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.

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

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

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

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. $\square$

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,

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

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

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

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

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

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

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

That is,

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

Thus

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

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

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

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

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

Also (2.18) requires,

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

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

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

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*

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

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

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

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

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

Now consider

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

Then

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

and

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

From the second equation of (2.32), we have

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

from this it follows that

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

and further, we have

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

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),

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

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.

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

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

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

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

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

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

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

Now consider

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

Then

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

Now from (2.46) and (2.47)

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

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

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

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)

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}(w_1{x_1}^2) \leq w_1\Big\{ &- 2D{x_1}^2 - 2a(y_1 + y^*){x_1}^2 - 2ax^*x_1y_1 \\ &+ b\gamma{x_1}^2 + b\gamma \int_0^\infty f(s){y_1}^2(t-s)\mathrm{d}s\Big\},\end{aligned} \tag{2.54}$$

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 ($ab \leq \frac{a^2}{2} + \frac{b^2}{2}$)

$$\frac{\mathrm{d}}{\mathrm{d}t}w_2\left(y_1 - y^* \ \log\left(\frac{y_1 + y^*}{y^*}\right)\right) = w_2cx_1y_1, \tag{2.55}$$

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}{V_0}^2(x_t) \leq &-D(2 - b\gamma T_f){x_1}^2 - 2\left(D\frac{a}{c} + ax^* - b\gamma\right)x_1y_1 \\ &- \left(2\frac{a}{c} - b\gamma T_f\right)(ax^* - b\gamma){y_1}^2 \\ &+ b\gamma(D + ax^* - b\gamma)\int_0^\infty f(s)\int_{t-s}^t {y_1}^2(u)\mathrm{d}u\mathrm{d}s,\end{aligned} \tag{2.56}$$

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}&\left\{w_1b\gamma\int_0^\infty f(s)\int_{t-s}^t {y_1}^2(u)\mathrm{d}u\mathrm{d}s\right\} = \\ &w_1b\gamma\left({y_1}^2 - \int_0^\infty f(s){y_1}^2(t-s)\mathrm{d}s\right)\end{aligned} \tag{2.57}$$

and

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

Now letting $w_2c = 2aw_1x^* + 2(D\frac{a}{c} + ax^* - b\gamma) > 0$ 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

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

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, $\|f\| = \sup_{0\le x<\infty}|f(x)|$. Obviously, if f is bounded, there exists a $H > 0$ such that $\|f\| \le H$.

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

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

$\eta > 0$ 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

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

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

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

which may be written as

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

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,

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

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

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

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

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

That is,

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

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

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

Then we have

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

From the second equation of (2.67), we have

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

and hence,

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

It follows from (2.71) that

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

Also

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

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

$$\begin{aligned} V'(t) &\le -Dx_1U_1(x_1) - ayU_1{}^2(x_1) \\ &\quad + y(t)U_1{}^2(x_1)\frac{1}{2}(aU(x^*)-b\gamma)c \\ &\quad \times \left[\frac{1}{\gamma+D}\left(1-e^{-(\gamma+D)\tau}\right) + \tau e^{-(\gamma+D)\tau}\right] \\ &\quad + \frac{1}{2}b\gamma c\left[\tilde{T_f} + T_f e^{-(\gamma+D)\tau}\right] y(t)U_1{}^2(x_1). \end{aligned} \tag{2.74}$$

Clearly $V'(t) < 0$ provided

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

where

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

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

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

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

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

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 $|U(x_1)| \le k|x_1|$ (a Lipschitz constant for U).

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

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

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,

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

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 $0 \le \tau < \tau^* = 0.00704$. 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 $0 \le \tau \le 5/16$ 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 $0 \le \tau < \tau^*$, 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 $T_f = \int_0^\infty sf(s)\mathrm{d}s < \infty$, $\quad T_g = \int_0^\infty sg(s)\mathrm{d}s < \infty$ 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,

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

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,

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

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 $c \le a$ 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 $U(x) \le L$ 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

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

utilizing the conditions, $U(x) \leq L$ 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.*

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

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,

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

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

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

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

we have

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

invoking the hypothesis on T_g.

Now define $\omega = \{(x, y) \in \mathbf{R}_+^2 : Dx + bDy \leq Dx_0\}$. 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 $t \geq t_0$ such that $(x, y) \in \mathbf{R}_+^2 - \omega$.

