_1 + \int_0^t \varphi_1(s)\mathrm{d}s \\ k_2 + \int_0^t \varphi_2(s)\mathrm{d}s \end{pmatrix} = \begin{pmatrix} \Phi_1(t) \\ \Phi_2(t) \end{pmatrix}$$

in which the functions $\varphi_1, \varphi_2 \in P_T^0, k_1, k_2 \in \mathbf{R}$, and $\Phi(t) \in P_T$ is to be a solution of (4.29). We now state and prove a result that establishes the existence of a T-periodic solution to the system (4.29) given by $(x(t), y(t)) \equiv (\Phi_1(t), \Phi(t)) = (k_1 + \int_0^t \varphi_1(s)\mathrm{d}s, k_2 + \int_0^t \varphi_2(s)\mathrm{d}s)$.

Theorem 4.26 *Assume that uptake function satisfies (A_1) and (A_2) and the delay kernels satisfy (H_1). Further, let $\min_{x\geq 0}\{d + aU(x(t)) - b\gamma\}\Big\} > 0$. Then (4.29) has a unique T-periodic solution provided there exists $r > 0$ such that*

$$\beta = \max\left\{\frac{ak\beta_1}{A_1}, \frac{|B_1| + aLT}{A_1}, \frac{ck\beta_1}{B_2}, \frac{2A_2r + cLT}{B_2}\right\} < 1, \tag{4.30}$$

in which $A_1 = \int_0^T D(t)\mathrm{d}t$,

$$B_1 = -b\gamma T, A_2 = dT,$$

$B_2 = (\gamma T + A_1) + 2d \int_0^T \int_0^t \phi_2(s)\mathrm{d}s\,\mathrm{d}t$,
$\beta_1 = Tr + \int_0^T \int_0^t \phi_2(s)\mathrm{d}s\,\mathrm{d}t$ *and k is the Lipschitz constant defined in (A_2).*

Proof We shall verify all the conditions of Lemma 4.25 now. First our aim is to find out constants k_1 and k_2 such that $\int_0^T F(t, \Phi_t)dt = 0$ as defined in condition (1) of Lemma 4.25 .

Assume that $\int_0^T F(t, \Phi_t)\mathrm{d}t = 0$ and let us try to solve it for k_1 and k_2. Therefore, $\int_0^T F_i(t, \Phi_t)\mathrm{d}t = 0, \quad i = 1, 2.$

Now $\int_0^T F_1(t, \Phi_t)\mathrm{d}t = 0$ implies that

$$\int_0^T \Big\{D(t)x_0(t) - D(t)\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)$$
$$-aU\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\Big(k_2 + \int_0^t \varphi_2(s)\mathrm{d}s\Big)$$
$$+b\gamma \int_{-\infty}^t f(t-s)\Big(k_2 + \int_0^s \varphi_2(z)dz\Big)\mathrm{d}s\Big\}\mathrm{d}t = 0.$$

That is,

$$\int_0^T D(t)x_0(t)\mathrm{d}t - k_1\int_0^T D(t)\mathrm{d}t - \int_0^T D(t)\int_0^t \varphi_1(s)\mathrm{d}s\,\mathrm{d}t$$
$$-a\int_0^T U\Big(k_1+\int_0^t \varphi_1(s)\mathrm{d}s\Big)\Big(k_2+\int_0^t \varphi_2(s)\mathrm{d}s\Big)\mathrm{d}t$$
$$+b\gamma k_2 T + b\gamma\int_0^T\int_{-\infty}^t f(t-s)\Big(\int_0^s \varphi_2(z)\mathrm{d}z\Big)\mathrm{d}s\,\mathrm{d}t = 0,$$

using the hypothesis (H_1) on f.

We observe that since $\int_0^t \varphi_2(s)\mathrm{d}s$ is T-periodic, for each $s\in\mathbf{R}$ we have

$$\int_0^T\int_{-\infty}^t f(t-s)\Big(\int_0^s \varphi_2(z)\mathrm{d}z\Big)\mathrm{d}s\,\mathrm{d}t = \int_0^T\int_{-\infty}^0 f(-s)\Big(\int_0^{t+s} \varphi_2(z)\mathrm{d}z\Big)\mathrm{d}s\,\mathrm{d}t$$
$$= \int_0^T\int_{-\infty}^0 f(-s)\mathrm{d}s\Big(\int_0^t \varphi_2(z)\mathrm{d}z\Big)\mathrm{d}t = \int_0^T\int_0^t \varphi_2(z)\mathrm{d}z\,\mathrm{d}t,$$

again using (H_1) on f. Using this in the above equation we get after rearrangement,

$$k_1\int_0^T D(t)\mathrm{d}t - b\gamma T k_2 - \int_0^T D(t)x_0(t)\mathrm{d}t$$
$$+\int_0^T D(t)\int_0^t \varphi_1(s)\mathrm{d}s\,\mathrm{d}t - b\gamma\int_0^T\int_0^t \varphi_2(s)\mathrm{d}s\,\mathrm{d}t$$
$$= -a\int_0^T \Big(k_2+\int_0^t \varphi_2(s)\mathrm{d}s\Big)U\Big(k_1+\int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t.$$

which can be written as

$$A_1k_1 + B_1k_2 + C_1 = -a\int_0^T \Big(k_2+\int_0^t \varphi_2(s)\mathrm{d}s\Big)U\Big(k_1+\int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t, \quad (4.31)$$

where $A_1=\int_0^T D(t)$, $B_1=-b\gamma T$, and $C_1=-\int_0^T D(t)x_0(t)\mathrm{d}t+\int_0^T D(t)\int_0^t \varphi_1(s)$ $\mathrm{d}s\,\mathrm{d}t - b\gamma\int_0^T\int_0^t \varphi_2(s)\mathrm{d}s\,\mathrm{d}t$.

Similarly the equation $\int_0^T F_2(t,\Phi_T)\mathrm{d}t = 0$ after some simplifications and rearrangements done as above yields

$$A_2k_2^2 + B_2k_2 + C_2 = c\int_0^T \Big(k_2+\int_0^t \varphi_2(s)\mathrm{d}s\Big)U\Big(k_1+\int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t, \quad (4.32)$$

where $A_2=dT$, $B_2=2d\int_0^T\int_0^t \varphi_2(s)\mathrm{d}s\,\mathrm{d}t + \int_0^T(\gamma+D(t))\mathrm{d}t$, and

$C_2=\int_0^T(\gamma+D(t))\int_0^t \varphi_2(s)\mathrm{d}s\,\mathrm{d}t + d\int_0^T(\int_0^t \varphi_2(s)\mathrm{d}s)^2\mathrm{d}t$.

We can solve equations (4.31) and (4.32) for the constants k_1 and k_2 once the functions U_1, φ_1, and φ_2 are known. But here under we employ the contraction mapping principle to obtain a unique pair of constants k_1 and k_2.

Now we rewrite (4.31) and (4.32), respectively, as

$$\begin{aligned} k_1 &= -\frac{B_1 k_2}{A_1} - \frac{C_1}{A_1} - \frac{a}{A_1}\int_0^T \Big(k_2 + \int_0^t \varphi_2(s)\mathrm{d}s\Big) U\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t \\ &\equiv G_1(k_1, k_2) \end{aligned}$$

and

$$\begin{aligned} k_2 &= -\frac{A_2 k_2^2}{B_2} - \frac{C_2}{B_2} - \frac{c}{B_2}\int_0^T \Big(k_2 + \int_0^t \varphi_2(s)\mathrm{d}s\Big) U\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t \\ &\equiv G_2(k_1, k_2). \end{aligned}$$

Now consider $u = G_1(u, v)$ and $v = G_2(u, v)$.

Our aim is to find a unique pair (u, v) satisfying the above equations. Now for some $r > 0$, consider the set,

$$Q_r = \{(u, v) \in \mathbf{R}^2 : \|(u, v)\| = |u| + |v| \le r\}.$$

Define a map $G : Q_r \to \mathbf{R}^2$ by $G(u, v) = (G_1(u, v), G_2(u, v))$ with $\|G\| = \max\{|G_1|, |G_2|\}$.

Now for any $(u, v), (u', v') \in Q_r$, we can show after some calculations that

$\|G(u, v) - G(u', v')\| \le \beta\|(u, v) - (u', v')\|$.

Then it follows that G is a contraction map on Q_r, and hence, G has a fixed point in Q_r for some r.

We shall now verify condition (ii) of Lemma 4.25. We shall prove that if there exists a constant $\alpha > 0$ such that $||\varphi|| \le \alpha$ then there corresponds an $L_\alpha > 0$ such that $|k_\varphi| \le L_\alpha$. From (4.32) we have

$$\begin{aligned} &\left|A_2 k_2 + B_2 - c\int_0^T U\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t\right| |k_2| \\ &\le |C_2| + c\int_0^T \left|\int_0^t \varphi_2(s)\mathrm{d}s\right| \left|U\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\right| \mathrm{d}t \\ &\le |C_2| + cL\left|\int_0^T \int_0^t \varphi_2(s)\mathrm{d}s\,\mathrm{d}t\right| \\ &\le |C_2| + cL\alpha\frac{T^2}{2}, \end{aligned}$$

using $|\varphi_2| \le ||\varphi|| \le \alpha$ and $|U(x)| \le L$ for all $x \in \mathbf{R}$.

$$\le \gamma\alpha\frac{T^2}{2} + \alpha p_1 + d\alpha^2\frac{T^3}{3} + cL\frac{\alpha T^2}{2},$$

since,

$$|C_2| = \left|\int_0^T (\gamma + D(t)) \int_0^t \varphi_2(s)\mathrm{d}s\,\mathrm{d}t + d\int_0^T \int_0^t (\varphi_2(s))^2 \mathrm{d}s\,\mathrm{d}t\right|$$
$$\leq \gamma\alpha\frac{T^2}{2} + \alpha p_1 + d\alpha^2\frac{T^3}{3},$$

where

$$p_1 = \int_0^T tD(t)\mathrm{d}t \leq l_2\frac{T^2}{2}.$$

Since the right-hand side of the above inequality depends only on the parameters of the system which are either fixed or at the control of the experimenter, corresponding to a given α, we can always find an $L_{2\alpha} > 0$ such that $|k_2| \leq L_{2\alpha}$. In case

$$\left|A_2k_2 + B_2 - c\int_0^T U\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t\right| = 0,$$

we have

$$|k_2| \leq \frac{|B_2|}{|A_2|} + \frac{cLT}{|A_2|},$$

which is again finite. Now from (4.31) and invoking the bound $L_{2\alpha}$ on k_2, we can easily show that there exists $L_{1\alpha} > 0$ such that $|k_1| \leq L_{1\alpha}$. Thus,

$$|k_\varphi| = |k_1| + |k_2| \leq L_{1\alpha} + L_{2\alpha} = L_\alpha \quad \text{(say)}.$$

It is easy to see that the function $E : P_T^0 \to P_T$ defined by $E(\varphi(t)) = \Phi(t) = k_\varphi + \int_0^t \varphi(s)\mathrm{d}s$ is continuous. This proves condition (2) of Lemma 4.25. It is clear that F carries bounded sets into bounded sets. This verifies condition (3) of Lemma 4.25. We shall now verify condition (4) of Lemma 4.25. For this let $X(t) = (x(t), y(t))^t$ be a T-periodic solution of $X'(t) = \breve{}F(t, X_t), \quad 0 < \lambda < 1$.

Consider the functional

$$V(t) \equiv V(x(t), y(t)) = |x(t)| + |\log(y(t))|.$$

Then $V(t)$ is T-periodic. Now,

$$D^+V(t) \leq \lambda\Big\{|D(t)x_0(t)| - D(t)|x(t)| - a|U(x(t))(y(t)|$$
$$+ b\gamma\int_{-\infty}^t f(t-s)|y(s)|\mathrm{d}s - (\gamma + D(t))$$
$$+ c\int_{-\infty}^t g(t-s)|U(x(s))|\mathrm{d}s - d|y(t)|\Big\}$$
$$\leq \lambda\Big\{ - D(t)|x(t)| - a|U(x(t))(y(t)| + b\gamma\int_{-\infty}^t f(t-s)|y(s)|\mathrm{d}s$$
$$- d|y(t)| + \gamma + l_2 + l_2m_2 + cL\Big\}$$

Integrating from 0 to T, we get

$$\begin{aligned}0 &= V(T) - V(0)\\ &\leq \lambda \int_0^T \Big\{ - D(t)|x(t)| - a|U(x(t))(y(t)| + b\gamma \int_{-\infty}^t f(t-s)|y(s)|\mathrm{d}s\\ &\qquad -d|y(t)| + \gamma + l_2 + l_2 m_2 + cL\Big\}\mathrm{d}t,\end{aligned}$$

from which we have

$$\int_0^T \Big[D(t)|x(t)| + \Big(d + a|U(x(t)| - b\gamma \Big)|y(t)| \Big]\mathrm{d}t \leq (\gamma + l_2 + l_2 m_2 + cL)T$$

which further implies that

$$\tilde{\alpha_1} \int_0^T (|x(t)| + |y(t)|)dt \leq M_1,$$

where $\tilde{\alpha_1} = \min \Big\{ l_1, \min_{x \geq 0}\{d + aU(x(t)) - b\gamma\} \Big\} > 0$ and $M_1 = (\gamma + l_2 + l_2 m_2 + cL)T$.

Now it is easy to see that

$$\begin{aligned}\int_0^T |X'(t)|\mathrm{d}t &\leq \int_0^T \Big[|D(t)x_0(t)| + |D(t)x(t)| + a|U(x(t))(y(t)|\\ &\qquad + b\gamma \int_{-\infty}^t f(t-s)|y(s)|\mathrm{d}s\\ &\qquad + c|y(t)| \int_{-\infty}^t g(t-s)|U(x(s))|\mathrm{d}s \Big]\mathrm{d}t\\ &\leq \int_0^T D(t)x_0(t)\mathrm{d}t\\ &\quad + \int_0^T \Big[|D(t)x(t)| + (aL + cL + b\gamma)|y(t)| \Big]\mathrm{d}t\\ &\leq \int_0^T D(t)x_0(t)\mathrm{d}t + \tilde{\alpha_2}\frac{M_1}{\tilde{\alpha_1}} = M_2 \text{ (say)}\end{aligned}$$

where $\tilde{\alpha_2} = \max\{l_2, aL + cL + b\gamma\} > 0$. Then it follows that there exists $M_3 > 0$ such that $||X(t)|| \leq M_3$. Therefore, all the conditions of Lemma 4.25 are satisfied and hence, the conclusion of the lemma follows. Thus the system (4.29) has a T-periodic solution. This completes the proof. □

We now give an example to illustrate the above result.

Example 4.27 Choose $\varphi_1(t) = \sin(t)$, $\varphi_2(t) = \cos(t)$ which are 2π-periodic functions of mean zero and let $U(x) = x/(N + x)$ which is the well known Michaelis–Menten uptake function for the nutrient uptake, N is the half-saturation constant.

Let $D(t) = \alpha_1 + \sin(t)$ and $x_0(t) = \alpha_2 + \cos(t)$, where $\alpha_1 > 1, \alpha_2 > 1$. Now,

$$U(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s) = 1 - \frac{N}{N + k_1 + 1 - \cos(t)}.$$

Then

$$\int_0^{2\pi} U\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t = 2\pi - N\int_0^{2\pi} \frac{1}{N + k_1 + 1 - \cos(t)}\mathrm{d}t.$$

Using elementary calculus we can show that

$$\int_0^{2\pi} U\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t = 2\pi - \frac{2\pi N}{\sqrt{(N + k_1 + 1)^2 - 1}}.$$

Similarly we can show that

$$\int_0^{2\pi} \Big(\int_0^t \varphi_2(s)\mathrm{d}s\Big)U\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t = 0.$$

Substituting in (4.31) and (4.32) and simplifying we get,

$$\begin{aligned} A_1k_1 + (B_1 + 2a\pi)k_2 + C_1 &= \frac{2\pi a k_2 N}{\sqrt{(N + k_1 + 1)^2 - 1}}, \\ A_2{k_2}^2 + (B_2 - 2c\pi)k_2 + C_2 &= -\frac{2\pi c k_2 N}{\sqrt{(N + k_1 + 1)^2 - 1}}. \end{aligned} \tag{4.33}$$

After some calculations we can see that, $A_1 = 2\pi\alpha_1, B_1 = -b\gamma 2\pi$, $C_1 = 2\pi\alpha_1(\alpha_2 + 1), A_2 = 2\pi d, B_2 = 2\pi(\gamma + \alpha_1)$, and $C_2 = \pi(d + 1)$. Now using (4.30), we can find a unique pair of constants k_1 and k_2 for the given functions φ_1 and φ_2 satisfying $\int_0^T F(t, \Phi_t)\mathrm{d}t = 0$ provided we have,

$$r < \min\left\{\frac{N\alpha_1}{a}, \frac{\gamma + \alpha_1 - c}{2d}\right\} \text{ and } \frac{b\gamma + a}{\alpha_1} < 1. \tag{4.34}$$

Clearly the inequality, $(b\gamma + a)/\alpha_1 < 1$, implies that $\gamma + \alpha_1 - c > 0$ in view of the assumption that $c \leq a$. This ensures the existence of $r > 0$.

It is easy to see that all other conditions are satisfied here and thus, we have

$$x(t) = k_1 + \int_0^t \varphi_1(s)\mathrm{d}s = k_1 + 1 - \cos(t)$$

and

$$y(t) = k_2 + \int_0^t \varphi_2(s)\mathrm{d}s = k_2 + \sin(t)$$

as a 2π-periodic solution of the given system.

Let us now consider system (4.1). We have Corollary 4.28.

Corollary 4.28 *Assume that uptake function satisfies* (A_1) *and* (A_2) *and the delay kernels satisfy* (H_1). *Then* (4.1) *has a* T*-periodic solution provided,*

$$min_{x>0}\{d + aU(x(t)) - b\gamma\} > 0.$$

Proof As in Theorem 4.26, we need to find real constants k_1 and k_2 such that $\int_0^T F(t, \Phi_t)\mathrm{d}t = 0$ and this equation yields two equations in k_1 and k_2 just as (4.31) and (4.32).

Rewriting (4.31) and (4.32) for this particular case, we have

$$A_1k_1 + B_1k_2 + C_1 = -a\int_0^T \Big(k_2 + \int_0^t \varphi_2(s)\mathrm{d}s\Big)U\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t \quad (4.35)$$

and

$$A_2k_2^2 + B_2k_2 + C_2 = c\int_0^T \Big(k_2 + \int_0^t \varphi_2(s)\mathrm{d}s\Big)U\Big(k_1 + \int_0^t \varphi_1(s)\mathrm{d}s\Big)\mathrm{d}t, \quad (4.36)$$

where $A_1 = DT$, $B_1 = -b\gamma T$, and
$C_1 = -Dx_0T + D\int_0^T\int_0^t \varphi_1(s)\mathrm{d}s\,\mathrm{d}t - b\gamma\int_0^T\int_0^t \varphi_2(s)\mathrm{d}s\,\mathrm{d}t$,
$A_2 = dT$, $B_2 = 2d\int_0^T\int_0^t \varphi_2(s)\mathrm{d}s\,\mathrm{d}t + (\gamma + D)T$ and
$C_2 = (\gamma + D)\int_0^T\int_0^t \varphi_2(s)\mathrm{d}s\,\mathrm{d}t + d\int_0^T(\int_0^t \varphi_2(s)\mathrm{d}s)^2\mathrm{d}t$.

Observe that the right-hand sides of (4.35) and (4.36) are functions of k_1 and k_2 and one is a constant multiple of the other. Combining these two equations, we get

$$\bar{A}_1k_1 + \bar{B}_1k_2 + \bar{C}_1 = \bar{A}_2k_2^2 + \bar{B}_2k_2 + \bar{C}_2$$

where $\bar{A}_1 = -\frac{A_1}{a}$, $\bar{B}_1 = -\frac{B_1}{a}$, $\bar{C}_1 = -\frac{C_1}{a}$ and $\bar{A}_2 = \frac{A_2}{c}$, $\bar{B}_2 = \frac{B_2}{c}$, $\bar{C}_2 = \frac{C_2}{c}$, which represents a parabola in the k_1k_2-plane. Thus, we can have any number of solutions k_1 and k_2 satisfying this equation corresponding to one set of functions φ_1 and φ_2 and when we require a unique periodic solution, we may look for condition similar to (4.30) on the parameters.

The rest of the proof is similar to Theorem 4.26 and hence, omitted. □

Remark 4.29 We now compare the hypotheses of Theorem 4.13 and Corollary 4.28. The assumptions on the uptake function and the delay kernels being the same, we need to compare the parametric conditions of these two. While the condition $\min_{x>0}\{d + aU(x)\} > b\gamma$ of Corollary 4.28 ensures the existence of periodic solutions to (4.1), Theorem 4.13 requires $D - aky^* > b\gamma + ck$, in addition to $\min_{x\geq x^*}\{d + aU(x)\} > b\gamma + ck$ for the global asymptotic stability of the equilibrium solution (x^*, y^*).

Thus, as long as the conditions of Corollary 4.28 are met, (4.1) has at least one periodic solution and when the conditions of Theorem 4.13 are also satisfied, this periodic solution tends to the positive equilibrium solution (x^*, y^*).

Thus, a startling fact is that the regulatory mechanism not only preserves the asymptotic stability of the system, but also induces sustainable oscillations in the system implying the model equations (4.1) admitting globally asymptotically stable periodic solutions.

For a unique T-periodic solution the parameters of (4.1) need to satisfy a condition similar to (4.30) of Theorem 4.26 which can be written as

$$\beta = \max\left\{\frac{ak\beta_1}{A_1}, \frac{|B_1| + aLT}{A_1}, \frac{ck\beta_1}{B_2}, \frac{A_2 2r + cLT}{B_2}\right\} < 1, \tag{4.37}$$

in which $A_1 = DT, B_1 = -b\gamma T, A_2 = dT, B_2 = (\gamma + D)T + 2d\int_0^T \int_0^t \phi_2(s)\mathrm{d}s\,\mathrm{d}t$, $\beta_1 = Tr + \int_0^T \int_0^t \phi_2(s)\mathrm{d}s\,\mathrm{d}t$.

Observe that the term $|B_1| + aLT/A_1$ is independent of r.
Further, $\beta < 1$ implies $(|B_1| + aLT)/A_1 < 1$ which means that $(b\gamma T + aLT)/DT < 1$. That is,

$$b\gamma + aL < D. \tag{4.38}$$

The following condition is necessary for the existence of a positive equilibrium solution to (4.1) (see discussion before Theorem 4.2).

$$\gamma + D < cL. \tag{4.39}$$

In view of the assumption that $c \le a$, (4.38) and (4.39) cannot occur simultaneously. Hence, we remark that the existence of a unique periodic solution itself enforces the nonexistence of a positive equilibrium solution for (4.1). Further, for nontrivial periodic $D(t)$ and $x_0(t)$ system (4.27) does not possess any (constant) equilibrium solution. In this context, we are prompted to study the asymptotic behavior of solutions of (4.27), and hence, of (4.1). The following result yields conditions under which the solutions of (4.27) are asymptotic to each other.

Theorem 4.30 *Assume that the delay kernels, in addition to* (H_1), *satisfy the conditions* $\int_0^\infty sf(s)\mathrm{d}s < \infty$, $\int_0^\infty sg(s)\mathrm{d}s < \infty$ *and* $U(x)$ *satisfies* (A_1) *and* (A_2). *Further, assume that there exists a continuously differentiable function* $W(t) = (w_1(t), w_2(t))$, $w_i(t) > 0$ *for* $i = 1, 2$, *bounded on* $0 \le t < \infty$ *such that*

$$\begin{aligned} w_1'(t) &= D(t)x_0(t) - D(t)w_1(t) - aU(w_1(t))w_2(t) \\ &\quad + b\gamma \int_0^\infty f(s)w_2(t-s)\mathrm{d}s + \mathcal{W}_1(t), \\ w_2'(t) &= w_2(t)\Big[-(\gamma + D(t)) + c\int_0^\infty g(s)U(w_1(t-s))\mathrm{d}s \\ &\quad - dw_2(t) + \mathcal{W}_2(t)\Big], \end{aligned}$$

where $\mathcal{W}_i(t)$, $i = 1, 2$ *are bounded on* $[0, \infty)$ *and* $\int_0^\infty |\mathcal{W}_i(t)|\mathrm{d}t < \infty$. *Then for any solution* $(x(t), y(t))$ *of* (4.27) *one has* $\lim_{t\to\infty}(x(t), y(t)) = (w_1(t), w_2(t))$ *provided*

$$l_1 - ck - akM_y > 0 \quad \textit{and} \quad \min_{w_1(t)>0}\{d - b\gamma + aU(w_1(t))\} > 0.$$

Proof We use the functional

$$\begin{aligned} V(t) \equiv V(x(t), y(t)) &= |x(t) - w_1(t)| + |\log\ y(t) - \log\ w_2(t)| \\ &\quad + b\gamma \int_0^\infty f(s) \int_{t-s}^t |y(u) - w_2(u)| \mathrm{d}u\, \mathrm{d}s \\ &\quad + c \int_0^\infty g(s) \int_{t-s}^t |U(x(u)) - U(w_1(u))| \mathrm{d}u\, \mathrm{d}s. \end{aligned}$$

Clearly, $V(w_1(t), w_2(t)) = 0$ and

$$V(t) \geq |x(t) - w_1(t)| + |\log\ y(t) - \log\ w_2(t)| > 0.$$

The upper Dini derivative of V along the solutions of (4.27) after some simplifications is given by

$$\begin{aligned} D^+V &= -D(t)|x(t) - w_1(t)| + c|U(x(t) - U(w_1(t))| \\ &\quad - (d - b\gamma)|y(t) - w_2(t)| - aU(w_1(t))|y(t) - w_2(t)| \\ &\quad + ay|U(x) - U(w_1(t))| + |\mathcal{W}_1(t)| + |\mathcal{W}_2(t)| \\ &\leq -(l_1 - ck - akM_y)|x(t) - w_1(t)| \\ &\quad - (d - b\gamma + aU(w_1(t)))|y(t) - w_2(t)| + |\mathcal{W}_1(t)| + |\mathcal{W}_2(t)|, \end{aligned}$$

where M_y is the bound on y defined in Theorem 4.24.

The negative definiteness of D^+V follows from the hypotheses and rest of the argument can be completed using standard arguments. This completes the proof. □

Now, for any two solutions $(x_1(t), y_1(t))$ and $(x_2(t), y_2(t))$ of (4.27) Theorem 4.30 implies that

$$\begin{aligned} &|x_1(t) - x_2(t)| + |y_1(t) - y_2(t)| = \\ &= |x_1(t) - w_1(t) + w_1(t) - x_2(t)| + |y_1(t) - w_2(t) + w_2(t) - y_2(t)| \\ &\leq |x_1(t) - w_1(t)| + |w_1(t) - x_2(t)| + |y_1(t) - w_2(t)| + |w_2(t) - y_2(t)| \\ &\to 0, \quad \text{as} \quad t \to \infty. \end{aligned}$$

Thus, all the solutions of (4.27) are asymptotic to each other. Hence, under the conditions of Theorem 4.26 they are all asymptotic to the unique T-periodic solution.

Now we come back to system (2.81) to establish the existence of periodic solutions to it. The choice, $d = 0, x_0(t) = x_0$, and $D(t) = D$ reduces (4.27) to (2.81) and similar to Corollary 4.28 we have Corollary 4.31.

Corollary 4.31 *Assume that uptake function satisfies* (A_1) *and* (A_2) *and the delay kernels satisfy* (H_1)*. Then* (2.81) *has a T-periodic solution provided,*

$$min_{x(t)>0}\{aU(x(t)) - b\gamma\} > 0.$$

Proof Since the proof of this corollary is similar to that of Theorem 4.26 or Corollary 4.28, we omit the details here. □

4.6 A Model with Discrete Delay in Growth Response

In this section we study the influence of self-regulatory mechanism on model (2.67). That is, we consider the system of equations,

$$\begin{aligned}\frac{\mathrm{d}x(t)}{\mathrm{d}t} &= D(x_0 - x(t)) - aU(x(t))y(t) + b\gamma\int_0^\infty f(s)y(t-s)\mathrm{d}s,\\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} &= -(\gamma + D)y(t) + cy(t)U(x(t-\tau)) - dy^2(t),\end{aligned} \tag{4.40}$$

with some positive initial conditions say (4.2).

Having done enough home work on such models, we directly proceed to the global stability of the positive equilibrium (x^*, y^*), which exists under the conditions of Theorem 4.2.

4.6.1 Stability Results

We shall obtain various sets of sufficient conditions on the parameters that establish the asymptotic stability of the positive equilibrium solution (x^*, y^*) of (4.40) and estimate the length of the delay for which these hold, employing a Lyapunov functional technique.

Before proceeding further, we make the following change of variables.

$$x_1(t) = x(t) - x^*,\ y_1(t) = \frac{y(t) - y^*}{y^*},\ U_1(x_1(t)) = U(x(t)) - U(x^*).$$

Then (4.40) after a rearrangement assumes the form

$$\begin{aligned}x_1'(t) &= -Dx_1(t) - ay^*U_1(x_1(t)) - ay^*U(x(t))y_1(t)\\ &\quad + b\gamma y^*\int_0^\infty f(s)y_1(t-s)\mathrm{d}s,\\ y_1'(t) &= (1 + y_1(t))\Big[cU_1(x_1(t-\tau)) - dy^*y_1(t)\Big].\end{aligned} \tag{4.41}$$

The following assumptions on the transformed uptake function U_1 are used in our subsequent discussion.

(A_3). $U \in C^1[0,\infty)$ and there exists a positive constant M_1 such that $\mathrm{d}U/\mathrm{d}x < M_1$.

In other words, $\mathrm{d}U_1/\mathrm{d}x_1 < M_1$ for $x_1 \in [-x^*, \infty)$.

(A_4). $x_1 U_1(x_1) > 0$ for all $x_1 \neq 0$ and there exist positive constants α_1, α_2 and β such that

$$\alpha_1 \le \frac{U_1(x_1)}{x_1} \le \alpha_2 \quad \text{for } x_1 \ge -x^* \text{ and } \quad \beta = \min_{x_1 \ge -x^*} \left\{ \frac{x_1}{U_1(x_1)} \right\}.$$

We now state and prove the main result of this section.

Theorem 4.32 *Assume that the delay kernel f satisfies (H_1), (H_2) and the uptake function U_1 satisfies (A_1), (A_3), and (A_4). The equilibrium solution $(0,0)$ of (4.41) is globally asymptotically stable for $0 \le \tau < \tau^*$, where τ^* may be estimated as follows with suitably chosen positive constants A and B.*

Case I $(D - \frac{b\gamma y^*}{2}) > 0$, $Bdy^* - \frac{Ab\gamma y^*}{2} > 0$.
Then

$$\tau^* = \min \left\{ \frac{2A\beta}{Bc},\ \frac{1}{2}\left(\frac{A_1}{B_1} + \frac{A_2}{B_2} - \sqrt{\left(\frac{A_1}{B_1} - \frac{A_2}{B_2} \right)^2 + \frac{4C_1^2}{B_1 B_2}} \right) \right\},$$

where

$$A_1 = A\left(D - \frac{b\gamma y^*}{2} \right), \quad B_1 = \frac{BcD}{2}, \quad 2C_1 = Aay^*L - Bc\alpha_2,$$

$$A_2 = Bdy^* - \frac{Ab\gamma y^*}{2} \quad \text{and} \quad B_2 = \frac{Bc}{2}[(D + 2ay^* + b\gamma y^*)M + b\gamma y^* + ay^*L^2],$$

Case II

$$A\left(D - \frac{b\gamma y^*}{2} - \frac{ay^*L}{2} \right) - \frac{Bc\alpha_2}{2} > 0$$

$$Bdy^* - \frac{A}{2}b\gamma y^* - \frac{A}{2}ay^*L - \frac{Bc\alpha_2}{2} > 0.$$

Then

$$\tau^* = \min \left\{ \tilde{A},\ \frac{2A\beta}{Bc},\ \tilde{B} \right\},$$

in which

$$\tilde{A} = \frac{A(D - \frac{b\gamma y^*}{2} - \frac{ay^*L}{2}) - \frac{Bc\alpha_2}{2}}{\frac{BcD}{2}}$$

and

$$\tilde{B} = \frac{Bdy^* - \frac{A}{2}b\gamma y^* - \frac{A}{2}ay^*L - \frac{Bc\alpha_2}{2}}{\frac{Bc}{2}[(D + 2ay^* + b\gamma y^*)M + b\gamma y^* + ay^*L^2]}.$$

Case III $A\Big(D + \frac{ay^*\alpha_1}{2} - \frac{b\gamma y^*}{2} - \frac{ay^*}{2}L\Big) - \frac{Bc\alpha_2}{2} > 0$ and

$Bdy^* - \frac{A}{2}b\gamma y^* - \frac{A}{2}ay^*L - \frac{Bc\alpha_2}{2} > 0.$

Then $\tau^* = \min\{m_1, m_2\}$, where

$$m_1 = \frac{A(D - \frac{b\gamma y^*}{2} + ay^*\alpha_1 - \frac{ay^*}{2}L) - \frac{Bc}{2}\alpha_2}{\frac{Bc}{2}(D + ay^*\alpha_2^2)},$$

$$m_2 = \frac{Bdy^* - \frac{Ab\gamma}{2}y^* - \frac{Aay^*}{2}L - \frac{Bc\alpha_2}{2}}{\frac{Bc}{2}[M(D + 2ay^* + b\gamma y^*) + b\gamma y^* + ay^*L^2]}.$$

Case IV $A\Big(D + \frac{ay^*\alpha_1}{2} - \frac{b\gamma y^*}{2}\Big) > 0,\ Bdy^* - \frac{A}{2}b\gamma y^* > 0.$

Then

$$\tau^* = \frac{1}{2}\left(\frac{A_1'}{B_1'} + \frac{A_2'}{B_2'} - \sqrt{\left(\frac{A_1'}{B_1'} - \frac{A_2'}{B_2'}\right)^2 + \left(\frac{4C_1'^2}{B_1'B_2'}\right)}\right),$$

where

$$A_1' = A\left(D - \frac{b\gamma y^*}{2} + ay^*\alpha_1\right),\quad B_1' = \frac{Bc}{2}(D + ay^*{\alpha_2}^2),$$

$C_1' = C_1,\quad A_2' = A_2,\quad$ and $\quad B_2' = B_2.$

In all the above, $M = M_1^2$, and M_1 is defined in (A_3).

Proof The foregoing discussion explains the construction of a Lyapunov functional that is useful in establishing the result.

Consider the functional,

$$V_1(t) \equiv V_1(x_1(t), y_1(t)) = \frac{A}{2}x_1^2(t) + B\Big[y_1(t) - \log(1 + y_1(t))\Big], \tag{4.42}$$

where A and B are positive constants which will be chosen appropriately.

