Global stability in chemostat-type plankton models with delayed nutrient recycling

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Abstract. In this paper, we consider chemostat-type plankton models in which plankton feeds on a limiting nutrient and the nutrient is supplied at a constant rate and is partially recycled after the death of plankton by bacterial decomposition. We use a distributed delay to describe nutrient recycling and a discrete delay to model the planktonic growth response to nutrient uptake. When one or both delays occur, by constructing Liapunov functionals, we obtain some sufficient conditions for the global attractivity of the positive equilibrium, which can be regarded as estimates of the delays for persistence of global attractivity.

Key words: Plankton models – Nutrient recycling – Time delay – Liapunov functionals – Global attractivity

1 Introduction

The method of continuous culture, known as the chemostat, provides an experimental system for researchers to simulate the growth of planktonic communities of microscopic algae and to investigate the consequences of the highly variable supply of their essential nutrient. It is the most simple idealization of a biological system where the parameters are measurable, the experiments are reasonable, and the mathematics is tractable. Tilman [32] provided theoretical, experimental and correlational information and Smith and Waltman [30] provided interesting mathematics on the chemostat.

As in Monod [20], the classical chemostat equations modeling plankton population dynamics originally related the growth rate of the cells to the nutrient concentration in the medium. It is assumed that the nutrient uptake

rate is proportional to the rate of reproduction. The constant of proportionality which converts units of nutrient to units of organisms is called the yield constant. Because of the assumed constant value of the yield, the classical Monod model is refereed to as the constant-yield model by Grover [17].

Droop [10] observed that under nonequilibrium correlations the nutrient concentration in the chemostat remained relatively high at the low dilution rates, a phenomenon that cannot be explained by the Monod model. This led him to introduce the notion of an internal nutrient pool and to propose that nutrient uptake is a function of the ambient nutrient concentration while growth rate varies with the internal nutrient level of the cells, called the cell quota, which may be viewed as the average amount of stored nutrient in each cell of the particular organism in the chemostat. The cell quota increases due to nutrient uptake and decreases due to cell division, which acts to spread the total stored nutrient over more cells. Grover [15, 17] refereed to the Droop model as the variable-yield or the variable-internal-store model.

Cunningham and Maas [7] observed damped oscillations in cell numbers when the dilution rate was increased in their experiments which involved the growth of a *Chlamydomonas reinhardii* population on a nitrogen substrate. It was hoped that the transient behavior of Droop model would explain the phenomenon. However, Cunningham and Nisbet [8] noted that the variable-yield Droop model could not reproduce these oscillations without the introduction of time delays into the equations. In fact, in the Droop model only the internal nutrient is immediately available for cell growth and nutrient storage by the cells introduces inevitably time delays between the environmental nutrient pool and population growth.

Though the nonequilibrium behavior of the constant-yield Monod model and the variable-yield Droop model differs considerably (see Grover [16]), at equilibria, the two models are equivalent (see Grover [17]). Moreover, Morel [21] found that the Droop model can be reduced to the Monod model by simple variable substitutions. Probably this is one of the reasons that many theoretical biologists think that the predictions of the variable-yield Droop model are identical to those of the simpler constant-yield Monod model. Recently, Smith and Waltman [29] confirmed mathematically that the Droop model makes the same predictions concerning the growth of a single population as the Monod model. Based on this fact, we shall only consider the simpler Monod model in this paper.

An important difference between a chemostat situation and a lake situation is that lakes generally have a residence time of nutrient and sediments measured in years (see Powell and Richerson [24]). This implies that in models of natural systems the washout rate is very small and the regeneration of nutrient due to bacterial decomposition of the dead biomass must be considered (see Svirezhev and Logofet [31]).

The effect of nutrient recycling on stability of closed ecosystems has been studied by Nisbet and Gurney [22], Nisbet, McKinstry and Gurney [23], and Ulanowicz [33], etc. Powell and Richerson [24] and Nisbet and Gurney [22] regarded nutrient recycling as an instantaneous term, thus neglecting the time

required to regenerate nutrient from dead biomass by bacterial decomposition. However, a delay in nutrient recycling is always present in a natural system and it increases when temperature decreases (see Whittaker [34]). Based on this observation, Beretta, Bischi and Solimano [1] proposed an open system with a single species feeding on a limit nutrient which is partially recycled after the death of the organisms. They used a distributed delay to model nutrient recycling and studied its effect on the stability of the positive equilibrium. Bischi [5] considered the same model and discussed the effect of the delay on resilience.

Following Caperon [6] and Cunningham and Nisbet [8], in a previous paper [26] one of us introduced a discrete delay in the growth response of the species to nutrient uptake in the model of Beretta, Bischi and Solimano [1]. By using the discrete delay as a bifurcation parameter, it was shown that the model undergoes a Hopf bifurcation. It was also found that both the distributed delay and the discrete delay do not change the property of persistence. Recently, Beretta and Takeuchi [2] used another distributed delay to describe the delayed growth response, namely, they considered a system of two retarded functional differential equations with two distributed delays. By constructing Liapunov functionals, they investigated the global asymptotic stability of the positive equilibrium for the case with a Lotka-Volterra coupling between nutrient and the biotic species. In two other papers, they extended the results to the cases that the biotic species has self-regulation which accounts for a finite carrying capacity of the environment (Beretta and Takeuchi [3]) and that the growth response is described by the Michaelis-Menten law (Beretta and Takeuchi [4]).