Clearly $V(t) \geq bx(t) + by(t) = b||X(t)||$, 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

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

and

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

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 $i = 1, 2, \ldots$. 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

$$\alpha_1 = \int_0^\infty s f_2(s) ds, \quad \beta_1 = \int_0^\infty s f_1(s) ds, \quad \textit{and} \quad A = D + a y^* U'(x^*)$$

in which f_1 *and* f_2 *are as defined earlier.*

Proof We consider the Lyapunov functional

$$\begin{aligned} V(X_t) &= v^2 + w_0 u^2 + V_0^2(X_t) \\ &\quad + \int_0^\infty \Big[f_1(s) + f_2(s) \Big] \int_{t-s}^t \mathrm{d}t_1 \\ &\quad \times \int_{t_1}^t \Big[v^2(z) + (\epsilon + \beta_0 - \alpha_0) u^2(z) \Big] \mathrm{d}z \mathrm{d}s, \end{aligned}$$

in which

$$\alpha_0 = \int_0^\infty f_2(s) \mathrm{d}s < \infty, \quad \beta_0 = \int_0^\infty f_1(s) \mathrm{d}s < \infty$$

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

$$V(0) = 0, \quad V(X_t) \geq \eta(v^2 + u^2),$$

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,

$$
\begin{aligned}
V'(X_t) \le &-\Big[2(\beta_0-\alpha_0)\delta + 2w_0\epsilon - (2(\beta_0-\alpha_0)+\epsilon)(\beta_1-\alpha_1)\Big]u^2 \\
&+2\Big[w_0 - 2(\beta_0-\alpha_0) + \delta\epsilon\Big]uv \\
&-\Big[2\delta - (2+\epsilon)(\beta_1-\alpha_1)\Big]v^2. \qquad (2.104)
\end{aligned}
$$

Using the definitions of α_0 and β_0 we may show that $\beta_0 > \alpha_0$.
Now letting $\epsilon = 0,\;\; \delta = A$, 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

$$
\begin{aligned}
V_{11}'(t) + V_{12}'(t) &\le -2Ax_1{}^2 - 2b\gamma(\frac{B}{C} - 1)x_1 y_1 + CT_f x_1{}^2 + I(t) \\
&\quad + C\int_0^\infty f(s)\int_{t-s}^t \int_0^\infty g(w)x_1{}^2(t-w)\mathrm{d}w\mathrm{d}z\mathrm{d}s \\
&\le -2Ax_1{}^2 - 2b\gamma(\frac{B}{C} - 1)x_1 y_1 + CT_f x_1{}^2 + I(t) \\
&\quad + CT_f\int_0^\infty g(s)x_1{}^2(t-s)\mathrm{d}s. \qquad (2.108)
\end{aligned}
$$

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),

$$V_1'(t) \le -2(A - CT_f)x_1{}^2 - 2b\gamma(\frac{B}{C} - 1)x_1 y_1 + I(t). \qquad (2.109)$$

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

$$
\begin{aligned}
V_2(t) &= \left[y_1 + \frac{C}{b\gamma}\int_0^\infty g(s)\int_{t-s}^t x_1(u)\mathrm{d}u\mathrm{d}s\right]^2 \\
&\quad + \left(\frac{C}{b\gamma}\right)^2\int_0^\infty g(s)\int_{t-s}^t\int_v^t x_1{}^2(u)\mathrm{d}u\mathrm{d}v\mathrm{d}s.
\end{aligned}
$$

After some simplifications, we can show that

$$V_2'(t) = \frac{2C}{b\gamma}x_1 y_1 + 2\left(\frac{C}{b\gamma}\right)^2 T_g x_1{}^2, \qquad (2.110)$$

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

$$
\begin{aligned}
V'(t) \le & -2\left[A - CT_f - \left(c\int_t^\infty f(s)\mathrm{d}s + B - C\right)T_g\right]{x_1}^2 \\
& + 2b\gamma x_1 y_1 \int_t^\infty f(s)\mathrm{d}s + I(t) \\
= & -2\left[A - CT_f - \left(c\int_t^\infty f(s)\mathrm{d}s + B - C\right)T_g\right]{x_1}^2 \\
& + 2b\gamma x_1 \int_t^\infty f(s)y_1(t-s)\mathrm{d}s, \quad \text{using (2.107)} \\
\le & -2\left[A - CT_f - \left(c\int_t^\infty f(s)\mathrm{d}s + B - C\right)T_g\right]{x_1}^2 \\
& + 2b\gamma x_1 \|\phi_2\| \int_t^\infty f(s)\mathrm{d}s \\
\le & -2\left[A - CT_f - \left(c\int_t^\infty f(s)\mathrm{d}s + B - C\right)T_g\right]{x_1}^2 \\
& + b\gamma {x_1}^2 \int_t^\infty f(s)\mathrm{d}s + b\gamma \|\phi_2\|^2 \int_t^\infty f(s)ds \\
= & -2\left[A - CT_f - (B-C)T_g\right]{x_1}^2 \\
& + [2cT_g + b\gamma]{x_1}^2 \int_t^\infty f(s)\mathrm{d}s + b\gamma\|\phi_2\|^2 \int_t^\infty f(s)\mathrm{d}s. \qquad (2.111)
\end{aligned}
$$