The time derivative of V_1 along the solutions of (4.41) is given by

$$\begin{aligned}
\frac{dV_1}{dt} &= Ax_1(t)\Big\{-Dx_1(t) - ay^*U_1(x_1(t)) \\
&\qquad - ay^*U(x(t))y_1(t) + b\gamma y^*\int_0^\infty f(s)y_1(t-s)ds\Big\} \\
&\qquad + By_1(t)\Big\{cU_1(x_1(t-\tau)) - dy^*y_1(t)\Big\} \\
&\le -A(D - \frac{b\gamma y^*}{2})x_1^2(t) - Aay^*U_1(x_1(t))x_1(t) \\
&\qquad - Aay^*U(x(t))x_1(t)y_1(t) + \frac{Ab\gamma y^*}{2}\int_0^\infty f(s)y_1^2(t-s)ds \\
&\qquad + Bcy_1(t)U_1(x_1(t-\tau)) - Bdy^*y_1^2(t).
\end{aligned} \tag{4.43}$$

Now consider

$$\begin{aligned}
y_1(t)U_1(x_1(t-\tau)) &= y_1(t)\Big[U_1(x_1(t)) - \int_{t-\tau}^{t} \frac{\mathrm{d}}{\mathrm{d}s}(U_1(x_1(s))\mathrm{d}s\Big] \\
&= y_1(t)\Big[U_1(x_1(t)) - \int_{t-\tau}^{t} \Big(\frac{\mathrm{d}U_1(x_1(s))}{\mathrm{d}x_1(s)} \cdot \frac{\mathrm{d}x_1(s)}{\mathrm{d}s}\Big)\mathrm{d}s\Big] \\
&= y_1(t)U_1(x_1(t)) - y_1(t)\int_{t-\tau}^{t} \left(\frac{\mathrm{d}U_1(x_1(s))}{\mathrm{d}x_1(s)}\right) \times \\
&\quad \times\Big\{-Dx_1(s) - ay^*U_1(x_1(s)) - ay^*U(x(s))y_1(s) \\
&\quad + b\gamma y^* \int_0^{\infty} f(s)y_1(s-u)du\Big\}\mathrm{d}s \\
&\le y_1(t)U_1(x_1(t)) \\
&\quad + \frac{1}{2}\left[D + 2ay^* + b\gamma y^*\right] y_1^2(t) \int_{t-\tau}^{t} \left(\frac{\mathrm{d}U_1(x_1(s))}{\mathrm{d}x_1(s)}\right)^2 \mathrm{d}s \\
&\quad + \frac{D}{2}\int_{t-\tau}^{t} x_1^2(s)\mathrm{d}s + \frac{ay^*}{2}\int_{t-\tau}^{t} U_1^2(x_1(s))\mathrm{d}s \\
&\quad + \frac{ay^*}{2}\int_{t-\tau}^{t} U^2(x(s))y_1^2(s)\mathrm{d}s \\
&\quad + \frac{b\gamma y^*}{2}\int_{t-\tau}^{t}\int_0^{\infty} f(u)y_1^2(s-u)\mathrm{d}u\,\mathrm{d}s.
\end{aligned}$$

Using this in (4.43), we get

$$\begin{aligned}
\frac{\mathrm{d}V_1}{\mathrm{d}t} \le& -A\left(D - \frac{b\gamma y^*}{2}\right)x_1^2(t) - Aay^*U(x(t))x_1(t)y_1(t) \\
&+ BcU_1(x_1(t))y_1(t) - B\Big[dy^* - \frac{c}{2}(D + 2ay^* + b\gamma y^*)M\tau\Big]y_1^2(t) \\
&- Aay^*U_1(x_1(t))x_1(t) + A\frac{b\gamma y^*}{2}\int_0^{\infty} f(s)y_1^2(t-s)\mathrm{d}s \\
&+ \frac{BcD}{2}\int_{t-\tau}^{t} x_1^2(s)\mathrm{d}s + B\frac{ay^*c}{2}\int_{t-\tau}^{t} U_1^2(x_1(s))\mathrm{d}s \\
&+ B\frac{ay^*c}{2}\int_{t-\tau}^{t} U^2(x(s))y_1^2(s)\mathrm{d}s \\
&+ B\frac{b\gamma y^*c}{2}\int_{t-\tau}^{t}\mathrm{d}s\int_0^{\infty} f(u)y_1^2(s-u)\mathrm{d}u\,\mathrm{d}s, \qquad (4.44)
\end{aligned}$$

using (A_3) and denoting $M = {M_1}^2$

Now consider the functional

$$\begin{aligned} V_2(t) &\equiv V_2(x_1(t), y_1(t)) \\ &= \frac{Bc}{2}\int_{t-\tau}^{t}\int_{s}^{t}\Big\{Dx_1^2(v) + ay^*U_1^2(x_1(v)) + ay^*U^2(x(v))y_1^2(v) \\ &\qquad + b\gamma y^*\int_0^\infty f(u)y_1^2(v-u)\mathrm{d}u\Big\}\mathrm{d}v. \end{aligned}$$

Then the time derivative of V_2 is given by,

$$\begin{aligned} \frac{\mathrm{d}V_2(t)}{\mathrm{d}t} &= \frac{Bc}{2}\Big\{Dx_1^2(t) + ay^*U_1^2(x_1(t)) + ay^*U^2(x(t))y_1^2(t) \\ &\qquad + b\gamma y^*\int_0^\infty f(u)y_1^2(t-u)\mathrm{d}u\Big\}\tau \\ &\quad - \frac{Bc}{2}\int_{t-\tau}^{t}\Big\{Dx_1^2(s) + ay^*U_1^2(x_1(s)) + ay^*U^2(x(s))y_1^2(s) \\ &\qquad + b\gamma y^*\int_0^\infty f(u)y_1^2(s-u)\mathrm{d}u\Big\}\mathrm{d}s. \end{aligned} \tag{4.45}$$

Now from (4.44) and (4.45), we have,

$$\begin{aligned} \frac{\mathrm{d}V_1}{\mathrm{d}t} + \frac{\mathrm{d}V_2}{\mathrm{d}t} &\le -A\left(D - \frac{b\gamma y^*}{2}\right)x_1^2(t) - Aay^*U(x(t))x_1(t)y_1(t) \\ &\quad - B\Big[dy^* - \frac{c}{2}(D + 2ay^* + b\gamma y^*)M\tau\Big]y_1^2(t) \\ &\quad - Aay^*U_1(x_1(t))x_1(t) + A\frac{b\gamma y^*}{2}\int_0^\infty f(s)y_1^2(t-s)\mathrm{d}s \\ &\quad + BcU_1(x_1(t))y_1(t) \\ &\quad + \frac{Bc}{2}\tau\Big\{Dx_1^2(t) + ay^*U_1^2(x_1(t)) + ay^*U^2(x(t))y_1^2(t)\Big\} \\ &\quad + \frac{Bc}{2}b\gamma y^*\tau\int_0^\infty f(u)y_1^2(t-u)\mathrm{d}u. \end{aligned} \tag{4.46}$$

Now define the functional

$$V_3(t) \equiv V_3(x_1(t), y_1(t)) = [A + Bc\tau]\frac{b\gamma y^*}{2}\int_0^\infty f(s)\int_{t-s}^{t} y_1^2(z)\mathrm{d}z\,\mathrm{d}s.$$

The time derivative of V_3 is given by,

$$\frac{\mathrm{d}V_3}{\mathrm{d}t} = [A + Bc\tau]\frac{b\gamma y^*}{2}\Big[y_1^2(t) - \int_0^\infty f(s)y_1^2(t-s)\mathrm{d}s\Big]. \tag{4.47}$$

We now define our main Liapunov functional

$$V(t) \equiv V(x_1(t), y_1(t)) = V_1(t) + V_2(t) + V_3(t).$$

Then clearly, $V(0,0) = 0$ and $V(x_1(t), y_1(t)) > 0$ for $x_1(t) > 0$, $y_1(t) > 0$.

Using (4.46) and (4.47), the time derivative of V along the solutions of (4.41) is given by

$$\begin{aligned}
\frac{\mathrm{d}V}{\mathrm{d}t} \leq & -A\left(D - \frac{b\gamma y^*}{2}\right)x_1^2(t) - Aay^*U(x(t))x_1(t)y_1(t)\\
& - B\left[dy^* - \frac{c}{2}(D + 2ay^* + b\gamma y^*)M\tau\right]y_1^2(t)\\
& - Aay^*U_1(x_1(t))x_1(t) + BcU_1(x_1(t))y_1(t)\\
& + \frac{Bc}{2}\Big[Dx_1^2(t) + ay^*U_1^2(x_1(t)) + ay^*U^2(x(t))y_1^2(t)\Big]\tau\\
& + [A + Bc\tau]\frac{b\gamma y^*}{2}y_1^2(t)\\
= & -\Big[A(D - \frac{b\gamma y^*}{2}) - \frac{Bc}{2}D\tau\Big]x_1^2(t)\\
& - \Bigg\{Bdy^* - A\frac{b\gamma y^*}{2}\\
& - \frac{Bc}{2}\Big[(D + 2ay^* + b\gamma y^*)M + b\gamma y^* + ay^*U^2(x(t))\Big]\tau\Bigg\}y_1^2(t)\\
& - Aay^*U(x(t))x_1(t)y_1(t) + Bc\Big(\frac{U_1(x_1(t))}{x_1(t)}\Big)x_1(t)y_1(t)\\
& - Aay^*U_1(x_1(t))x_1(t) + \frac{Bcay^*}{2}\tau U_1^2(x_1(t)).
\end{aligned} \tag{4.48}$$

Case I Let $\left(D - \frac{b\gamma y^*}{2}\right) > 0$ and $Bdy^* - A\frac{b\gamma y^*}{2} > 0$.

Now inequality (4.48) upon further simplification and rearrangement yields

$$\begin{aligned}
\frac{\mathrm{d}V}{\mathrm{d}t} \leq -\Bigg\{ & \left[A\left(D - \frac{b\gamma y^*}{2}\right) - \frac{BcD}{2}\tau\right]x_1^2(t)\\
& + \Big[Aay^*U(x(t)) - Bc\alpha_2\Big]x_1(t)y_1(t)\\
& + \Big[Bdy^* - A\frac{b\gamma y^*}{2}\\
& -\frac{Bc}{2}\tau\Big[(D + 2ay^* + b\gamma y^*)M + \quad b\gamma y^* + ay^*U^2(x(t))\Big]\Big]y_1^2(t)\Bigg\}\\
& -\Big[Aay^*\beta - \frac{Bc}{2}ay^*\tau\Big]U_1^2(x_1(t)),
\end{aligned}$$

where α_2 and β are as defined in (A_4).

Then $\mathrm{d}V/\mathrm{d}t$ is negative definite if,

$$Aay^*\beta > \frac{Bc}{2}ay^*\tau \quad \text{and} \quad C_1^2 < (A_1 - B_1\tau)(A_2 - B_2\tau), \tag{4.49}$$

where

$$2C_1 = Aay^*L - Bc\alpha_2,\ A_1 = A\left(D - \frac{b\gamma y^*}{2}\right),\ B_1 = \frac{BcD}{2},$$

$$A_2 = Bdy^* - \frac{Ab\gamma y^*}{2} \quad \text{and} \quad B_2 = \frac{Bc}{2}[(D + 2ay^* + b\gamma y^*)M + b\gamma y^* + ay^*L^2)],$$

using that $U(x) \leq L$.

Now the second inequality of (4.49) implies that,

$$B_1B_2\tau^2 - (A_1B_2 + A_2B_1)\tau + A_1A_2 - C_1^2 > 0.$$

Consider

$$B_1B_2\tau^2 - (A_1B_2 + A_2B_1)\tau + (A_1A_2 - C_1^2) = 0. \tag{4.50}$$

A necessary condition for the second inequality in (4.49) to hold is $C_1^2 < A_1A_2$. This condition implies that both the roots of (4.50) are real, distinct, and positive, since A_1, A_2, B_1, and B_2 are all be positive.

Let τ_1 and τ_2 represent the two roots of (4.50) and without loss of generality, let $\tau_1 < \tau_2$. Clearly, $\tau_1 \leq A_1/B_1 \leq \tau_2$ and $\tau_1 \leq A_2/B_2 \leq \tau_2$.

Therefore, if we choose $\tau^* = \min\{\tau_1, \frac{2A\beta}{Bc}\}$ where,

$$\tau_1 = \frac{1}{2}\Big(\frac{A_1}{B_1} + \frac{A_2}{B_2} - \sqrt{\Big(\frac{A_1}{B_1} - \frac{A_2}{B_2}\Big)^2 + \frac{4C_1^2}{B_1B_2}}\Big),$$

then $\mathrm{d}V/\mathrm{d}t < 0$ for $0 \leq \tau \leq \tau^*$. We now consider Case II.

Case II Let $A(D - \frac{b\gamma y^*}{2} - \frac{ay^*}{2}L) - \frac{Bc\alpha_2}{2} > 0$ and $Bdy^* - \frac{Ab\gamma y^*}{2} - \frac{Aay^*}{2}L - \frac{Bc\alpha_2}{2} > 0$.

Now we observe that inequality (4.48) may be simplified to yield

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} \leq &-\left\{A\left(D - \frac{b\gamma y^*}{2}\right) - \frac{Aay^*}{2}U(x(t)) - \frac{Bc\alpha_2}{2} - \frac{BcD}{2}\tau\right\} x_1^2(t)\\ &-\left\{Bdy^* - \frac{Ab\gamma y^*}{2} - \frac{Aay^*}{2}U(x(t)) - \frac{Bc\alpha_2}{2}\right.\\ &\quad\left. - \frac{Bc\tau}{2}[(D + 2ay^* + b\gamma y^*)M + b\gamma y^* + ay^*U^2(x(t))]\right\} y_1^2(t)\\ &-\left\{Aay^*\beta - \frac{Bc}{2}ay^*\tau\right\}U_1^2(x_1(t)).\end{aligned}$$

Then $\mathrm{d}V/\mathrm{d}t < 0$ if we choose $0 \le \tau < \tau^*$, where

$$\tau^* = \min\left\{\tilde{A},\ \frac{2A\beta}{Bc},\ \tilde{B}\right\},$$

in which

$$\tilde{A} = \frac{A(D - \frac{b\gamma y^*}{2} - \frac{ay^*L}{2}) - \frac{Bc\alpha_2}{2}}{\frac{BcD}{2}}$$

and

$$\tilde{B} = \frac{Bdy^* - \frac{A}{2}b\gamma y^* - \frac{A}{2}ay^*L - \frac{Bc\alpha_2}{2}}{\frac{Bc}{2}[(D + 2ay^* + b\gamma y^*)M + b\gamma y^* + ay^*L^2]}.$$

Upon eliminating the arbitrary constants A and B from the above, we obtain

$$dy^*(2D - b\gamma y^* - ay^*L) - Dc\alpha_2 > 0,$$

which gives a sufficient condition for the existence of $\tau^* > 0$.

We now simplify (4.48) as,

$$\begin{aligned}
\frac{\mathrm{d}V}{\mathrm{d}t} \le &-\left[A\left(D - \frac{b\gamma y^*}{2}\right) - \frac{BcD}{2}\tau\right]x_1^2(t)\\
&-\left[Bdy^* - \frac{Ab\gamma}{2}y^*\right.\\
&\left.\quad -\frac{Bc}{2}\left[M(D + 2ay^* + b\gamma y^*) + b\gamma y^* + ay^*L^2\right]\tau\right]y_1^2(t)\\
&-Aay^*U(x(t))x_1(t)y_1(t) + Bc\alpha_2 x_1(t)y_1(t)\\
&-\left[Aay^*\left(\frac{U_1(x_1(t))}{x_1(t)}\right) - \tau\frac{Bc}{2}ay^*\left(\frac{U_1(x_1(t))}{x_1(t)}\right)^2\right]x_1^2(t)\\
\le &-\left[A(D - \frac{b\gamma y^*}{2} + ay^*\alpha_1) - \frac{Bc}{2}(D + ay^*\alpha_2^2)\tau\right]x_1^2(t)\\
&\quad -[Aay^*U(x(t)) - Bc\alpha_2]x_1(t)y_1(t)\\
&-\left[Bdy^* - \frac{Ab\gamma y^*}{2}\right.\\
&\left.\quad -\frac{Bc}{2}\left[M(D + 2ay^* + b\gamma y^*) + b\gamma y^* + ay^*L^2\right]\tau\right]y_1^2(t).
\end{aligned} \tag{4.51}$$

We now have Case III.

Case III Let $A(D - \frac{b\gamma y^*}{2} + ay^*\alpha_1 - \frac{ay^*}{2}L) - \frac{Bc\alpha_2}{2} > 0$ and $Bdy^* - A\frac{b\gamma y^*}{2} - \frac{Aay^*L}{2} - \frac{Bc}{2}\alpha_2 > 0$.

Now the inequality (4.51) upon using the inequality $xy \le \frac{1}{2}(x^2 + y^2)$ and rearranging, assumes the form

$$\frac{\mathrm{d}V}{\mathrm{d}t} \leq -\Bigg[A\left(D - \frac{b\gamma y^*}{2} + ay^*\alpha_1 - \frac{ay^*}{2}U(x)\right) - \frac{Bc\alpha_2}{2} - \frac{Bc}{2}(D + ay^*\alpha_2^2)\tau\Bigg]x_1^2(t)$$
$$-\Bigg[Bdy^* - A\frac{b\gamma}{2}y^* - \frac{A}{2}ay^*U(x) - \frac{Bc}{2}\alpha_2 - \frac{Bc}{2}\tau\Big[M(D + 2ay^* + b\gamma y^*) + b\gamma y^* + ay^*L^2\Big]\Bigg]y_1^2(t).$$

Therefore, for $0 \leq \tau < \tau^* = \min\{m_1, m_2\}$, where

$$m_1 = \frac{A(D - \frac{b\gamma y^*}{2} + ay^*\alpha_1 - \frac{ay^*}{2}L) - \frac{Bc}{2}\alpha_2}{\frac{Bc}{2}(D + ay^*\alpha_2^2)},$$
$$m_2 = \frac{Bdy^* - \frac{Ab\gamma}{2}y^* - \frac{Aay^*}{2}L - \frac{Bc\alpha_2}{2}}{\frac{Bc}{2}[M(D + 2ay^* + b\gamma y^*) + b\gamma y^* + ay^*L^2]},$$

we have $\mathrm{d}V/\mathrm{d}t < 0$.

Case IV Let

$$D - \frac{b\gamma y^*}{2} + ay^*\alpha_1 > 0 \text{ and } Bdy^* - \frac{Ab\gamma y^*}{2} > 0.$$

Now from (4.51), we have $\mathrm{d}V/\mathrm{d}t < 0$ provided,

$$C_1'^2 < (A_1' - B_1'\tau)(A_2' - B_2'\tau), \tag{4.52}$$

that is,

$$B_1'B_2'\tau^2 - (A_1'B_2' + A_2'B_1')\tau + (A_1'A_2' - C'^2_1) > 0, \text{ in which}$$
$$A_1' = A\left(D - \frac{b\gamma y^*}{2} + ay^*\alpha_1\right), \; B_1' = \frac{Bc}{2}(D + ay^*\alpha_2^2),$$
$$C_1' = \frac{1}{2}(Aay^*L - Bc\alpha_2), \; A_2' = Bdy^* - \frac{Ab\gamma y^*}{2}$$

and

$$B_2' = \frac{Bc}{2}[M(D + 2ay^* + b\gamma y^*) + b\gamma y^* + ay^*L^2].$$

Arguing as in Case I, it can be shown that the equation,

$$B_1'B_2'\tau^2 - (A_1'B_2' + A_2'B_1')\tau + (A_1'A_2' - C'^2_1) = 0 \tag{4.53}$$

has two distinct, positive, real roots, say, $\tilde{\tau_1}, \tilde{\tau_2} (> \tilde{\tau_1})$. Further, it is easy to see that $\tilde{\tau_1} \leq A'_1/B'_1 \leq \tilde{\tau_2}$ and $\tilde{\tau_1} \leq A'_2/B'_2 \leq \tilde{\tau_2}$.

Therefore, for

$$\tau^* = \tilde{\tau_1} = \frac{1}{2}\Big(\frac{A'_1}{B'_1} + \frac{A'_2}{B'_2} - \sqrt{\Big(\frac{A'_1}{B'_1} - \frac{A'_2}{B'_2}\Big)^2 + \frac{4C'^2_1}{B'_1 B'_2}}\Big),$$

we have, $\mathrm{d}V/\mathrm{d}t < 0$.

We have established the negative definiteness of $\mathrm{d}V/\mathrm{d}t$ in each of the Cases I, II, III, or IV depending on the choice of τ^* estimated separately for each of the case. Therefore, the functional V constructed above is the required Lyapunov functional and now the conclusion of the theorem follows from standard arguments. □

The following example illustrates the above result.

Example 4.33 Consider the system (4.40) with $D = 1, a = 4, b = 0.2, \gamma = 1, c = 3$, and $d = 20$. That is,

$$x'(t) = (x_0 - x(t)) - 4U(x(t))y(t) + (0.2)\int_0^\infty f(s)y(t-s)\mathrm{d}s,$$
$$y'(t) = -2y(t) + 3U(x(t-\tau)) - 20y^2(t),$$

in which $x_0 = 9.68$ (approx.) and $U(x) = x/(1+x)$.

Clearly, $(x^*, y^*) = (8, \frac{1}{30})$ and $U(x^*) = \frac{8}{9}$. Further, $M = 1, \beta = 9, \alpha_2 = \frac{1}{9}$, and $\alpha_1 = 0.0122$, assuming the bound $x(t) \leq x_0 + (b\gamma cL)/(dD)$, given in Sect. 4.2.

Then for the choice of $A = 1$ and $B = 1$ we have, from Theorem 4.32,

(I). $\tau_1 = 0.3043, \quad \tau_2 = 0.6724$, and $\frac{2A\beta}{Bc} = 6$, and thus, $\tau^* = 0.3043$,
(II). $\tau^* = 0.202$,
(III). $m_1 = 0.5093, \quad m_2 = 0.203$ and thus, $\tau^* = 0.203$, and
(IV). $\tilde{\tau_1} = 0.3055, \quad \tilde{\tau_2} = 0.673$, and $\tau^* = \tilde{\tau_1} = 0.3055$.

We observe that the estimates on τ^* in these cases may be improved by proper choice of the parameters A and B. For example, the choice $A = 0.75$ and $B = 1$ yields, $\tau^* = 0.211$ and $\tau^* = 0.212$, respectively, in cases(II) and (III).

Remark 4.34 A researcher, who is familiar with Lyapunov function(al)s, observes that stability region obtained depends on the selection of Lyapunov function(al) and any modification of this function(al) either in terms of functions used or the parameters included in the functional may produce a different portion of the stability region of the system. It is the observation of the authors that, in general, no two Lyapunov function(al)s produce the same stability region for the system under consideration. At this juncture, we draw the attention of the readers to the normalization of y in (4.41). Theorem 4.32 may be tried without a normalization of y to obtain a different estimation on the delay τ. For example, Cases I and II of Theorem 4.32 with a nonnormalized y (i.e., $y_1 = y - y^*$) assume the form, *Case I (a)* $(D - \frac{b\gamma}{2}) > 0$, $Bdy - \frac{Ab\gamma y^*}{2} > 0$ and

$$\tau^* = \min\left\{\frac{2A\beta}{Bc},\ \frac{1}{2}\Big(\frac{A_1}{B_1} + \frac{A_2}{B_2} - \sqrt{\Big(\frac{A_1}{B_1} - \frac{A_2}{B_2}\Big)^2 + \frac{4C_1^2}{B_1 B_2}}\Big)\right\},$$

where

$$A_1 = A\left(D - \frac{b\gamma}{2}\right),\ B_1 = \frac{BcD}{2},\ 2C_1 = AaL - Bc\alpha_2,$$

$$A_2 = Bd - \frac{Ab\gamma}{2} \quad \text{and} \quad B_2 = \frac{Bc}{2}[(D + a(1 + y^*) + b\gamma)M + b\gamma + aL^2],$$

and

Case II (a)

$$A\Big(D - \frac{b\gamma}{2} - \frac{aL}{2}\Big) - \frac{Bc\alpha_2}{2} > 0,$$

$$Bd - \frac{A}{2}b\gamma - \frac{A}{2}aL - \frac{Bc\alpha_2}{2} > 0$$

with

$$\tau^* = \min\left\{\frac{A(D - \frac{b\gamma}{2} - \frac{aL}{2}) - \frac{Bc\alpha_2}{2}}{\frac{BcD}{2}}, \frac{2A\beta}{Bc}, \frac{Bd - \frac{A}{2}b\gamma - \frac{A}{2}aL - \frac{Bc\alpha_2}{2}}{\frac{Bc}{2}[(D + a(1 + y^*) + b\gamma)M + b\gamma + aL^2]}\right\}.$$

For these estimations, we get for the parametric values of Example 4.33, for Case I(a),

$\tau_1 = 0.5507$, $\tau_2 = 0.6724$, and $(2A\beta)/(Bc) = 6$, and hence, $\tau^* = 0.5507 = \tau_1$.

Thus, in this case we have obtained a better estimation on τ than Case I of Theorem 4.32. But we note that Case II(a) cannot be applied here as the first condition

$$\Big(D - \frac{b\gamma}{2} - \frac{aL}{2}\Big) - \frac{Bc\alpha_2}{2} > 0$$

fails to hold for the above parametric values.

It would be interesting to know what changes the nonnormalized term y brings in the other cases. Further, the functional used in the proof of Theorem 4.32 is not unique and an enthusiastic reader may try different ones for few more stability conditions.

Now we use the procedure of Theorem 4.10 to find one more sufficient condition.

Letting $x_1(t) = x(t) - x^*$, $y_1(t) = y(t) - y^*$, and $U_1(x_1(t)) = U(x(t)) - U(x^*)$, we rewrite system (4.40) as,

$$x_1'(t) = -Dx_1(t) - aU(x(t))y_1(t) - ay^*U_1(x_1(t)) + b\gamma \int_0^\infty f(s)y_1(t-s)\mathrm{d}s,$$
$$y_1'(t) = (y_1(t) + y^*)[cU_1(x_1(t-\tau)) - dy_1(t)]. \tag{4.54}$$

In the following result we replace the assumptions (A_3) and (A_4) on U_1 by (A_2).

Theorem 4.35 *Assume that the delay kernel f satisfies (H_1), (H_2) and the uptake function U_1 satisfies (A_1) and (A_2). The equilibrium solution $(0,0)$ of (4.54) is globally asymptotically stable for*

$$0 \le \tau < \tau^* = \min\left\{ \frac{D - ck - aky^*}{(D + ay^*)ck}, \frac{d + a\bar{\alpha} - b\gamma}{(aL + b\gamma)ck} \right\},$$

provided $D - ck - aky^* > 0$ and $d + a\bar{\alpha} - b\gamma > 0$, in which $\bar{\alpha} = \min_{x \ge x^*}\{U(x)\}$.

Proof We consider the functional, $V(t) = V_1(t) + V_2(t)$ where

$$V_1(t) = |x_1(t)| + \left|\log\left(\frac{y_1(t) + y^*}{y^*}\right)\right| + b\gamma \int_0^\infty f(s) \int_{t-s}^t |y(u)|\mathrm{d}u\,\mathrm{d}s$$

and

$$V_2(t) = ck\Big[D \int_{t-\tau}^t \mathrm{d}s \int_s^t |x_1(u)|\mathrm{d}u + aL \int_{t-\tau}^t \mathrm{d}s \int_s^t |y_1(u)|\mathrm{d}u + ay^* \int_{t-\tau}^t \mathrm{d}s \int_s^t |U_1(x_1(u))|\mathrm{d}u + b\gamma \int_{t-\tau}^t \mathrm{d}s \int_0^\infty f(z) \int_{s-z}^t |y_1(u)|\mathrm{d}u\,\mathrm{d}z\Big].$$

Consider

$$D^+V_1(t) \le -D|x_1(t)| - aU(x(t))|y_1(t)| - ay^*|U_1(x_1(t))| + c|U_1(x_1(t-\tau))| + b\gamma|y_1(t)| - d|y_1(t)|.$$

Now we have,

$$\begin{aligned}|U_1(x_1(t-\tau))| &\le k|x_1(t-\tau)| = k\left|x_1(t) - \int_{t-\tau}^t x_1'(s)\mathrm{d}s\right| \\ &= k\Big|x_1(t) - \int_{t-\tau}^t \Big[-Dx_1(s) - aU(x(s))y_1(s) \\ &\qquad - ay^*U_1(x_1(s)) + b\gamma \int_0^\infty f(z)y_1(s-z)\mathrm{d}z\Big]\mathrm{d}s\Big|\end{aligned}$$

$$\leq k|x_1(t)| + k\Big[D\int_{t-\tau}^{t}|x_1(s)|\mathrm{d}s + aL\int_{t-\tau}^{t}|y_1(s)|\mathrm{d}s$$
$$+ ay^*\int_{t-\tau}^{t}|U_1(x_1(s))|\mathrm{d}s$$
$$+ b\gamma\int_{t-\tau}^{t}\int_0^\infty f(z)|y_1(s-z)|\mathrm{d}z\,\mathrm{d}s\Big].$$

Thus, we have

$$\begin{aligned} D^+V_1(t) \leq &-(D-ck-aky^*)|x_1(t)| - (d+aU(x)-b\gamma)|y_1(t)| \\ &+ck\Big[D\int_{t-\tau}^{t}|x_1(s)|\mathrm{d}s + aL\int_{t-\tau}^{t}|y_1(s)|\mathrm{d}s \\ &+ay^*\int_{t-\tau}^{t}|U_1(x_1(s))|\mathrm{d}s + b\gamma\int_{t-\tau}^{t}\int_0^\infty f(z)|y_1(s-z)|\mathrm{d}z\,\mathrm{d}s\Big]. \end{aligned} \tag{4.55}$$

Now

$$\begin{aligned} D^+V_2(t) \leq &\, ck\Big[D|x_1(t)|\tau + aL|y_1(t)|\tau + ay^*|U_1(x_1(t))| + b\gamma|y_1(t)|\tau\Big]\tau \\ &-ck\Big[D\int_{t-\tau}^{t}|x_1(s)|\mathrm{d}s + aL\int_{t-\tau}^{t}|y_1(s)|\mathrm{d}s \\ &+ay^*\int_{t-\tau}^{t}|U_1(x_1(s))|\mathrm{d}s + b\gamma\int_{t-\tau}^{t}\int_0^\infty f(z)|y_1(s-z)|\mathrm{d}z\,\mathrm{d}s\Big]. \end{aligned} \tag{4.56}$$

Using (4.55) and (4.56) we have after some simplifications

$$\begin{aligned} D^+V(t) &\leq -(D-ck-aky^*)|x_1(t)| - (d+aU(x)-b\gamma)|y_1(t)| \\ &\quad + ck(D+aky^*)\tau|x_1(t)| + ck(aL+b\gamma)\tau|y_1(t)| \\ &= -\Big(D-ck-aky^*-ck(D+aky^*)\tau\Big)|x_1(t)| \\ &\quad -\Big(d+aU(x)-b\gamma-ck(aL+b\gamma)\tau\Big)|y_1(t)|. \end{aligned}$$

The negative definiteness of $D^+V(t)$ follows from the hypotheses. The remainder of the proof may be completed employing standard arguments. □

The following result is a simple consequence of Theorem 4.32 which provides sufficient conditions for the global asymptotic stability of the equilibrium solution $(0,0)$ of (4.6.2) when $\tau = 0$.

Corollary 4.36 *Assume that the delay kernel f satisfies (H_1), (H_2) and the uptake function U_1 satisfies (A_1), (A_3), and (A_4). The equilibrium solution $(0,0)$ of (4.41) is globally asymptotically stable for $\tau = 0$ provided there exist positive constants A and B such that the following conditions hold:*

$A_1 = A(D - \frac{b\gamma y^*}{2}) > 0$, $A_2 = Bdy^* - \frac{Ab\gamma y^*}{2} > 0$, *and* $A_1 A_2 > {C_1}^2$, *where* $2C_1 = Aay^*L - Bc\alpha_2$.

The following results are for the case $\tau = 0$ in (4.40). These results are special cases of Theorems 4.17 and 4.18, respectively. The results may be established by employing the same functionals used in Theorems 4.17 and 4.18 and the procedure as well. Thus, the details are omitted.

Theorem 4.37 *Assume that the delay kernel* f *satisfies* (H_1) *and* (H_2) *and the uptake function satisfies* (A_1) *and* (A_2). *The equilibrium solution* $(0, 0)$ *of* (4.41) *is globally asymptotically stable for* $\tau = 0$ *provided the parameters satisfy*

$$dy^* > \left[\frac{1}{4} + \left(\frac{b\gamma}{a}\right)^2\right]c.$$

Theorem 4.38 *Assume that the delay kernel* f *satisfies* (H_1) *and* (H_2) *and the uptake function satisfies* (A_1) *and* (A_2). *The equilibrium solution* $(0, 0)$ *of* (4.41) *is globally asymptotically stable for* $\tau = 0$ *provided the inequalities*

$$x^* < x_0, \quad dy^* > \left(\frac{b\gamma}{a}\right)^2 \frac{ac}{4U(x^*)(aU(x^*) - b\gamma)}.$$

Now we give examples to compare Corollary 4.36 with Theorems 4.37 and 4.38.

Example 4.39 Consider the system (4.41) with $D = 1.3, a = 8, b = 0.8, \gamma = 2, c = 7.6$, and $d = 10$. That is

$$x'(t) = (1.3)(x_0 - x(t)) - 8U(x(t))y(t) + (1.6)\int_0^\infty f(s)y(t-s)\mathrm{d}s,$$
$$y'(t) = -(3.3)y(t) + (7.6)U(x(t)) - 10y^2(t),$$

in which $x_0 = 1.0923$ (approx.) and $U(x) = x/(1 + x)$.

Clearly, $(x^*, y^*) = (1, \frac{1}{20})$ and $U(x^*) = \frac{1}{2}$.

It is easy to see that all the hypotheses of Corollary 4.36 are satisfied for the choice of $A = 5, B = 1$ and hence, (x^*, y^*) is globally asymptotically stable by virtue of Corollary 4.36. It may be observed that parametric conditions of both the Theorems 4.37 and 4.38 are violated, and hence, they are not applicable here.

Example 4.40 Consider the system,

$$x'(t) = (x_0 - x(t)) - 20U(x(t))y(t) + 2\int_0^\infty f(s)y(t-s)\mathrm{d}s,$$
$$y'(t) = -5y(t) + 16U(x(t)) - 2y^2(t),$$

in which $D = 1, a = 20, b = 0.5, \gamma = 4, c = 16, d = 2, x_0 = 22$, and $U(x) = x/(3 + x)$.

Clearly, $(x^*, y^*) = (9, \frac{7}{2})$ and $U(x^*) = \frac{3}{4}$.

Since $D - (b\gamma y^*)/2 < 0$, Corollary 4.36 cannot be applied here, while both Theorems 4.37 and 4.38 ensure the global asymptotic stability of (x^*, y^*) in this case.

It is evident from the above examples that Corollary 4.36 is independent of Theorems 4.37 and 4.38.

4.7 Discussion

In this chapter we have obtained several independent sets of sufficient conditions for the global asymptotic stability of the positive equilibrium besides establishing the survival of species (persistence). It is easy to see that Theorems 4.10 and 4.13 reduce to Theorems 2.33 and 2.35, respectively, in the special case $d = 0$. But we cannot think of the counter parts of Theorems 4.11 and 4.12 for (2.81) in this sense. Thus, these two theorems establish the stability of (x^*, y^*) under conditions that are definitely not possible for (2.81). May be due to the presence of the supporting term "$-dy^2$," we are able to describe the stability region of (4.1) better.

The results of Sect. 4.5 uphold the popular notion that the transition from instability to stability is via oscillations. Further these results reestablish the occurrence of oscillations observed in experiments (see Sect. 1.8 of Chap. 1).

It is interesting to note that delay-independent results (stability, no matter how large the delay is) would severely restrict the parameters of the system. Due to these restrictions, delay-independent stability results become less applicable. Moreover, these results are of little interest in the back ground that increasing time delays always destabilizes the system. Hence, it is worthwhile to discuss results which depend on the delay (that is, delay dependent stability results) for which the equilibrium is stable. This is the starting point of our discussion in the Sect. 4.6. We have not placed any apriori conditions on the parameters for the stability of the positive equilibrium of the delay-free system. Thus, the method followed here applies to the delay-free system, as well (that is, when $\tau = 0$).

4.8 Notes and Remarks

Theorem 4.32 gives the length of the delay for which the system is stable when the system has a finite carrying capacity ($d > 0$). But for large d, we have from the equilibrium solutions (4.4) that y^* takes small values and eventually $y^* \to 0$ as $d \to \infty$. From the conditions on the parameters of the system in Theorem 4.32, we can see that τ^* increases for increasing d, but is always bounded (by $cL - \gamma - D$), eventually tending to $cU(x_0) - \gamma - D$. But when $d \to \infty$, $y^* \to 0$ which means that the consumer population becomes extinct. Surely, this is not desirable. This means that the system when it has a definite carrying capacity can tolerate a delay in the growth response of the species and under the conditions of Theorem 4.32, the species survive.

We observed in Sect. 2.5 (see Example 2.42 and Remarks) that we need a better condition for establishing the survival of species when $aU(x) < b\gamma$ for $x > x^*$ and our study here reveals that the introduction of the term $-dy^2$ has definitely answered this problem, allowing $U(x)$ to be smaller than $b\gamma$. Hence, we may conclude that the finite carrying capacity of the environment help stabilize the situation in the sense expressed above.

Another way of viewing the results in this chapter is that at low levels of nutrient consumption (supply), the resulting death due to the intraspecies competition, represented by $-dy^2$ in (4.1) helps in stabilizing the populations and under the sufficient conditions we have presented in Sect. 4.4, the populations tend toward the positive equilibrium solution.

Note that we have not allowed any recycling from the dead biomass represented by $-dy^2$. An enthusiastic reader may further explore the influence of recycling from this biomass also.

A question of more general interest is to discuss the case where in the self-regulatory effect, being nonlinear, need not necessarily be quadratic in nature. Thus, it is reasonable to consider the model (4.1) in which the term dy^2 may be replaced by dy^p for some $p > 0$. Mathematically, the model is more complicated to analyze in view of the fact that solutions of (4.1) when $0 < p < 1$ fail to possess uniqueness property.

We have noted from (4.37) and (4.38) that the uniqueness of T-periodic solution excludes the possibility of existence of a positive equilibrium solution to (4.1). This situation has arisen due to the assumption that the growth rate coefficient (c) is no more than the consumption rate (a). It could be of some interest to see what happens when $a < c$, growth rate is bigger than the consumption rate as in the case of a fast expanding virus, for example. In such case the system (4.1) may have a positive equilibrium solution besides a unique T-periodic solution.

Since persistence also implies survival in some sense, results on persistence for models (2.1)–(2.6) could be of interest. However, the existence of $\delta > 0$ such that $x(t) > \delta$ for $t \to \infty$ may represent a surviving population but we are not fully convinced that this population may be in a position to reproduce and improve the population even when the circumstances are conducive for a growth. We have to interpret the persistence of the solutions of system (4.1) in the light of the finite carrying capacity of environment which enforces the death of some of the species while Theorem 4.7 ensures the survival of at least some of the species.