In this paper, we consider the model proposed in [26], a system of two retarded functional differential equations with a distributed delay and a discrete delay, and its special cases. By using Liapunov functional methods, we obtain some sufficient conditions for the global asymptotic stability of the positive equilibrium. We show that global stability of the positive equilibrium persists if the delays are sufficiently small and we give explicit estimates of the delays. The paper is organized as follows. In Sect. 2, we first consider the model with continuously delayed nutrient recycling. In Sect. 3, we suppose that the delay describing nutrient recycling is a discrete (constant or variable) delay. The general case with a distributed delay and a discrete delay is considered in Sect. 4. Finally, a discussion is carried out in Sect. 5.

2 Continuously delayed nutrient recycling

Consider the following integrodifferential model of plankton-nutrient interaction with a distributed time delay describing nutrient recycling

$$
\begin{aligned}
\dot{N} &= D(N^0 - N) - aU(N)P + b\gamma \int_0^\infty f(s)P(t-s)ds, \\
\dot{P} &= P[-\gamma + D) + cU(N)],
\end{aligned}
\tag{2.1}
$$

where N is the limiting nutrient concentration and P is a measure of plankton concentration at any time.

In system (2.1), all parameters are positive constants. N^0 is the input concentration of the limiting nutrient, a is the maximum uptake rate of nutrient, $c\,(\leqq a)$ is the maximum specific growth rate of plankton, $b\,(0 < b < 1)$ is the fraction of the nutrient recycled by bacterial decomposition of the dead plankton, γ is the death rate of plankton and D is the washout rate, so $\gamma + D$ represents the total loss rate of the plankton.

The function $U(N)$ describes the nutrient uptake rate of plankton. We assume the following general hypotheses on $U(N)$:

(i) $U(N)$ is non-negative, increasing and vanishes when there is no nutrient;

(ii) there is a saturation effect when the nutrient is very abundant.

That is, $U(N)$ is a differentiable function defined on $[0, \infty)$ and

$$U(0) = 0, \qquad \frac{dU}{dN} > 0, \qquad \lim_{N \to \infty} U(N) = 1.$$

These hypotheses are satisfied by the Michaelis-Menten function (Caperon [6])

$$U(N) = \frac{N}{k + N},$$

where $k > 0$ is the half-saturation constant or Michaelis-Menten constant.

The delay-kernel $f(s)$ is a non-negative bounded function defined on $[0, \infty)$ and describes the contribution of the plankton population dead in the past to the nutrient recycled at time t. The presence of the distributed time delay must not affect the equilibrium values, so we normalize the kernel such that

$$\int_0^\infty f(s)\,ds = 1. \tag{2.2}$$

According to MacDonald [19], we define the average time lag as

$$T_f = \int_0^\infty s f(s)\,ds. \tag{2.3}$$

In particular, the exponential kernel $f(s) = \alpha e^{-\alpha s}$, $\alpha > 0$, is called a weak kernel, it is frequently used in biological modeling (see Cushing [9] and Cunningham and Nisbet [8]). For the weak kernel, the average time lag is $T_f = 1/\alpha$.

Note that $E_0 = (N^0, 0)$ is always an equilibrium for system (2.1), and if

$$\gamma + D < c \quad \text{and} \quad U^{-1}\!\left(\frac{\gamma + D}{c}\right) < N^0, \tag{2.4}$$

system (2.1) has a positive interior equilibrium $E^* = (N^*, P^*)$ with

$$N^* = U^{-1}\!\left(\frac{\gamma + D}{c}\right), \qquad P^* = \frac{D(N^0 - N^*)}{aU(N^*) - b\gamma}. \tag{2.5}$$

Model (2.1) was proposed by Beretta, Bischi and Solimano [1]. They studied the local stability of the positive equilibrium. Bischi [5] considered the effect of delay on resilience, that is, the rate at which a system returns to a stable steady state following a perturbation. His results show that when the system is characterized by oscillating behavior, an increase of the delay can have a stabilizing effect. The results in [26] indicate that if the kernel $f(s)$ is a weak kernel, then the system (2.1) is uniformly persistent, a term used to describe long term survival of the interacting species. Global stability of some models related to system (2.1) has been studied by Beretta and Takeuchi [2–4]. In Sect. 4 of [2], they discussed the global stability of system (1.1) with a Lotka-Volterra coupling between nutrient and the plankton; in Sect. 4 of [3], they considered the global stability of system (1.1) with an additional negative term $-dP$ in the second equation, i.e., they supposed that the planktonic species has self-regulation, but their results cannot be applied to the case when $d = 0$; in Sect. 4 of [4], they studied the global stability of system (1.1) with the response function being of the Michaelis-Menten form. Also, they derived global stability conditions for solutions with initial conditions in $Q_H = \{\phi : \|\phi\| < H\}$ and depending on K, the upper bound of the solutions. In the following result, we do not require such restrictions on initial conditions and the response function.