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,

$$V(t) + 2(A - Q(\epsilon)) \int_T^t {x_1}^2(s)\mathrm{d}s \leq V(T) + b\gamma\|\phi_2\|^2 \int_0^\infty sf(s)\mathrm{d}s.$$

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,

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

Now observing that $c \leq a$, $b\gamma < \gamma$, 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, $V'(t) \leq -DV(t) + Dx_0$, from which it follows that

$$V(t) = V(x(t), y(t)) \leq V(0)e^{-Dt} + x_0.$$

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

$$\begin{aligned}x'(t) &= -D(x(t) - x^*) - aU(x(t))(y(t) - y^*) - ay^*(U(x(t)) - U(x^*)) \\ &\qquad + b\gamma \int_{0}^{\infty} f(s)(y(t-s) - y^*)\mathrm{d}s, \\ y'(t) &= cy(t)\int_{0}^{\infty} g(s)(U(x(t-s)) - U(x^*))\mathrm{d}s.\end{aligned} \tag{2.114}$$

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,*

$$D - (c - ay^*)k > 0 \quad \textit{and} \quad \Delta \equiv \min_{x\geq x^*}\{aU(x) - b\gamma\} > 0.$$

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,

$$D^+V < -(D + aky^* - ck)|x(t) - x^*| - \frac{\Delta}{k_1}|\log y(t) - \log y^*| \quad < 0, \tag{2.115}$$

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 $t \in (t_4, t_5)$,

$$\begin{aligned}
D^+V(t) &\leq -\beta V(t) + ck[\int_T^\infty g(s)M\,\mathrm{d}s + \int_0^T g(s)(\bar{\sigma}+\epsilon)\mathrm{d}s] \\
&\quad + b\gamma[\int_T^\infty f(s)M\,\mathrm{d}s + \int_0^T f(s)(\bar{\sigma}+\epsilon)\mathrm{d}s] \\
&\leq -\beta(\bar{\sigma} - \epsilon) + (b\gamma + ck)M\epsilon + (b\gamma + ck)(\bar{\sigma} + \epsilon) \\
&< -[\beta - (b\gamma + ck)]\bar{\sigma}/2 \\
&< 0, \qquad (2.118)
\end{aligned}$$

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*

$$\begin{aligned} {T_f}^* &= \frac{1}{\gamma + D}\int_0^\infty f(s)\left(e^{[\gamma+D]s} - 1\right)ds < \infty \quad \textit{and} \\ {T_g}^* &= \frac{1}{c - \gamma - D}\int_0^\infty g(s)\left(e^{[c-\gamma-D]s} - 1\right)ds < \infty. \end{aligned}$$

Further let

$$b\gamma c\left({T_f}^* + T_f + (c - \gamma - D)T_f {T_g}^*\right) + c(aU(x^*) - b\gamma)e^{cT_g}(T_g + {T_g}^*) < 2a.$$

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

$$\begin{aligned} V_1(t) = &\int_0^{x_1(t)} U_1(u)\mathrm{d}u \\ &+ \frac{1}{2}b\gamma c \int_0^{\infty} f(s) \int_{t-s}^{t} \int_{w}^{t} P(u) \int_0^{\infty} g(v)\mathrm{d}v\mathrm{d}u\mathrm{d}w\mathrm{d}s \\ &+ \frac{1}{2}b\gamma c T_f \int_0^{\infty} g(s) \int_{t-s}^{t} P(u+s){U_1}^2(x_1(u))\mathrm{d}u\mathrm{d}s, \end{aligned}$$

in which

$$P(t) = y^* \mathrm{e}^{y_1(t)}$$

and

$$\begin{aligned} V_2(t) = &\int_0^{z(t)} (\mathrm{e}^s - 1)\mathrm{d}s \\ &+ \frac{1}{2}c^2\mathrm{e}^{cT_g} \int_0^{\infty} g(s) \int_{t-s}^{t} \mathrm{e}^{y_1(v+s)} \int_{v}^{t} {U_1}^2(x_1(u))\mathrm{d}u\mathrm{d}v\mathrm{d}s, \end{aligned}$$

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.

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