It is clear that both persistence and global stability ensure the eventual survival of species, requiring, respectively, that $\liminf_{t\to\infty} u(t) \geq \delta_1 > 0$ and $\liminf_{t\to\infty} u(t) = u^* > 0$. Especially, when $\delta,\ u^*$ assume insignificantly low values, how to understand this kind of survivability remains as an open question. Would biology support the thought that the eventual growth of the populations limited to small (insignificant) numbers mean survival of the ecosystem?

The following example substantiates our contention.

Consider the following model (see Example 4.20)

$$x'(t) = 2(x_0 - x(t)) - 25U(x(t))y(t) + 3\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s$$
$$y'(t) = -8y(t) + 20y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - 315y^2(t)$$

in which $U(x) = x/(4+x), b = 1/2, \gamma = 6, D = 2$, and $x_0 = 4.030$ approximately.

The equilibrium solutions are $x^* = 4$ and $y^* = 0.00635$ with $U(x^*) = \frac{1}{2}$ and $k = 1/4$.

This system is globally asymptotically stable by virtue of Theorems 4.17 or 4.18.

Note that the equilibrium value $y^* = 0.00635$ is very insignificant when compared to other parameters of the system.

Does not it mean that the concepts of survivability and stability are not adequately handled by the mathematical definitions? This unquestionably calls for a more intensive introspection into our existing mathematical formulations. Understandably, results of the kind discussed in the literature remain only as mathematical results and do not evince any interest in biologists. On the other hand, local stability analysis is certainly a disturbing factor under the above state of affairs when global stability itself, presumably, has a little influence in the sense described above.

It appears, therefore, reasonable to visualize the growth of y beyond equilibrium value but with controllable size.

Also, another issue that demands the attention of mathematicians is the question of survival of the consumer species when the nutrient (may be a chemical feed) supplied may have an adverse affect on the normal growth cycle of consumer population resulting in the survivability of individuals that may not have the ability to contribute to the growth of the ecosystem.

The results of Sect. 4.2–4.4 provided by Sree Hari Rao and Raja Sekhara Rao [86, 87]. Details of the proofs of Theorems 4.17 and 4.18 can be had from the work of Beretta and Takeuchi [11]. Sects. 4.5 and 4.7 are contributions of Sree Hari Rao and Raja Sekhara Rao [87, 91]. Extending model (4.1) to a system of n-competing consumer species, Fergola, Jiang, and Ma [31] obtained similar results. Similar models with two or more competing species are considered by Freedman and Xu [39] and Ruan and He [80]. Of course, some of them assume no delay in growth response.

4.9 Exercises

1. Explain why Lyapunov functionals of the type used in Theorems 4.11 and 4.12 are not suitable for system (2.8)?
2. Show that Theorems 4.10 and 4.13 reduce to Theorems 2.33 and 2.35, respectively.

3. What conclusions can be drawn from Examples 2.42 and 4.21? Does this suggest killing of some species when food supply is not good enough ?
4. Give examples of delay kernels f and g satisfying the conditions $\int_0^\infty sf(s)\mathrm{d}s = \infty$ but $\int_0^\infty f(s)\mathrm{d}s = 1$ so that Example 4.16 holds only for Theorem 4.13 but not for Theorems 4.10 and 4.11.
5. Extend Theorem 4.26 for different time periods T_1 and T_2, for $D(t)$ and $x_0(t)$ respectively.
6. Show that the unique periodic solution of (4.1) is asymptotically stable (Choose $W_1(t) = W_2(t) = 0$ and $D(t) = D_0, x_0(t) = x_0$ in Theorem 4.30).
7. Following Corollary 4.30, find conditions for the uniqueness of periodic solution. Can one conclude that the uniqueness of periodic solution implies nonexistence of positive equilibrium for (2.81)? (See discussion before Theorem 4.31).
8. It is seen in Chaps. 2 and 3 that the time delays induce oscillations. Now from Corollary 4.30, periodic solutions exist to system (2.81) and self-regulation also induces oscillations. Discuss how to differentiate these two types of oscillations?
9. Is it possible to establish the existence of limit cycles to systems (2.81) and (4.1)? (see Beretta, Bischi, and Solimano [7]).
10. If the term dy^2 is replaced by $dy^p, 0 < p < 1$ in system (4.1), solutions need not be unique. Using the transformation $z = y^{1-p}$ study the stability of the resulting system. The problem is still open.
11. Supply the details to establish that the map $G : Q_r \to \mathbf{R}^2$ defined in Theorem 4.26 (in order to establish the existence of a unique solution (k_1, k_2) for (4.31) and (4.32)) is a contraction mapping.
12. Try delay independent global stability results for (4.40).

    (a) Use the procedure used in results from among Theorems 4.9–4.18.
    (b) Can the results of Section (2.4) derived for equation (2.67) be modified for this model?

    Design suitable Lyapunov functionals in these cases
13. See how models described in earlier sections become special cases of (4.40).

Choice of parameters	Model
$d = 0$	(2.67)/(2.5)
$d = 0, \tau{=}0$	(2.40)
$d = 0, f(s) = \delta(s)$	(2.29)
$d = 0, b = 0, f(s) = \delta(s)$	(2.2)
$d = 0, f(s) = \delta(s), \gamma = 0$	(2.7)
$d = 0, \gamma = 0, f(s) = \delta(s)\tau = 0,$	(1.5).

Can the results of Section 4.6 be modified to these models? If yes, establish the global stability of positive equilibrium in each case. Otherwise, give reasons and substantiate them.

Chapter 5
Wall Growth

5.1 Introduction

Often, the microorganisms grow not only in the growth medium (container), but also along the walls of the container. This is either due to the ability of the microorganisms to stick on to the walls of the container or the flow rate is not fast enough to wash these organisms out of the system. This phenomenon is generally referred to as the "wall growth."

One of the basic assumptions in a simple chemostat is that the washout rate is fast enough that it does not allow any wall growth. But when one uses a chemostat to describe a bio reactor, wall growth becomes an important factor to be considered (e.g., growth of microflora in large intestine of mammals, etc [103]). Again when we consider a lake situation, where the flow rate is very low, we can observe the growth of algae and fungi along the walls or banks. These observations motivate us to study the influence of wall growth on the dynamics of limited nutrient-consumer system and we appropriately modify our model equations (2.81) in order to incorporate the wall growth into our model.

Naturally, we regard the consumer population y as an aggregate of two categories of populations, namely, one in the growth medium (y_1) and the other on the walls of the container (y_2). Any time the individuals may switch their categories, that is, the microorganisms on the walls may join those in the growth medium or the biomass in the medium may prefer walls. If r_1 and r_2 represent the rates at which the species stick on to and shear from the walls, respectively, then $r_1 y_1$ and $r_2 y_2$ represent the corresponding terms of species changing the categories. Thus, the growth of microorganisms is now represented by two equations, one corresponding to that sticks onto the wall and the other for the one in the medium. The nutrient is equally available to both the categories. Therefore, it is assumed that both the categories consume same amount of nutrient and at the same rate.

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With these observations, we now present our model equations as follows:

$$\begin{aligned}
x'(t) &= D(x_0 - x(t)) - aU(x(t))y_1(t) - aU(x(t))y_2(t) \\
&\quad + b\gamma \int_{-\infty}^{t} f(t-s)y_1(s)\mathrm{d}s, \\
y_1'(t) &= -(\gamma + D)y_1(t) + cy_1(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s \\
&\quad - r_1 y_1(t) + r_2 y_2(t), \\
y_2'(t) &= -\gamma y_2(t) + cy_2(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s \\
&\quad + r_1 y_1(t) - r_2 y_2(t).
\end{aligned} \tag{5.1}$$

Observe that only the dead biomass in the medium, y_1 contributes to the material recycling. Moreover, since the microorganisms on the wall are not washed out of the system, we have not included the term $-Dy_2$ in the last equation representing the growth of y_2. Further, the natural death factor γ is assumed to be the same for both these categories.

Our aim in this chapter is to discuss the influence of wall growth on the behavior of solutions of the model equations, in particular, on the stability of the positive equilibrium solution of (5.1). Since the variables x, y_1, and y_2 represent the concentrations, we assume nonnegative initial conditions

$$x \equiv \phi(t), \quad y_i \equiv \phi_i(t), \quad i = 1, 2 \text{ and } -\infty < t \le 0, \tag{5.2}$$

where ϕ and ϕ_i are bounded, continuous, nonnegative functions.

We begin our study with a description of the properties of the solutions of (5.1) in Sect. 5.2.

5.2 Basic Properties of Solutions

As in the earlier chapters, we assume that the consumption function U satisfies (A_1) and (A_2) and the delay kernels are nonnegative and satisfy (H_1) and (H_2). For brevity, we shall list these assumptions below.

(A_1). $U(x)$ is continuous real valued function defined on $\mathbf{R}_+ = [0, \infty)$ such that

$$U(0) = 0, U(x) > 0 \quad \text{for } x > 0 \text{ and } \lim_{x\to\infty} U(x) = L_1 < \infty.$$

$|U(x)| \le L$ for all x, for some $L > 0$.

(A_2). There exists a constant $k > 0$ such that for all x_1, $x_2 \in \mathbf{R}_+$,

$$|U(x_1) - U(x_2)| \leq k|x_1 - x_2|.$$

$$(H_1). \quad \int_0^\infty f(s)\mathrm{d}s = 1, \quad \int_0^\infty g(s)\mathrm{d}s = 1,$$

$$(H_2). \quad \int_0^\infty sf(s)\mathrm{d}s < \infty, \quad \int_0^\infty sg(s)\mathrm{d}s < \infty.$$

In view of the local Lipschitz condition (A_2) on U, we can prove the local existence and uniqueness of solutions of (5.1). Further, we can extend the results of Sect. 2.5 of Chap. 2, to establish the local existence and uniqueness of solutions of (5.1) and the uptake function need not necessarily be of Lipschitzian type in that case. Therefore, we tacitly assume throughout this chapter that system (5.1) has solutions which are unique and continuable on their maximal interval of existence.

We shall now show that all the solutions of (5.1) are nonnegative for all $t > 0$.

Theorem 5.1 *All the solutions of the system* (5.1) *are nonnegative for all* $t > 0$ *corresponding to the initial conditions* (5.2).

Proof We shall show that once a solution enters the octant

$$\Omega = \{(x, y_1, y_2)/x > 0, y_1 > 0, y_2 > 0\},$$

it remains there forever. By continuity each solution has to take the value 0 before it assumes a negative value. If $y_i = 0$ with $y_j \geq 0, i \neq j$, then $y_i' = r_j y_j \geq 0$ for i = 1,2, which means that y_i is at least nondecreasing at $y_i = 0$. This rules out the possibility of $y_i, i = 1, 2$ taking a negative value. Again when $x = 0$, we have

$$x'(t) = Dx_0 + b\gamma \int_{-\infty}^{t} f(t-s)y_1(s)\mathrm{d}s > 0,$$

since $y_i \geq 0$. Therefore, x is increasing at $x = 0$. When $y_1 = 0 = y_2$, $x'(t) = Dx_0 - Dx$, and again at $x = 0$, $x'(t) = Dx_0 > 0$ and hence, x is increasing at $x = 0$. □

Thus, we can conclude that the solutions of (5.1) are nonnegative for all $t > 0$.

We shall now show that the solutions are bounded. We employ a Lyapunov function technique as in Theorem 2.28 and obtain a set of conditions on the delay kernels.

Theorem 5.2 *All solutions of* (5.1) *are uniformly bounded in* $\mathbf{R}_+^3 = \{(x, y_1, y_2) \in \mathbf{R}^3 : x \geq 0, y_i \geq 0, i = 1, 2\}$, *provided the following conditions hold.*

$$T_g = \int_0^\infty sg(s)\mathrm{d}s < \min\left\{\frac{bD}{ar_1L}, \frac{b\gamma}{ar_2L}, \frac{a-bc}{acL}\right\},$$
$$T_f = \int_0^\infty sf(s)\mathrm{d}s < \frac{1}{\gamma}.$$

Proof We consider the functional

$$\begin{aligned} V(t) &\equiv V(x, y_1, y_2) \\ &= x(t) + by_1(t) + b\gamma \int_0^\infty f(s) \int_{t-s}^t y_1(u)\, \mathrm{d}u\, \mathrm{d}s \\ &\quad + by_2(t) + a(y_1(t) + y_2(t)) \int_0^\infty g(s) \int_{t-s}^t U(x(u))\, \mathrm{d}u\, \mathrm{d}s. \end{aligned}$$

The time derivative of V along the solutions of (5.1) after some rearrangements becomes

$$\begin{aligned} \frac{\mathrm{d}V}{\mathrm{d}t} &= Dx_0 - Dx(t) - a(\gamma + D + r_1)y_1(t) \int_0^\infty g(s) \int_{t-s}^t U(x(u))\, \mathrm{d}u\, \mathrm{d}s \\ &\quad - a(\gamma + r_2)y_2(t) \int_0^\infty g(s) \int_{t-s}^t U(x(u))\, \mathrm{d}u\, \mathrm{d}s \\ &\quad - bDy_1(t) + ar_1 y_1(t) \int_0^\infty g(s) \int_{t-s}^t U(x(u))\, \mathrm{d}u\, \mathrm{d}s \\ &\quad - b\gamma y_2(t) + ar_2 y_2(t) \int_0^\infty g(s) \int_{t-s}^t U(x(u))\, \mathrm{d}u\, \mathrm{d}s \\ &\quad - \left[a - bc - ac \int_0^\infty g(s) \int_{t-s}^t U(x(u))\, \mathrm{d}u\, \mathrm{d}s\right] \times \\ &\quad \times y_1(t) \int_0^\infty g(s)\, U(x(t-s))\, \mathrm{d}s \\ &\quad - \left[a - bc - ac \int_0^\infty g(s) \int_{t-s}^t U(x(u))\, \mathrm{d}u\, \mathrm{d}s\right] \times \\ &\quad \times y_2(t) \int_0^\infty g(s)\, U(x(t-s))\, \mathrm{d}s. \end{aligned}$$

Ignoring the third and fourth terms on the right-hand side which are negative and using $U(x) \leq L$ for all x, we have

$$\begin{aligned} \frac{\mathrm{d}V}{\mathrm{d}t} &\leq Dx_0 - Dx(t) - (b\gamma - ar_2 LT_g)y_2(t) - (bD - ar_1 LT_g)y_1(t) \\ &\quad - (a - bc - acLT_g)y_1(t) \int_0^\infty g(s)\, U(x(t-s))\, \mathrm{d}s \\ &\quad - (a - bc - acLT_g)y_2(t) \int_0^\infty g(s)\, U(x(t-s))\, \mathrm{d}s \\ &\leq Dx_0 - Dx(t) - (b\gamma - ar_2 LT_g)y_2(t) - (bD - ar_1 LT_g)y_1(t), \end{aligned}$$

invoking the bound on T_g.

Thus,

$$\frac{dV}{dt} \le Dx_0 - Dx(t) - \alpha_1 y_1(t) - \alpha_2 y_2(t),$$

where $\alpha_1 = bD - ar_1 LT_g$ and $\alpha_2 = b\gamma - ar_2 LT_g$.

Now define $\omega = \{(x, y_1, y_2) \in \mathbf{R}^3_+ : Dx + \alpha_1 y_1 + \alpha_2 y_2 \le Dx_0\}$.

Case I Consider $\mathbf{R}^3_+ - \omega$. If a trajectory starts from $t_0 > 0$ in $\mathbf{R}^3_+ - \omega$, then the functional $V(x, y_1, y_2)$ along a trajectory starting from this point would be decreasing for all times $t \ge t_0$ such that $(x, y_1, y_2) \in \mathbf{R}^3_+ - \omega$. Clearly $V(t) \ge bx(t) + by_1(t) + by_2(t) = b||X(t)||$, since $0 < b < 1$. Using the initial conditions, we have

$$\begin{aligned}\frac{dV}{dt} &\le \phi + b\phi_1 + b\gamma T_f \phi_1 + aLT_g\phi_1 + b\phi_2 + aLT_g\phi_2 \\ &\le 3\eta||\Phi||,\end{aligned}$$

where $\eta = \max\{1, b\gamma T_f + aLT_g, b + aLT_g\}$ and $||\Phi|| = \sup_{t\in(-\infty,0)}\{|\phi|, |\phi_1|, |\phi_2|\}$. Let $\beta = 3\eta||\Phi||$. Then we have $b||X(t)|| \le V(x, y_1, y_2) \le \beta$ which implies the uniform boundedness of the solutions of (5.1) here.

Case II If $(x, y_1, y_2) \in \omega$ for all t then by definition of ω, all the solutions are uniformly bounded.

Case III Suppose that a trajectory enters the plane ω at t_0 and leaves ω at t_1. Then for all $t \in (t_0, t_1)$,

$$\begin{aligned}V(x, y_1, y_2) \le{}& x_0\left(1 + \frac{bD}{\alpha_1} + \frac{bD}{\alpha_2} + \frac{aDLT_g}{\alpha_1} + \frac{aDLT_g}{\alpha_2}\right) \\ &+ b\gamma \int_0^\infty f(s) \int_{t-s}^t y_1(u)\mathrm{d}u\,\mathrm{d}s.\end{aligned}$$

Since $y_1(u) \le (1/b)V(x, y_1, y_2) \le \beta/b$ for $u \in (-\infty, t_0)$ and $y_1 \le (Dx_0)/(\alpha_1)$ for $u \in (t_0, t_1)$, we have for $t \in (t_0, t_1)$,

$$\begin{aligned}V(x, y_1, y_2) \le{}& x_0\left(1 + \frac{bD}{\alpha_1} + \frac{bD}{\alpha_2} + \frac{aDLT_g}{\alpha_1} + \frac{aDLT_g}{\alpha_2}\right) \\ &+ \gamma T_f \max\left\{\beta, \frac{bDx_0}{\alpha_1}\right\} = \beta_1 \text{ (say).}\end{aligned}$$

Suppose the trajectory that leaves ω at $t = t_1$ re-enters ω at $t = t_2$ and leaves again at $t = t_3$ and so on. Continuing the above process for the interval (t_n, t_{n+1}), we can show that

$$\begin{aligned}V(x, y_1, y_2) \le{}& x_0\left(1 + \frac{bD}{\alpha_1} + \frac{bD}{\alpha_2} + \frac{aDLT_g}{\alpha_1} + \frac{aDLT_g}{\alpha_2}\right) \\ &+ \gamma T_f \max\left\{\beta, \frac{bDx_0}{\alpha_1}, \beta_1, \beta_2, \ldots, \beta_n\right\} = \beta_{n+1} \text{ (say).}\end{aligned}$$

It is easy to see that

$$\beta_n \leq \max\left\{\beta, \frac{x_0}{1-\gamma T_f}\left(1+\frac{bD}{\alpha_1}+\frac{bD}{\alpha_2}+\frac{aDLT_g}{\alpha_1}+\frac{aDLT_g}{\alpha_2}\right)\right\}$$

and moreover $\beta_i \leq \beta_{i+1}$ for $i = 1, 2, \ldots$ By the hypothesis that $T_f < (1/\gamma)$ we have $\{\beta_n\}$ is bounded and thus for $t \geq t_0$,

$$\begin{aligned} b\|X(t)\| &< V(x, y_1, y_2) \\ &\leq \max\left\{\beta, \frac{x_0}{1-\gamma T_f}\left(1+\frac{bD}{\alpha_1}+\frac{bD}{\alpha_2}+\frac{aDLT_g}{\alpha_1}+\frac{aDLT_g}{\alpha_2}\right)\right\}. \end{aligned}$$

The proof of the theorem is complete. □

In Sect. 5.3 we study the existence of equilibria of (5.1) and their global asymptotic stability.

5.3 Global Dynamics

We now study the global behavior of solutions of (5.1). By the following change of variables:

$$\alpha(t) = \frac{y_1(t)}{y_1(t)+y_2(t)} \quad \text{and} \quad z(t) = y_1(t) + y_2(t),$$

the system (5.1) assumes the form,

$$\begin{aligned} x'(t) &= D(x_0 - x(t)) - aU(x(t))z(t) \\ &\quad + b\gamma \int_{-\infty}^{t} f(t-s)\alpha(s)z(s)\mathrm{d}s, \\ z'(t) &= -\gamma z(t) - D\alpha(t)z(t) \\ &\quad + cz(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s, \\ \alpha'(t) &= -D\alpha(t)(1-\alpha(t)) - r_1\alpha(t) + r_2(1-\alpha(t)). \end{aligned} \tag{5.3}$$

For any positive solutions y_1 and y_2 of (5.1) we have $0 < \alpha(t) < 1$ for all t. Further $\alpha'(0) = r_2 > 0$ and $\alpha'(1) = -r_1 < 0$. Thus (0,1) is a positively invariant region for $\alpha(t)$.

Observe that the equation for α is independent of x and z. The equilibrium points for this equation are given by

$$\alpha^* = \frac{D + r_1 + r_2 \pm \sqrt{(D+r_1+r_2)^2 - 4Dr_2}}{2D}.$$

It is clear that the root $\alpha^* = \left(D + r_1 + r_2 - \sqrt{(D + r_1 + r_2)^2 - 4Dr_2}\right)/2D$ is the one that lies in the interval (0, 1) and the second root is bigger than 1. Moreover, it is easy to see that $\alpha(t) \to \alpha^*$ as $t \to t^*$ and hence, α^* is an asymptotically stable rest point.

Eliminating the third equation in (5.3) and replacing $\alpha(t)$ by α^* in the first two equations we have for sufficiently large t,

$$\begin{aligned} x'(t) &= D(x_0 - x(t)) - aU(x(t))z(t) \\ &\quad + b\gamma\alpha^* \int_{-\infty}^{t} f(t-s)z(s)\mathrm{d}s, \\ z'(t) &= -\gamma z(t) - D\alpha^* z(t) \\ &\quad + cz(t) \int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s. \end{aligned} \tag{5.4}$$

The equilibria for this system are given by

$$\begin{aligned} Dx_0 - Dx^* - aU(x^*)z^* + b\gamma\alpha^* z^* &= 0, \\ (cU(x^*) - \gamma - D\alpha^*)z^* &= 0. \end{aligned} \tag{5.5}$$

By definition of $\alpha(t), z(t), z^* = 0$ cannot be a solution of this system. Therefore, the required positive equilibrium point (x^*, z^*) is given by

$$U(x^*) = \frac{\gamma + D\alpha^*}{c} \quad \text{and} \quad z^* = \frac{Dx_0 - Dx^*}{aU(x^*) - b\gamma\alpha^*}, \tag{5.6}$$

which exists provided, $(\gamma + D\alpha^*)/c < L$ and $(x_0 - x^*)(aU(x^*) - b\gamma\alpha^*) > 0$ hold.

Henceforth, we tacitly assume that the positive equilibrium (x^*, z^*) exists and is unique.

Now we establish the global asymptotic stability of (x^*, z^*).

Using (5.5) after eliminating z^* from the second equation, we rewrite (5.4) as

$$\begin{aligned} x'(t) &= -D(x(t) - x^*) - aU(x(t))(z(t) - z^*) \\ &\quad - az^*(U(x(t)) - U(x^*)) \\ &\quad + b\gamma\alpha^* \int_0^{\infty} f(s)(z(t-s) - z^*)\mathrm{d}s, \\ z'(t) &= cz(t) \int_0^{\infty} g(s)(U(x(t-s)) - U(x^*))\mathrm{d}s. \end{aligned} \tag{5.7}$$

We now state and prove our first result.

Theorem 5.3 *Assume that the delay kernels satisfy* (H_1) *and* (H_2) *and the uptake function* $U(x)$ *satisfies* (A_1) *and* (A_2). *The equilibrium point* (x^*, z^*) *of* (5.4) *is globally asymptotically stable provided,*

$$D-(c-az^*)k>0 \quad \text{and} \quad \bar{\Delta} \equiv \min_{x\geq x^*}\{aU(x)-b\gamma\alpha^*\}>0.$$

Proof We consider the functional,

$$\begin{aligned} V(t) \equiv V(x(t),z(t)) &= |x(t)-x^*| + |\log\,(z(t)) - \log z^*| \\ &\quad + b\gamma\alpha^* \int_0^\infty f(s) \int_{t-s}^t |z(u)-z^*| \mathrm{d}u\,\mathrm{d}s \\ &\quad + c \int_0^\infty g(s) \int_{t-s}^t |U(x(u))-U(x^*)| \mathrm{d}u\,\mathrm{d}s. \end{aligned}$$

Clearly, $V(x^*, z^*) = 0$ and

$$V(x(t),z(t)) \geq |x(t)-x^*| + |\log\,(z(t)) - \log z^*| > 0.$$

The upper Dini derivative of V along the solutions of (5.4) and using (5.7) becomes after some simplifications

$$\begin{aligned} D^+V &\leq -D|x(t)-x^*| - aU(x(t))|z(t)-z^*| - az^*|U(x(t))-U(x^*)| \\ &\quad + b\gamma\alpha^*|z(t)-z^*| + c|U(x(t))-U(x^*)| \\ &= -D|x(t)-x^*| + (c-az^*)|U(x)-U(x^*)| \\ &\quad - (aU(x)-b\gamma\alpha^*)|z(t)-z^*|. \end{aligned}$$

If $c \leq az^*$, then the condition $\min_{x\geq x^*}\{aU(x)-b\gamma\} > 0$ is alone sufficient to ensure the negative definiteness of D^+V. Hence, we assume that $c > az^*$. Then we have,

$$\begin{aligned} D^+V &\leq -D|x(t)-x^*| + (c-az^*)|U(x)-U(x^*)| \\ &\quad -(aU(x)-b\gamma\alpha^*)|z(t)-z^*| \\ &< -(D+akz^*-ck)|x(t)-x^*| - \bar{\Delta}|z(t)-z^*| < 0, \end{aligned}$$

invoking the hypotheses.

Thus,

$$D^+V < -(D+akz^*-ck)|x(t)-x^*| - \frac{\bar{\Delta}}{k_3}|\log z(t) - \log z^*| < 0, \tag{5.8}$$

where $k_1 > 0$ is such that $|\log\ z(t) - \log\ z^*| \leq k_3|z(t)-z^*|$.

Now integrating (5.8) with respect to t from 0 to t, we get

$$V(t) + (D - ck + az^*k)\int_0^t |x(s) - x^*|\mathrm{d}s + \frac{\bar{\Delta}}{k_1}\int_0^t |\log z(s) - \log z^*|\mathrm{d}s \le V(0).$$

Therefore, $V(t) \equiv V(x(t), z(t))$ is bounded on $[0, \infty)$ and since $x(t), z(t)$ are bounded on $[0, \infty)$, $|x(t) - x^*|$ and $|\log z(t) - \log z^*|$ are bounded on $[0, \infty)$ and these imply the boundedness of their derivatives on $[0, \infty)$. Now the conclusion follows from standard arguments. □

Remark 5.4 From (5.6) it easy to see that $aU(x^*) > b\gamma\alpha^*$ when the positive equilibrium exists. Thus, if U is monotone increasing then the second condition (on parameters) of Theorem 5.3 is automatically true. We now scale down the parameters by dividing each by D and measuring the nutrient in terms of x_0, letting $\gamma = 0, a = a/D = c/D = c = 1$. This reduces the first condition on the parameters in Theorem 5.3 to $1 + kz^* > k$ or $k < 1/(1 - z^*)$. With this change of parameters, the equilibrium solution is given by $U(x^*) = \alpha^* < 1$ and $\alpha^* z^* = 1 - x^* < 1$. We observe that for all the uptake functions that are generally used in a chemostat (see Sect. 1.6) $k \le 1$, and hence, $k < 1/(1 - z^*)$ holds.

Thus, the existence of positive equilibrium itself ensures the global asymptotic stability here and for which the necessary and sufficient condition is $U(1) > 1$. This is what exactly Theorem 5.1 of Pilyugin and Waltman [74] established for model equations (1.5).

Now we present another set of sufficient conditions for the global asymptotic stability of (x^*, z^*). Using (5.5), we rewrite (5.4) as

$$\begin{aligned} x'(t) &= -D(x(t) - x^*) - a(U(x(t) - U(x^*))z(t) \\ &\qquad -aU(x^*)(z(t) - z^*) + b\gamma\alpha^* \int_0^\infty f(s)z(t-s)\mathrm{d}s, \\ z'(t) &= cz(t)\int_0^\infty g(s)U(x(t-s))\mathrm{d}s. \end{aligned} \tag{5.9}$$

We shall state and prove our next result.

Theorem 5.5 *Assume that the delay kernels satisfy* (H_1) *and* (H_2) *and the uptake function* $U(x)$ *satisfies* (A_1) *and* (A_2). *The equilibrium point* (x^*, z^*) *of* (5.4) *is globally asymptotically stable provided,*

$$D - ck > 0 \quad and \quad aU(x^*) - b\gamma\alpha^* > 0.$$

Proof We consider the functional,

$$V(t) \equiv V(x(t), z(t)) = |x(t) - x^*| + |\log(z(t)) - \log z^*| + b\gamma\alpha^* \int_0^\infty f(s) \int_{t-s}^t |z(u) - z^*| \mathrm{d}u \, \mathrm{d}s + c \int_0^\infty g(s) \int_{t-s}^t |U(x(u)) - U(x^*)| \mathrm{d}u \, \mathrm{d}s.$$

Then the upper right derivative of V along the solutions of (5.9) becomes after some simplifications

$$\begin{aligned} D^+V &\leq -D|x(t) - x^*| - az|U(x(t)) - U(x^*)| - aU(x^*)|z(t) - z^*| \\ &\quad + c|U(x(t)) - U(x^*)| + b\gamma\alpha^*|z(t) - z^*| \\ &\leq -(D - ck)|x(t) - x^*| - (aU(x^*) - b\gamma\alpha^*)|z(t) - z^*| \\ &< 0, \end{aligned}$$

by hypotheses. The rest of the argument is similar to that of Theorem 5.3, and hence, omitted. □

Note that the condition $aU(x^*) > b\gamma\alpha^*$ is necessary for the existence of a positive equilibrium (see Remark 5.4).

In the next result we relax hypothesis (H_2) on the delay kernels. Since the proof is similar to Theorem 2.33, we only state the result.

Theorem 5.6 *Assume that* (H_1), (A_1) *and* (A_2) *hold. The positive equilibrium solution* (x^*, z^*) *of* (5.4) *is globally asymptotically stable provided,*

$$b\gamma\alpha^* + ck < \min\{D, \min_{x \geq x^*}\{aU(x)\}\}.$$

We now give another result which is analogous to Theorem 2.34. Since the proof of our next result follows from it with a slight modification of the parameters, we do not intend to prove the theorem but give only its statement.

Theorem 5.7 *Assume that the uptake function satisfies* (A_1) *and* (A_2) *and the delay kernels, in addition to* (H_1) *and* (H_2), *satisfy*

$$T_f^* = \frac{1}{(\gamma + D\alpha^*)} \int_0^\infty f(s)[\exp(\gamma + D\alpha^*)s - 1]\mathrm{d}s < \infty,$$

$$T_g^* = \frac{1}{cL - \gamma - D\alpha^*} \int_0^\infty g(s)[\exp(cL - \gamma - D\alpha^*)s - 1]\mathrm{d}s < \infty$$

and

$$\int_0^\infty sg(s)[\exp(cL-\gamma-D\alpha^*)s-1]\mathrm{d}s<\infty.$$

The positive equilibrium (x^*, z^*) *of* (5.4) *is globally asymptotically stable provided,*

$$bc\gamma\alpha^*[T_f^*+T_f+T_fT_g^*(cL-\gamma-D\alpha^*)] \\ +c(aU(x^*)-b\gamma\alpha^*)\exp(cT_g(T_g+T_g^*)<2a.$$

Observe the similarities between systems (5.4) and (2.81) and also between the corresponding results, namely, Theorems 5.3, 5.6, and 2.33, 2.35 etc., except for the term α^* in Theorems 5.3, and 5.6. Therefore, it is not difficult to see that the results of this section are independent of each other. Thus, the examples cited in Sect. 2.5, may be modified to illustrate the results of this section and to prove independence of each of these results from others.

Remark 5.8 Since $0<\alpha^*<1$, we observe that the conditions on the parameters in Theorems 5.3, and 5.6 are stronger than the corresponding conditions in Theorems 2.33 and 2.35, respectively. Therefore, we can remark that wall growth truly contributes to the stability of the equilibrium. To substantiate this, we now illustrate how wall growth contributes to the stability of the system recalling the model defined in Example 2.42 of Chap. 2. Note that the stability of this model could not be decided by methods followed in Sect. 2.5.

Example 5.9 Consider the model,

$$x'(t)=1.7(x_0-x(t))-20U(x(t))y(t) \\ +(0.78)\int_{-\infty}^t f(t-s)y(s)\mathrm{d}s,$$

$$y'(t)=-3y(t)+19y(t)\int_{-\infty}^t g(t-s)U(x(s))\mathrm{d}s,$$

where

$$U(x)=\begin{cases}\frac{x}{10+x^2} & ,0\le x<30\\ \frac{3}{91} & ,\text{otherwise}\end{cases}$$

and $b=0.6$, $\gamma=1.3$ and $x_0=3.2$.

Now choosing $r_1=1$, $r_2=2$, and incorporating wall growth, we modify above model to

$$x'(t)=1.7(x_0-x(t))-20U(x(t))y(t) \\ +(0.78)\int_{-\infty}^t f(t-s)y(s)\mathrm{d}s,$$

$$\begin{aligned}
y_1'(t) &= -3y_1(t) + 19y_1(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s, \\
&\quad -y_1(t) + 2y_2(t), \\
y_2'(t) &= -1.3y_2(t) + 19y_2(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s \\
&\quad +y_1(t) - 2y_2(t).
\end{aligned}$$

For these values of D, r_1, and r_2, we can see that $\alpha^* = 0.5254$.
This transforms above system to [as in (5.4)],

$$\begin{aligned}
x'(t) &= 1.7(x_0 - x(t)) - 20U(x(t))z(t) \\
&\quad +(0.4098)\int_{-\infty}^{t} f(t-s)z(s)\mathrm{d}s, \\
z'(t) &= -1.3z(t) - (0.89318)z(t) + 19z(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s.
\end{aligned}$$

Clearly, $(x^*, z^*) = (1.3704, 1.6385)$ is the equilibrium point with $U(x^*) = 0.1154$.

It is easy to see that all the hypotheses of Theorem 5.3 are satisfied, and hence, (1.3704, 1.6385) is globally asymptotically stable.

5.4 Discussion

In this chapter, we have introduced the concept of wall growth into a model of limited nutrient-consumer dynamics. This allows us to consider the growth of microorganisms that are in the medium and also on the walls of the container. The model (2.81) has been suitably modified to incorporate the phenomenon of wall growth. We have obtained various independent sets of sufficient conditions for the global asymptotic stability of the positive equilibrium. Comparing the corresponding parametric conditions in Chaps. 3 and 5, we note that (as already noted in Remark 5.8) since $0 < \alpha^* < 1$, the condition $aU(x) > b\gamma\alpha^*$ of Theorem 5.3 is definitely a better condition than the corresponding condition ($aU(x) > b\gamma$) in Theorem 2.33. Same is the case with Theorems 5.6 and 2.35. Thus, wall growth also allows us to study the survival of species at low levels of nutrient supply or consumption than those envisaged by Theorems 2.33 and 2.35. Thus, we can conclude that wall growth truly contributes to the stability of the equilibrium (enriches the stability properties of the equilibrium).

5.5 Notes and Remarks

A successful attempt to introduce the concept of wall growth into the chemostat was made by Pilyugin and Waltman [74] for the basic model (1.5) without time delays. Now we have seen the results of this chapter for the general model (2.81) contributed by Sree Hari Rao and Raja Sekhara Rao [89]. Freter [41, 42] discusses some important biological situations where mathematical models incorporating wall growth may be studied. The readers who are interested in those aspects may go through these articles and references there in. The influence of wall growth on the models right from (2.1) to (2.5) has not been pursued, at least to our knowledge. Therefore, an attempt may be made in this direction to enrich the literature.

At the end of Chap. 2 (Sect. 2.6), we remarked that material recycling (with or without a time delay) has a stabilizing effect on the system. In case of wall growth, we have noted that the biomass sticking onto the walls is just consuming the nutrient available but not contributing to the recycling after death. Thus, the nutrient pool is not receiving its share as usual. What type of influence is this going to have on our system?

To understand this, we now compare the conclusions of Theorems 4.10 and 5.3 when applied to the system given by the model in Example 2.42, already provided by Examples 4.21 and 5.9, respectively. In Example 4.21 we have $x^* = \sqrt{10}, \quad y^* = 0.02523$ and in Example 5.9 $x^* = 1.3704, \quad y^* = 1.6385$ as the corresponding asymptotically stable equilibrium solutions with a constant input concentration $x_0 = 3.2$.

It is obvious that in case of self-regulation the equilibrium value x^* is close to its input concentration x_0 while in case of model with wall growth it is considerably away form x_0. The y population in case of self-regulation on y is very low and hence, less consumption of nutrient and vice versa. In case of wall growth, the consumer population y shoots up, consuming the nutrient more. This is complemented by low recycling of nutrient due to wall growth. This is not quite unexpected!

5.6 Exercises

1. Apply the concept of wall growth to models (2.1)–(2.5) and discuss its influence.
2. What is the influence of wall growth on models with and without material recycling?
3. Study the influence of wall growth on models with discrete delays.
4. Do wall growth and self-regulation fit in the same model? Explain?
5. Construct Lyapunov functions to study (5.1) directly (use the techniques of Sect. 2.5). Discuss the influence of wall growth on the consumption provided by the condition $aU(x) > b\gamma$.