Theorem 2.1. *Assume that*
 (a) *the inequalities in* (2.4) *hold;*
 (b) $T_f < \infty$, $T_f^* < \infty$, *and*

$$\gamma [T_f^* + T_f] < \frac{2a}{bc}, \tag{2.6}$$

where

$$T_f = \int_0^\infty s f(s)\,ds, \qquad T_f^* = \frac{1}{\gamma + D}\int_0^\infty f(s)\left[e^{(\gamma + D)s} - 1\right]ds. \tag{2.7}$$

Then the positive equilibrium E^* of system (2.1) *is globally asymptotically stable.*

Proof. We first prove the global attractivity of E^*. Define

$$x_1 = N - N^*, \qquad x_2 = \ln(P/P^*) \tag{2.8}$$

and

$$\xi(x_1) = U(x_1 + N^*) - U(N^*), \tag{2.9}$$

such that $-N^* < x_1 < +\infty$, $-\infty < x_2 < +\infty$, $-U(N^*) \leqq \xi(x_1) < 1 - U(N^*)$. Then

$$N = x_1 + N^*, \qquad P = P^* e^{x_2}$$

and $x_1 \xi(x_1) > 0$ for any $x_1 \in (-\infty, +\infty)$ and $x_1 \xi(x_1) = 0$ if and only if $x_1 = 0$. By the variable change (2.8), system (2.1) can be written as follows:

$$\dot{x}_1(t) = -Dx_1(t) - aP^* e^{x_2(t)} \xi(x_1(t)) - aP^* U(N^*)\left[e^{x_2(t)} - 1\right]$$

$$+ b\gamma P^* \int_0^\infty f(s\left[e^{x_2(t-s)} - 1\right]ds, \tag{2.10}$$

$$\dot{x}_2(t) = c\xi(x_1(t)),$$

in which now the positive equilibrium has been transformed to the trivial equilibrium $x_1 = x_2 = 0$.

Using the second equation in (2.10) and (2.2), we can rewrite the first equation in (2.10) in the following form

$$
\begin{aligned}
\dot{x}_1(t) = {} & -Dx_1(t) - aP^* e^{x_2(t)} \xi(x_1(t)) - aP^* U(N^*) [e^{x_2(t)} - 1] \\
& + b\gamma P^* \left(\left[\int_0^t f(s)\, ds \right] [e^{x_2(t)} - 1]\, ds + \int_t^\infty f(s) [e^{x_2(t-s)} - 1]\, ds \right. \\
& \left. - \int_0^t f(s) \int_{t-s}^t e^{x_2(u)} \dot{x}_2(u)\, du\, ds \right) \\
= {} & -Dx_1(t) - aP^* e^{x_2(t)} \xi(x_1(t)) - P^* \left[aU(N^*) - b\gamma + b\gamma \int_t^\infty f(s)\, ds \right] \\
& \times [e^{x_2(t)} - 1] + \frac{1}{2} b\gamma P^* \int_t^\infty f(s) [e^{x_2(t-s)} - 1]\, ds \\
& - bc\gamma P^* \int_0^t f(s) \int_{t-s}^t e^{x_2(u)} \xi(x_1(u))\, du\, ds \,. \qquad (2.11)
\end{aligned}
$$

Now define

$$
V_1(x_1) = \int_0^{x_1} \xi(u)\, du \,. \qquad (2.12)
$$

Then $V_1(x_1) \geqq 0$ and, along the solutions of (2.11),

$$
\begin{aligned}
\dot{V}_1(t) = {} & \xi(x_1(t)) \dot{x}_1(t) \\
= {} & -Dx_1(t) \xi(x_1(t)) - aP^* e^{x_2(t)} \xi^2(x_1(t)) \\
& - P^* \left[aU(N^*) - b\gamma + b\gamma \int_t^\infty f(s)\, ds \right] \xi(x_1(t)) [e^{x_2(t)} - 1] \\
& + b\gamma P^* \xi(x_1(t)) \int_t^\infty f(s) [e^{x_2(t-s)} - 1]\, ds \\
& - \frac{1}{2} bc\gamma P^* \xi(x_1(t)) \int_0^t f(s) \int_{t-s}^t e^{x_2(u)} \xi(x_1(u))\, du\, ds \\
\leqq {} & -Dx_1(t) \xi(x_1(t)) - aP^* e^{x_2(t)} \xi^2(x_1(t)) \\
& - P^* \left[aU(N^*) - b\gamma + b\gamma \int_t^\infty f(s)\, ds \right] \xi(x_1(t)) [e^{x_2(t)} - 1] \\
& + b\gamma P^* \xi(x_1(t)) \int_t^\infty f(s) \, [e^{x_2(t-s)} - 1]\, ds \\
& + \frac{1}{2} bc\gamma P^* \left[\left(\int_0^\infty f(s) \int_{t-s}^t e^{x_2(u)}\, du\, ds \right) \xi^2(x_1(t)) \right. \\
& \left. + \int_0^\infty f(s) \int_{t-s}^t e^{x_2(u)} \xi^2(x_1(u))\, du\, ds \right] \,. \qquad (2.13)
\end{aligned}
$$