6. Construct numerical examples to check the independence of the stability results in this chapter.
7. Provide an example to establish that even wall growth may not stabilize the system. (See if one of the conditions on parameters fails, or show that $aU(x) < b\gamma\alpha^*$ for $x > x^*$).

Chapter 6
Zones of No Activation

6.1 Introduction

Excess consumption of nutrient may lead to abnormalities in the growth of biotic species. Further, excess consumption of nutrient should be controlled in order to utilize the resources properly, especially, when the resources are not abundantly available (limited nutrient). When the populations are at equilibrium or once they are completely fed, they show no tendency to consume food any more at least for a while. Based on these observations, we introduce in this chapter a new notion called a "zone of no activation" for the consumer species. That means near the equilibrium the microorganisms do not consume nutrient any more and the same consumption level is maintained near the equilibrium for a while. Such a nonconsumption state is called a zone of no activation. This is to be understood in the context that the nutrient uptake is, in general, assumed to be a monotonically increasing function.

The presence of a zone of no activation may imply that the consumption of nutrient has a saturation near equilibrium. But this saturation is altogether different from the saturation in the supply of nutrient uptake as envisaged in the assumption (A_1) on the uptake function $U(x)$ (see Sect. 2.5). In a zone of no activation, since the consumer species are completely fed, they show no tendency to consume nutrient any more at that stage while the saturation effect on $U(x)$ implies that consumption of the nutrient does not increase even when the populations require more nutrient. Mathematically, this phenomenon may be expressed as the uptake function $U(x)$ maintaining the same value $U(x^*)$ not only at x^* (equilibrium value), but also in a certain neighborhood of x^*.

The following discussion provides a good understanding of the zones of no activation with regard to plants growing under the application of fertilizers. Consider a situation where a plant biomass feeds on a fertilizer. It may be true that a continuous use of fertilizer enriches the nutrient levels of the soil, thus, leading to an enhanced plant growth. At the same time, excess use of the fertilizers leads to imbalances in the nutrient levels of the soil causing abnormalities in the plant growth, thus, effecting the yield. Therefore, a situation arises when a constant supply of

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the fertilizer should be considered, or even the supply of the fertilizer should be stopped till such a time that the soil has balanced nutrient levels. This we consider by $U(x) = U(x^*)$ (maintenance of nutrient uptake at equilibrium level) in a certain neighbourhood of x^* and this neighbourhood may be regarded as a "zone of no activation."

Our aim in this chapter is to understand how the introduction of a zone of no activation influences the stability properties of the positive equilibrium. In other words, we understand the presence of a zone of no activation as a measure of restoring stability in a situation where excess consumption of nutrient leads to abnormalities in the biomass growth which may, in turn, lead to instability of the system. Observe that the zone of no activation does not depend on the size of the population but it represents a basic property of the biotic species themselves. Since such zones of no activation exist in any biological system, we try to understand them through systems (2.81) and (4.1), keeping in view the importance of these models in the present context.

We now study the influence of the presence of a zone of no activation on the stability properties of system (2.81).

6.2 Global Stability for the System (2.81)

In this section, we consider system (2.81). That is,

$$\begin{aligned} x'(t) &= D(x_0 - x(t)) - aU(x(t))y(t) \\ &\quad + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s, \\ y'(t) &= -(\gamma + D)y(t) + cy(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s \end{aligned} \tag{6.1}$$

with nonnegative initial conditions,

$$x(s) = \phi_1(s),\ \ y(s) = \phi_2(s),\ \ -\infty < s \le 0. \tag{6.2}$$

We assume that the system (6.1) has unique continuable solutions in their maximal intervals of existence and they are nonnegative and bounded, recalling the results of Sect. 2.5. Further, the uptake function U satisfies (A_1) and (A_2) stated in Sect. 2.5 and the delay kernels are nonnegative and satisfy (H_1) and (H_2). For completeness we shall restate these basic assumptions.

(A_1). $U(x)$ is continuous real valued function defined on $\mathbf{R}_+ = [0, \infty)$ such that

$$U(0) = 0, U(x) > 0 \quad \text{for} \quad x > 0 \text{ and } \lim_{x\to\infty} U(x) = L_1 < \infty.$$

$|U(x)| \leq L$ for all x, for some $L > 0$.
(A_2). There exists a constant $k > 0$ such that for all $x_1,\ x_2 \in \mathbf{R}_+$,

$$|U(x_1) - U(x_2)| \leq k|x_1 - x_2|.$$

$$(H_1). \qquad \int_0^\infty f(s)\mathrm{d}s = 1, \quad \int_0^\infty g(s)\mathrm{d}s = 1,$$

$$(H_2). \qquad \int_0^\infty sf(s)\mathrm{d}s < \infty, \quad \int_0^\infty sg(s)\mathrm{d}s < \infty.$$

We recall that (6.1) has a unique positive equilibrium given by

$$U(x^*) = \frac{\gamma + D}{c}, \quad y^* = \frac{D(x_0 - x^*)}{aU(x^*) - b\gamma}.$$

Now, we make the following change of variables:

$$u(t) = x(t) - x^*,\ v(t) = y(t) - y^*,\ \text{and} \quad G(u) = U(x) - U(x^*)$$

which transforms system (6.1) into

$$\begin{aligned} u'(t) &= -Du(t) - a(G(u(t)) + U(x^*))v(t) - ay^*G(u(t)) \\ &\quad + b\gamma \int_{-\infty}^{t} f(t-s)v(s)\mathrm{d}s, \\ v'(t) &= (v(t) + y^*)\left[c\int_{-\infty}^{t} g(t-s)G(u(s))\mathrm{d}s\right]. \end{aligned} \tag{6.3}$$

In the zone of no activation we define the uptake function denoted by $G(u)$ as

$$G(u) = \begin{cases} G_1(u), \text{ for } & u > \delta_1, \\ G_2(u), \text{ for } & u < -\delta_1, \\ 0, \qquad \text{for } & |u| \leq \delta_1 \end{cases} \tag{6.4}$$

for some $\delta_1 \geq 0$.
In view of the continuity of $U(x)$, we have

$$\lim_{u \to \delta_1{}^+} G_1(u) = 0 = \lim_{u \to -\delta_1{}^-} G_2(u).$$

We observe that $(0, 0)$ is an equilibrium solution of (6.3) corresponding to (x^*, y^*) of (6.1).
The following is the first result in this section.

Theorem 6.1 *Assume that the delay kernels satisfy* (H_1) *and* (H_2) *and the uptake function satisfies* (A_1) *and* (A_2). *The equilibrium solution* $(0, 0)$ *of* (6.3) *is globally asymptotically stable provided,*

$$\mu = \min\{D - (c - ay^*)k_1, D - (c - ay^*)k_2\} > 0,$$

$$\nu_1 = \min_{u>\delta_1}\{a(G_1(u) + U(x^*)) - b\gamma\} > 0 \text{ and}$$

$$\nu_2 = \min_{u<-\delta_1}\{a(G_2(u) + U(x^*)) - b\gamma\} > 0$$

in which $k_1 > 0$ *and* $k_2 > 0$ *are such that*

$$|G_1(u)| \le k_1|u| \quad \text{for} \quad u > \delta_1 \quad \text{and} \quad |G_2(u)| \le k_2|u| \quad \text{for} \quad u < -\delta_1.$$

Remark 6.2 The existence of the positive constants k_1 and k_2 is assured by the assumption (A_2) on $G(u)$. In case $\delta_1 = 0$, we have $k_1 = k_2 = k$, the Lipschitz constant defined in (A_2).

Proof of Theorem 6.1 We consider functional

$$V(t) = |u(t)| + |\log \frac{v(t) + y^*}{y^*}| + b\gamma \int_0^\infty f(s) \int_{t-s}^t |v(z)| \mathrm{d}z \, \mathrm{d}s + c \int_0^\infty g(s) \int_{t-s}^t |G(u(z))| \mathrm{d}z \, \mathrm{d}s.$$

The upper Dini derivative of V along the solutions of system (6.3) is given by

$$\begin{aligned} D^+V &\le -D|u(t)| - a(G(u(t)) + U(x^*))|v(t)| - ay^*|G(u(t))| \\ &\quad + b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s + c \int_0^\infty g(s)|G(u(t-s))|\mathrm{d}s \\ &\quad + b\gamma|v(t)| - b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \\ &\quad + c|G(u(t))| - c \int_0^\infty g(s)|G(u(t-s))|\mathrm{d}s \\ &= -D|u(t)| + (c - ay^*)|G(u(t))| - [a(G(u) + U(x^*)) - b\gamma]|v(t)|, \end{aligned}$$

and from (6.4) we have

$$D^+V \le - \begin{cases} [D - (c - ay^*)k_1]|u(t)| \\ +[a(G_1(u) + U(x^*)) - b\gamma]|v(t)| \text{ for } & u(t) > \delta_1 \\ [D - (c - ay^*)k_2]|u(t)| \\ +[a(G_2(u) + U(x^*)) - b\gamma]|v(t)| \text{ for } & u(t) < -\delta_1 \\ D|u(t)| + (aU(x^*) - b\gamma)|v(t)| \quad \text{for} & |u(t)| \le \delta_1 \end{cases}$$

Let $\nu = \min\{\nu_1, \nu_2\}$. Then it follows that

$$D^+V \leq -[\mu|u(t)| + \nu|v(t)|]\,.$$

Integrating this from 0 to t, we get

$$V(t) + \mu \int_0^t |u(s)|\mathrm{d}s + \nu \int_0^t |v(s)|\mathrm{d}s \leq V(0),$$

which implies that

$$V(t) + \mu \int_0^t |u(s)|\mathrm{d}s + \nu \int_0^t |\log \frac{v(s) + y^*}{y^*}|\mathrm{d}s \leq V(0).$$

Therefore $V(t)$ is bounded on $[0, \infty)$ and since the solutions of system (6.1) are bounded, it follows that $u(t)$ and $\log\ (v(t) + y^*)/y^*$ are bounded, implying that D^+V is bounded. Now the conclusion follows from standard arguments.

Remark 6.3 In the hypotheses of the above theorem, it is taken that $c - ay^* > 0$. In case $c - ay^* < 0$, we have the upper Dini derivative after some simplifications given by

$$\begin{aligned} D^+V &\leq -D|u(t)| + (c - ay^*)|G(u(t))| \\ &\quad -(a(G(u(t) + U(x^*)) - b\gamma)|y(t) - y^*| \\ &< 0, \end{aligned}$$

since $\nu_1 > 0$, $\nu_2 > 0$.

Thus, we observe that hypotheses, $\nu_1 > 0$, $\nu_2 > 0$, are alone sufficient to ensure the global asymptotic stability of $(0, 0)$ in this case.

In the next result we relax the condition (H_2) on the delay kernels at the expense of placing more restrictions on the parameters of the system (6.3).

Theorem 6.4 *Assume that the delay kernels satisfy* (H_1)*, the uptake function satisfies* (A_1) *and* (A_2)*. The equilibrium solution* $(0, 0)$ *of system* (6.3) *is globally asymptotically stable provided,*

$$b\gamma + ck_1 < \min\{D - ak_1y^*, \min_{u(t)>\delta_1}\{a(G_1(u) + U(x^*))\}\} = \beta_1 \text{ (say)},$$

$$b\gamma < \min\{D, aU(x^*)\} = \beta \quad \text{(say)}, \quad \textit{and}$$

$$b\gamma + ck_2 < \min\left\{D - ak_2y^*, \min_{u(t)<-\delta_1}\{a(G_2(u) + U(x^*))\}\right\} = \beta_2 \text{ (say)},$$

where k_1 *and* k_2 *are as in Theorem* 6.1.

Proof Consider the functional

$$V(t) = V(u(t), v(t)) = |u(t)| + \left|\log\left(\frac{v(t) + y^*}{y^*}\right)\right|.$$

Clearly, $V(0,0) = 0,\ V(t) > 0 \quad$ for $u(t) + v(t) > 0$.
The upper Dini derivative of V along the solutions of (6.3) is given by

$$\begin{aligned}
D^+V &\le -D|u(t)| - a(G(u) + U(x^*))|v(t)| - ay^*|G(u(t))| \\
&\quad + b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s + c\int_0^\infty g(s)|G(u(t-s)|\mathrm{d}s \\
&\le \begin{cases}
-(D - ak_1y^*)|u(t)| - [a(G_1(u) + U(x^*))]|v(t)| \\
+ b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \\
+ c\int_0^\infty g(s)|G_1(u(t-s))|\mathrm{d}s \quad \text{for } u(t) > \delta_1 \\
-(D - ak_2y^*)|u(t)| - [a(G_2(u) + U(x^*))]|v(t)| \\
+ b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \\
+ c\int_0^\infty g(s)|G_2(u(t-s))|\mathrm{d}s \quad \text{for } u(t) < -\delta_1 \\
-D|u(t)| - (aU(x^*))|v(t)| \\
+ b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \quad \text{for } |u(t)| \le \delta_1,
\end{cases}
\end{aligned}$$

using (6.4).

$$\le \begin{cases}
-\beta_1 V(t) + b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \\
+ ck_1\int_0^\infty g(s)|u(t-s)|\mathrm{d}s \quad \text{for } u > \delta_1 \\
-\beta_2 V(t) + b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \\
+ ck_2\int_0^\infty g(s)|u(t-s)|\mathrm{d}s \quad \text{for } u < -\delta_1 \\
-\beta V(t) + b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \quad \text{for } |u| \le \delta_1
\end{cases}$$

$$\le \begin{cases}
-\beta_1 V(t) + b\gamma \int_0^\infty f(s)V(t-s)\mathrm{d}s \\
+ ck_1\int_0^\infty g(s)V(t-s)\mathrm{d}s \quad \text{for } u > \delta_1 \\
-\beta_2 V(t) + b\gamma \int_0^\infty f(s)V(t-s)\mathrm{d}s \\
+ ck_2\int_0^\infty g(s)V(t-s)\mathrm{d}s \quad \text{for } u < -\delta_1 \\
-\beta V(t) + b\gamma \int_0^\infty f(s)V(t-s)ds \quad \text{for } |u| \le \delta_1
\end{cases}$$

<0, using the hypotheses.

Since the rest of the proof is similar to that of Theorem 2.33, we omit the details here. □

Remark 6.5 In the zone of no activation, that is for $|u(t)| \le \delta_1$, $\mathrm{d}V/\mathrm{d}t < 0$ follows from Theorem 6.1 directly and the strain on the parameters in Theorem 6.4 is reduced considerably, and hence, the equilibrium $(0, 0)$ is globally asymptotically stable as long as $|u(t)| \le \delta_1$. Therefore, by the appropriate choice of $\delta_1 > 0$, we can maintain the stability of the equilibrium. In other words, the stability depends on how large $\delta_1 > 0$ can be chosen to create a zone of no activation there.

6.3 Global Stability with Self-regulation and Zones

For a better understanding of the influence of a zone of no activation we discuss, in this section, the global asymptotic stability of the equilibrium solution of a limited nutrient-consumer system with a self-regulation (system (4.1)), when the uptake functions have zones of no activation as described in Sect. 6.1. We present several examples for illustration.

We consider system (4.1) along with the initial conditions(4.2). That is

$$x'(t) = D(x_0 - x(t)) - aU(x(t))y(t) + b\gamma \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s,$$
$$y'(t) = -(\gamma + D)y(t) + cy(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - \mathrm{d}y^2(t), \quad (6.5)$$

and

$$x(s) = \phi_1(s),\ y(s) = \phi_2(s), \quad -\infty < s \le 0, \quad (6.6)$$

where ϕ_j for $j = 1, 2$ are bounded, continuous, nonnegative functions on $(-\infty, 0]$.

We assume that there exists a unique positive equilibrium (x^*, y^*) for system (4.1) and (4.1) has solutions which are unique, nonnegative, and bounded in view of the study of (4.1) in Chap. 4.

By the following change of variables

$$u(t) = x(t) - x^*,\ v(t) = y(t) - y^*,\ \text{and } G(u) = U(x) - U(x^*)$$

system (6.5) assumes the form,

$$u'(t) = -Du(t) - a(G(u(t)) + U(x^*))v(t) - ay^*G(u(t))$$
$$+ b\gamma \int_{-\infty}^{t} f(t-s)v(s)\mathrm{d}s,$$
$$v'(t) = (v(t) + y^*)[c\int_{-\infty}^{t} g(t-s)G(u(s))\mathrm{d}s - dv(t)]. \quad (6.7)$$

We observe that $(0, 0)$ is an equilibrium solution of (6.7).

In the zone of no activation we consider the uptake function $G(u)$ defined by

$$G(u) = \begin{cases} G_1(u), & \text{for} \quad u > \delta_1, \\ G_2(u), & \text{for} \quad u < -\delta_1, \\ 0, & \text{for} \quad |u| \le \delta_1 \end{cases} \quad (6.8)$$

for some $\delta_1 \ge 0$.

We now state and prove our first result in this section.

Theorem 6.6 *Assume that the delay kernels satisfy the conditions* (H_1) *and* (H_2) *and the uptake function satisfies* (A_1). *The equilibrium solution* $(0, 0)$ *of* (6.7) *is globally asymptotically stable provided there exist constants* $\eta_1 > 0$ *and* $\eta_2 > 0$ *such that*

$$\min\left\{D - \frac{b\gamma}{4\eta_1} + A_1, D - \frac{b\gamma}{4\eta_1} + A_2, D - \frac{b\gamma}{4\eta_1}\right\} > 0,\ d - \frac{c}{4\eta_2} - b\gamma\eta_1 > 0$$

$$\textit{and}\ \ a^2L^2 < 4B[d - \frac{c}{4\eta_2} - b\gamma\eta_1]\ \textit{where}$$

$$B = \min\left\{D - \frac{b\gamma}{4\eta_1} + A_1, D - \frac{b\gamma}{4\eta_1} + A_2, D - \frac{b\gamma}{4\eta_1}\right\} > 0,$$

$$A_1 = \min_{u>\delta_1}\left\{ay^*\left(\frac{G_1(u)}{u}\right) - c\eta_2\left(\frac{G_1(u)}{u}\right)^2\right\}\ \textit{and}$$

$$A_2 = \min_{u<-\delta_1}\left\{ay^*\left(\frac{G_2(u)}{u}\right) - c\eta_2\left(\frac{G_2(u)}{u}\right)^2\right\}.$$

Proof Consider the functional

$$V(t) \equiv V(u(t), v(t)) = \frac{u^2(t)}{2} + \int_0^{v(t)} \frac{z}{z + y^*}\mathrm{d}z$$

$$+ c\eta_2 \int_0^\infty g(s) \int_{t-s}^t G^2(u(t_1)\mathrm{d}t_1\mathrm{d}s + b\gamma\eta_1 \int_0^\infty f(s) \int_{t-s}^t v^2(t_1)\mathrm{d}t_1\mathrm{d}s.$$

Clearly $V(0, 0) = 0$ and $V(u(t), v(t)) \geq \frac{u^2(t)}{2} + \int_0^{v(t)} \frac{z}{z+y^*}\mathrm{d}z > 0$.

The time derivative of V along the solutions of system (6.7) is given by

$$\begin{aligned}
\frac{\mathrm{d}V}{\mathrm{d}t} &= u(t)u'(t) + \frac{v(t)}{v(t) + y^*}v'(t) \\
&\quad + c\eta_2 G^2(u(t)) - c\eta_2 \int_0^\infty g(s)G^2(u(t-s))\mathrm{d}s \\
&\quad + b\gamma\eta_1 v^2(t) - b\gamma\eta_1 \int_0^\infty f(s)v^2(t-s)\mathrm{d}s \\
&= -Du^2(t) - a(G(u(t)) + U(x^*))u(t)v(t) - ay^*G(u(t))u(t) \\
&\quad + b\gamma \int_0^\infty f(s)u(t)v(t-s)\mathrm{d}s + c\int_0^\infty g(s)v(t)G(u(t-s))\mathrm{d}s - dv^2(t) \\
&\quad + c\eta_2 G^2(u(t)) - c\eta_2 \int_0^\infty g(s)G^2(u(t-s))\mathrm{d}s \\
&\quad + b\gamma\eta_1 v^2(t) - b\gamma\eta_1 \int_0^\infty f(s)v^2(t-s)\mathrm{d}s.
\end{aligned}$$

Utilizing Lemma 4.10 with $\eta = \eta_1$ and $\eta = \eta_2$ in the fourth and fifth terms of the right-hand side of the above equation, invoking (H_1) on the delay kernels and simplifying, we get

$$\frac{\mathrm{d}V}{\mathrm{d}t} \leq -\left(D - \frac{b\gamma}{4\eta_1}\right)u^2(t) - a(G(u) + U(x^*))u(t)v(t)$$
$$-\left[d - \frac{c}{4\eta_2} - b\gamma\eta_1\right]v^2(t) - ay^*G(u)u(t) + c\eta_2 G^2(u(t)).$$

Now from (6.8) we have

$$\frac{\mathrm{d}V}{\mathrm{d}t} \leq -\begin{cases} \left(D - \frac{b\gamma}{4\eta_1} + A_1\right)u^2(t) + a(G_1(u) + U(x^*))u(t)v(t) \\ +\left(d - \frac{c}{4\eta_2} - b\gamma\eta_1\right)v^2(t) \quad \text{for } u > \delta_1 \\ \left(D - \frac{b\gamma}{4\eta_1} + A_2\right)u^2(t) + a(G_2(u) + U(x^*))u(t)v(t) \\ +\left(d - \frac{c}{4\eta_2} - b\gamma\eta_1\right)v^2(t) \quad \text{for } u < -\delta_1 \\ \left(D - \frac{b\gamma}{4\eta_1}\right)u^2(t) + aU(x^*)u(t)v(t) \\ +\left(d - \frac{c}{4\eta_2} - b\gamma\eta_1\right)v^2(t) \quad \text{for } |u| \leq \delta_1. \end{cases}$$

Thus, we have

$$\frac{\mathrm{d}V}{\mathrm{d}t} \leq -\left[Bu^2(t) + a(G(u) + U(x^*))u(t)v(t) + \left(d - \frac{c}{4\eta_2} - b\gamma\eta_1\right)v^2(t)\right]. \tag{6.9}$$

Then $\mathrm{d}V/\mathrm{d}t$ is negative definite provided,

$$[a(G(u) + U(x^*))]^2 < 4B\left[d - \frac{c}{4\eta_2} - b\gamma\eta_1\right].$$

Since $G(u) + U(x^*) \leq L$, for all u, it follows that $\mathrm{d}V/\mathrm{d}t$ is negative definite if

$$a^2L^2 < 4B\left[d - \frac{c}{4\eta_2} - b\gamma\eta_1\right].$$

Now let $Q(t) = (u(t), v(t))^T$,

$$P = \begin{pmatrix} B & \frac{aL}{2} \\ \frac{aL}{2} & d - \frac{c}{4\eta_2} - b\gamma\eta_1 \end{pmatrix}.$$

Then from (6.9) we have

$$\frac{\mathrm{d}V}{\mathrm{d}t} \leq -Q(t)^T PQ(t) \leq -\bar{\lambda}(u^2(t) + v^2(t)),$$

for some $\bar{\lambda} > 0$, which exists by our hypotheses, implying the negative definiteness of $\mathrm{d}V/\mathrm{d}t$. Now the conclusion follows easily.

The proof is complete. □

The following examples illustrate Theorem 6.6.

Example 6.7 Consider the system (6.7) with

$$G(u) = \begin{cases} \dfrac{u-\delta_1}{p+u-\delta_1} & \text{for} \quad u > \delta_1 \\ 0 & \text{for} \quad |u| \leq \delta_1 \\ \dfrac{u+\delta_1}{p+u+\delta_1} & \text{for} \quad u < -\delta_1 \end{cases}$$

where $p = 1 + x^*$, x^* being the equilibrium solution of (6.5).

This uptake function corresponds to Michaelis–Menten kinetics.

Clearly $uG_1(u) > 0$ and $uU_2(u) > 0$ and

$$\lim_{u\to\infty} \frac{G_1(u)}{u} = 0 = \lim_{u\to\infty} \frac{G_2(u)}{u},$$

$$\text{where} \quad G_1(u) = \frac{u-\delta_1}{p+u-\delta_1} \text{ and } G_2(u) = \frac{u+\delta_1}{p+u+\delta_1}.$$

Therefore, $A_1 = A_2 = 0$.

Thus, the equilibrium solution $(0, 0)$ of (6.7) is globally asymptotically stable provided,

$$D-\frac{b\gamma}{4\eta_1} > 0, d-b\gamma\eta_1-\frac{c}{4\eta_2} > 0 \quad \text{and} \quad a^2L^2 < 4\left[D - \frac{b\gamma}{4\eta_1}\right]\left[d - b\gamma\eta_1 - \frac{c}{4\eta_2}\right].$$

Example 6.8 Consider the system (6.7) with

$$G(u) = \begin{cases} z(\delta_1)(u-\delta_1) & \text{for} \quad u > \delta_1 \\ 0 & \text{for} \quad |u| \leq \delta_1 \\ z(\delta_1)(u+\delta_1) & \text{for} \quad u < -\delta_1 \end{cases}$$

where $z(\delta_1)$ satisfies $\lim_{\delta_1\to 0} z(\delta_1) = (ay^*)/(c\eta_2)$, with $G_1(u) = z(\delta_1)(u-\delta_1)$, $G_2(u) = z(\delta_1)(u+\delta_1)$.

We have $A_1 = A_2 = z(\delta_1)ay^* - z^2(\delta_1)c\eta_2 = A$ (say).

The condition $D - (b\gamma/4\eta_1) + A > 0$ gives an estimate for $z(\delta_1)$ and is given by

$$z(\delta_1) < \frac{ay^* + \sqrt{a^2y^{*2} + 4c\eta_2(D - \frac{b\gamma}{4\eta_1})}}{2c\eta_2}.$$

Now, the equilibrium solution $(0, 0)$ of (6.7) is globally asymptotically stable if,

$$D - \frac{b\gamma}{4\eta_1} > 0,\ d - b\gamma\eta_1 - \frac{c}{4\eta_2} > 0,\ \text{and}$$

$$a^2L^2 < 4\left[D - \frac{b\gamma}{4\eta_1} + A\right]\left[d - b\gamma\eta_1 - \frac{c}{4\eta_2}\right].$$

From the definitions of A_1 and A_2 in Theorem 6.6 and as seen in the above examples, it follows that the functions $G_1(u)$ and $G_2(u)$ cannot be super linear in "u." For, if $G_1(u)$ and $G_2(u)$ are super linear, the values of A_1 and A_2 may be in the extended real number system. The following theorem accommodates the super linear uptake functions which have saturation effects and accordingly we define $G(u)$ as follows:

$$G(u) = \begin{cases} G_1^*(u) & \text{for} \quad u(t) > \delta_1 \\ 0 & \text{for} \quad |u(t)| \le \delta_1 \\ G_2^*(u) & \text{for} \quad u(t) < -\delta_1, \end{cases}$$

where

$$G_1^*(u) = \begin{cases} P_1(u) & \text{for} \quad \delta_1 < u \le \alpha_1 \\ P_1(\alpha_1) & \text{for} \quad u > \alpha_1 \quad \text{and,} \end{cases}$$

$$G_2^*(u) = \begin{cases} P_2(u) & \text{for} \quad -\alpha_2 \le u < -\delta_1 \\ P_2(-\alpha_2) & \text{for} \quad u < -\alpha_2. \end{cases}$$

in which α_1, α_2 are positive real numbers and P_1, P_2 are continuous and can be super linear in their arguments.

Theorem 6.9 *Assume that the delay kernels satisfy the conditions* (H_1) *and* (H_2). *The equilibrium solution* $(0, 0)$ *of* (6.7) *is globally asymptotically stable provided,*

$$\min\left\{D - \frac{b\gamma}{4\eta_1} + A_1^*, D - \frac{b\gamma}{4\eta_1} + A_2^*, D - \frac{b\gamma}{4\eta_1}\right\} > 0,$$

$$d - b\gamma\eta_1 - \frac{c}{4\eta_2} > 0 \quad \text{and} \quad a^2L^2 < 4B^*\left[d - b\gamma\eta_1 - \frac{c}{4\eta_2}\right] \quad \text{where}$$

$$B^* = \min\left\{D - \frac{b\gamma}{4\eta_1} + A_1^*, D - \frac{b\gamma}{4\eta_1} + A_2^*, D - \frac{b\gamma}{4\eta_1}\right\} > 0,$$

$$A_1^* = \min_{u>\delta_1}\left\{ay^*\left[\frac{P_1(u)}{u}\right] - c\eta_2\left[\frac{P_1(u)}{u}\right]^2\right\} \quad \text{and}$$

$$A_2^* = \min_{u<-\delta_1}\left\{ay^*\left[\frac{P_2(u)}{u}\right] - c\eta_2\left[\frac{P_2(u)}{u}\right]^2\right\}.$$

Proof The proof of this theorem is similar to that of Theorem 6.6 and hence, omitted. □

Theorem 6.10 *Assume that the delay kernels satisfy* (H_1) *and* (H_2) *and the uptake function satisfies* (A_1) *and* (A_2). *The equilibrium solution* $(0, 0)$ *of* (6.7) *is globally asymptotically stable provided,*

$$\mu = \min\{D - (c - ay^*)k_1, D - (c - ay^*)k_2\} > 0,$$

$$\nu_1 = \min_{u>\delta_1}\{d + a(G_1(u) + U(x^*)) - b\gamma\} > 0 \quad \text{and}$$

$$\nu_2 = \min_{u<-\delta_1}\{d + a(G_2(u) + U(x^*)) - b\gamma\} > 0$$

in which $k_1 > 0$ *and* $k_2 > 0$ *are as defined in Theorem* 6.1.

Proof We consider the following functional

$$V(t) = |u(t)| + |log\,\frac{v(t) + y^*}{y^*}| + b\gamma \int_0^\infty f(s) \int_{t-s}^t |v(z)|\mathrm{d}z\,\mathrm{d}s$$
$$+ c \int_0^\infty g(s) \int_{t-s}^t |G(u(z))|\mathrm{d}z\,\mathrm{d}s.$$

The upper Dini derivative of V along the solutions of system (6.7), after some simplifications, is given by

$$D^+V \leq -D|u(t)| + (c - ay^*)|G(u(t))| - [d + a(G(u) + U(x^*)) - b\gamma]|v(t)|$$

and from (6.8) we have,

$$D^+V \leq -\begin{cases} [D - (c - ay^*)k_1]|u(t)| & \\ + [d + a(G_1(u) + U(x^*)) - b\gamma]|v(t)| \text{ for} & u(t) > \delta_1 \\ [D - (c - ay^*)k_2]|u(t)| & \\ + [d + a(G_2(u) + U(x^*)) - b\gamma]|v(t)| \text{ for} & u(t) < -\delta_1 \\ D|u(t)| + (d + aU(x^*) - b\gamma)|v(t)| \quad \text{for} & |u(t)| \leq \delta_1. \end{cases}$$

Let $\nu = \min\{\nu_1, \nu_2\}$. Then it follows that

$$D^+V \leq -[\mu|u(t)| + \nu|v(t)|].$$

Integrating this from 0 to t, we get

$$V(t) + \mu \int_0^t |u(s)|\mathrm{d}s + \nu \int_0^t |v(s)|\mathrm{d}s \leq V(0),$$

which implies that

$$V(t) + \mu \int_0^t |u(s)|\mathrm{d}s + \nu \int_0^t \left|\log \frac{v(s) + y^*}{y^*}\right| \mathrm{d}s \le V(0).$$

Therefore $V(t)$ is bounded on $[0, \infty)$ and since the solutions of system (6.5) are bounded, it follows that $u(t)$ and $\log\,((v(t) + y^*)/y^*)$ are bounded, implying that D^+V is bounded. Now the conclusion follows from standard arguments. □

In the next result we relax the condition (H_2) on the delay kernels.

Theorem 6.11 *Assume that the delay kernels satisfy* (H_1), *the uptake function satisfies* (A_1) *and* (A_2). *The equilibrium solution* $(0, 0)$ *of system* (6.7) *is globally asymptotically stable provided,*

$$b\gamma + ck_1 < \min\{D - ak_1 y^*, \min_{u(t)>\delta_1} \{d + a(G_1(u) + U(x^*))\}\} = \beta_1 \,(say),$$

$$b\gamma < \min\{D, d + aU(x^*)\} = \beta, \quad (say), \quad and$$

$$b\gamma + ck_2 < \min\{D - ak_2 y^*, \min_{u(t)<-\delta_1} \{d + a(G_2(u) + U(x^*))\}\} = \beta_2 \,(say)$$

Proof Consider the functional

$$V(t) = V(u(t), v(t)) = |u(t)| + \left|\log\,(\frac{v(t) + y^*}{y^*})\right|.$$

Clearly, $V(0, 0) = 0$, $V(t) > 0$ for $u(t) + v(t) > 0$.
The upper Dini derivative of V along the solutions of (6.7) is given by

$$\begin{aligned} D^+V \le& -D|u(t)| - a(G(u) + U(x^*))|v(t)| - ay^*|G(u(t))| \\ &+ b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s + c\int_0^\infty g(s)|G(u(t-s)|\mathrm{d}s - d|v(t)|. \\ \le& \begin{cases} -(D - ak_1 y^*)|u(t)| - [d + a(G_1(u) + U(x^*))]|v(t)| \\ +b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \\ +c\int_0^\infty g(s)|G_1(u(t-s))|\mathrm{d}s \quad \text{for } u(t) > \delta_1 \\ -(D - ak_2 y^*)|u(t)| - [d + a(G_2(u) + U(x^*))]|v(t)| \\ +b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \\ +c\int_0^\infty g(s)|G_2(u(t-s))|\mathrm{d}s \quad \text{for } u(t) < -\delta_1 \\ -D|u(t)| - (d + aU(x^*))|v(t)| \\ +b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \quad \text{for } |u(t)| \le \delta_1, \end{cases} \end{aligned}$$

using (6.8).

$$\leq \begin{cases} -\beta_1 V(t) + b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \\ +ck_1 \int_0^\infty g(s)|u(t-s)|\mathrm{d}s \quad \text{for } u > \delta_1 \\ -\beta_2 V(t) + b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \\ +ck_2 \int_0^\infty g(s)|u(t-s)|\mathrm{d}s \quad \text{for } u < -\delta_1 \\ -\beta V(t) + b\gamma \int_0^\infty f(s)|v(t-s)|\mathrm{d}s \quad \text{for } |u| \leq \delta_1 \end{cases}$$

$$\leq \begin{cases} -\beta_1 V(t) + b\gamma \int_0^\infty f(s)V(t-s)\mathrm{d}s \\ +ck_1 \int_0^\infty g(s)V(t-s)\mathrm{d}s \quad \text{for } u > \delta_1 \\ -\beta_2 V(t) + b\gamma \int_0^\infty f(s)V(t-s)\mathrm{d}s \\ +ck_2 \int_0^\infty g(s)V(t-s)\mathrm{d}s \quad \text{for } u < -\delta_1 \\ -\beta V(t) + b\gamma \int_0^\infty f(s)V(t-s)\mathrm{d}s \quad \text{for } |u| \leq \delta_1 \end{cases}$$

< 0, using the hypotheses.

Since the rest of the proof is similar to that of Theorem 4.12, we omit the details here. □

The following examples illustrate that Theorems 6.6 and 6.10 are independent of each other.

Example 6.12 Consider the model

$$\begin{aligned} x'(t) &= 2.75(x_0 - x(t)) - 18U(x(t))y(t) \\ &\quad + (0.0625)\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s, \\ y'(t) &= -3y(t) + 16y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - 44y^2(t) \end{aligned}$$

in which $U(x) = x/(4+x), b = 0.25, \gamma = 0.25, x_0 = 2.9,$ and $D = 2.75$.

The equilibrium solutions are $(x^*, y^*) = (\frac{8}{3}, 0.0773)$ with $U(x^*) = \frac{2}{5}$.

For this system define,

$$G_1(u) = G_2(u) = \frac{9u}{5(3u+20)}.$$

Clearly, $k_1 = k_2 = \frac{1}{4}$.

We observe that $D - ck_1 + ak_1y^* < 0, D - ck_2 + ak_2y^* < 0$ and hence, Theorem 6.10 cannot be applied here.

We verify the hypotheses of Theorem 6.6.

Clearly, for the choice of $\eta_1 = 1, \eta_2 = 2,$ and $\delta_1 = 1$, we see that $A_1 = -0.086, A_2 = -0.51$ and accordingly, $B = 2.1775$. It is easy to see that all conditions of Theorem 6.6 are satisfied and $(x^*, y^*) = (\frac{8}{3}, 0.0773)$ is globally asymptotically stable in view of Theorem 6.6.

Example 6.13 Consider the following system

$$x'(t) = 2(x_0 - x(t)) - 18U(x(t))y(t)$$
$$+ (0.25)\int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s$$
$$y'(t) = -3y(t) + 16y(t)\int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s - 3y^2(t)$$

in which $U(x) = x/(4+x)$, $b = 0.25, \gamma = 1,$ and $D = 2.$

The equilibrium solutions are $(x^*, y^*) = (\frac{8}{3}, 1.133)$ with

$$U(x^*) = \frac{2}{5} \quad \text{and} \quad x_0 = 29.716, \text{ approximately.}$$

Define $G_1(u)$ and $G_2(u)$ as in Example 6.12.

We note that Theorem 6.6 cannot be applied as the following inequality

$$a^2L^2 < 4B\left[d - \frac{c}{4\eta_2} - b\gamma\eta_1\right]$$

is not satisfied for any choice of η_1 and η_2. However, we observe that with $k_1 = k_2 = 1/4$, all the hypotheses of Theorem 6.10 are satisfied, and hence, (x^*, y^*) is globally asymptotically stable.

6.4 Discussion

In this chapter, we have introduced a notion called a "zone of no activation" for the consumer species. We have studied the influence of the zones of no activation on the dynamics of a limited nutrient-consumer system (2.81) and also under the influence of self-regulatory control mechanism (system (4.1)). In each case we have obtained various independent sets of sufficient conditions for the global asymptotic stability of the positive equilibrium solution.

As already observed in Sect. 6.1, zones of no activation may be considered (created) in two situations: one that naturally occurs when the equilibrium renders the nonconsumption of nutrient any more near the equilibrium and second, when excess consumption of nutrient leads to abnormalities in the growth of populations, adversely affecting the stability of the system. In a zone of no activation ($U(x) = U(x^*)$, i.e., $G(u) = 0$), we see that the conditions of Theorem 6.10 directly imply the global asymptotic stability, while the strain on the parameters in Theorems 6.6 and 6.11 is considerably released. Thus, by the appropriate choice of "δ_1," we see that the zone of no activation may be extended and the stability of the equilibrium is maintained.

Finally, when the nutrient consumption is increasing (i.e., $U(x)$ is monotone increasing function), we reduce the consumption by creating a zone of no activation with $U(x) = U(x^*)$ for all $x > x^*$. In case the consumption is very less (i.e., $aU(x) < b\gamma$ for $x > \bar{x} > x^*$), we create a zone of no activation at the appropriate time, to raise it to see that $aU(x) \geq b\gamma$ or otherwise by maintaining $U(x) = U(x^*)$ recalling that $aU(x^*) > b\gamma$ is necessary for the existence of a positive equilibrium solution, which controls both types of fluctuations stated above. Thus, we conclude that zones of no activation help us in restoring or preserving the stability of the system.

6.5 Notes and Remarks

Though, we have defined the uptake function $G(u)$ by (6.4) or (6.8) around the equilibrium (a natural zone of no activation), a more useful way of defining the uptake function in a zone of no activation could be

$$G(u) = \begin{cases} G_1(u) & \text{for} \quad u(t) > \delta_1 \\ G^* & \text{for} \quad \delta_2 \leq u(t) \leq \delta_1 \\ G_2(u) & \text{for} \quad u(t) < \delta_2 \end{cases}, \tag{6.10}$$

where G^* is any value $G(u)$ takes on $[-x^*, \infty)$ such that $\lim_{u \to \delta_2^-} G_2(u) = G^* = \lim_{u \to \delta_1^+} G_1(u)$, in which $\delta_2 \leq u \leq \delta_1$ defines the zone of no activation created. Note that this type of zone of no activation may be created anywhere in the interval of definition of G. This value G^* need not be the value at equilibrium but any desired value. Further the definition (6.10) enables us to decide the length of a zone as per system requirements by choosing δ_1 and δ_2 appropriately. This may help us realize the ideas of the last paragraph of the discussion above. For example, we may extend the zone to the right indefinitely if the situation demands a minimum of G^* consumption forever for a survival.

But this is not the natural zone we have defined in (6.4) or (6.8) that evolves in the situations described in Sect. 6.1. But using (6.10), a zone may be created by an experimenter basing on the requirements of his system and observations during the experiment.

The length of a zone defined by (6.10) is fixed once δ_1 and δ_2 are selected. But a sudden change of situation may demand the continuation of the zone for some more time or a reduction of it. In such a case we should think of a "variable zone." A variable zone may be raised by defining $\delta_1 \equiv \delta_1(t)$ and $\delta_2 \equiv \delta_2(t)$, both as functions of time t. By appropriate definitions of the functions $\delta_i(t),\ i = 1, 2$ the length of zones can be varied suitably.

Note that the choice $\delta_1 = \delta_2$ defines a zone of length zero. A zone of length zero is present everywhere in any system. If the situation demands more than one zone, instead of fitting a zone each time, how about creating a "moving zone." This idea is something like a "rescue and relief team" – whenever there is a trouble – create a zone immediately. The following case illustrates a case of creation of two zones during the intervals I_1 and I_2 of time t when the system demands it.

Zone 1 : $\delta_1(t) = \delta_{11}(t), \quad \delta_2(t) = \delta_{21}(t)$ for $t \in I_1$.
Zone 2 : $\delta_1(t) = \delta_{12}(t), \quad \delta_2(t) = \delta_{22}(t)$ for $t \in I_2$.
Finally, $\delta_1(t) = \delta_2(t)$ for $t \in \mathbf{R} - \{\mathbf{I_1} \cup \mathbf{I_2}\}$.

The idea of a zone was introduced by Sree Hari Rao and Raja Sekhara Rao [87] for chemostat models. The concept of zone is worked out only for models (2.81) and (4.1) in this article. Nothing has been done for models (2.1)–(2.5) so far and may be pursued by interested researchers. This idea may also be extended to general prey–predator models as a zone of no activation appears more prevalent in animals. For example, a lion under normal conditions does not hunt more than twice a week if he finds a prey that can sufficiently feed him. Further, animals that ruminate consume continuously for a part of the day and relax. Does it apply to human beings who have developed a habit of continuous eating?

6.6 Exercises

1. Define a zone of no activation for models (2.1) – (2.5) and obtain various stability conditions.
2. Study the influence of a zone on model (3.1) for which we have established the instability.
3. Study the combined effect of a zone of no activation and wall growth on the same model. Does it help reduce the fall of nutrient levels due to wall growth?
4. Use the definitions of (6.10) in models instead of (6.4) in the results of this section. What observations do you make?
5. Can the uptake function take the value G^* before x takes x^*? (In such a case the system may not possess an equilibrium value.)
6. Visualize the concept of a variable zone. Determine $G(u)$ appropriately in variable zone.
7. Elaborate the concept of moving zone. Explain how a moving zone and a variable zone are better than a fixed zone (6.4) or (6.10)?
8. Apply the concept of a zone to other biological models such as Lotka–Volterra model.

Chapter 7
Influence of the Control Mechanisms

7.1 Introduction

The study of Example 2.42 has revealed that the mechanisms introduced in Chaps. 4–6 have definitely contributed toward the stability of the positive equilibrium whose status is undecided as far as model equations (2.81) are concerned. We shall now see the strength of these mechanisms when the system given by model (2.81) is established to exhibit the instability tendencies observed in Sects. 3.2 and 3.2.

We use the following notation throughout this chapter.

$$F_1 = \int_0^\infty f(s)\mathrm{d}s < \infty, \quad G_1 = \int_0^\infty g(s)\mathrm{d}s < \infty \qquad (I)$$

and

$$T_f = \int_0^\infty sf(s)\mathrm{d}s < \infty, \quad T_g = \int_0^\infty sg(s)\mathrm{d}s < \infty. \qquad (II)$$

Clearly T_f and T_g are the average time delays in material recycling and growth response of the species, respectively. This enables us to find directly the influence of time delays on the stability of the system. We have already used this notation in Sect. 3.2

7.2 Stability Under Self-Regulatory Control Mechanism

In this section, we introduce our first mechanism known as self-regulatory control mechanism into system (2.81) to contain the influence of the consumption and the delay in recycling. We have already established in Chap. 4 its strength when the nutrient supply/consumption is low. The attempt here is to see how far it works when the delays (through nonnormalized kernels) influence the dynamics of the system.

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Introduction of this control mechanism modifies (2.81) to (see (4.1))

$$\begin{aligned} x'(t) &= D(x_0 - x(t)) - aU(x(t))y(t) \\ &\quad + b\gamma \int_0^\infty f(s)y(t-s)\mathrm{d}s, \\ y'(t) &= -(\gamma + D)y(t) \\ &\quad + cy(t)\int_0^\infty g(s)U(x(t-s))\mathrm{d}s - \mathrm{d}y^2(t). \end{aligned} \tag{7.1}$$

System (7.1) has already been discussed in detail in Chap. 4. We shall now discuss the stability of the positive equilibrium solution of (7.1) directly.

Note that the system (7.1) has a different set of nontrivial equilibrium solutions from (2.81) due to the presence of the term $-\mathrm{d}y^2$.

The equilibria of (7.1) are the solutions of the algebraic system

$$\begin{aligned} Dx_0 - Dx - aU(x)y + b\gamma F_1 y &= 0, \\ \Big[cU(x)G_1 - \gamma - D - \mathrm{d}y\Big]y &= 0. \end{aligned} \tag{7.2}$$

Clearly $(x_0, 0)$ is a solution of (7.2), which is the axial equilibrium solution of (7.1), which incidentally is the axial equilibrium solution of (2.81) also.

An interior equilibrium of (7.1) is given by a nonzero solution of (7.2) and is denoted by

$$\begin{aligned} x^* &= x_0 - \frac{(aU(x^*) - b\gamma F_1)(cU(x^*)G_1 - \gamma - D)}{dD}, \\ y^* &= \frac{cU(x^*)G_1 - \gamma - D}{d} \end{aligned} \tag{7.3}$$

We can see that (x^*, y^*) is positive if and only if

$$U(x^*) > \frac{\gamma + D}{cG_1}$$

or

$$\frac{\gamma + D}{cG_1} < L$$

and

$$\big(aU(x^*) - b\gamma F_1\big)\big(cU(x^*)G_1 - \gamma - D\big) < x_0 dD.$$

Theorem 4.2 now becomes as follows.

Theorem 7.1 *A necessary and sufficient condition for the existence of a positive equilibrium is*

$$\frac{\gamma + D}{cG_1} < U(x^*) < \frac{1}{2}\left\{\frac{\gamma + D}{cG_1} + \frac{b\gamma F_1}{a} + \sqrt{\left(\frac{\gamma + D}{cG_1} - \frac{b\gamma F_1}{a}\right)^2 + 4\frac{x_0 dD}{acG_1}}\right\}. \tag{7.4}$$

The following theorem establishes that the solutions of (7.1) are bounded. We observe that the conditions below Theorem 2.28 are sufficient to ensure the uniform boundedness of the solutions of (7.1) but these conditions depend on the delay kernels more.

Let

$$x(t) = \phi_1(t) \quad \text{and} \quad y(t) = \phi_2(t), \quad t \in (-\infty, t_0],\ t_0 \in \mathbf{R}$$

be the initial conditions for (7.1).

Theorem 7.2 *Let $\phi_j(t) \geq 0,\ j = 1, 2$ and not identically zero on any interval, and let the delay kernels satisfy (I). Then*

$$x(t) \leq \max\left\{x_0 + b\gamma F_1 M, \sup_{-\infty<t\leq 0}\{\phi_1(t)\}\right\},$$
$$y(t) \leq \max\left\{\frac{cL}{d}G_1, \sup_{-\infty<t\leq 0}\{\phi_2(t)\}\right\} = M(say)\forall t\,.$$

Remark 7.3 It is shown in Sect. 3.2 that system (2.81) may have unbounded solutions under the conditions of Corollary 3.6. For the boundedness of the solutions of (2.81) additional conditions are required as specified in Theorem 2.28 or inequalities below it. Now it is obvious from Theorem 7.2 that the solutions of (7.1) are always bounded. Hence, we remark that the introduction of self-regulatory mechanism into (2.81) regulates this type of disturbance (unbounded nature) of the solutions of (2.81).

However, the following result shows that the conditions for the stability of the axial equilibrium remain unaltered by the presence of the term $-\mathrm{d}y^2$. Proof of this result is similar to that of Theorem 4.8, and hence, omitted.

Theorem 7.4 *If $(\gamma + D/cG_1) > L$, the axial equilibrium $(x_0, 0)$ is globally asymptotically stable.*

In the remainder of the section we assume that the positive equilibrium solution (x^*, y^*) exists and is given by (7.3).

The following results modify Theorems 4.9 and 4.12.

Theorem 7.5 *Assume (A_1) and (A_2) on the uptake function U and let f and g satisfy (I) and (II). The positive equilibrium (x^*, y^*) of (7.1) is globally asymptotically stable provided*

$$G_1 < \frac{D + aky^*}{ck} \quad \textit{and} \quad F_1 < \min_{x\geq x^*}\left\{\frac{d + aU(x)}{b\gamma}\right\}. \tag{7.5}$$

Theorem 7.6 *Assume that the uptake function satisfies* (A_1), (A_2) *and the delay kernels satisfy* (I). *The positive equilibrium solution* (x^*, y^*) *of* (7.1) *is globally asymptotically stable provided,*

$$b\gamma F_1 + ckG_1 < \min\left\{D - aky^*, \min_{x \geq x^*}\{d + aU(x)\}\right\} = \mu \ (say). \tag{7.6}$$

Remark 7.7 Comparing the hypotheses of Theorems 7.5 and 7.6, we can observe that Theorem 7.6 does not require (II) on the delay kernels. Since, the values $\int_0^\infty sf(s)\mathrm{d}s = T_f$ and $\int_0^\infty sg(s)\mathrm{d}s = T_g$ denote the average time delays in material recycling and growth response of the species, relaxation of (II) on the delay kernels implies that the system can tolerate any lengths of delays if the other parameters and the consumption are as specified in Theorem 7.6. A straightforward computation shows that the condition (7.6) of Theorem 7.6 is weaker than condition (7.5) of Theorem 7.5 on the parameters of the system. This is, of course, tolerable in view of the relaxation on the delay kernels.

Remark 7.8 It may be established as in Sect. 4.5 that the condition $aU(x) > b\gamma F_1$ for $x > 0$ is sufficient to ensure the existence of a periodic solution to (2.81) establishing the oscillatory growth thereby implying the survival of species y. Here, we notice that the stability of (x^*, y^*) of system (2.81) can also be established under the conditions of Theorem 7.5 by letting $d = 0$. From this we understand that when the supply/consumption of nutrient is sufficiently high so that the system can tolerate a delay in material recycling (i.e., $aU(x) > b\gamma F_1$ for $x > x^*$) we need no mechanism on (2.81) for the stability assuming that the first condition of (7.5) holds. But when the consumption levels are falling down after attaining equilibrium value ($aU(x) < b\gamma F_1$ for $x > x^*$), a delay in material recycling is not tolerable and the stability of system (2.81) is in doubt. In such a case the introduction of self-regulatory mechanism with appropriately chosen $d > 0$ satisfying the second condition of (7.5) can preserve the stability of (x^*, y^*) of (7.1) establishing the eventual survival of both x and y. As the presence of the term $d > 0$ implies the death of some of the species, the consumer species survive in less numbers when supply/consumption of nutrient is less, which is realistic in nature. It also suggests that reduction in the size of consumer population is a natural, immediate remedy to survive at low nutrient supply/consumption.

If $G_1 < 1$, the condition $U(x^*) > (\gamma + D/cG_1)$ for the existence of a positive equilibrium for (7.1) (see inequality (7.4)) appears to be a weaker condition than the corresponding condition of system (2.81). But once $U(x)$ attains the equilibrium value, Theorems 7.5 and 7.6 suggest that if the other parameters of the system are properly controlled, the system becomes globally asymptotically stable even if the consumption starts decreasing thereafter and touches its lowest values.

Our next theorem provides an estimate for d, thereby specifying the direct influence of the carrying capacity of the environment on the global asymptotic stability of the positive equilibrium (x^*, y^*) of system (7.1). Further, we replace the assumption (A_2) on U by a gradient-type condition.

The following transformation is useful.
Let $x_1 = x - x^*$, $y_1 = y - y^*$, and $\xi_1(x_1) = U(x) - U(x^*)$.
Using this we may rewrite (7.7) as

$$\begin{aligned} x_1'(t) &= -Dx_1 - a(\xi_1(x_1) + U(x^*))y_1 - ay^*\xi_1(x_1) \\ &\quad + b\gamma \int_0^\infty f(s)y_1(t-s)\mathrm{d}s, \\ y_1'(t) &= (y_1 + y^*)\left[c\int_0^\infty g(s)\xi_1(x_1(t-s))\mathrm{d}s - \mathrm{d}y_1\right]. \end{aligned} \tag{7.7}$$

Clearly (0,0) is the equilibrium solution of (7.7) corresponding to (x^*, y^*) of (7.1).

Proof of this result runs on the lines similar to those of Theorem 4.16 and hence, the details are omitted.

Theorem 7.9 *Assume that the delay kernels satisfy* (*I*) *and* (*II*) *and the uptake function, in addition to* (A_1), *satisfies*

$$x_1\xi_1(x_1) \geq 0, \xi_1(x_1) \neq 0 \quad \text{for } x_1 \neq 0.$$

The equilibrium solution (0,0) *of* (7.7) *is globally asymptotically stable provided*

$$d > \frac{(b\gamma c)^2\left[\sqrt{1 + \frac{a^2 L}{(b\gamma)^2}} + \frac{a\sqrt{L}}{b\gamma}\right]^2}{4\eta G_1 D\tilde{\alpha}(cG_1U(x^*) - \gamma - D)} \tag{7.8}$$

in which $\tilde{\alpha} = \min_{x \geq x^*}\left\{\frac{x_1}{\xi_1(x_1)}\right\} > 0$ *and* $\eta = \max\{1, F_1\}$.

The following example helps us understand the influence of self-regulatory mechanism on the stability of system (2.81) when Theorem 3.13 establishes the instability of (x^*, y^*).

Example 7.10 Consider the model

$$\begin{aligned} x'(t) &= (0.25)(6 - x(t)) - 10U(x)y(t) + \frac{1}{4}\int_0^\infty \mathrm{e}^{-\frac{1}{4}s}y(t-s)\mathrm{d}s, \\ y'(t) &= -10y(t) + 5y(t)\int_0^\infty \mathrm{e}^{-\frac{1}{4}s}U(x(t-s))\mathrm{d}s \end{aligned}$$

in which $\gamma = 9.75$, $b = 1/39$, $U(x) = x/(4+x)$, and $f(s) = e^{-\frac{1}{4}s} = g(s)$.

Clearly $F_1 = 4 = G_1$. The equilibrium values are $U(x^*) = (\gamma + D)/(cG_1) = 1/2$, $x^* = 4$, and $y^* = 1/8$. Also $U'(x^*) = 1/16$.

Clearly $U'(x^*)(aU(x^*) - b\gamma F_1) > 0$. Therefore, the instability discussed in Theorem 3.11 does not arise.

Now with $p = q$, condition (3.43) becomes

$$2p(A + p)^2 - B < 0.$$

Here $p = 1/4$, $A = D + ay^*U'(x^*) = 21/64$, and $B = acy^*U(x^*)U'(x^*) = 25/2$, clearly satisfy above inequality. Therefore, $(4, \frac{1}{8})$ is unstable by virtue of Theorem 3.15.

Now introducing the self-regulatory mechanism into the system with $d = 725/9$, we have

$$x'(t) = (0.25)(6 - x(t)) - 10U(x)y(t) + \frac{1}{4}\int_0^\infty e^{-\frac{1}{4}s} y(t-s)\mathrm{d}s,$$
$$y'(t) = -10y(t) + 5y(t)\int_0^\infty e^{-\frac{1}{4}s} U(x(t-s))\mathrm{d}s - \frac{725}{9}y^2(t) ,$$

with γ, b, $U(x)$ defined as earlier.

Because of the introduction of $-\mathrm{d}y^2$ term, the equilibrium state changes to $U(x^*) = 7/12$, $x^* = 5.6$, and $y^* = 3/145$.

Clearly $\tilde{\alpha} = 9.6$, $L = 1$ and we have

$$\frac{(b\gamma c)^2\left[\sqrt{1 + \left(\frac{a}{b\gamma}\right)^2} + \frac{a}{b\gamma}\right]^2}{4\eta G_1 D\tilde{\alpha}[cG_1U(x^*) - \gamma - D]} = 39.064 < d = \frac{725}{9}.$$

Also it is easy to see that all the other hypotheses of Theorem 7.9 are satisfied here and hence, $(x^*, y^*) = (5.6, 3/145)$ is globally asymptotically stable by virtue of Theorem 7.9.

Conclusions of this example may be seen in Figs. 7.1 and 7.2.

Remark 7.11 It is now clear that when a positive equilibrium of (2.81) exists and is established to be unstable in view of Theorem 3.13, Example 7.10 explains a case where the introduction of self-regulatory mechanism provides a globally asymptotically stable (interior) equilibrium by virtue of Theorem 7.7. Hence, we remark that this mechanism may help restore the stability of a system that has a tilt toward instability.

7.3 Stability Under Wall Growth Mechanism

The second control mechanism we introduce into system (2.81) is the phenomenon of wall growth described in Chap. 5. The model (2.81) with the wall growth may be represented by (see Chap. 5 for details)

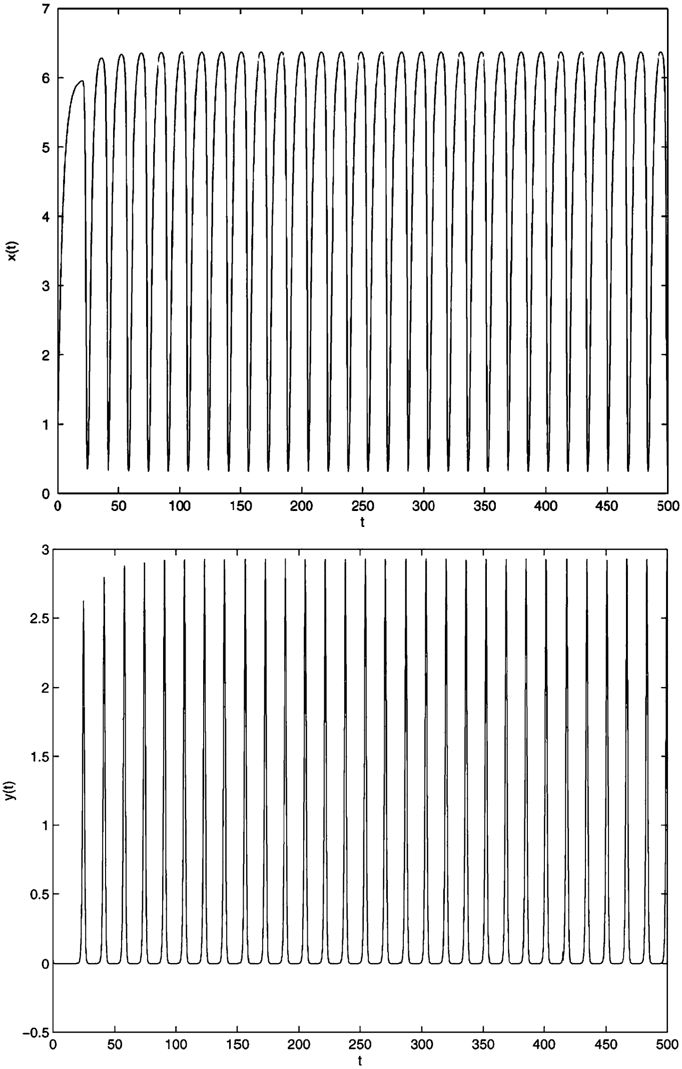

Fig. 7.1 Oscillations in populations x and y, respectively, in the absence of self-regulation

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x)z(t) \\ &\quad + b\gamma\alpha^* \int_0^\infty f(s)z(t-s)\mathrm{d}s, \\ z'(t) &= -\gamma z(t) - D\alpha^* z(t) \\ &\quad + cz(t)\int_0^\infty g(s)U(x(t-s))\mathrm{d}s. \end{aligned} \tag{7.9}$$

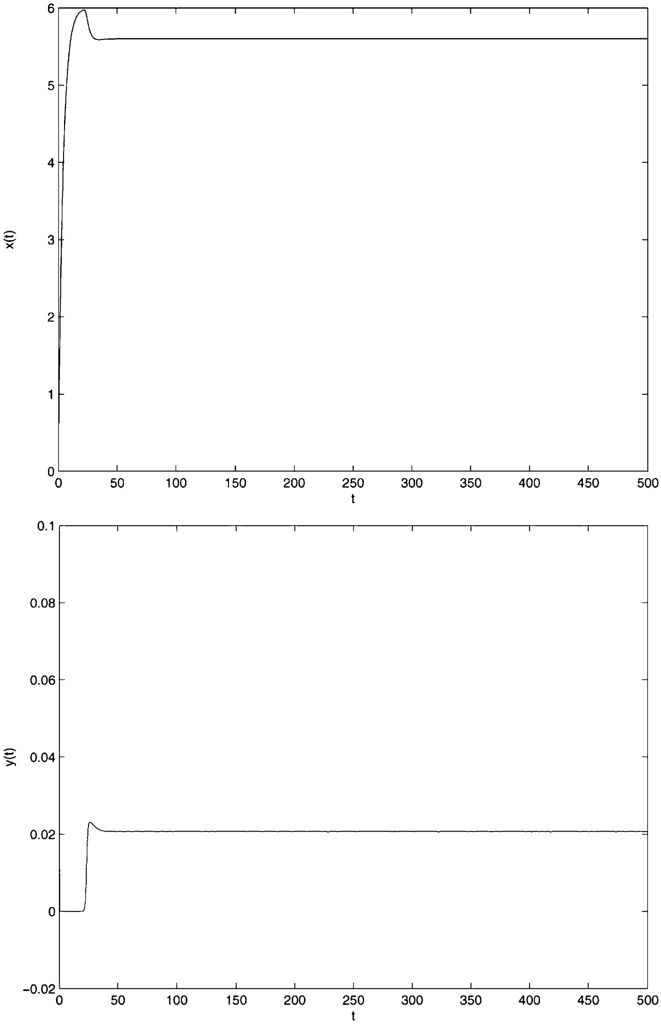

Fig. 7.2 Stabilization of populations x and y under self-regulatory mechanism

Note that since, $z(t) = y_1 + y_2$ is the aggregate of the populations, the stability of system (7.9) implies the eventual survival of both x and y of (2.81).

We now discuss the existence of equilibria for (7.9).

If the equilibria for (7.9) exist, they should satisfy

$$\begin{aligned} Dx_0 - Dx^* - aU(x^*)z^* + b\gamma\alpha^* z^* F_1 &= 0, \\ (cU(x^*)G_1 - \gamma - D\alpha^*)z^* &= 0. \end{aligned} \tag{7.10}$$

Keeping in view the definitions of $\alpha(t)$ and $z(t)$, we exclude the possibility of $z^* = 0$. Thus (7.10) will have only nontrivial (nonaxial) equilibria.

A nontrivial solution (x^*, z^*) of (7.10) is given by

$$U(x^*) = \frac{\gamma + D\alpha^*}{cG_1} \quad \text{and} \quad z^* = \frac{Dx_0 - Dx^*}{aU(x^*) - b\gamma\alpha^* F_1}, \tag{7.11}$$

which exists and is positive provided

$$\frac{\gamma + D\alpha^*}{cG_1} < L \quad \text{and} \quad (x_0 - x^*)(aU(x^*) - b\gamma\alpha^* F_1) > 0 \tag{7.12}$$

hold.

Uniqueness of (x^*, z^*) follows from its global asymptotic stability discussed later.

Now we proceed to discuss the global asymptotic stability of (x^*, z^*) assuming its existence, that is (7.12) holds. Since the results are only modifications of their counter parts in Chap. 5, we omit the proofs.

Theorem 7.12 *Assume that the uptake function satisfies* (A_1) *and* (A_2) *and the delay kernels satisfy* (*I*) *and* (*II*). *The equilibrium solution* (x^*, z^*) *of* (7.9) *is globally asymptotically stable provided*

$$G_1 < \frac{D + akz^*}{ck} \quad \textit{and} \quad F_1 < \min_{x \geq x^*} \left\{ \frac{aU(x)}{b\gamma\alpha^*} \right\}. \tag{7.13}$$

Theorem 7.13 *Assume* (A_1) *and* (A_2) *on the uptake function and let* f *and* g *satisfy* (*I*). *The positive equilibrium* (x^*, z^*) *of* (7.9) *is globally asymptotically stable provided*

$$b\gamma F_1\alpha^* + ckG_1 < \min\{D - akz^*, \min_{x \geq x^*}\{aU(x)\}\}. \tag{7.14}$$

The following examples illustrate the aforementioned results and also explain how the introduction of wall growth renders an unstable equilibrium state.

Example 7.14 Consider the system

$$\begin{aligned} x'(t) &= 2(6 - x(t)) - 10U(x)y(t) \\ &\quad + 1/2 \int_0^\infty \mathrm{e}^{-\frac{s}{11}}\, y(t-s)\mathrm{d}s, \\ y'(t) &= -6y(t) + 6y(t) \int_0^\infty \mathrm{e}^{-\frac{s}{2}}\, U(x(t-s))\mathrm{d}s \end{aligned} \tag{7.15}$$

in which $\gamma = 4, b = 1/8$, and $U(x) = x/(4 + x)$.

Clearly $F_1 = 11$ and $G_1 = 2$. The equilibrium values are

$$U(x^*) = 1/2, \; x^* = 4, \quad \text{and} \quad y^* = -8.$$

Since $x_0 = 6 > x^* = 4$ and $aU(x^*) - b\gamma F_1 = -1/2 < 0$, the earlier system does not have a positive equilibrium.

Now introducing wall growth into (7.15) with $r_1 = 1$ and $r_2 = 2$, we get

$$x'(t) = 2(6 - x(t)) - 10U(x)z(t) + 1/2 \int_0^\infty e^{-\frac{s}{11}} \alpha(t-s)z(t-s)ds,$$
$$z'(t) = -4z(t) - 2\alpha(t)z(t) + 6z(t) \int_0^\infty e^{-\frac{s}{2}} U(x(t-s))ds,$$
$$\alpha'(t) = -2\alpha(t)(1-\alpha(t)) - 1\alpha(t) + 2(1-\alpha(t)).$$

We have

$$\alpha^* = \frac{D + r_1 + r_2 - \sqrt{(D_1 + r_1 + r_2)^2 - 4Dr_2}}{2D} = 1/2$$

Thus for large t, as in (7.9), we have

$$\begin{aligned} x'(t) &= 12 - 2x(t) - 10U(x)z(t) \\ &\quad +1/4 \int_0^\infty e^{-1/11s} z(t-s)ds, \\ z'(t) &= -5z(t) + 6z(t) \int_0^\infty e^{-1/2s} U(x(t-s))ds \end{aligned} \tag{7.16}$$

The equilibrium solutions of (7.16) are

$$U(x^*) = 5/12, x^* = 20/7, \text{and } z^* = 4.4372.$$

It is easy to see that the parametric conditions (7.13) of Theorem 7.12 are satisfied with $k = 7/48$ and hence, $(x^*, z^*) = (20/7, 4.4372)$ is globally asymptotically stable by virtue of Theorem 7.12

Conclusions of this example may be seen in Figs. 7.3 and 7.4.

Example 7.15 Consider the system

$$\begin{aligned} x'(t) &= 2(4 - x(t)) - 10U(x)y(t) \\ &\quad +(0.4) \int_0^\infty e^{-\frac{s}{11}} y(t-s)ds, \\ y'(t) &= -6y(t) + 6y(t) \int_0^\infty e^{-\frac{s}{2}} U(x(t-s))ds, \end{aligned} \tag{7.17}$$

in which $\gamma = 4$, $b = 10$, and $U(x) = x/(4+x)$. Clearly $F_1 = 11, G_1 = 2$ as in the earlier example.The equilibrium solutions are $U(x^*) = (\gamma + D)/cG_1 = 1/2, x^* = 4$.

Also $aU(x^*) - b\gamma F_1 = 0.6 > 0$.

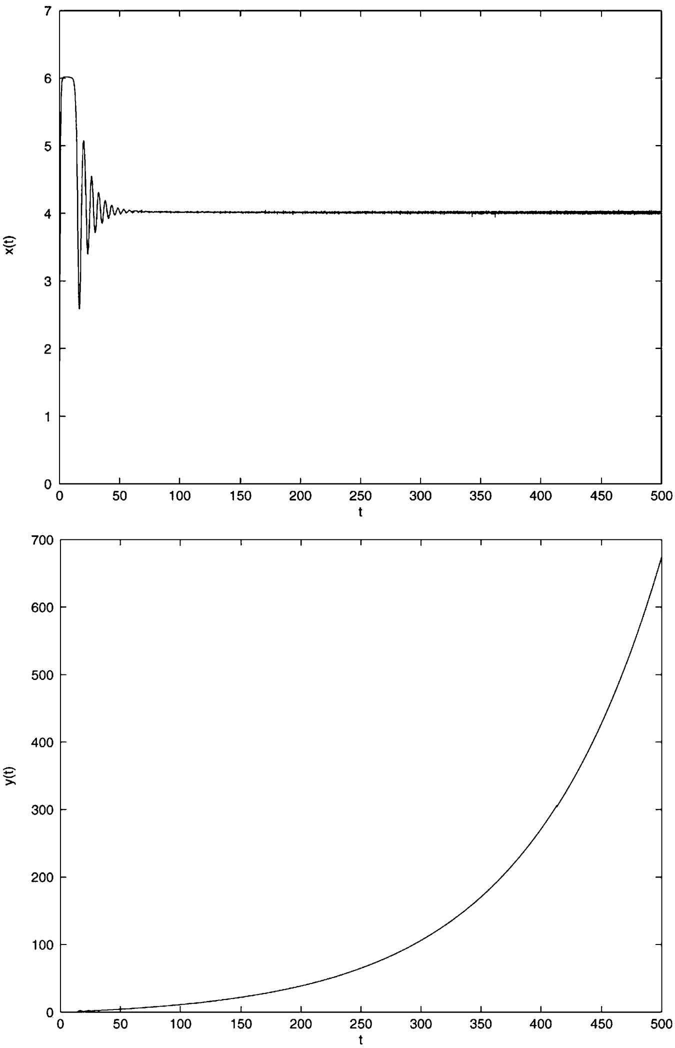

Fig. 7.3 System (7.15): possessing no positive equilibrium solution and population y exhibiting unbounded growth

But $y^* = [D(x_0 - x^*)]/[aU(x^*) - b\gamma F_1] = 0$ as $x_0 = x^* = 4$ in this case. Therefore (7.17) has no positive equilibrium. Introducing wall growth into (7.17) with $r_1 = 1$ and $r_2 = 2$ again and proceeding as in Example (7.14) we have

$$\alpha^* = 1/2, U(x^*) = (\gamma + D\alpha^*)cG_1 = 5/12, x^* = 20/7, \text{and}$$
$$z^* = [D(x_0 - x^*)]/[aU(x^*) - b\gamma\alpha^* F_1] = 1.1622 \text{ (approx)}.$$

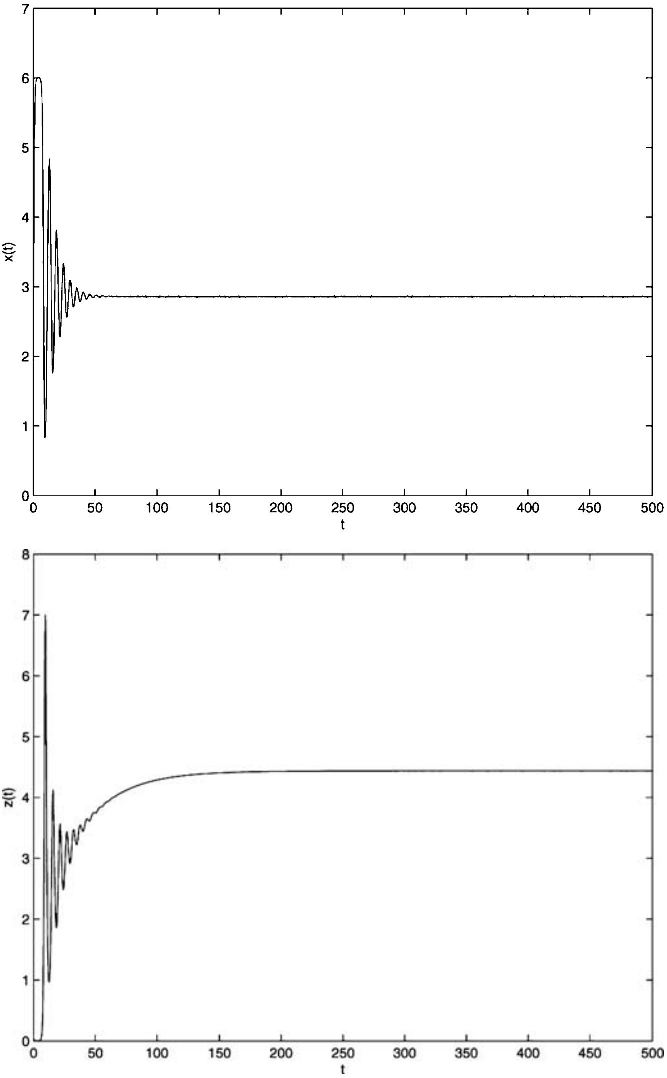

Fig. 7.4 Population x and aggregate population z approaching positive equilibrium solution under the influence of wall growth

Clearly all the parametric conditions are satisfied with $k = 7/48$. Therefore, by virtue of Theorem 7.12, $(x^*, z^*) = (20/7, 1.1622)$ is globally asymptotically stable.