Let $x(t) = (x_1(t), x_2(t))$ and

$$V_2(x(t)) = \frac{1}{2} bc\gamma P^* \int_0^\infty f(s) \int_{t-s}^t \int_v^t e^{x_2(u)} \xi^2(x_1(u)) \, du \, dv \, ds . \qquad (2.14)$$

From (2.13) and (2.14), we have

$$\frac{d}{dt}(V_1 + V_2)(x(t)) \leqq - Dx_1(t)\xi(x_1(t)) - aP^* e^{x_2(t)} \xi^2(x_1(t))$$

$$- P^* \left[aU(N^*) - b\gamma + b\gamma \int_t^\infty f(s) \, ds \right] \xi(x_1(t))[e^{x_2(t)} - 1]$$

$$+ b\gamma P^* \xi(x_1(t)) \int_t^\infty f(s) \left[e^{x_2(t-s)} - 1 \right] ds$$

$$+ \frac{1}{2} bc\gamma P^* \left[\left(\int_0^\infty f(s) \int_{t-s}^t e^{x_2(u)} \, du \, ds \right) \right.$$

$$\left. + T_f e^{x_2(t)} \right] \xi^2(x_1(t)) . \qquad (2.15)$$

On the other hand, from the second equation of (2.1) one can see that

$$\dot{P}(t) \geqq - (\gamma + D)P(t) ,$$

which implies that

$$\ln \frac{P(t)}{P(s)} \geqq - (\gamma + D)(t - s) \quad \text{for } t \geqq s > 0 .$$

Thus, we have

$$P(s) \leqq e^{(\gamma + D)(t-s)} P(t) \quad \text{for } t \geqq s > 0 \qquad (2.16)$$

and

$$P^* \int_0^\infty f(s) \int_{t-s}^t e^{x_2(u)} \, du \, ds = \int_0^\infty f(s) \int_{t-s}^t P(u) \, du \, ds$$

$$\leqq \left(\int_0^\infty f(s) \int_{t-s}^t e^{(\gamma + D)(t-u)} \, du \, ds \right) P(t)$$

$$= \frac{1}{\gamma + D} \left[\int_0^\infty f(s) (e^{(\gamma + D)s} - 1) \, ds \right] P(t)$$

$$= T_f^* P(t). \qquad (2.17)$$

By (2.15) and (2.17), we obtain

$$\frac{d}{dt}(V_1 + V_2)(x(t)) \leqq -Dx_1(t)\xi(x_1(t)) - aP^* e^{x_2(t)}\xi^2(x_1(t))$$

$$- P^*\left[aU(N^*) - b\gamma + b\gamma \int_t^\infty f(s)\,ds\right]\xi(x_1(t))[e^{x_2(t)} - 1]$$

$$+ b\gamma P^* \xi(x_1(t)) \int_t^\infty f(s)[e^{x_2(t-s)} - 1]\,ds$$

$$+ \tfrac{1}{2}bc\gamma[T_f^* + T_f]P(t)\xi^2(x_1(t)) . \tag{2.18}$$

Let

$$V_3(x_2)(t) = \frac{P^*}{c}\left[aU(N^*) - b\gamma + b\gamma \int_t^\infty f(s)\,ds\right]\int_0^{x_2(t)}[e^s - 1]\,ds \tag{2.19}$$

and

$$V(t) = V_1(x_1)(t) + V_2(x)(t) + V_3(x_2)(t) . \tag{2.20}$$

Then $V(t) \geqq 0$. From (2.20), (2.18) and (2.19),

$$\dot{V}(t) \leqq -Dx_1(t)\xi(x_1(t)) + b\gamma\xi(x_1(t)) \int_t^\infty f(s)[P(t-s) - P^*]\,ds$$

$$+ P\xi^2(x_1(t))[-a + \tfrac{1}{2}bc\gamma(T_f^* + T_f)] . \tag{2.21}$$

Since $|\xi(x_1)| \leqq 1$, we have

$$\dot{V}(t) \leqq -Dx_1(t)\xi(x_1(t)) - [a - \tfrac{1}{2}bc\gamma(T_f^* + T_f)]P\xi^2(x_1(t))$$

$$+ b\gamma\left[\sup_{-\infty < s \leqq 0} P(s) + P^*\right]\int_t^\infty f(s)\,ds . \tag{2.22}$$

Notice that $\int_0^t \int_t^\infty f(s)\,ds\,du \leqq \int_0^\infty sf(s)\,ds = T_f < \infty$. Integrating (2.22) from 0 to $t > 0$ and using the assumption (b), we obtain

$$V(t) + D\int_0^t x_1(s)\xi(x_1(s))\,ds \leqq V(0) + b\gamma\left[\sup_{-\infty < s \leqq 0} P(s) + P^*\right]T_f . \tag{2.23}$$