Conclusions of this example may be seen in Figs. 7.5 and 7.6.

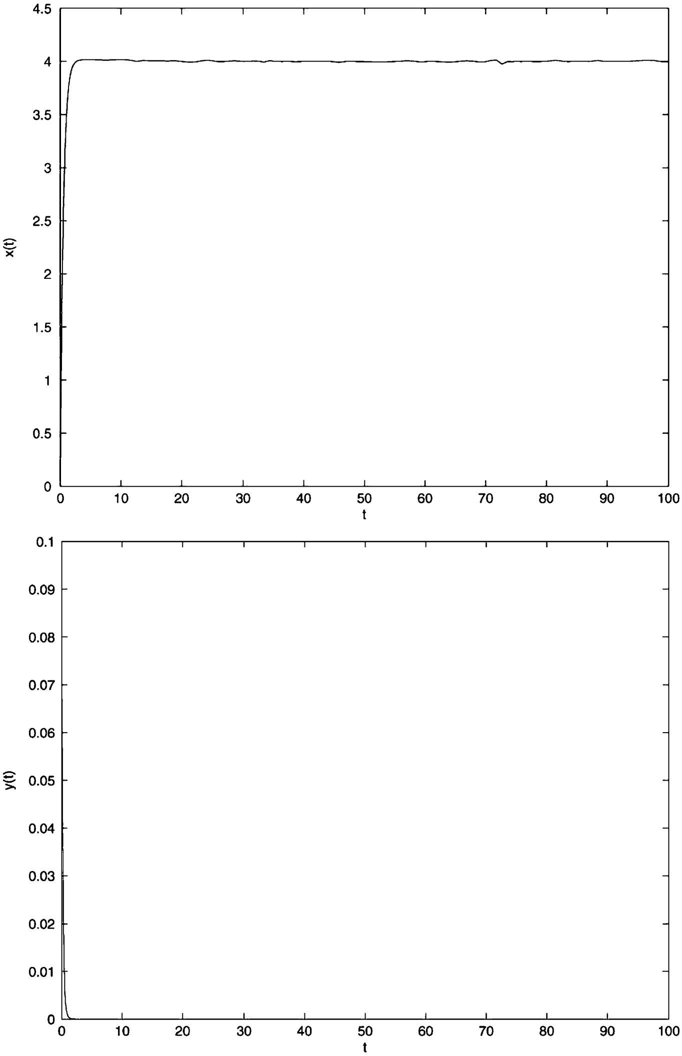

Fig. 7.5 Populations approaching axial equilibrium $(4, 0)$ implying the extinction of species y

The following example illustrates Theorem 7.13.

Example 7.16 Consider the model

$$\begin{aligned} x'(t) &= 4(6.5 - x(t)) - 12U(x)y(t) \\ &\quad +(0.4)\int_0^{\infty} f(s)y(t-s)\mathrm{d}s, \\ y'(t) &= -8y(t) + 10y(t)\int_0^{\infty} g(s)U(x(t-s))\mathrm{d}s. \end{aligned} \tag{7.18}$$

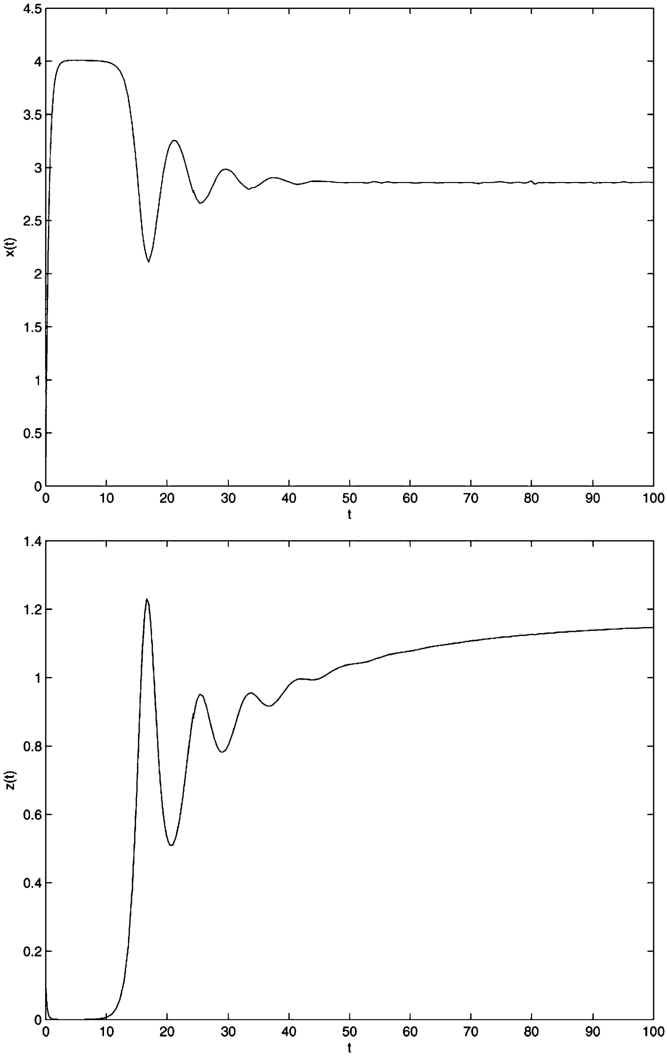

Fig. 7.6 Populations x and z (aggregate population) approaching positive equilibrium solution under the influence of wall growth mechanism, implying the survival of species

in which $\gamma = 4, b = 1/10$, and $U(x) = x/(4+x)$. Choose f and g such that $F_1 = \int_0^\infty f(s)\mathrm{d}s = 2,\ G_1 = \int_0^\infty g(s)\mathrm{d}s = 1$.

The equilibrium solutions are

$$U(x^*) = 4/5 \text{ and } x^* = 16.$$

Observe that $aU(x^*) - b\gamma F_1 > 0$ while $x_0 - x^* < 0$ implying that $y^* < 0$.

Thus, system (7.18) does not possess a positive equilibrium.

Again letting $r_1 = 1$ and $r_2 = 2$, introducing wall growth and proceeding as in Example (7.14), we obtain $\alpha^* = 1/2, U(x^*) = 3/5, x^* = 6$, and $z^* = 1/4.6$.

Now with $k = 1/4$, $D - akz^* = 3.337$, and $\min_{x \geq x^*}\{aU(x)\} = 9.6$, condition (7.14) of Theorem 7.13 is satisfied. Also all the other conditions of Theorem 7.3.2 are satisfied here. Therefore, $(x^*, z^*) = (6, 1/4.6)$ is globally asymptotically stable by virtue of Theorem 7.13.

Example 7.17 Consider the model

$$\begin{aligned} x'(t) &= 2(3.5 - x(t)) - 10U(x)y(t) \\ &\quad +(1/2)\int_0^\infty \mathrm{e}^{-\frac{s}{11}} y(t-s)\mathrm{d}s, \\ y'(t) &= -6y(t) + 6y(t)\int_0^\infty \mathrm{e}^{-\frac{s}{2}} U(x(t-s))\mathrm{d}s, \end{aligned}$$

in which $U(x) = x/(4 + x)$, $\gamma = 4$, $b = 1/8$, and $x_0 = 3.5$.

The equilibrium values are $U(x^*) = 1/2, x^* = 4$, and $y^* = 2$. Note that $U'(x^*) > 0$ and $aU(x^*) - b\gamma F_1 = -1/2 < 0$.

Therefore, $(x^*, y^*) = (4, 2)$ is unstable by virtue of Theorem 3.13 (condition (a)).

Again, introducing wall growth with $r_1 = 1$ and $r_2 = 2$, and proceeding as in Example 7.14, we get $\alpha^* = 1/2$, $U(x^*) = 5/12x^* = 20/7$, and $z^* = 4.4372$.

It may be seen that all the conditions of Theorem 7.12 are satisfied and hence, (x^*, z^*) is globally asymptotically stable by virtue of Theorem 7.12.

We record the conclusions of our study in this section as follows.

Remark 7.18 It is may be noticed from Example 7.14, 7.15 and 7.16 that when the system (2.81) does not possess an interior equilibrium solution, the introduction of wall growth mechanism has enabled the (modified) system to possess a positive equilibrium solution whose global asymptotic stability may then be established by virtue of Theorem 7.12 or Theorem 7.13 as the case may be.

Further, Example 7.17 shows that when system (2.81) possess a positive equilibrium whose instability is ensured by Theorem 3.13 (Corollary 3.14), the corresponding positive equilibrium solution of system (7.9) may be globally asymptotically stable.

7.4 Stability Under Zones of No Activation

A necessary condition for the existence of a positive equilibrium for (2.81) is that the consumption takes the value $(\gamma + D)/cG_1$ for some $x = x^* > 0$. The condition (7.3) says that the self-regulatory mechanism necessarily requires $U(x)$ to take a value bigger than $(\gamma + D)/cG_1$ for some $x > 0$ to have a positive equilibrium for system (7.1). At the same time, the introduction of wall growth mechanism enables the consumption to attain the equilibrium at an early stage, well before $(\gamma + D)/cG_1$ (since $(\gamma + D\alpha^*)/cG_1 < (\gamma + D)/cG_1$ as $\alpha^* < 1$). Having dealt with the stability of system (2.81) in these two cases, we now consider the situation where the consumption remains unaltered at $(\gamma + D)/cG_1$ not only at the equilibrium value $x = x^*$ but also in a neighborhood of it. In other words, we study the dynamics of (2.81) when the consumption is maintained at the equilibrium value $U(x) = U(x^*) = (\gamma + D)/cG_1$ when $x \in (x^* - \delta, x^* + \delta)$ for some $\delta > 0$.

Before defining a zone of no activation for (2.81) we assume that the system (2.81), that is,

$$\begin{aligned} z'(t) &= D(x_0 - x(t)) - aU(x(t))y(t) \\ &\quad + b\gamma \int_0^\infty f(s)y(t-s)\mathrm{d}s, \\ y'(t) &= -(\gamma + D)y(t) \\ &\quad + cy(t)\int_0^\infty g(s)U(x(t-s))\mathrm{d}s \end{aligned} \tag{7.19}$$

has a positive equilibrium (x^*, y^*) satisfying $U(x^*) = (\gamma + D)/cG_1$.

The transformation $u(t) = x(t) - x^*$, $v(t) = y(t) - y^*$, and $\xi(u) = U(x) - U(x^*)$ takes the system (7.19) to

$$\begin{aligned} u'(t) &= -Du(t) - a[\xi(u) + U(x^*)]v(t) \\ &\quad - ay^*\xi(u(t)) + b\gamma \int_0^\infty f(s)v(t-s)\mathrm{d}s, \\ v'(t) &= (v(t) + y^*)c \int_0^\infty g(s)\xi(u(t-s))\mathrm{d}s. \end{aligned} \tag{7.20}$$

A zone of no activation in consumption for the consumer species may be defined by

$$\xi(u) = \begin{cases} \xi_1(u), & \text{for} \quad u > \delta_2, \\ \xi_2(u), & \text{for} \quad u < \delta_1, \\ 0, & \text{for} \quad \delta_1 \le u \le \delta_2, \end{cases} \tag{7.21}$$

where δ_1 and δ_2 are real constants.

Further,

$$\lim_{u \to \delta_1^-} \xi_1(u) = \lim_{u \to \delta_2^+} \xi_2(u), \tag{7.22}$$

where $\xi_1(u)$ and $\xi_2(u)$ are continuous, bounded and satisfy

$$|\xi_i(x_1) - \xi_i(x_2)| \le k_i|x_1 - x_2| \quad \forall\, x_1, x_2, \quad i = 1, 2. \tag{7.23}$$

for some positive constants k_i, $i = 1, 2$.

Note that (0,0) is the equilibrium solution of (7.20) corresponding to (x^*, y^*) of (7.19).

We directly proceed to the global asymptotical stability of the equilibrium (0,0) of (7.20) under the influence of the zone of no activation (7.21). The proof is omitted since it is a repetition of that of Theorem 6.1.

Theorem 7.19 *Assume that* (7.21)–(7.23) *hold and the delay kernels satisfy* (*I*) *and* (*II*). *The equilibrium solution* $(0, 0)$ *of* (7.20) *is globally asymptotically stable provided*

$$\min\left\{D - (cG_1 - ay^*)k_1, D - (cG_1 - ay^*)k_2\right\} > 0,$$
$$aU(x^*) - b\gamma F_1 > 0,$$
$$\min_{u>\delta_2}\left\{a[\xi_2(u) + U(x^*)] - b\gamma F_1\right\} > 0,$$
$$\textit{and}$$
$$\min_{u<\delta_1}\left\{a[\xi_1(u) + U((x^*)] - b\gamma F_1\right\} > 0.$$

Remark 7.20 Notice that in the zone of no activation, that is for $\delta_1 \leq u \leq \delta_2$ (see proof of Theorem 6.1),

$$D^+V \leq -D|u(t)| - (aU(x^*) - b\gamma F_1)|v(t)|\,.$$

Thus D^+V is negative definite if $aU(x^*) - b\gamma F_1 > 0$. Then clearly, this condition is alone sufficient to ensure the global asymptotic stability of the equilibrium $(0, 0)$.

Recalling the condition (b) of Theorem 3.13 for the instability of (x^*, y^*) namely

$$U'(x^*) < 0 \quad \text{and} \quad aU(x^*) - b\gamma F_1 > 0.$$

Theorem 7.19 implies that a natural remedy to fight out this type of instability is to introduce a zone of no activation here.

The following theorem is of some interest to us as it relaxes the delay kernels from condition (II).

Theorem 7.21 *Assume* (7.21)–(7.23) *on the uptake function. Assume* (*I*) *on the delay kernels. The equilibrium solution* $(0, 0)$ *of* (7.20) *is globally asymptotically stable provided*

$$ck_1G_1 + b\gamma F_1 < \min\left\{D - ak_1y^*, \min_{u<\delta_1}\left\{a[\xi(u) + U(x^*)]\right\}\right\},$$
$$ck_2G_1 + b\gamma F_1 < \min\left\{D - ak_2y^*, \min_{u>\delta_2}\left\{a[\xi(u) + U(x^*)]\right\}\right\},$$
$$\textit{and} \quad b\gamma F_1 < \min\left\{D,\ aU(x^*)\right\}.$$

Remark 7.22 In the zone of no activation, $\delta_1 \le u \le \delta_2$ we have, $aU(x^*) - b\gamma F_1 > 0$ and $D > b\gamma F_1$ are sufficient for the global asymptotic stability of (0,0). Since $U'(x^*) = 0$ in $\delta_1 \le u \le \delta_2$, the condition $aU(x^*) - b\gamma F_1 > 0$ rules out the possibility of instability specified by condition (b) of Theorem 3.13 and (0,0) is globally asymptotically stable by virtue of Theorem 7.21.

7.5 Discussion

Up till now in the literature, mathematical analysis of the models representing the growth in a lake known as chemostat-like models are confined to the survival of species expressed in terms of their persistence and global asymptotic stability of the positive equilibrium especially when the time delays present in such systems tend to destabilize the equilibrium. These studies have dealt with the question of preserving the stability of the system. But this instability dilemma calls for an adequate understanding of the instability tendencies in growth process of microbial populations feeding on a nutrient, so as to develop effective biocontrol mechanisms to contain these tendencies.

In an attempt to dwell upon this view point, which in our opinion makes the study more realistic, we propose three different mechanisms termed as self-regulatory mechanism, wall growth, and creation of a zone of no activation. The main thrust of this work is embodied in providing a mathematical support to these biologically relevant ideas besides paving way for the clear understanding of the restoration of stability. The present study establishes that the first mechanism besides controlling the wild growth renders in bringing the populations to have a globally asymptotically stable growth (see results of Sect 7.2 and remarks there in). Further we notice that this mechanism comes into play when the nutrient supply is low and competition is inevitable.

The second mechanism contributes significantly to have populations approach globally asymptotically the positive equilibrium when the existence of such an equilibrium to the original model equations is in doubt. This conclusion has been supported by several examples that deal with a variety of situations that are concerned with the nonexistence of positive equilibrium for the original model equations (see Sect. 7.3). This helps when the inflows are very high and thus, wall growth is an immediate resort.

The third mechanism related to the creation of a zone of no activation is a biologically welcoming process that particularly helps preventing a situation that leads to possible instability when the supply of nutrient is abundant in the system. Further the importance of this mechanism requires a deeper study as selecting a zone is important. This zone need not be the equilibrium value but an appropriate one depending on the supply.

7.6 Notes and Remarks

We have understood three types of situations that arise during a season-cycle and the response of species to these seasonal changes. Let us now get back to our basic problem of a limited nutrient–consumer system. If one wants to develop such a system in a laboratory or for commercial purposes, one may choose one of the models (2.1)–(2.6) suitably and apply these mechanisms. When resources are low our study recommends a self-regulatory mechanism, if the resources are high, go in for wall growth and zones whenever necessary.

The purpose of a zone becomes very clear now. Two zones appear to be very useful and some times inevitable. One zone is between a low supply state and a high supply state. The second is during a transition from high supply state to the low one. The zones need not be the ones defined at equilibrium value, i.e., (6.8) but may be the one defined by (6.10), when achieving an equilibrium state is difficult. These zones act as controllers. Further, if one plans for the total resources that the system requires for a whole season, one can have a number of zones for an optimal utilization of resources.

Our attempt here is only a beginning and much needs to be done in this direction. We conjecture that these mechanisms can be applied to a number of biological models and tested at each stage. We feel that the working principles of these mechanisms will be more clear if the inflow and outflow rates are distinguished from each other. Note that we have used the parameter D to represent both of these. Attempts are made on some models but systems (2.1)–(2.6) need to be reconsidered under the present circumstances posed by the control mechanisms. The contents of this chapter are taken from a recent work of Sree Hari Rao and Raja Sekhara Rao [95].

Examples 7.10, 7.14, and 7.15 are simulated using Matlab 6.5 release 13 invoking ode113. By defining,

$$w_1(t) = \int_{-\infty}^{t} f(t-s)y(s)\mathrm{d}s, \quad w_2(t) = \int_{-\infty}^{t} g(t-s)U(x(s))\mathrm{d}s,$$

and $f(s) = \mathrm{e}^{-\alpha s}$, $g(s) = \mathrm{e}^{-\beta s}$, $\alpha > 0, \beta > 0$, we transform system (2.81) into a fourth-order system of ordinary differential equations of the following form

$$\begin{aligned}
x'(t) &= D(x_0 - x(t)) - aU(x)y(t) + b\gamma w_1(t),\\
y'(t) &= -(\gamma + D)y(t) + cy(t)w_2(t),\\
w_1'(t) &= y(t) - \alpha w_1(t),\\
w_2'(t) &= U(x(t)) - \beta w_2(t)
\end{aligned}$$

and apply the above package.

7.7 Exercises

1. Modify the other results of Chaps. 4–6 to understand the effect of nonnormalized kernels.
2. We have broadly classified the season-cycle into (a) a low supply period say summer for self-regulation, (b) a high supply period, for example, rainy season, to introduce wall growth, and (c) transition periods, high supply to low supply and vice versa, to introduce zones. Are there any more new classifications based on the seasonal effects to be introduced to develop new mechanisms?
3. What new environmental conditions may be included in our models to introduce more mechanisms?

Chapter 8
Parameter Estimation Using Dynamic Optimization

8.1 Introduction

Until now, we have studied the stability, instability, and oscillatory behaviors of the system (2.81) (Chap. 2) and mechanisms that can regulate the instability characteristics of the systems in Chaps. 4–7. We have observed that due to the variations in nutrient supply (inflow) and washout (outflow), the system is subject to disturbances. In fact, this has lead to formulation of various models (2.1)–(2.6) and the mechanisms in earlier chapters. The inflow and outflow rates are represented by the parameter D in our models. Thus, on the whole, D seems to be king pin in determining the characteristics of these biological models. Such a parameter is called a key parameter. But if we know that the system can be brought under control by restricting this parameter, we may call this D, a control parameter. Then it becomes very important to estimate this control parameter. Once D is estimated, the tendency (stability or instability) of the system under consideration may be understood from the results of Chaps. 2 and 3. Accordingly the control parameter may be varied to change the dynamics of the system from instability to stability or vice-versa. Even in case D is only a key parameter and cannot be controlled by us, its estimation helps us in deciding whether mechanisms are required and which mechanism, if required.

In case of a chemostat, D is under the control of experimenter. Therefore, by our stability analysis, we can fix a range for D in which the system is going to be stable, once the other parameters are known. But this is not the case with a lake. The inflows as well as outflows are entirely dependent on nature/season. Thus, D in this case is beyond our control and the best we can do is to estimate it. Once D is estimated and a stability analysis is made, we can decide upon the necessity for a control mechanism. If the system is stable, we are comfortable. Also the value of D decides the type of mechanism we should go in for as discussed in Chaps. 4–6. In these cases, D is only a key parameter and no more the control parameter. Then our task extends to estimation of those parameters that represent the control mechanisms which, thus, become the new control parameters.

But how to estimate these parameters? We apply optimal control theory for estimating these vital parameters. The method of differential transforms is introduced to find an approximate solution of the given system as a power series of the time

Vadrevu Sree Hari Rao and Ponnada Raja Sekhara Rao, *Dynamic Models and Control of Biological Systems*, DOI 10.1007/978-1-4419-0359-4_8,

variable. We provide an algorithm to estimate the key/control parameters. At the same time, finding an optimal path for the system is important for biological models since optimization of growth/population of the consumer (predator) or food (prey) or the consumption of prey provides clues about the behavior of the system on the whole. Since the systems under consideration are nonlinear dynamical systems, the method is termed dynamic optimization using nonlinear programming techniques.

We now begin our next section with a detailed description of the dynamic optimization method we are going to employ here.

8.2 Dynamic Optimization

Static optimization problems deal with maximization/minimization of a linear/nonlinear functional with constraints satisfying linear/nonlinear inequalities or equations. There are various techniques to solve these problems. For instance, a problem of optimization of a linear functional in two variables, subject to a set of linear equality/inequality constraints, requires graphing of these constraints, yielding a closed convex region known as "feasible region." A simple and well-known technique is the corner point method, which suggests that the functional attains maxima/minima at one of the corner points of the feasible region. A close look at this technology suggests that static (classical) optimization is purely a domain-dependent property.

The methods of calculus are used to find the unconstrained maxima and minima of functions of several variables. Particular problems with equality constraints are solved using Lagranges method and inequality constraints are solved by Kuhn–Tucker's optimality conditions. Depending on the physical structure of the optimization problem, we choose linear, nonlinear, multioptimal control theory, neural network, and fuzzy system techniques to find an optimal solution.

On the other hand, the constraints of an optimization problem may exhibit a tendency to respond to the changes (disturbances) in the environment (external factors) and in such a case one has to consider dynamical constraints for the system. Constraints that may, thus, form a dynamical system characterize dynamic optimization problems. It means that dynamic optimization problems are concerned with the dynamical systems described, for example, by differential equations, difference-differential equations, integral equations, integro-differential equations, etc. The dynamics described by these equations depend on the state and control functions of the system. Therefore, an obvious difference between the static optimization and dynamic optimization problems lies in the choice of constraints (algebraic equations/inequalities and dynamical systems). Thus, "dynamic optimization is a process of determining control and state histories for a dynamical system over a finite time period to optimize performance indexes."

The main objective of a dynamic optimization problem is "to find an admissible control function u which transforms the system from its initial state to a desired state within a stipulated time ($t = T$) and optimizes the objective (cost) functional." Mathematically, dynamic optimization problem consists of the following:

- Description of the constraints represented as a dynamical system with initial conditions
- Defining the boundary conditions
- Defining the admissible set of controls
- Selection of the performance criterion function (usually known as objective function)

Generally in all the dynamic optimization problems we need to identify key parameters associated with control function $u(t)$, which govern the dynamics of the system of state variables. The block diagram of a dynamic optimization problem is represented in Fig. 8.1 (later).

To accomplish dynamic optimization, it is possible to use a number of approaches such as the classical calculus of variations, dynamic programming, the Pontryagin's maximum principle, etc.

The following example illustrates how calculus of variation problem by Euler may be transformed into a dynamic optimization problem. Optimize

$$\int_{t_0}^{T} f(t, x(t), x'(t))\mathrm{d}t \tag{8.1}$$

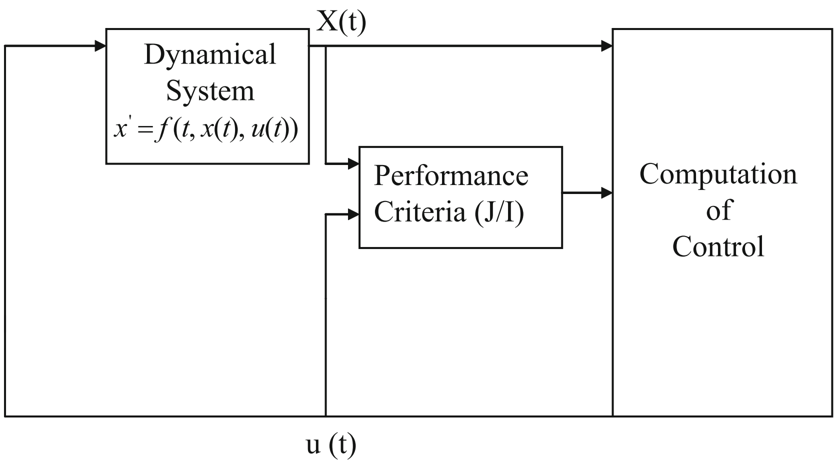

Fig. 8.1 Block diagram of a dynamic optimization problem

subject to $x(t_0) = p_0$, where f, x are continuously differentiable in $t_0 \le t \le T$. By the transformation

$$x' = u.$$

(8.1) may be written as

optimize

$$\int_{t_0}^{T} f(t, x(t), u(t))\mathrm{d}t, \tag{8.2}$$

subject to

$$x' = u, \quad x(t_0) = p_0,$$

where x is the state variable and u is the control variable . This provides us a basic structure of a dynamic optimization problem. A generalization of this problem is as follows:

Optimize

$$\int_{t_0}^{T} f(t, x(t), u(t))\mathrm{d}t, \tag{8.3}$$

subject to

$$x' = g(t, x(t), u(t)), \quad x(t_0) = p_0. \tag{8.4}$$

The functions f, g are continuously differentiable with respect to their arguments, x, the state function, and u, the control function of the dynamical system.

We shall follow the techniques provided in the book by Kamien and Schwartz [57] and the following procedure explains the basic method of obtaining the optimal solution to the given system.

For any functions x and u satisfying (8.4), to help us in optimizing (8.3), we choose a multiplier function λ, similar to a Lagrange multiplier function, which is a continuously differentiable function of t on $t_0 \le t \le T$. We shall provide the other specifications of λ a little later. Now (8.3) may be written as,

$$\int_{t_0}^{T} f(t, x(t), u(t))\mathrm{d}t = \int_{t_0}^{T} \Big[f(t, x(t), u(t)) + \lambda(t) g(t, x(t), u(t)) - \lambda(t) x'(t) \Big] \mathrm{d}t, \tag{8.5}$$

since $\lambda(t) g(t, x(t), u(t)) - \lambda(t) x'(t) = 0$, from (8.4), for any $\lambda(t)$. Now consider the last term of (8.5),

$$-\int_{t_0}^{T} \lambda(t) x'(t)\mathrm{d}t = -\lambda(T)x(T) + \lambda(t_0)x(t_0) + \int_{t_0}^{T} \lambda'(t) x(t)\mathrm{d}t. \tag{8.6}$$

Using (8.6) in (8.5), we have

$$\int_{t_0}^{T} f(t,x(t),u(t))\mathrm{d}t = \int_{t_0}^{T} \Big[f(t,x(t),u(t)) + \lambda(t)g(t,x(t),u(t)) + \lambda'(t)x(t)\Big]\mathrm{d}t - \lambda(T)x(T) + \lambda(t_0)x(t_0).$$

It is clear that $\int_{t_0}^{T} f(t,x(t),u(t))\mathrm{d}t$ is maximum when the right hand side of the aforementioned equality is maximum.

If we denote $H = f(t,x(t),u(t)) + \lambda(t)g(t,x(t),u(t)) + \lambda'(t)x(t)$, then from elementary calculus, we have the necessary conditions for H to be maximum as $\frac{\partial H}{\partial x} = 0$ and $\frac{\partial H}{\partial u} = 0$. Thus, we have,

Necessary Conditions

1. $\lambda'(t) = -\Big(\dfrac{\partial f}{\partial x} + \lambda\dfrac{\partial g}{\partial x}\Big)$
2. $\lambda(T) = 0$
3. $\dfrac{\partial f}{\partial u} + \lambda\dfrac{\partial g}{\partial u} = 0$

Sufficient Conditions

f and g are concave functions of x and u.

The choice of $\lambda(T) = 0$ reduces our work and helps us define λ precisely. The concavity of f and g provide us local maxima or minima at least. We shall now apply this technique to find an optimal solution for our chemostat model. To make matters simple and have a better understanding of the techniques, we consider the basic model of chemostat, namely, system (1.5).

8.3 Application to Basic Chemostat Model

We now consider system (1.5), that is,

$$\begin{aligned} x'(t) &= Dx_0 - Dx(t) - aU(x(t))y(t), \\ y'(t) &= ay(t)U(x(t)) - Dy(t). \end{aligned} \tag{8.7}$$

This may be written as

$$
\begin{aligned}
x' &= g(x, y), \\
y' &= f(x, y).
\end{aligned}
\tag{8.8}
$$

Integrating the second equation of (8.8) with respect to t from t_0 to t, we get

$$y(t) - y(t_0) = \int_{t_0}^{t} f(x(t), y(t))\mathrm{d}t.$$

Then system (8.8) may be viewed as the following optimization problem: optimize

$$\int_{t_0}^{T} f(x(t), y(t), u(t))\mathrm{d}t,$$

subject to

$$x' = g(x(t), y(t), u(t)), \quad x(t_0) = x^0, \quad y(t_0) = y^0 \tag{8.9}$$

for any initial conditions $x(t_0) = x^0$, $y(t_0) = y^0$ and terminal value of time T. Notice that we are optimizing consumer species y here. In view of our observations throughout, we assume the parameter D as the key parameter that controls the dynamics of the system. This allows us to define the control function $u \equiv D$. With this setup, we now find an optimum solution for the system (8.9) using the necessary and sufficient conditions provided in earlier section.

Now $f(x, y, D) = aU(x)y - Dy$ and $g(x, y, D) = Dx_0 - Dx - aU(x)y$. Let λ be our multiplier function. Then the third necessary condition

$$\frac{\partial f}{\partial D} + \lambda \frac{\partial g}{\partial D} = 0$$

yields

$$-y + \lambda x_0 - \lambda x = 0.$$

This after a rearrangement gives

$$\lambda = \frac{y}{x_0 - x}. \tag{8.10}$$

Differentiating this λ with reference to t and rearranging we get

$$\lambda' = \frac{y' + x'\lambda}{x_0 - x}. \tag{8.11}$$

Now the first necessary condition

$$\lambda'(t) = -\left(\frac{\partial f}{\partial x} + \lambda \frac{\partial g}{\partial x}\right)$$

yields

$$\lambda' = -\left[aU'(x)y - D\lambda - aU'(x)y\lambda\right], \tag{8.12}$$

with second necessary condition requiring $\lambda(T) = 0$ for some $T \geq t_0$. Using (8.11) in (8.12), we get

$$\frac{y' + x'\lambda}{x_0 - x} = D\lambda + a(\lambda - 1)U'(x)y.$$

Using the value of $\lambda = \frac{y}{x_0 - x}$ on the right hand side of the aforementioned equation, we get

$$y' + x'\lambda = Dy + aU'(x)y(x + y - x_0).$$

Using (8.7) for x', y', and λ as above in this equation, we get

$$aU(x)y - Dy + (Dx_0 - Dx - aU(x)y)\frac{y}{x_0 - x} = Dy - aU'(x)y(x_0 - x - y).$$

This yields

$$aU(x)y\frac{x_0 - x - y}{x_0 - x} = Dy - aU'(x)y(x_0 - x - y).$$

Thus, we have either

Case 1. $y = 0$ or
Case 2.

$$aU(x)\frac{x_0 - x - y}{x_0 - x} = D - aU'(x)(x_0 - x - y).$$

This after a simple rearrangement gives

$$D = a\left[\frac{U(x)}{x_0 - x} + U'(x)\right](x_0 - x - y)$$

or

$$y = (x_0 - x)\left[1 - \frac{D}{aU(x) + a(x_0 - x)U'(x)}\right]. \tag{8.13}$$

From the discussion in previous section it follows that this gives an optimal value for system (8.7). We shall see how far this solution fits into our framework.

Before this, we recall some basic properties of solutions of (8.7) from Chap. 1.

Adding the two equations of (8.7) we get

$$x' + y' = Dx_0 - D(x + y),$$

which is a first-order linear equation in $x + y$ whose solution is given by

$$x(t) + y(t) = x_0 + [x(t_0) + y(t_0) - x_0]\mathrm{e}^{-D(t-t_0)}. \tag{8.14}$$

Now from (8.13), we have

$$x + y = x_0 - \frac{D(x_0 - x)}{aU(x) + (x_0 - x)U'(x)}. \tag{8.15}$$

Clearly, $x + y \to x_0$ eventually for large values of t.

The following observations may be derived from (8.13) and (8.14).

1. When $x \to x_0$, we have $y \to 0$.
2. When the consumption is maximum, we have $U'(x) = 0$ for some $x = \bar{x}$. Then y is given by
$$y = (x_0 - \bar{x})\left[1 - \frac{D}{aU(\bar{x})}\right].$$
In particular if $\bar{x} = x^*$, the equilibrium value of x, then using $aU(x^*) = D$ we have $y \to 0$.
This hints at the case where the consumption falls after x attains x^*. Then $aU(x)$ becomes less than D and hence, from the second equation of (8.7) $y \to 0$.
3. Again at $x = x^*$, we have $aU(x^*) = D$. Then
$$\begin{aligned} y &= (x_0 - x^*)\left[1 - \frac{D}{D + a(x_0 - x^*)U'(x^*)}\right] \\ &= (x_0 - x^*)\frac{a(x_0 - x^*)U'(x^*)}{D + a(x_0 - x^*)U'(x^*)}. \end{aligned}$$
Then, for sufficiently small values of D, $y \to x_0 - x^*$. But $x_0 - x^* = y^*$ at the equilibrium state. Thus, equilibrium solution is the optimal solution for small values of D. It is justified by the observation that when D is small, equilibrium state is attained even at low levels of consumption $U(x^*) = \frac{D}{a}$. However, when $(x_0 - x^*)U'(x^*) << D$ then clearly $y \to 0$. This is justified by the observation that at these high levels of washout, it is difficult for the microorganism y to survive.
4. When $aU(x) < D$, we have
$$\begin{aligned} y &= (x_0 - x)\left[1 - \frac{D}{aU(x) + a(x_0 - x)U'(x)}\right] \\ &< (x_0 - x)\left[1 - \frac{D}{D + a(x_0 - x)U'(x)}\right] \to 0, \end{aligned}$$
for large values of D. This also explains the case where the system can not have a positive equilibrium solution, and hence, $x \to x_0$.

We have noticed in Chap. 1 that $x + y$ always remains in the cone bounded by $x \geq 0,\ y \geq 0$ and $x + y = x_0$. Thus, $x = x_0,\ y = 0$ and $x = 0,\ y = x_0$ are optimal values that are corner points of the feasible region. Also one may notice in all the earlier cases that the respective optimal solutions are within this range. Thus, our optimal solution (8.13) is the one we are looking for.

We shall now consider a simple rearrangement of system (8.7),

$$\begin{aligned} x' &= Dx_0 - Dx - aU(x)e^z, \\ z' &= aU(x) - D, \end{aligned} \tag{8.16}$$

obtained from (8.7) by letting $\log y = z$. This system may be viewed as the following optimization problem:

Optimize

$$\int_{t_0}^{T} f(x(t), z(t), D)\mathrm{d}t,$$

subject to

$$x' = g(x(t), z(t), D), \quad x(t_0) = x^0, \quad z(t_0) = z^0. \tag{8.17}$$

Here $f(x, z, D) = aU(x) - D$ and $g(x, z, D) = Dx_0 - Dx - aU(x)e^z$. Proceeding exactly as above, we have

$$\frac{\partial f}{\partial D} + \lambda \frac{\partial g}{\partial D} = 0 \quad \text{gives} \quad -1 + \lambda(x_o - x) = 0 \quad \text{or} \;\; \lambda = \frac{1}{x_0 - x},$$

and

$$\lambda' = -\left\{ \frac{\partial f}{\partial x} + \lambda \frac{\partial g}{\partial x} \right\} = -\left\{ aU'(x) - D\lambda - \lambda a U'(x)e^z \right\}.$$

Using the values of λ, λ', and x' in the earlier equation, we get upon some eliminations and rearrangements,

$$y = e^z = \frac{U'(x)(x_0 - x)^2}{U(x) + U'(x)(x_0 - x)}.$$

We record the following *observations*:

1. When $x \to x_0$ we have $y \to 0$.
2. When $x = \bar{x}$ is a value of x such that $U'(x) = 0$, $y \to 0$.
3. If there exists a value $\tilde{x}$ for x such that $U(\tilde{x}) = 0$ and $U'(\tilde{x}) \neq 0$, then $y \to x_0 - \tilde{x}$. In particular if $\tilde{x} = 0$ then $y \to x_0$.
4. At the equilibrium value, $U(x^*) = \frac{D}{a}$ and

$$\begin{aligned} y = \frac{U'(x^*)(x_0 - x^*)^2}{U(x^*) + U'(x^*)(x_0 - x^*)} &= \frac{aU'(x^*)(x_0 - x^*)^2}{D + aU'(x^*)(x_0 - x^*)} \\ \to x_0 - x^*, \end{aligned}$$

for small values of D. This is the case where the equilibrium condition of $x^* + y^* = x_0$ is satisfied and the equilibrium solution is an optimal solution.