This, together with the definition of the nonnegative function V, implies that $x(t) = (x_1(t), x_2(t))$ is bounded and $x_1(t)\xi(x_1(t)) \in L_1[0, \infty)$. Note that ξ is uniformly continuous on $[0, \infty)$. It then follows from the system (2.10) that $x(t)$ and hence $\dot{x}(t)$ are uniformly continuous. Using Barbalat's lemmas (see Lemmas 1.2.2 and 1.2.3 in Gopalsamy [13]), $\lim_{t\to\infty} x_1(t)\xi(x_1(t)) = 0$, which leads to $\lim_{t\to\infty} x_1(t) = 0$, and $\lim_{t\to\infty} \dot{x}_1(t) = 0$. That is, $\lim_{t\to\infty}(N(t), \dot{N}(t)) = (N^*, 0)$. Now taking the limit $t \to \infty$ on both sides of the first equation in (2.1), we obtain

$$\lim_{t\to\infty}\left[aU(N^*)P(t) - b\gamma \int_0^\infty f(s)P(t-s)\,ds\right] = D(N^0 - N^*) . \tag{2.24}$$

Since $P(t)$ is bounded eventually, $\limsup_{t\to\infty} P(t) = p_1 < \infty$. Hence, there exists a sequence $\{t_n\}$ satisfying $t_n \geq t_m$ for $n \geq m$ and $t_n \to \infty$ as $n \to \infty$ such that $\lim_{n\to\infty} P(t_n) = p_1$. Thus, from (2.24)

$$aU(N^*)p_1 \leq D(N^0 - N^*) + b\gamma p_1,$$

that is, $p_1 \leq P^*$. Similarly, one can show that $\liminf_{t\to\infty} P(t) = p_2 \geq P^*$. Therefore, $\lim_{t\to\infty} P(t) = P^*$. This proves the global attractivity of E^*.

Following Theorem 5 in [4], we know that E^* is locally asymptotically stable if

$$\gamma T_f < \frac{1}{b}\left[\frac{D}{ck} + \frac{a}{c}\right] \tag{2.25}$$

with $k = U'(N^*)P^*$. From (2.7), one can see that $T_f^* > T_f$. It then follows from (2.6) that $\gamma T_f < a/bc$, which implies that (2.25) holds. This, together with the global attractivity of E^*, leads to the global asymptotic stability of E^*. The proof is completed. $\qquad\square$

Remark 2.2. The local asymptotic stability condition $\gamma T_f < 1/b[D/ck + a/c]$ was derived in [4] by considering the associated characteristic equation of the linearized system of (2.1) at the equilibrium E^*. Following the idea of the construction of the Liapunov functional in the proof of Theorem 2.1, one can obtain the same condition on the local asymptotic stability of E^*.

3 Discretely delayed nutrient recycling

In this section, we suppose that the delay describing nutrient recycling is discrete. We first consider the following equations

$$\begin{aligned}
\dot{N} &= D(N^0 - N) - aU(N)P + b\gamma P(t - \tau), \\
\dot{P} &= P[-(\gamma + D) + cU(N)],
\end{aligned} \tag{3.1}$$

where $\tau > 0$ is a constant. Notice that if the inequalities in (2.4) hold, then the positive equilibrium E^* given by (2.5) exists.

Theorem 3.1. *Assume that*

    (a) *the inequalities in (2.4)* hold;
    (b) $\tau > 0$ *is finite such that*

$$\gamma\left[\frac{1}{\gamma + D}[e^{(\gamma + D)\tau} - 1] + \tau\right] < \frac{2a}{bc}. \tag{3.2}$$

Then the positive equilibrium E^* of (3.1) is globally attractive.

Proof. By using the transformation (2.8), the system (3.1) can be written as follows:

$$x_1(t) = -Dx_1(t) - aP^* e^{x_2(u)} \xi(x_1(t)) - aP^* U(N^*)[e^{x_2(t)} - 1]$$
$$+ b\gamma P^* [e^{x_2(t-\tau)} - 1], \tag{3.3}$$

$$\dot{x}_2(t) = c\xi(x_1(t)).$$

Define $V_1(x_1)$ as in (2.12), then along the solutions of (3.3) we have

$$\dot{V}_1(x_1(t)) = \xi(x_1(t))\dot{x}_1(t)$$

$$\leq -Dx_1(t)\xi(x_1(t)) - aP^* e^{x_2(t)}\xi^2(x_1(t))$$

$$- P^*[aU(N^*) - b\gamma]\xi(x_1(t))[e^{x_2(t)} - 1]$$

$$+ \tfrac{1}{2} bc\gamma P^* \left[\left(\int_{t-\tau}^{t} e^{x_2(u)} du \right) \xi^2(x_1(t)) + \int_{t-\tau}^{t} e^{x_2(u)} \xi^2(x_1(u)) du \right] \tag{3.4}$$

for $t \geq \tau$. Now define

$$W_2(x(t)) = \frac{1}{2} bc\gamma P^* \int_{t-\tau}^{t} \int_{v}^{t} e^{x_2(u)} \xi^2(x_1(u)) \, du \, dv. \tag{3.5}$$

From (3.4) and (3.5), it follows that

$$\frac{d}{dt}(V_1 + W_2)(x(t)) \leq -Dx_1(t)\xi(x_1(t)) - aP^* e^{x_2(t)} \xi^2(x_1(t))$$

$$- P^*[aU(N^*) - b\gamma]\xi(x_1(t))[e^{x_2(t)} - 1]$$

$$+ \frac{1}{2} bc\gamma P^* \left[\left(\int_{t-\tau}^{t} e^{x_2(u)} du \, ds \right) + \tau e^{x_2(t)} \right] \xi^2(x_1(t)). \tag{3.6}$$

Using (2.16) and following the argument in (2.17), we obtain

$$P^* \int_{t-\tau}^{t} e^{x_2(u)} du \leq \frac{1}{\gamma + D}[e^{(\gamma + D)\tau} - 1] P(t). \tag{3.7}$$

Hence, (3.6) becomes

$$\frac{d}{dt}(V_1 + W_2)(x(t)) \leq -Dx_1(t)\xi(x_1(t)) - aP^* e^{x_2(t)} \xi^2(x_1(t))$$

$$- P^*[aU(N^*) - b\gamma]\,\xi(x_1(t))[e^{x_2(t)} - 1]$$

$$+ \frac{1}{2} bc\gamma \left[\frac{1}{\gamma + D}(e^{(\gamma + D)\tau} - 1) + \tau \right] P(t)\xi^2(x_1(t)). \tag{3.8}$$

Let $W_3(x_2) = \int_0^{x_2} [e^s - 1] ds$. We can choose α such that

$$\alpha c = P^*[aU(N^*) - b\gamma].$$

Define a Liapunov functional as follows

$$W(x)(t) = V_1(x)(t) + W_2(x)(t) + \alpha W_3(x)(t) . \tag{3.9}$$

Then from (3.8) and (3.9), we have

$$\dot{W}(x)(t) \leqq - Dx_1(t)\xi(x_1(t))$$
$$+ P\xi^2(x_1(t))\left[- a + \frac{1}{2}bc\gamma\left(\frac{1}{\gamma + D}[e^{(\gamma + D)\tau} - 1] + \tau\right)\right]. \tag{3.10}$$

Using (3.10) and the same argument used in the proof of Theorem 2.1, one can show that the positive equilibrium E^* of (3.1) is globally attractive. This completes the proof. $\qquad\square$

We next consider the following equations with a variable delay

$$\dot{N} = D(N^0 - N) - aU(N)P + b\gamma P(t - \tau(t)),$$
$$\dot{P} = P[- (\gamma + D) + U(N)], \tag{3.11}$$

where $\tau(t)$ is differentiable and satisfies

$$0 \leqq \tau(t) \leqq T, \qquad 0 \leqq \dot{\tau}(t) < 1. \tag{3.12}$$

Denote $\sigma(t) = t - \tau(t)$, then its inverse $\sigma^{-1}(t)$ exists and denote $q(t) = \sigma^{-1}(t) - t$. By modifying the Liapunov functionals constructed in the proof of Theorem 3.1, we have the following result.

Theorem 3.2. *Assume that*

(a) *the inequalities in (2.4) hold;*
(b) *the delay $\tau(t)$ satisfies (3.12) and*

$$\gamma\left[\frac{1}{\gamma + D}[e^{(\gamma + D)\tau(t)} - 1] + q(t)\right] < \frac{2a}{bc}, \tag{3.13}$$

where $q(t) = \sigma^{-1}(t) - t$ and $\sigma(t) = t - \tau(t)$.
Then the positive equilibrium E^* of (3.11) is globally attractive.

Proof. Under the transformation (2.8), we can rewrite (3.11) as follows:

$$\dot{x}_1(t) = - Dx_1(t) - aP^*e^{x_2(t)}\xi(x_1(t)) - aP^*U(N^*)[e^{x_2(t)} - 1]$$
$$+ b\gamma P^*[e^{x_2(t - \tau(t))} - 1], \tag{3.14}$$
$$\dot{x}_2(t) = c\xi(x_1(t)) .$$

Define $V_1(x_1)$ as in (2.12), then along the solutions of (3.14), we have

$$\dot{V}_1(x_1(t)) = \xi(x_1(t))\dot{x}_1(t) \leqq - Dx_1(t)\xi(x_1(t)) - aP^*e^{x_2(t)}\xi^2(x_1(t))$$
$$- P^*[aU(N^*) - b\gamma]\xi(x_1(t))[e^{x_2(t)} - 1]$$
$$+ \frac{1}{2}bc\gamma P^*\left[\left(\int_{t-\tau(t)}^{t} e^{x_2(u)}\,du\right)\xi^2(x_1(t)) + \int_{t-\tau(t)}^{t} e^{x_2(u)}\xi^2(x_1(u))\,du\right]$$
$$\tag{3.15}$$

for $t \geqq T$. Now define

$$W_4(x(t)) = \frac{1}{2}bc\gamma P^* \int_t^{\sigma^{-1}(t)} \int_{\sigma(s)}^t e^{x_2(u)}\xi^2(x_1(u))\,du\,dv . \tag{3.16}$$

Then by (3.15) and (3.16), we obtain

$$\frac{d}{dt}(V_1 + W_4)(x(t)) \leqq -Dx_1(t)\xi(x_1(t)) - aP^*e^{x_2(t)}\xi^2(x_1(t))$$

$$- P^*[aU(N^*) - b\gamma]\xi(x_1(t))[e^{x_2(t)} - 1]$$

$$+ \frac{1}{2}bc\gamma P^*\left[\left(\int_{t-\tau(t)}^t e^{x_2(u)}\,du\,ds\right) + q(t)e^{x_2(t)}\right]\xi^2(x_1(t)) . \tag{3.17}$$