8.4 Method of Differential Transforms

The concept of differential transforms was proposed by Pukhov [76, 77]. In this, a source x is transformed to its image X. Since x is carried into its image X by differential operations, it is called a differential transform. The inversion is carried out by means of Taylor series expansion. Differential transform is, therefore, sometimes called a $T-$transform.

Let x be a function of the continuous variable t and $X(k)$ denote its discrete image, which is a function of the argument $k = 0, 1, 2, \ldots, \infty$. Then we define

$$X(k) = \frac{1}{k!}\left(\frac{\mathrm{d}^k x}{\mathrm{d}t^k}\right)_{t=t_0} \tag{8.18}$$

and

$$x(t) = \sum_{k=0}^{\infty} X(k)(t - t_0)^k. \tag{8.19}$$

The differential transforms of some standard functions for $t_0 = 0$ are given here.

$$x(t) \equiv 1 : \quad X(k) = \begin{cases} 1, & k = 0, \\ 0, & k \neq 0; \end{cases}$$

$$x(t) \equiv t : \quad X(k) = \begin{cases} 1, & k = 1, \\ 0, & k \neq 1; \end{cases}$$

$$x(t) \equiv t^r : \quad X(k) = \begin{cases} 1, & k = r, \\ 0, & k \neq r; \end{cases}$$

$$x(t) \equiv \mathrm{e}^{\lambda t} : \quad X(k) = \frac{\lambda^k}{k!};$$

$$x(t) \equiv \sin \omega t : \quad X(k) = \frac{\omega^k}{k!}\ \sin \frac{\pi k}{2};$$

and

$$x(t) \equiv \cos \omega t : \quad X(k) = \frac{\omega^k}{k!}\ \cos \frac{\pi k}{2}$$

The following results may be obtained from the definitions (8.18) and (8.19) (see [2]).

1. If $x(t) = v(t) \pm w(t)$ then $X(k) = V(k) \pm W(k)$.
2. If $x(t) = cv(t)$ then $X(k) = cV(k)$, for any constant c.
3. If $x(t) = \frac{\mathrm{d}^n v(t)}{\mathrm{d}t^n}$ then $X(k) = \frac{(k+n)!}{k!} V(k+n)$.

4. If $x(t) = v(t)w(t)$ then $X(k) = \sum_{k_1=0}^{k} V(k_1)W(k-k_1)$.
5. If $x(t) = \int_{t_0}^{T} v(t)$ then $X(k) = \frac{V(k-1)}{k}$.

Here $V(k)$ and $W(k)$ denote the differential transforms of $v(t)$ and $w(t)$, respectively.
In particular, we have, from formula 3

$$\text{if} \quad z(t) = x'(t) \quad \text{then} \quad Z(k) = (k+1)X(k+1). \tag{8.20}$$

We attempt to understand the earlier formulas and definitions by applying them to our system (8.7). Adding the two equations of (8.7), we get

$$x' + y' = Dx_0 - D(x+y).$$

Applying the formulas given above along with (8.20), we get

$$(k+1)X(k+1) + (k+1)Y(k+1) = Dx_0\,\delta(k) - D(X(k)+Y(k)),$$

in which $k = 0, 1, 2\ldots, \infty$ and

$$\delta(k) = \begin{cases} 1, & k = 0, \\ 0, & k \neq 0. \end{cases}$$

That is,

$$X(k+1) + Y(k+1) = \frac{Dx_0\,\delta(k) - D(X(k)+Y(k))}{k+1}. \tag{8.21}$$

Letting $k = 0, 1, 2, \ldots$ in (8.21), we get

$$\begin{aligned}
X(1) + Y(1) &= Dx_0\,\delta(0) - D(X(0)+Y(0)) \\
&= -D(X(0)+Y(0)-x_0) \\
X(2) + Y(2) &= \frac{Dx_0\,\delta(1) - D(X(1)+Y(1))}{2} \\
&= -\frac{D(X(1)+Y(1))}{2} \\
&= -\frac{D}{2!}[-D(X(0)+Y(0)-x_0)] \\
&= (-1)^2\frac{D^2}{2!}(X(0)+Y(0)-x_0) \\
X(3) + Y(3) &= -\frac{D(X(2)+Y(2))}{3} \\
&= (-1)^3\frac{D^3}{3!}(X(0)+Y(0)-x_0)
\end{aligned}$$

$$X(4) + Y(4) = (-1)^4 \frac{D^4}{4!}(X(0) + Y(0) - x_0),$$
$$\dots$$
$$X(k) + Y(k) = (-1)^k \frac{D^k}{k!}(X(0) + Y(0) - x_0),$$

and so on. Now using the transform (8.19), we have

$$\begin{aligned}
x(t) + y(t) &= \sum_{k=0}^{k=\infty} (X(k) + Y(k))(t - t_0)^k \\
&= X(0) + Y(0) + (X(0) + Y(0) - x_0) \times \\
&\quad \sum_{k=1}^{k=\infty} (-1)^k \frac{D^k}{k!}(t - t_0)^k \\
&= x_0 + (X(0) + Y(0) - x_0) \sum_{k=0}^{k=\infty} (-1)^k \frac{D^k}{k!}(t - t_0)^k \\
&= x_0 + (X(0) + Y(0) - x_0)e^{-D(t-t_0)},
\end{aligned}$$

which is exactly the solution in (8.14). Thus, it is clear that this method produces desired results.

We shall now apply this method to system (8.7) again to find expressions for $x(t)$ and $y(t)$ separately. However, to avoid complications at this stage, we assume that the uptake function $U(x)$ takes the form $U(x) = \frac{x}{N+x}$, where $N > 0$ is a constant. System (8.7) is

$$\begin{aligned}
x' &= Dx_0 - Dx - a\frac{x}{N + x}y, \\
y' &= -Dy + a\frac{x}{N + x}y.
\end{aligned} \tag{8.22}$$

This may be written as

$$\begin{aligned}
Nx' + xx' &= Dx_0N + D(x_0 - N)x - Dx^2 - axy, \\
Ny' + xy' &= -DNy + (a - D)xy.
\end{aligned} \tag{8.23}$$

Applying our formulas 1–4 along with (8.20), we get

$$N\ (k + 1)X(k + 1) + \sum_{k_1=0}^{k} X(k_1)\ (k + 1 - k_1)X(k + 1 - k_1)$$
$$= Dx_0N\ \delta(k) + D(x_0 - N)X(k) - D\sum_{k_1=0}^{k} X(k_1)X(k - k_1)$$

$$-a\sum_{k_1=0}^{k} X(k_1)Y(k-k_1)$$

$$N\ (k+1)Y(k+1)+\sum_{k_1=0}^{k} X(k_1)\ (k+1-k_1)Y(k+1-k_1)$$

$$=-DNY(k)+(a-D)\sum_{k_1=0}^{k} X(k_1)Y(k-k_1).$$

The first equation may be written as

$$N\ (k+1)X(k+1)+X(0)(k+1)X(k+1)$$
$$+\sum_{k_1=1}^{k} X(k_1)\ (k+1-k_1)X(k+1-k_1)$$
$$=Dx_0N\ \delta(k)+D(x_0-N)X(k)-D\sum_{k_1=0}^{k} X(k_1)X(k-k_1)$$
$$-a\sum_{k_1=0}^{k} X(k_1)Y(k-k_1).$$

This gives

$$X(k+1)=-\frac{\sum_{k_1=1}^{k}(k+1-k_1)X(k_1)X(k+1-k_1)}{(N+X(0))(k+1)}+\frac{Dx_0N\ \delta(k)+D(x_0-N)X(k)}{(N+X(0))(k+1)}-\frac{\sum_{k_1=0}^{k} X(k_1)\Big[DX(k-k_1)+aY(k-k_1)\Big]}{(N+X(0))(k+1)}.$$

Similarly,

$$Y(k+1)=-\frac{\sum_{k_1=1}^{k}(k+1-k_1)X(k_1)Y(k+1-k_1)}{(N+X(0))(k+1)}+\frac{(-DN)Y(k)+(a-D)\sum_{k_1=0}^{k} X(k_1)Y(k-k_1)}{(N+X(0))(k+1)},$$

where $k=0,1,2,\ldots$. Using these recurrence relations, we may compute the values of $X(k)$ and $Y(k)$ and obtain the corresponding functions

$$x(t) = \sum_{k=0}^{\infty} X(k)(t-t_0)^k \quad \text{and} \quad y(t) = \sum_{k=0}^{\infty} Y(k)(t-t_0)^k, \tag{8.24}$$

which give the required solution to (8.22).

8.4.1 Estimation of Washout Rate D

We shall now explain briefly the procedure, that will be adopted, to estimate the key/control parameters. To simplify the things, we consider the system

$$x' = f(t, x(t), v(t)), \quad x(t_0) = p_0, \tag{8.25}$$

where $t \in [t_0, T]$ is time variable with the terminal value T, x is the state function, and v is the control function taken from a feasible class of controls $\bar{V}$. f is continuously differentiable with respect to all its arguments. For terminal control problems the system (8.25) satisfies the boundary condition

$$S[x(T), T] = 0. \tag{8.26}$$

Now we define the following functional on the solution space of equation (8.25) under the feasible control class $v \in \bar{V}$:

$$I_j = \theta_j(T, x(T), v(T)) + \int_{t_0}^{T} \Phi_j(t, x(t), v(t))\mathrm{d}t, \tag{8.27}$$

where $j = 1, 2, \ldots, n$, and the functions Φ_j and θ_j for $j = 1, 2, \ldots, n$ have continuous partial derivatives with respect to $x, \ v$ in their domains of definition. The functional I_j is optimized over the feasible region

$$0 \le I_j \le A_j, \quad j = 1, 2, \ldots, n, \tag{8.28}$$

where A_j are real constants. The optimal control problem aims at determining the extremals $x^*(t), v^*(t), I^* \in I, t \in [0, T]$, by optimizing the functional (8.27) under differential constraints given by (8.25) and terminal boundary condition (8.26). The computational complexity of the system depends on the dimensions of the control functions and the state functions. To overcome the complexities in this case we use quasi-analog modeling principles and mathematical tools of the differential transforms. We determine the solution for the given differential system (8.25)–(8.27) over a class of analytic functions $v(t, C)$, where C is a free parameter (called the control parameter). We consider the differential transform, denoted by

$$\underline{x(t)} = X(k) = \frac{h^k}{k!}\left(\frac{\mathrm{d}^k(x(t))}{\mathrm{d}t^k}\right)_{t=t_0}, \tag{8.29}$$

where $\underline{x(t)}$ is the transform that is a real, analytic function of the real argument t. $X(k)$ is a discrete function of numerical argument $k = 0, 1, 2 \ldots$ and is known as the differential spectrum of $x(t)$, at the point $t = t_0$ and h is a scale factor. Application of the differential transform (8.29) to the control function $v(t, C)$ determines its differential spectrum at $h = T$ and $t_0 = 0$:

$$\underline{v(t)} = V(k) = \frac{h^k}{k!}\left(\frac{\mathrm{d}^k}{\mathrm{d}t^k}(v(t))\right)_{t=t_0}. \tag{8.30}$$

Equation (8.25) via differential transforms (8.29), (8.30) reduces to the following recurrence relation

$$X(k+1, C) = \frac{T}{k+1}\Big[\underline{f}(\underline{t}, X(k, C), V(k, C)\Big]. \tag{8.31}$$

From (8.31), we can determine the differential spectrum $X(k, C)$ of the state function $x(t, C)$, given the differential spectrum (8.30) of the control function $v(t, C)$. The terminal state function $x(T, C)$ in terms of the differential spectrum $X(k, C)$ is defined by

$$x(T, C) = \sum_{k=0}^{\infty} \frac{T^k}{k!} X(k, C). \tag{8.32}$$

Now we construct the objective functions I_js from the solution space of the system (8.25). Using (8.25), (8.31) in (8.27), we get

$$I_j(T, C) = \theta_j(T, x(T), V(T)) + T \sum_{k=0}^{\infty} \frac{\Phi(X(k, C), V(k, C), \underline{t})}{k+1}. \tag{8.33}$$

From these vector functionals we determine the optimal control vector $v(t, C)$, by using the following necessary condition of optimality

$$\begin{aligned} &\tfrac{\partial I}{\partial C} = 0, \quad \tfrac{\partial^2 I}{\partial C^2} \geq 0 \quad \text{(for minima)}, \\ &\tfrac{\partial I}{\partial C} = 0, \quad \tfrac{\partial^2 I}{\partial C^2} \leq 0 \quad \text{(for maxima)}. \end{aligned} \tag{8.34}$$

Sufficient conditions follow from strict inequalities in the second terms of (8.34).

We adopt this procedure for estimation of the key parameters for system (8.7), which is viewed as a control problem with washout rate D as the control parameter. The main advantage of the earlier quasi- analog simulations using differential transforms lies in the fact that the time-dependent functions are eliminated and are expressed by a differential spectrum in the image domain.

Before we adopt this procedure, we shall make ready our system for this. Consider (8.7), that is,

$$x'(t) = D(x_0 - x(t)) - aU(x(t))y(t),$$
$$y'(t) \quad = -Dy(t) + aU(x(t))y(t), \tag{8.35}$$

with $U(x) = \frac{x}{N+x}$ (see (8.23)).

Applying formulas 1–4 the first equation of (8.35) gives (see discussion below equation (8.23))

$$\sum_{k_1=0}^{k} X(k_1)(k+1-k_1)X(k+1-k_1) + N(k+1)X(k+1)$$
$$= Dx_0X(k) + NDx_0\delta(k) - D\sum_{k_1=0}^{k} X(k_1)X(k-k_1)$$
$$-DNX(k) - a\sum_{k_1=0}^{k} X(k_1)Y(k-k_1).$$

At $k = 0$, let $X(0) = \bar{a}$ and $Y(0) = \bar{b}$. Then we have

$$\begin{aligned} X(0)X(1) + NX(1) &= Dx_0X(0) + NDx_0\delta(0) - DX(0)X(0) \\ &\quad -DNX(0) - aX(0)Y(0) \\ X(1)(X(0)+N) &= Dx_0\bar{a} + NDx_0 - D\bar{a}^2 - DN\bar{a} - a\bar{a}\bar{b}. \end{aligned}$$

That is,

$$X(1) = D\frac{(x_0\bar{a} + Nx_0 - \bar{a}^2 - N\bar{a})}{\bar{a}+N} - \frac{\bar{a}a\bar{b}}{\bar{a}+N} \quad \text{or} \quad X(1) = AD + B,$$

where

$$A = \frac{(x_0\bar{a} + Nx_0 - \bar{a}^2 - N\bar{a})}{\bar{a}+N} = x_0 - \bar{a} \text{ and } B = -\frac{\bar{a}a\bar{b}}{\bar{a}+N}.$$

Similarly, the second equation of (8.35) gives (see the relation above (8.24))

$$\sum_{k_1=0}^{k} X(k_1)(k+1-k_1)Y(k+1-k_1) + N(k+1)Y(k+1)$$
$$= -D\sum_{k_1=0}^{k} X(k_1)Y(k-k_1) - DNY(k) + a\sum_{k_1=0}^{k} X(k_1)Y(k-k_1).$$

Again at $k = 0$,

$$X(0)Y(1) + NY(1) = -DX(0)Y(0) - DNY(0) + aX(0)Y(0),$$

that is

$$Y(1)(\bar{a} + N) = -D\bar{a}\bar{b} - DN\bar{b} + a\bar{a}\bar{b},$$

which gives

$$Y(1) = D\frac{(-\bar{a}\bar{b} - N\bar{b})}{\bar{a} + N} + \frac{\bar{a}a\bar{b}}{\bar{a} + N} \text{ or } Y(1) = E_1 D + E_2,$$

where

$$E_1 = \frac{(-\bar{a}\bar{b} - N\bar{b})}{\bar{a} + N} = -\bar{b} \text{ and } E_2 = \frac{\bar{a}a\bar{b}}{\bar{a} + N} - B.$$

Now for $k = 1$, first equation of (8.35) yields

$$\begin{aligned} 2X(0)X(2) + X(1)X(1) + 2NX(2) = {} & Dx_0X(1) - D[X(0)X(1) + X(1)X(0)] \\ & -DNX(1) - a[X(0)Y(1) + X(1)Y(0)] \end{aligned}$$

$$\begin{aligned} X(2)(2\bar{a} + 2N) = {} & -(AD + B)^2 + Dx_0(AD + B) - 2D\bar{a}(AD + B) \\ & -DN(AD + B) - a\bar{a}(E_1D + E_2) - a(AD + B)\bar{b} \end{aligned}$$

or

$$\begin{aligned} (2\bar{a} + 2N)X(2) = {} & D^2[-A^2 + x_0A - 2\bar{a}A - NA] \\ & +D[-2AB + x_0B - 2\bar{a}B - NB - a\bar{a}E_1 - aA\bar{b}] \\ & +[-B^2 - a\bar{a}E_2 - aB\bar{b}]. \end{aligned}$$

That is,

$$\begin{aligned} X(2) = {} & D^2\frac{[-A^2 + x_0A - 2\bar{a}A - NA]}{(2\bar{a} + 2N)} \\ & +D\frac{[-2AB + x_0B - 2\bar{a}B - NB - a\bar{a}C - aA\bar{b}]}{(2\bar{a} + 2N)} \\ & +\frac{[-B^2 - a\bar{a}E_2 - aB\bar{b}]}{(2\bar{a} + 2N)}. \end{aligned}$$

That is

$$X(2) = D^2F + DG + H,$$

where

$$F = \frac{[-A^2 + x_0A - 2\bar{a}A - NA]}{(2\bar{a} + 2N)},$$

$$G = \frac{[-2AB + x_0 B - 2\bar{a}B - NB - a\bar{a}E_1 - aA\bar{b}]}{(2\bar{a} + 2N)},$$
$$H = \frac{[-B^2 - a\bar{a}E_2 - aB\bar{b}]}{(2\bar{a} + 2N)}.$$

Again at $k = 1$, second equation of (8.35) yields

$$2X(0)Y(2) + X(1)Y(1) + 2NY(2) = -D[X(0)Y(1) + X(1)Y(0)]$$
$$-DNY(1) + a[X(0)Y(1) + X(1)Y(0)]$$

or

$$\begin{aligned} Y(2)(2\bar{a} + 2N) = &-(AD + B)(E_1 D + E_2) - D[\bar{a}(E_1 D + E_2) \\ &+\bar{b}(AD + B)] - DN(E_1 D + E_2) \\ &+a[\bar{a}N(E_1 D + E_2) + (AD + B)\bar{b}]. \end{aligned}$$

This gives

$$\begin{aligned} Y(2) = &\, D^2 \frac{[-AE_1 - \bar{a}E_1 - \bar{b}A - NE_1]}{(2\bar{a} + 2N)} \\ &+D\frac{[-BE_1 - AE_2 - \bar{a}E_2 - \bar{b}B - NE_2 + a\bar{a}NE_1 + a\bar{b}A]}{(2\bar{a} + 2N)} \\ &+\frac{[-BE_2 + a\bar{a}NE_2 + \bar{b}Ba]}{(2\bar{a} + 2N)} \\ = &\, D^2 J + DK + L \quad \text{(say)}, \end{aligned}$$

where

$$J = \frac{[-AE_1 - \bar{a}E_1 - \bar{b}A - NE_1]}{(2\bar{a} + 2N)},$$
$$K = \frac{[-BE_1 - AE_2 - \bar{a}E_2 - \bar{b}B - NE_2 + a\bar{a}NE_1 + a\bar{b}A]}{(2\bar{a} + 2N)},$$
$$L = \frac{[-BE_2 + a\bar{a}NE_2 + \bar{b}Ba]}{(2\bar{a} + 2N)}.$$

Continuing this way, we have

$$x(T) = \bar{a} + T(AD + B) + T^2(D^2 F + DG + H) + \ldots,$$
$$y(T) = \bar{b} + T(E_1 D + E_2) + T^2(D^2 J + DK + L) + \ldots.$$

A rearrangement leads to

$$x(T) = \bar{a} + BT + T^2H + D(AT + GT^2) + D^2T^2F + \dots,$$
$$y(T) = \bar{b} + TE_2 + T^2L + D(TE_1 + KT^2) + D^2T^2J + \dots,$$

which provide expressions for a solution of (8.22) (i.e., (8.35)) in terms of the parameter D at a time T.

We shall now define our objective function to apply the procedure discussed. We choose $I_1(T, D) = x(T)+y(T)$ and $I_2(T, D) = 1+x(T)y(T)$ as the components of our objective function I. The reason is simply this. I_1 is chosen to reflect the growth in x and y and the term xy in I_2 reflects the interaction between x and y. One may notice that these are obtained from (8.27) with

$$\theta_1 = x(t_0) + y(t_0);\ \Phi_1 = x' + y',$$
$$\theta_2 = x(t_0)y(t_0);\ \Phi_2 = \frac{1}{T - t_0} + x'y'.$$

Since x and y are bounded solutions of (8.35), the condition (8.28) is automatically satisfied.

We shall now optimize

$$I = \alpha_1 I_1 + \alpha_2 I_2,$$

which is a linear combination of I_1 and I_2 and $\alpha_1 > 0, \alpha_2 > 0$ are such that $\alpha_1 + \alpha_2 = 1$. This objective function is the simplest one though several choices are available in literature (see [35]), subject to (8.35) for any set of initial values $x(t_0)$ and $y(t_0)$. However, in order to avoid the complexity of computations, we restrict ourselves to

$$x(T) = M + DP + D^2O,$$
$$y(T) = Q + RD + D^2S,$$

ignoring terms of $O(D^3)$ and higher order. This is reasonable in view of the discussion in last section and earlier part of this section that the system may have an nonzero optimal solution for small values of D. Here, $M = \bar{a} + BT + T^2H$, $P = AT + GT^2$, $O = T^2F$, $Q = \bar{b} + TE_2 + T^2L$, $R = TE_1 + KT^2$, and $S = T^2J$.

We shall now consider our objective function choosing $\alpha_1 = \alpha^*,\ \alpha_2 = 1 - \alpha^*$, $0 < \alpha^* < 1$.

$$\begin{aligned} I &= \alpha^* I_1 + (1 - \alpha^*)I_2 \\ &= \alpha^*[(M + DP + D^2O) + (Q + RD + D^2S)] \\ &\quad +(1 - \alpha^*)[1 + (M + DP + D^2O)(Q + RD + D^2S)]. \end{aligned}$$

That is,

$$
\begin{aligned}
I = & D^4[OS(1-\alpha^*)] + D^3[(1-\alpha^*)(RO + PS)] \\
& + D^2[(1-\alpha^*)(SM + PR + QO) + \alpha^* S + \alpha^* O] \\
& + D[\alpha^* P + \alpha^* R + (1-\alpha^*)[PQ + MR] \\
& + [\alpha^* M + \alpha^* Q + (1-\alpha^*)[1 + MQ].
\end{aligned}
$$

The optimality conditions (8.34) are given by

$$
\begin{aligned}
\frac{\partial I}{\partial D} = & 4D^3[OS(1-\alpha^*)] + 3D^2[(1-\alpha^*)(RO + PS)] \\
& + 2D[(1-\alpha^*)(SM + PR + QO) + \alpha^* \beta S + \alpha^* \alpha O] \\
& + [\alpha^* \alpha P + \alpha^* \beta R + (1-\alpha^*)[PQ + MR] = 0
\end{aligned} \tag{8.36}
$$

and

$$
\begin{aligned}
\frac{\partial^2 I}{\partial D^2} = & 12D^2[OS(1-\alpha^*)] \\
& + 6D[(1-\alpha^*)(RO + PS)] \\
& + 2[(1-\alpha^*)(SM + PR + QO) + \alpha^* \beta S + \alpha^* \alpha O]
\end{aligned} \tag{8.37}
$$

whose sign needs to be verified. Our aim here is to find the value of D satisfying the above. This we illustrate by the following example.

Example 8.1 Consider the system

$$
\begin{aligned}
x' &= 6D - Dx - 10\frac{x}{4+x}y, \\
y' &= -Dy + 10\frac{x}{4+x}y,
\end{aligned}
$$

with $\bar{a} = X(0) = 0.1$ and $\bar{b} = Y(0) = 1$ and $T = 1$. We have after some calculations, $A = 5.9$, $B = -0.243$, $E_1 = -1$, $E_2 = 0.243$, $F = -2.95$, $G = -6.6776$, $H = 0.259$, $J = 0.5$, $K = 6.4702$, $L = -0.1706$, $M = 0.116$, $P = -0.7776$, $O = -2.95$, $Q = 1.0724$, $S = 0.5$, and $R = 5.4702$. Some of the values are approximated to three digits only. For the choice of $\alpha^* = 0.5$, (8.36) becomes

$$
-2.956D^3 - 24.7889D^2 - 9.8092D + 2.2466 = 0.
$$

This has only one positive root given by $D \approx 0.1617$.
One may verify that (8.37) becomes

$$
\frac{\partial^2 I}{\partial D^2} = -\left(8.85D^2 + 49.5777D + 19.6184\right) < 0,
$$

for this value of D. Thus, $D = 0.1617$, maximizes the objective function.

For this value of D, the above system has an equilibrium solution given by $x^* = 0.06574$, $y^* = 5.93426$. At the equilibrium value of $x^* = 0.06574$, the optimal value of y estimated by case 3 of section 8.3 is $y = 5.333$ which is a reasonable estimate for our lazy second order approximations. We may also notice that for $0<D<10$, the above system can have a positive equilibrium which is stable

8.5 Discussion

In the present chapter, we have introduced the concept of dynamic optimization as applicable to our systems. This provided ways to obtain optimal solution to our dynamical system. The method of differential transforms to find approximate solutions to a given system is also introduced. These concepts/methods are applied to our basic chemostat model of Chap. 1 for an easy understanding. An optimal control problem is defined and the method of differential transforms is used to find approximately the control parameter D (the washout) that plays a key role in deciding the fate of microorganisms of the system. Thus, a new perception is provided for the researchers working on biological models.

8.6 Notes and Comments

Motivation for this work stems from those of Baranov et al. [3], Sree Hari Rao and Venkata Ratnam [96]. Techniques of dynamic optimization may be found in the book by Kamien and Schwartz [57]. Some literature on dynamic optimization for models with discrete time delays is also available in that book but it is highly necessary to develop theory that applies to our models. An attempt has been made by Sree Hari Rao and Venkata Ratnam [96] to develop theory of dynamic optimization for systems of integro-differential equations (systems with continuous time delays). We remark here that the application of the differential transforms method for models involving time delays is a promising area of research.

8.7 Exercises

1. Use dynamic optimization technique of Sect. 8.3 on models (1.13), (1.22), and on (2.2)–(2.4) in the absence of time delays, that is, when $\tau = 0$.
2. Develop techniques to apply dynamic optimization method to discrete delay models (2.2)–(2.4) for $\tau > 0$ (see [57]).
3. Apply the method of differential transforms to models (2.2)–(2.4) for $\tau = 0$.
4. Define the differential transform of a function with time delay and apply on system (2.2).
5. For convenience, we have chosen $\alpha^* = 0.5$ in Example 8.1. Try various other values for $0 < \alpha^* < 1$ to modify the value of D.

Appendix A
Derivatives and Definitions

In this appendix, we shall include some definitions and results that are frequently used in the text. Not only that! These are quite useful and handy for a reader who deals with the convergence and stability of solutions of the systems described by mathematical models.

We shall begin with what is known as Leibnitz rule for differentiation under the integral sign and is used many times in this book while dealing with Lyapunov functionals involving integral terms.

$$\frac{\mathrm{d}}{\mathrm{d}\alpha}\left\{\int_{\phi(\alpha)}^{\psi(\alpha)} f(x,\alpha)\mathrm{d}x\right\} = \int_{\phi(\alpha)}^{\psi(\alpha)} \frac{\partial}{\partial\alpha} f(x,\alpha)\mathrm{d}x + f[\psi(\alpha),\alpha]\,\frac{\mathrm{d}\psi}{\mathrm{d}\alpha} - f[\phi(\alpha),\alpha]\frac{\mathrm{d}\phi}{\mathrm{d}\alpha}.$$

The Dini derivatives of a function f at a point $x = x_0$ are defined by

$$D^+ f(x_0) = \limsup_{x\to x_0+} \frac{f(x)-f(x_0)}{x-x_0}, \quad D_+ f(x_0) = \liminf_{x\to x_0+} \frac{f(x)-f(x_0)}{x-x_0},$$

$$D^- f(x_0) = \limsup_{x\to x_0-} \frac{f(x)-f(x_0)}{x-x_0}, \quad D_- f(x_0) = \liminf_{x\to x_0-} \frac{f(x)-f(x_0)}{x-x_0}.$$

These are also known as the upper right derivative (D^+), the lower right derivative (D_+), the upper left derivative (D^-), and the lower left derivative (D_-) of f at $x = x_0$, respectively. Further, f is said to have at $x = x_0$

1. Right derivative if $D^+ f(x_0) = D_+ f(x_0)$.
2. Upper derivative if $D^+ f(x_0) = D^- f(x_0)$.

The left derivative and lower derivative are defined in a similar manner. We say that f' exists at an interior point $x = x_0$ if all the above derivatives exist and are equal to each other.

In general, $D_- f(x) \le D^- f(x)$ and $D_+ f(x) \le D^+ f(x)$. Thus, a set of necessary and sufficient conditions for f' to exist is $D^+ f(x_0) \le D_- f(x_0)$ and $D^- f(x_0) \le D_+ f(x_0)$. It may also be noted that $D^+(f+g) \le D^+ f + D^+ g$.

The following definitions are useful.

Definition A.1 *If $g(x)$ is a differentiable function on any interval I then*

$$D^+|g(x)| = \text{sgn } g(x) \frac{\mathrm{d}g}{\mathrm{d}x}.$$

Definition A.2 *A continuous function $w: [0,\infty) \to [0,\infty)$ with $w(0) = 0$, $w(s) > 0$ for $s > 0$ and strictly increasing is called a wedge.*

Definition A.3 *A function $g: [0,\infty) \times D \to [0,\infty)$ is said to be*

1. *Positive definite if $g(t,0) = 0$ and there exists a wedge w_1 such that $g(t,x) \ge w_1(|x|)$*
2. *Negative definite if $-g(t,x)$ is positive definite*
3. *Decrescent if there is a wedge w_2 such that $g(t,x) \le w_2(|x|)$ and strongly decrescent if $g(t,x) < w_2(|x|)$ holds;*

Consider the system

$$x'(t) = G(t, x(.)), \tag{A.1}$$

in which G is a continuous function defined on $\mathbf{R}^+ \times D$ such that $G(t,0) = 0$ for any open set D.

The following criteria is useful to establish that a given function is positive definite and decrescent as well.

Theorem A.4 *A scalar functional $V(t, x(.))$ is uniformly positive definite and strongly decrescent if there are continuous functions $Q, W: [0,\infty) \times \mathbf{R}^n \to [0,\infty)$, wedges w_1 and w_2, a continuous scalar function $\alpha(t) \ge \alpha$, a continuous scalar function*
$J(t, W(s, x(s)))$, $\alpha(t \le s \le t)$ and a constant $m < 1$ with

$$W(t, x(t)) \le V(t, x(.)) \le Q(t, x(t)) + J(t, W(t, x(.))),$$
$$J(t, W(t, x(.))) \le m \sup_{\alpha(t) \le s \le t} W(s, x(s))$$

and

$$w_1(|x|) \le W(t,x) \le Q(t,x) \le w_2(|x|).$$

Theorem A.5 *The function $H(x,y) = Ax^2 + Bxy + Cy^2$ is*

1. *Positive definite if and only if $A > 0$ and $B^2 < 4AC$*
2. *Negative definite if and only if $A < 0$ and $B^2 < 4AC$.*

Appendix B
Results on Boundedness and Convergence

Consider the following system of retarded functional differential equations

$$X'(t) = F(t, X_t),\ X_t = X(t+\theta), \tag{B.1}$$

where

$$X(t_0) = X(t_0+\theta) = \phi(\theta), \quad -\infty < \theta \le 0$$

is the initial condition. Here the function ϕ is chosen from the space of all bounded, continuous functions on $(-\infty, 0]$, denoted by $BC(-\infty, 0]$ with appropriate norm. We assume that $X'(t_0) = F(t_0, \phi)$. Then

Theorem B.1 *Suppose that* $\Omega \subseteq \mathbf{R} \times \mathbf{BC}(-\infty, \mathbf{0}]$ *is open and that the map* $F(t, \phi)$ *is continuous and satisfies a local Lipschitz condition in* ϕ, *that is,*

$$|F(t,\phi) - F(t,\psi)| \le k\rho(\phi,\psi),$$

where ρ *is any metric on* $BC(-\infty, 0]$. *If* $(t_o, \phi) \in \Omega$ *then for some* $\delta > 0$ *there exists a unique solution of* (B.1) *on* $[t_0, t_0+\delta)$ *which depends on the initial data.*

The following result is due to Burton [15, Theorem 8.4.3, p. 265] which provides conditions under which the solutions of (B.1) are bounded.

Theorem B.2 *Let* $V(t, x(.))$ *be continuous and locally Lipschitz in* x, *uniformly positive definite and strongly decrescent:*

$$W(t, x(t)) \le V(t, x(.)) \le Q(t, x(t)) + m \sup_{\alpha(t)\le s\le t} W(s, x(s))$$

for a continuous function $\alpha(t) \ge \alpha \ge -\infty$ *and* $m < 1$. *Suppose there is a positive number* $\tilde{U}$ *with* $V'_{(B.1)} \le 0$ *if* $Q(t, x(t)) \ge \tilde{U}$. *Then the solutions of* (B.1) *are uniformly bounded.*

The following convergence result is due to Reissig, Sansone, and Conti [78, Lemma 1, p. 601–602].

Theorem B.3 *Let $f(t)$ be defined, continuous and piecewise continuously differentiable for $t \geq 0$ and let $f(t)$ and $f'(t)$ be bounded. Let $G(x)$ be defined, continuous and positive definite for all x. Further, let $\int_0^\infty G(f(t))\mathrm{d}t < \infty$. Then* $\lim_{t\to\infty} f(t) = 0$.

Proof Assume that for $t \geq 0$, $|f(t)| \leq a$, $|f'(t)| \leq a'$ and we set $\int_0^\infty G(f(t))\mathrm{d}t = g < \infty$. If the conclusion is false then for every number $\epsilon > 0$, there exists a positive, monotone increasing divergent series $\{t_k\}$ with $|f(t_k)| \geq 2\epsilon$. Here we may assume that $t_1 \geq \delta$ and $t_{k+1} - t_k \geq 2\delta$ for a suitably chosen $\delta > 0$. From the estimate,

$$\int_0^\infty G(f(t))\mathrm{d}t \geq \sum_{k=1}^\infty \int_{t_k-\delta}^{t_k+\delta} G(f(t))\mathrm{d}t$$

in conjugation with the relation

$$|f(t)| \geq |f(t_k)| - |f(t) - f(t_k)| \geq 2\epsilon - \delta a' = \epsilon \quad \left(\delta = \frac{\epsilon}{a'}\right)$$

which is valid for $t_k - \delta \leq t \leq t_k + \delta$, it follows that

$$g = \int_0^\infty G(f(t))\mathrm{d}t > k\gamma\epsilon, \quad k = 1, 2, ..., \quad \gamma = \inf_{\epsilon \leq |x| \leq a} G(x) > 0.$$

But this is impossible. Thus, the conclusion follows. □

Theorem B.4 (Barbalat's Lemma, [4]). *If the function $g(t)$ is defined and differentiable for $t \geq 0$ and if further, $-\infty < \lim_{t\to\infty} g(t) = g_0 < \infty$, and $g'(t)$ is uniformly continuous for $t \geq 0$ then* $\lim_{t\to\infty} g'(t) = 0$.

Proof Suppose $\limsup_{t\to\infty} g'(t) = g_0' > 0$. ($g_0' < 0$ leads to contradiction. Why?) Then there exists a strictly increasing divergent positive sequence $\{t_n\}$ such that $g'(t_n) \geq (1/2)g_0'$. On account of the uniform continuity of $g'(t)$, we can find a $\delta_0 > 0$ such that $|g'(t+h) - g'(t)| \leq \epsilon_0 = (1/4)g_0'$ for $0 \leq h \leq \delta_0$. This means that $g(t_n + \delta_0) - g(t_n) \geq (1/4)g_0'\delta_0$, contradicting Cauchy's convergence criterion: $|g(t+h) - g(t)| \leq \epsilon$ (chosen smaller than $(1/4)g_0'\delta_0$) for $h \geq 0$, $t \geq T(\epsilon)$.