Using (2.16) and following the argument in (2.17), we have

$$P^*\int_{t-\tau(t)}^t e^{x_2(u)}\,du \leqq \frac{1}{\gamma + D}\left[e^{(\gamma + D)\tau(t)} - 1\right]P(t) .$$

Hence from (3.17)

$$\frac{d}{dt}(V_1 + W_2)(x(t)) \leqq -Dx_1(t)\xi(x_1(t)) - aP^*e^{x_2(t)}\xi^2(x_1(t))$$

$$- P^*[aU(N^*) - b\gamma]\xi(x_1(t))[e^{x_2(t)} - 1]$$

$$+ \frac{1}{2}bc\gamma\left[\frac{1}{\gamma + D}(e^{(\gamma + D)\tau(t)} - 1) + q(t)\right]P(t)\xi^2(x_1(t)) . \tag{3.18}$$

Let W_3 be defined as in the proof of Theorem 3.1. One can select α such that $\alpha c = P^*[aU(N^*) - b\gamma]$. Then

$$V(x)(t) = V_1(x)(t) + W_4(x)(t) + \alpha W_3(x)(t)$$

is the required Liapunov functional. This completes the proof.   □

Remark 3.3. As pointed out in Remark 2.2, one can use the idea of constructing the Liapunov functionals for Theorems 3.1 and 3.2 to derive the local asymptotic stability conditions for the positive equilibrium E^* of systems (3.1) and (3.11).

4 Delayed growth response

In the chemostat, there are two obvious sources of delays. One is, as pointed out by one referee, due to the possibility that the species takes up nutrient in excess of immediate needs and stores the nutrient to be used later when nutrient is scarce, so that the "free" nutrient concentration does not reflect the

nutrient available for growth. An internal-store model (without time delays) was considered by Grover [15–17] and Smith and Waltman [29]. Another one is due to the cell cycle, which characterizes the time delay between consumption and growth. Consequently there is a delay in the growth term of the species equation but no delay in the consumption term in the nutrient equation. In this section, we consider the second type of delay model with an added nutrient recycling term. We suppose that there is a discrete delay in the growth response of plankton to nutrient uptake, that is, we consider the following system:

$$\dot{N} = D(N^0 - N) - aU(N)P + b\gamma \int_0^\infty f(s)P(t - s)\,ds,$$

$$\dot{P} = P[-\gamma + D) + cU(N(t - \tau))],$$

(4.1)

where $\tau \geq 0$ is a constant. Notice that system (2.1) is a special case of system (4.1) when $\tau = 0$. If the inequalities in (2.4) hold, then there is a positive equilibrium E^* given by (2.5).

System (4.1) was considered in [26]. It was shown that the solutions are bounded, the discrete delay could destabilize the positive equilibrium E^* and Hopf bifurcations may occur. In the following, we will give estimates of the delay such that the global attractivity of the positive equilibrium persists.

Theorem 4.1 *Assume that*

(a) *the inequalities in (2.4) holds;*
(b) *the delay $\tau > 0$ and the kernel f satisfy*

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

(4.2)

where

$$T_\tau = \frac{c}{2}[aU(N^*) - b\gamma]\left[\frac{1}{\gamma_1}(e^{\gamma_1 \tau} - 1) + re^{\gamma_1 \tau}\right],$$

$$T_{\tau, f} = \tfrac{1}{2}bc\gamma\left[T_\gamma^* + T_f e^{\gamma_1 \tau}\right]$$

with $\gamma_1 = c - (\gamma + D) > 0$ and T_f^* defined by (2.7).
Then the positive equilibrium E^* of (4.1) is globally attractive.

Proof. Let $x(t) = (x_1(t), x_2(t))$ be defined by (2.8) and $\xi(x_1)$ be defined by (2.9). Then it follows from (4.1) that

$$\dot{x}_1(t) = -Dx_1(t) - aP^*e^{x_2(t)}\xi(x_1(t)) - aU(N^*)P^*[e^{x_2(t)} - 1]$$

$$+ b\gamma P^* \int_0^\infty f(s)[e^{x_2(t - s)} - 1]\,ds,$$

(4.3)

$$\dot{x}_2(t) = c\xi(x_1(t - \tau)).$$

Define

$$V_1(x_1(t)) = \int_0^{x_1(t)} \xi(s)\,ds, \qquad V_2(x_2(t)) = \int_0^\infty [e^s - 1]\,ds.$$

(4.4)