Similarly, we can show that $\liminf_{t\to\infty} g'(t) \neq 0$ is excluded. This proves the lemma. □

Lemma B.5 *Let $f : [t_0, \infty) \to [0, \infty)$ be continuously differentiable such that $f \in L_1[t_0, \infty)$ and* $\mathrm{d}f/\mathrm{d}t \in L_1[t_0, \infty)$. *Then* $\lim_{t\to\infty} f(t) = 0$.

Proof Since $\mathrm{d}f/\mathrm{d}t \in L_1[t_0, \infty)$, for every $\epsilon > 0$ there exists a positive number $T > t_0$ such that for $t_2 > t_1 > T$

$$\left|\int_{t_1}^\infty \frac{\mathrm{d}f(t)}{\mathrm{d}t}\mathrm{d}t\right| < \frac{\epsilon}{2}; \quad \left|\int_{t_2}^\infty \frac{\mathrm{d}f(t)}{\mathrm{d}t}\mathrm{d}t\right| < \frac{\epsilon}{2}.$$

We have

$$
\begin{aligned}
\left|f(t_2) - f(t_1)\right| &= \left|\int_{t_1}^{t_2} \frac{\mathrm{d}f(t)}{\mathrm{d}t}\mathrm{d}t\right| \\
&= \left|\int_{t_2}^{\infty} \frac{\mathrm{d}f(t)}{\mathrm{d}t}\mathrm{d}t - \int_{t_1}^{\infty} \frac{\mathrm{d}f(t)}{\mathrm{d}t}\mathrm{d}t\right| \\
&\leq \left|\int_{t_1}^{\infty} \frac{\mathrm{d}f(t)}{\mathrm{d}t}\mathrm{d}t\right| + \left|\int_{t_1}^{\infty} \frac{\mathrm{d}f(t)}{\mathrm{d}t}\mathrm{d}t\right| \\
&< \frac{\epsilon}{2} + \frac{\epsilon}{2} = \epsilon.
\end{aligned}
$$

Thus, $\lim_{t\to\infty} f(t)$ exists. This together with the assumptions that $f(t) \geq 0$ and $f \in L_1[t_0, \infty)$ will imply that $\lim_{t\to\infty} f(t) = 0$. The proof is complete. □

Appendix C
Uniqueness and Stability

Consider the system of differential equations

$$x' = f(t, x), \tag{C.1}$$

in which $f : \mathbf{R}^n \to \mathbf{R}^n$. Let $x(t_0) = x_0$.

Let $S \subset \mathbf{R}^{n+1}$ be (not necessarily an open) subset of $\mathbf{R}^{n+1}$, and let $f : \mathbf{R}^n \to \mathbf{R}^n$. Then, given $(t_0, x_0) \in S$, a solution of the initial value problem

$$x' = f(t, x), \;\; x(t_0) = x_0, \tag{C.2}$$

is a differentiable function x on any interval J that contains the initial point t_0, such that $(t, x(t)) \in J$ for all $t \in J$, and the initial condition $x(t_0) = x_0$. If J contains either of its end points then $x'(t)$ is interpreted as a one-sided derivative at that point. For any $\xi \in \mathbf{R}^n$ we define its norm as $\|\xi\| = \sum_{i=1}^{n} |\xi_i|$.

Now we state and prove the following result on the uniqueness of solutions of the initial value problem (C.2). The following result provides conditions weaker than Lipschitz condition for uniqueness and it is due to Norris and Driver [71].

Theorem C.1 *Let $f : S \to \mathbf{R}^n$ be continuous and satisfy the following condition. Each point in S has an open neighborhood U, a constant $K > 0$, an integer $m \geq 0$, and functions h_j and γ_j for $j = 1, 2, \ldots, m$, such that*

$$\|f(t, \xi) - f(t, \eta)\| \leq K\|\xi - \eta\| + K \sum_{j=1}^{m} |g_j(h_j(t, \xi)) - g_j(h_j(t, \eta))| \tag{C.3}$$

on $U \cap S$, where $h_j : U \to \mathbf{R}$ is continuously differentiable with

$$\frac{\partial h_j(t, \xi)}{\partial t} + \sum_{i=1}^{n} \frac{\partial h_j(t, \xi)}{\partial \xi_i} f_i(t, \xi) \neq 0 \;\text{ on }\; U \cap S, \tag{C.4}$$

and each $g_j : \mathbf{R} \to \mathbf{R}$ is continuous and of bounded variation on bounded subintervals. Then the initial value problem (C.2) with any point $(t_0, X_0) \in S$ has at most one solution on any interval J.

Note that the theorem does not guarantee the existence of a solution to the initial value problem on a nontrivial interval J. One can conclude that existence follows if S is open.

Proof Suppose x and y are two different solutions of the initial value problem on some interval $J = [t_0, b)$ where $b > t_0$. and the argument for the case $J = (b, t_0]$ is similar. Let

$$a \equiv \inf\{t \in (t_0, b) : x(t) \neq y(t)\}.$$

Then $x(a) = y(a)$. For the point $(a, x(a)) \in S$ let U, K, m, h_j, and g_j be as in the hypotheses of the theorem. Without loss of generality, assume that for each j the expression in (C.4) is positive at $(a, x(a))$. Then reducing U if necessary, the continuity of the derivatives of h_j assures that there exist positive constants p and M such that for $j = 1, \ldots, m$,

$$\frac{\partial h_j(t,\xi)}{\partial t} + \sum_{i=1}^{n} \frac{\partial h_j(t,\xi)}{\partial \xi_i} f_i(t,\xi) \geq p \text{ on } U \cap S \tag{C.5}$$

and

$$\|h_j(t,\xi) - h_j(t,\eta)\| \leq M\|\xi - \eta\| \text{ on } U. \tag{C.6}$$

Choose a bounded interval $[\alpha_j, \beta_j]$ which contains $h_j(U \cap S)$, reducing U if necessary. Then g_j is the difference of two continuous nondecreasing functions on $[\alpha_j, \beta_j]$, and each of them may be extended to a continuous nondecreasing function on $\mathbf{R}$ by defining it to be constant on $(-\infty, \alpha_j]$ and constant on $[\beta_j, \infty)$. Without loss of generality, we shall assume that each g_j is itself nondecreasing on $\mathbf{R}$ and that

$$g_j(h_j(a, x(a))) = 0. \tag{C.7}$$

Define

$$z(t) = \int_a^t \|x'(s) - y'(s)\| \mathrm{d}s \text{ for } a \leq t < b.$$

Then $z(a) = 0$, $z'(a) = 0, z$ and z' are continuous, $z'(t) \geq 0$ and $\|x(t) - y(t)\| \leq z(t)$ on $[a, b)$.

Choose $c \in (a, b]$ sufficiently small so that $(s, x(s))$ and $(s, y(s))$ remain in U for $a \leq s < c$. Then from (C.6),

$$h_j(s, x(s)) - Mz(s) \leq h_j(s, y(s)) \leq h_j(s, x(s)) + Mz(s),$$

and from (C.5)

$$\frac{\mathrm{d}}{\mathrm{d}s} h_j(s, x(s)) \geq p$$

for $a \leq s < c$ and $j = 1, \ldots, m$.

Thus for $a \le t < c$, using (C.3) and the monotonicity of g_j we get

$$\begin{aligned}
z(t) &\le K \int_a^t \left\{ \|x(s) - y(s)\| + \sum_{j=1}^m |g_j(h_j(s, x(s))) - g_j(h_j(s, y(s)))| \right\} \mathrm{d}s \\
&\le K(t-a)z(t) + \frac{K}{p} \sum_{j=1}^m \int_a^t \Big[g_j(h_j(s, x(s)) + Mz(s)) \\
&\qquad\qquad - g_j(h_j(s, x(s)) - Mz(s)) \Big] \frac{\mathrm{d}}{\mathrm{d}s} h_j(s, x(s)) \mathrm{d}s \\
&= K(t-a)z(t) + \frac{K}{p} \sum_{j=1}^m \int_{h_j(t,x(t))-Mz(t)}^{h_j(t,x(t))+Mz(t)} g_j(u)\mathrm{d}u \\
&\quad - \frac{K}{p} \sum_{j=1}^m \int_a^t \Big[g_j(h_j(s, x(s)) + Mz(s)) + g_j(h_j(s, x(s)) \\
&\qquad\qquad - Mz(s)) \Big] \times Mz'(s) \mathrm{d}s.
\end{aligned}$$

Choose $\delta_1 > 0$ such that for each j

$$|g_j(u)| < \frac{p}{6mKM} \quad \text{when} \quad |u - h_j(a, x(a))| < \delta_1.$$

Then choose $\delta \in (0, \frac{1}{6K})$ such that $a + \delta \le c$ and, for each j,

$$|h_j(t, x(t)) - h_j(a, x(a))| + Mz(t) < \delta_1 \quad \text{when} \quad a \le t < a + \delta.$$

Now for $a < t < a + \delta$ one obtains $z(t) \le 5z(t)/6$. This contradiction completes the proof. □

We now consider the following special case of the system (C.1)

$$x' = Px. \tag{C.8}$$

in which p is an $n \times n$ real matrix.

We say that system (C.8) is stable if for any admissible (physically possible) initial condition provided, $\lim_{t\to\infty} x(t) = 0$ for any solution $x(t)$ of (C.8). The solutions of system may be bounded without being stable. Finally, the system is unstable if it is neither bounded nor stable.

We shall present a condition that helps us to determine the stability of the system (C.8) if the coefficient matrix P has all its elements real constants.

Theorem C.2 *The system (C.8) is stable for all initial conditions if and only if all the eigen values of P have negative real parts.*

A matrix is said to be "stable" if all its eigen values have negative real parts. For matrices of small order it may not be difficult to determine the eigen values and recognize their signs. But as the order of the matrix increases it becomes very difficult at least to have an idea of their signs leave aside determining them explicitly. In such a case, the following method comes in handy many times. This process is known as Routh–Hurwitz method.

We know that the characteristic polynomial of (C.8) is given by $|P - \lambda I|$. Suppose that all the coefficients of this polynomial are real.
Let

$$|P - \lambda I| = a_0\lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} + a_3\lambda^{n-3} + \cdots + a_{n-1}\lambda + a_n = 0$$

denote the characteristic equation of (C.8).

Consider the matrix

$$H = \begin{pmatrix} a_1 & a_3 & a_5 & \cdots & a_{2n-1} \\ a_0 & a_2 & a_4 & \cdots & a_{2n-2} \\ 0 & a_1 & a_3 & \cdots & a_{2n-3} \\ 0 & a_0 & a_2 & \cdots & a_{2n-4} \\ 0 & 0 & a_1 & \cdots & a_{2n-5} \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & \cdots & \cdots & \cdots & a_n \end{pmatrix}.$$

This is known as the Hurwitz matrix. This is transformed into an upper triangular matrix say

$$R = \begin{pmatrix} b_1 & b_2 & b_3 & \cdots & b_n \\ 0 & c_1 & c_2 & \cdots & c_{n-1} \\ 0 & d_1 & d_2 & \cdots & d_{n-2} \\ \cdots & \cdots & \cdots & \cdots & \cdots \end{pmatrix}.$$

in which $b_n = a_{2n-1},\ n = 1, 2, \ldots, n$ and all other elements being obtained from H through elementary row operations. R is known as Routh matrix. We now have

Theorem C.3 (Routh's Theorem). *The number of roots of polynomial equation $|P - \lambda I| = 0$ with positive real part is equal to the number of changes of sign in the sequence*

$$b_1,\ c_1,\ d_1,\ \ldots$$

Theorem C.4 (Routh's Criterion). *The polynomial equation $|P - \lambda I| = 0$ has all its roots with negative real part if all the terms $b_1,\ c_1,\ d_1,\ \ldots$ are nonzero and have the same sign.*

It is assumed that none of the terms $b_1,\ c_1,\ \ldots$ is on the principal diagonal nonzero. If any of them vanishes and there is at least one nonzero element in that row, then we replace the zero element on the principal diagonal by a small real number ϵ and form a Routh matrix as above. This does not interfere with the number of sign changes given by Routh's theorem.

More useful formulation of the Routh–Hurwitz method is obtained by determining the Hurwitz determinants, namely,

$$D_1 = a_1, \ D_2 = \begin{vmatrix} a_1 & a_3 \\ a_0 & a_2 \end{vmatrix}, \ D_3 = \begin{vmatrix} a_1 & a_3 & a_5 \\ a_0 & a_2 & a_4 \\ 0 & a_1 & a_3 \end{vmatrix}, \ldots, D_n = |H|.$$

Now we have

Theorem C.5 (Routh–Hurwitz criterion). *A set of necessary and sufficient condition that all the characteristic roots of* $|P - \lambda I| = 0$ *have negative real parts is*

$$a_0 > 0, \quad D_i > 0, \quad \forall i = 1, 2, \ldots, n.$$

Here all the terms in D_i *with indices larger than* n *or having negative indices are replaced by* 0.

Another useful procedure that reduces the number of calculations is the following.

Theorem C.6 (Lienard and Chipart Criterion). *Let* D_k *denote the* kth *order Hurwitz determinant defined above. Suppose that all the coefficients of the characteristic polynomial are positive. Then all the roots of* $|P - \lambda I| = 0$ *have negative real parts if and only if any one of the following four conditions is true.*

1. $a_{n-2k+2} > 0, \quad D_{2k-1} > 0, \quad 1 \le k \le n/2$
2. $a_{n-2k+2} > 0, \quad D_{2k} > 0, \quad 1 \le k \le n/2$
3. $a_n \quad a_{n-2k-1} > 0, \quad D_{2k-1} > 0, \quad 1 \le k \le n/2$
4. $a_n \quad a_{n-2k-1} > 0, \quad D_{2k} > 0, \quad 1 \le k \le n/2.$

The advantage of this criterion over Routh–Hurwitz criterion is that it requires the computation of only half of the Hutwitz determinants.

We shall now turn our attention toward the Lyapunov stability.

Consider the system

$$X'(t) = F(t, X_t). \tag{C.9}$$

Theorem C.7 *A continuous function* $V : [0, \infty) \times D \to [0, \infty)$ *that is locally Lipschitz in* x *and satisfies*

$$V'(t, x) = \limsup_{h \to 0+} \Big[\frac{V(t + h, x) - V(t, x)}{h} \Big] \le 0$$

on $[0, \infty) \times D$ *is called a Lyapunov function for the system* (C.9).

Since we deal with the autonomous systems mostly, we consider the system

$$X'(t) = F(X(t)) \tag{C.10}$$

where F is continuous in X for $X \in \bar{G}$. Here G is an open set in $\mathbf{R}^n$.

Definition C.8 *$V(X)$ is a Lyapunov function in G for (C.10) if $V' = grad V.F \leq 0$ on G.*

Let $X = 0$ be a critical point of F in (C.10).

Theorem C.9 *If there exists a Lyapunov function V for (C.10) then the critical point $X = 0$ is stable. Further if $V' < 0$ (negative definite), the critical point is asymptotically stable.*

Define $E = \{X \in \bar{G}/V'(X) = 0\}$ and let M be the largest invariant set in E. In case $V' \leq 0$, the following result is useful in establishing the asymptotic stability of the critical point.

Theorem C.10 *If V is a Lyapunov function in G for (C.10) then each bounded solution $X(t) \subseteq G$ of (C.10) approaches M.*

The following results on local and global stability for functional differential equations of the form

$$X'(t) = F(t, X_t), \quad F(0) = 0 \tag{C.11}$$

are used in the text.

By $w_i(s),\ s \geq 0$ we mean scalar continuous nondecreasing functions such that $w_i(0) = 0$, $w_i(s) > 0$ for $s > 0$ and $\lim_{s\to\infty} w_i(s) = \infty$.

Theorem C.11 (Burton, page 237–246 [15]). *Let $V(t, X_t)$ be a continuous scalar functional which is locally Lipschitz in X_t for $X_t \in X_H(t)$ for some $H > 0$ and $t \geq 0$.*

1. *If $w_1(\|X(t)\|) \leq V(t, X_t)$, $V(t, 0) = 0$, $V'_{(C.11)}(t, X_t) \leq 0$ for $t \geq t_0$, then $X = 0$ is stable.*
2. *In addition to (1), if $V(t, X_t) \leq w_2(\|X(t)\|)$, then $X = 0$ is uniformly stable.*
3. *Let (1) hold and suppose there is an $M > 0$ such that $X_t \in X_H(t)$, $t_0 \leq t < \infty$ imply that $|F(t, X_t)| < M$ and $V'_{(C.11)}(t, X_t) \leq -w_3(\|X(t)\|)$, then $X = 0$ is asymptotically stable.*

Note that when the system is autonomous and $F(X_t)$ is uniform Lipschitz for any $t \geq t_0$, $t_0 \in \mathbf{R}$ and any $X_t, Y_t \in X_H(t)$, the assumption in (3) concerning $F(X_t)$ is trivially true. Finally, since the system is autonomous, the asymptotic stability implies the uniform asymptotic stability.

Consider the autonomous system

$$X'(t) = F(X_t), \ F(0) = 0 \tag{C.12}$$

with the initial conditions ϕ which are BC functions on $(-\infty, 0]$ and such that $\phi \in Q_H$, then the following theorem holds:

Theorem C.12 *Let $V(X_t)$ be a scalar functional such that $V : X_H(t) \to [0, \infty)$ and it is uniform Lipschitz on $X_{\mathrm{H}}(t)$ for any $H > 0$. If furthermore,*

$$w_1(\|X(t)\|) \leq V(X_t), \quad V(0) = 0, \quad V'_{(C.12)}(X_t) \leq -w_2(\|X(t)\|),$$

for all $t \geq t_0$. Then the trivial equilibrium of (C.12) is globally (uniformly) asymptotically stable.

The term “globally” is justified by the arbitrariness of the choice of $H > 0$ for the space $X_{\mathrm{H}}(t)$. This arbitrary nature allows us to consider the trajectories of (C.12), which start at $t = t_0$ arbitrarily far from the equilibrium $X(t) = 0$ for $t \in (-\infty, \infty)$. Theorem C.11, apart from the arbitrariness of H, is almost the same which may be found in Hale [46] concerning asymptotic stability of functional differential equations. According to Hale, in (C.12) only the positive definiteness of $w_2(\|X\|)$ is required.

Finally, we close this appendix with the following definition that plays an important role in understanding the survival of a biological species.

Definition C.13 *A component $u(t)$ of a given system is said to persist if for any $u(0) > 0$ it follows that $u(t) > 0$ for $t > 0$ and $\liminf_{t\to\infty} u(t) > 0$. Further, if there exists $\delta > 0$ such that $u(t)$ persists and $\liminf_{t\to\infty} u(t) \geq \delta$ independent of $\phi(t) > 0, -\infty < t \leq 0$, where $\phi(t)$ is an initial condition, then $u(t)$ is said to uniformly persist. A system uniformly persists if each component does.*

References

1. R.A. Armstrong and R. McGehee, Competitive exclusion, *Am. Nat.*, 115(1980), 151–170.
2. A. Arikoglu and I. Ozkol, Solution of boundary value problems for integro-differential equations by using differential transform method, *Appl. Math. Comput*, 168(2005), 1145–1158.
3. V.L. Baranov, N.S. Zalogin, O.S. Uruskiy, G.L. Baranov, and E. Yu. Komarenko, Quasianalog multictriteria models for dynamic process optimization problems, *Eng. Simulat.*, 14(1997), 1–12.
4. I. Barbălat, Systèmes d'équations différentielles d'oscillations nonlinéaires, *Rev. Math. Pures Appl.*, 4(1959), 267–270.
5. H. Bereketoglu, G.I. Bischi, and I. Győri, Global asymptotic stability in a nonautonomous Lotka–Volterra type system with infinite delay, *J. Math. Anal. Appl.*, 210(1997), 279–291.
6. E. Beretta and G.I. Bischi, Stability and Hopf bifurcations in some limited nutrient-species models with nutrient recycling and time lags, J. Eisenfeld and D.S. Levine (Eds.), in Biomedical Modeling and Simulation, J.C. Baltzer A.G., Scientific Publishing Co.(c), IMACS, 1989, pp. 175–181.
7. E. Beretta, G.I. Bischi, and F. Solimano, Oscillations in a system with material cycling, *J. Math. Biol.*, 26(1988), 143–167.
8. E. Beretta, G.I. Bischi, and F. Solimano, Stability in chemostat equations with delayed nutrient recycling, *J. Math. Biol.*, 28(1990), 99–111.
9. E. Beretta and Y. Kuang, Global stability in a well known delayed chemostat model, *Commun. Appl. Anal.*, 4(2000), 147–155.
10. E. Beretta and Y. Takeuchi, Qualitative properties of chemostat equations with time delays: Boundedness, local and global asymptotic stability, *Diff. Equat. Dyn. Syst.*, 2(1994), 19–40.
11. E. Beretta and Y. Takeuchi, Qualitative properties of chemostat equations with time delays – II, *Differ. Equa. Dyn. Syst.*, 2(1994), 263–288.
12. E. Beretta and Y. Takeuchi, Global stability for chemostat equations with delayed nutrient recycling, *Nonlinear World*, 1(1994), 291–306.
13. G.I. Bischi, Effects of time lags in transient characteristics of nutrient cycling model, *Math. Biosci.*, 109(1992), 151–175.
14. B. Boon and H. Laudelout, Kinetics of nitrate oxidation by Nicrobacter Winogradskyi, *Biochem. J.*, 85(1962), 440–447.
15. T.A. Burton, *Volterra Integral and Differential Equations*, *Mathematics in Science and Engineering,* Vol. 167, Academic, Orlando, FL, 1983.
16. T.A. Burton and B. Zhang, Periodicity in delay equations by direct fixed point mapping, *Differe. Equat. Dyn. Syst.*, 6(1998), 413–424.
17. A.W. Bush and A.E. Cook, The effect of time delay and growth rate inhibition in the bacterial decomposition of waste water, *J. Theor. Biol.*, 63(1975), 385–395.
18. G.J. Butler, S.B. Hsu, and P. Waltman, Coexistence of competing predators in a chemostat, *J. Math. Biol.*, 17(1983), 133–151.
19. G.J. Butler, S.B. Hsu, and P. Waltman, A mathematical model of the chemostat with periodic washout rate, *SIAM J. Appl. Math.*, 45(1985), 435–449.

20. G.J. Butler and P. Waltman, Bifurcation from a limit cycle in a two predator-one prey ecosystem modeled on a chemostat, *J. Math. Biol.*, 12(1981), 295–310.
21. G.J. Butler and G.S.K. Wolkowicz, A mathematical model of the chemostat with a general class of functions describing the nutrient uptake, *SIAM J. Appl. Math.*, 45(1985), 138–151.
22. G.J. Butler and G.S.K. Wolkowicz, Predator-mediated competition in the chemostat, *J. Math. Biol.*, 24(1986), 167–191.
23. J. Caperon, Time lag in population growth response of isochrysis galbana to a variable nitrate environment, *Ecology*, 50(1969), 188–192.
24. H. Caswell, A simulation study of a time lag population model, *J. Math. Biol.*, 24(1986), 167–191.
25. A. Cunningham and R.M. Nisbet, Transients and oscillations in continuous culture, M. Bazin (Ed.), in *Mathematics in Microbiology*, Academic, London, 1983, pp. 77–103.
26. J.M. Cushing, *Integrodifferential equations and delay models in population dynamics*, Lecture Notes in Biomathematics, Vol. 20, Springer, New York, NY, 1997.
27. V. D'Ancona, *The Struggle for Existence*, E.J. Brill, Leiden 1954.
28. M.R. Droop, Vitamin B_{12} and marine ecology III, An experiment with a chemostat, *J. Mar. Biol. Assoc. UK*, 46(1966), 659–671.
29. H.M. El-Owaidy and M. Ismail, Asymptotic behaviour of the chemostat model with delayed response in growth, *Chaos, Solitons, and Fractals*, 13(2002), 787–795.
30. S.F. Ellermeyer, Competition in the chemostat: Global asymptotic behavior of a model with delayed response in growth, *SIAM J. Appl. Math.*, 54(1994), 456–465.
31. P. Fergola, L. Jiang, and Z. Ma, On the dynamics of a chemostat model with delayed nutrient recycling, *Int. J. Appl. Math. Comput. Sci.*, 10(2000), 81–96.
32. L.H. Erbe, H.I. Freedman, and V. Sree Hari Rao, Three-species food-chain models with mutual interference and time delays, *Math. Biosci.*, 80(1986), 57–80.
33. T. Fisher and T. Bellows (Eds.), *Hand Book of Biological Control: Principles and Applications of Biological Control*, Elsevier, India, 2005.
34. H.I. Freedman, Deterministic mathematical models in population ecology, *in Monographs and Textbooks in Pure and Applied Mathematics*, Vol. 57, Marcel Dekker, New York, NY, 1980.
35. H.I. Freedman, J.W.-H. So, and P. Waltman, Chemostat competition with time delays, J. Eisenfeld and D.S. Levine (Eds.), in *Biomedical Systems Modelling and Simulation (Paris, 1988)*, volume 5 of *IMACS Ann. Comput. Appl. Math.*, Baltzer, Basel, 1989, pp. 171–173.
36. H.I. Freedman, J.W.-H. So, and P. Waltman, Coexistence in a model of competition in the chemostat incorporating discrete delays, *SIAM J. Appl. Math.*, 49(1989), 859–870.
37. H.I. Freedman, and V. Sree Hari Rao, The trade-off between mutual interference and time lags in predator-prey systems, *Bull. Math. Biol.*, 45(1983), 991–1004.
38. H.I. Freedman, V. Sree Hari Rao, and K. Jaya Lakshmi, Stability, persistence, and extinction in a predator-prey system with discrete and continuous time delays, R.P. Agarwal (Ed.), in *Recent trends in Differential Equations*, World Sci. Ser. Appl. Anal., Vol.1, World Scientific, River Edge, NJ, 1992. pp. 221–238.
39. H.I. Freedman and Y.T. Xu, Models of competition in the chemostat with instantaneous and delayed nutrient recycling, *J. Math. Biol.*, 31(1993), 513–527.
40. H.I. Freedman and F. Yang, Competing predators for a prey in a chemostat model with periodic nutrient input *J. Math. Biol.*, 29(1991), 715–732.
41. R. Freter, Mechanism that controls microflora in the large intestine, in D.J. Hentges, Editor, *Human Intestinal Microflora in Health and Disease*, Academic, New York, NY, 1983, pp. 33–54.
42. R. Freter, An understanding of colonization of the large intestine requires mathematical analysis, *Microbiol. Ther.*, 16(1986), 147–155.
43. T.C. Gard, A new Lyapunov function for the simple chemostat, *Nonlinear Anal. Real World Appl.*, 3(2002), 211–226.
44. K. Gopalsamy, Stability and oscillations in delay differential equations of population dynamics, in *Mathematics and its Applications*, Kluwer, Dordrecht, 1992.

45. K. Gopalsamy and P.X. Weng, Global attractivity and "level crossings" in a periodic partial integrodifferential equation, *Houston J. Math.*, 18(1992), 551–575.
46. J.K. Hale, Theory of functional differential equations, Springer, New York, NY, Second Edition, 1977.
47. J.K. Hale and A.S. Somolinos, Competition for fluctuating nutrient, *J. Math. Biol.*, 18(1983), 255–280.
48. S.R. Hansen and S.P. Hubbell, Single nutrient microbial competition: Agreement between experimental and theoretical forecast outcomes, *Science*, 20(1980), 1491–1493.
49. A. Hastings, Multiple limit cycles in predator–prey models, *J. Math. Biol.*, 11(1981), 51–63.
50. X.Z. He and S. Ruan. Global stability in chemostat-type plankton models with delayed nutrient recycling, *J. Math. Biol.*, 37(1998), 253–271.
51. X.Z. He, S. Ruan, and H. Xia, Global stability in chemostat-type plankton models with delayed nutrient recycling, *SIAM J. Math. Anal.*, 29(1998), 681–696.
52. M.W. Hirsch, S. Smale, and R.L. Devaney, *Differential Equations, Dynamical Systems, and an Introduction to Chaos*, Elsevier, India, Second Edition, 2004.
53. S.B. Hsu, Limiting behavior for competing species, *SIAM J. Appl. Math.*, 34(1978), 760–763.
54. S.B. Hsu, A competition model for a seasonally fluctuating nutrient, *J. Math. Biol.*, 9(1980), 115–132.
55. S.B. Hsu, S. Hubbell, and P. Waltman, A mathematical theory for single nutrient in continuous cultures of micro organisms modeling two species competition, *SIAM J. Appl. Math.*, 32(1997), 366–383.
56. S.B. Hsu, P. Waltman, and S.F. Ellermeyer, A remark on the global asymptotic stability of a dynamical system modeling two species competition, *Hiroshima Math. J.*, 24(1994), 435–445.
57. M.I. Kamien and N.L. Schwartz, Dynamic optimization, in *The Calculus of Variations and Optimal Control in Economics and Management Series*, Vol. 4, North-Holland Publishing Co., New York, NY, 1981.
58. J. Kato and J. Pan, Stability domain of a chemostat system with delay, S. Ruan, G.S.K. Wolkowicz, and J. Wu (Eds.), in *Differential Equations with Applications to Biology (Halifax, NS, 1997)*, Volume 21 of *Fields Inst. Commun.*, American Mathematical Society, Providence, RI, 1999, pp. 307–315.
59. J.P. Keener, Oscillatory coexistence in the chemostat: A codimension two unfolding, *SIAM J. Appl. Math.*, 43(1983), 1005–1018.
60. V.B. Kolmanovskiĭ and V.R. Nosov, Stability of functional differential equations, Academic Press, London, 1986.
61. V.B. Kolmanovskiĭ, L. Torelli, and R. Vermiglio, Stability of some test equations with delay, *SIAM J. Math. Anal.*, 25(1994), 948–961.
62. Y. Kuang, Limit cycles in a chemostat-related model, *SIAM J. Appl. Math.*, 49(1989), 1759–1767.
63. Y. Kuang, Delay differential equations with applications in population dynamics, Academic Press, Boston, MA, 1993.
64. B. Li, Global asymptotic behavior of the chemostat: general response functions and different removal rates, *SIAM J. Appl. Math.*, 59(1998), 411–422.
65. N. MacDonald, *Time lags in biological models*, Lecture Notes in Biomathematics, Vol. 27, Springer, Berlin, 1978.
66. J. Monod, Recherches sur la Croissance des Cultures Bacteriennes, Hermann et cie., Paris, 1942.
67. J.D. Murray, *Mathematical Biology, I & (II): An Introduction*, Springer, India, Third Edition, 2004.
68. H. Nakajima and D.L. De Angelis, Resilience and local stability in a limited nutrient-consumer system, *Bull. Math. Biol.*, 51(1989), 501–510.
69. R.M. Nisbet and W.S.C. Gurney, *Modelling Fluctuating Populations*, Wiley, New York, NY, 1982.
70. R.M. Nisbet, J. Mckinstry, and W.S.C. Gurney, A strategic model of material recycling in a closed ecosystem, *Math. Biosci.*, 64(1983), 99–113.

71. M.J. Norris and R.D. Driver, A uniqueness theorem for ordinary differential equations, *SIAM J. Math. Anal.*, 12(1981), 141–144.
72. A. Novick and L. Szilard, Experiments with the chemostat on spontaneous mutations of bacteria, *Proc. Nat. Acad. Sci.*, 36(1950), 708–719.
73. L.M. Perko, Differential equations and dynamical systems, Springer, New York, NY, Third Edition, 2001.
74. S.S. Pilyugin and P. Waltman, The simple chemostat with wall growth, *SIAM J. Appl. Math.*, 59(1999), 1552–1572.
75. T. Powell and P.J. Richerson, Temporal variation, spatial heterogeneity and competition for resources in plankton systems: A theoretical model, *Am. Nat.*, 125(1985), 431–464.
76. G.E. Pukhov, Differential transforms of mathematical models, *Elektronnoe Modelirovanie*, 1(1979), 17–25.
77. G.E. Pukhov, Expansion formulas for Differential transforms, Translated from '*Kibernetika*', 4(1981), 30–32.
78. R. Reissig, G. Sansone, and R. Conti, *Non-linear Differential Equations of Higher Order*, Translated from the German, Noordhoff International Publishing, Leyden, 1974.
79. S. Ruan, The effect of delays on stability and persistence in plankton models, *Nonlinear Anal.*, 24(1995), 575–585.
80. S. Ruan and X.Z. He, Global stability in chemostat-type competition models with nutrient recycling, *SIAM J. Appl. Math.*, 58(1998), 170–192.
81. Y. Sanling and H. Maoan, Bifurcation analysis of a chemostat model with two distributed delays, *Chaos, Solitons Fractals*, 20(2004), 995–1004.
82. Y. Sanling, H. Maoan, and M. Zhien, Competition in the chemostat: Convergence of a model with delayed response in growth, *Chaos, Solitons Fractals*, 17(2003), 659–667.
83. Y. Sanling, Y. Song, and H. Maoan, Direction and stability of bifurcating periodic solutions of a chemostat model with two distributed delays, *Chaos, Solitons Fractals*, 21(2004), 1109–1123.
84. H.L. Smith, Competitive coexistence in an oscillating chemostat, *SIAM J. Appl. Math.*, 40(1981), 498–522.
85. H.L. Smith and P. Waltman, *The Theory of Chemostat*, Cambridge University Press, London, 1995.
86. V. Sree Hari Rao and P. Raja Sekhara Rao, Global stability of chemostat models involving time delays, *Differ. Equat. Dyn. Syst.*, 8(2000), 1–28.
87. V. Sree Hari Rao and P. Raja Sekhara Rao, Global stability of chemostat models involving time delays and zones of no activation, *Can. Appl. Math. Q.,* 9(2001), 273–300.
88. V. Sree Hari Rao and P. Raja Sekhara Rao, Mathematics of the chemostat, *Bull. Marathwada. Math. Soc.,* 2(2001), 129–139.
89. V. Sree Hari Rao and P. Raja Sekhara Rao, Global stability in chemostat models involving time delays and wall growth, *Nonlinear Anal. Real World Appl.*, 5(2004), 141–158.
90. V. Sree Hari Rao and P. Raja Sekhara Rao, Mathematical models of the microbial populations and issues concerning stability, *Chaos Solitons Fractals*, 23(2005), 657–670.
91. V. Sree Hari Rao and P. RajaSekhara Rao, Oscillations induced by the time lags in limited nutrient-consumer dynamic models, *Chaos Solitons Fractals*, 25(2005), 11–23.
92. V. Sree Hari Rao and P. Raja Sekhara Rao, Stability analysis of resource-consumer dynamic models, *ANZIAM J.*, 47(2006), 413–438.
93. V. Sree Hari Rao and P. Raja Sekhara Rao, Mathematical models and stabilizing bio-control mechanisms for microbial populations in a cultured environment, *Chaos Solitons Fractals*, 28(2006), 1222–1251.
94. V. Sree Hari Rao and P. Raja Sekhara Rao, Basic chemostat model revisited, *Differ. Equat. Dyn. Syst.*, 17(2009), 3–23.
95. V. Sree Hari Rao, P. Raja Sekhara Rao and K. Venkata Ratnam, Parameter estimation using dynamic optimization in limited nutrient-consumer hybrid dynamical systems, *Nonlinear Anal.*, 64(2006), 263–287.

96. V. Sree Hari Rao and K. Venkata Ratnam, Multiparameter dynamic optimization algorithms and application to a problem of bioinformatics relating to the spread of an epidemic, *Electron. Model.*, 26(2006), 105–116.
97. G. Stépán, *Retarded Dynamical Systems: Stability and Characteristic Functions*, Pitman Research Notes in Mathematics Series, Vol. 210, Longman Scientific & Technical, Harlow, 1989.
98. Y.M. Svirezhev and D.O. Logofet, *Stability of Biological Communities*, Translated from the Russian by Alexey Voinov [A. A. Voinov], “Mir”, Moscow, 1983.
99. R.E. Ulanowicz, Mass and energy flows in closed ecosystems, *J. Theor. Biol.*, 34(1972), 419–439.
100. P. Waltman, *Competition Models in Population Biology*, CBMS-NSF Regional Conference Series in Applied Mathematics, Vol. 45, Society for Industrial and Applied Mathematics (SIAM), Philadelphia, PA, 1983.
101. P. Waltman, Coexistence in chemostat-like models, *Rocky Mountain J. Math.*, 20(1990), 777–807.
102. R.H. Whittaker, *Communities and Ecosystems*, Macmillan, New York, NY, 1975.
103. F.M. Williams, Dynamics of microbial populations Mechanism that controls microflora in the large intestine, In *B.C. Pattern, Editor, Systems Analysis and Simulation in Ecology*, Academic, New York, NY, 1971.
104. G.S.K. Wolkowicz, Successful invasion of a food web in a chemostat, *Math. Biosci.*, 93(1989), 249–268.
105. G.S.K. Wolkowicz and Z. Lu, Global dynamics of a mathematical model of competition in the chemostat: General response functions and differential death rates, *SIAM J. Appl. Math.*, 52(1992), 222–233.
106. G.S.K. Wolkowicz, H. Xia, and S. Ruan, Competition in the chemostat: A distributed delay model and its global asymptotic behavior, *SIAM J. Appl. Math.*, 57(1997), 1281–1310.

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