Then along the solutions of system (4.3) we have

$$\dot{V}_1(x_1(t)) = -Dx_1(t)\xi(x_1(t)) - aP^*e^{x_2(t)}\xi^2(x_1(t))$$

$$- P^*\left[aU(N^*) - b\gamma + b\gamma\int_t^\infty f(s)\,ds\right]\xi(x_1(t))\,[e^{x_2(t)} - 1]$$

$$+ b\gamma P^*\,\xi(x_1(t))\int_t^\infty f(s)[e^{x_2(t-s)} - 1]\,ds$$

$$- b\gamma P^*\,\xi(x_1(t))\int_0^t f(s)\int_{t-s}^t e^{x_2(u)}\dot{x}_2(u)\,du\,ds$$

$$= -Dx_1(t)\xi(x_1(t)) - aP^*e^{x_2(t)}\xi^2(x_1(t))$$

$$- P^*\left[aU(N^*) - b\gamma + b\gamma\int_t^\infty f(s)\,ds\right]\xi(x_1(t))[e^{x_2(t+\tau)} - 1]$$

$$+ P^*\left[aU(N^*) - b\gamma + b\gamma\int_t^\infty f(s)\,ds\right]\xi(x_1(t))[e^{x_2(t+\tau)} - e^{x_2(t)}]$$

$$+ b\gamma P^*\xi(x_1(t))\int_t^\infty f(s)[e^{x_2(t-s)} - 1]\,ds$$

$$- bc\gamma P^*\xi(x_1(t))\int_0^t f(s)\int_{t-s}^t e^{x_2(u)}\xi(x_1(u-\tau))\,du\,ds \qquad (4.5)$$

and

$$\dot{V}_2(x_2(t+\tau)) = c\xi(x_1(t))[e^{x_2(t+\tau)} - 1]\,. \qquad (4.6)$$

Choose $\alpha(t) = P^*/c[aU(N^*) - b\gamma + b\gamma\int_t^\infty f(s)\,ds]$ and

$$V_3(t) = V_1(x_1(t)) + \alpha(t)V_2(x_2(t+\tau))\,. \qquad (4.7)$$

Then it follows that

$$\dot{V}_3(t) \leqq -Dx_1(t)\xi(x_1(t)) - aP^*e^{x_2(u)}\xi^2(x_1(t))$$

$$+ cP^*\left[aU(N^*) - b\gamma + b\gamma\int_t^\infty f(s)\,ds\right]\xi(x_1(t))$$

$$\times \int_t^{t+\tau} e^{x_2(u)}\xi(x_1(u-\tau))\,du$$

$$+ b\gamma P^*\,\xi(x_1(t))\int_t^\infty f(s)[e^{x_2(t-s)} - 1]ds$$

$$- bc\gamma P^*\,\xi(x_1(t))\int_0^t f(s)\int_{t-s}^t e^{x_2(u)}\xi(x_1(u-\tau))\,du\,ds$$

$$\leqq - Dx_1(t)\xi(x_1(t)) - aP(t)\xi^2(x_1(t))$$

$$+ \frac{1}{2}cP^* \left[aU(N^*) - b\gamma + b\gamma \int_t^\infty f(s)\,ds \right]$$

$$\times \int_t^{t+\tau} e^{x_2(u)} \left[\xi^2(x_1(t)) + \xi^2(x_1(u-\tau)) \right] du$$

$$+ b\gamma P^* \xi(x_1(t)) \int_t^\infty f(s) \left[e^{x_2(t-s)} - 1 \right] ds$$

$$+ \frac{bc\gamma P^*}{2} \int_0^\infty f(s) \int_{t-s}^t e^{x_2(u)} \left[\xi^2(x_1(t)) + \xi^2(x_1(u-\tau)) \right] du\,ds . \quad (4.8)$$

Now define a nonnegative function as follows

$$V(t) = V_3(x(t)) + V_4(t) , \qquad (4.9)$$

in which

$$V_4(t) = \frac{1}{2}cP^* \left[aU(N^*) - b\gamma + b\gamma \int_t^\infty f(s)\,ds \right]$$

$$\times \int_{t-\tau}^t \int_v^t e^{x_2(u+\tau)} \xi^2(x_1(u))\,dv\,du$$

$$+ \frac{1}{2}b\gamma c \left[\int_0^\infty f(s) \int_{t-s}^t \int_v^t P(u)\xi^2(x_1(u-\tau))\,dv\,du\,ds \right.$$

$$\left. + T_f \int_{t-\tau}^t P(s+\tau)\xi^2(x_1(s))\,ds \right] .$$

Note that $|\xi(x_1)| \leqq 1$. Thus we have

$$\dot{V}(t) \leqq - Dx_1(t)\xi(x_1(t)) - aP(t)\xi^2(x_1(t))$$

$$+ \frac{1}{2}cP^* \left[aU(N^*) - b\gamma + b\gamma \int_t^\infty f(s)\,ds \right]$$

$$\times \left[\int_t^{t+\tau} e^{x_2(u)}\,du + \tau e^{x_2(t+\tau)} \right] \xi^2(x_1(t))$$

$$+ \frac{1}{2}bc\gamma \left[\left(\int_0^\infty f(s) \int_{t-s}^t P(u)\,du\,ds \right) + T_f P(t+\tau) \right] \xi^2(x_1(t))$$

$$+ b\gamma \left[\sup_{-\infty < s \leqq s} P(s) + P^* \right] \int_t^\infty f(s)\,ds . \qquad (4.10)$$

On the other hand, from the second equation of system (4.1), we have

$$\dot{P}(t) \leqq [c - (\gamma + D)]P = \gamma_1 P$$

and hence

$$P(s) \leqq P(t)e^{\gamma_1(s-t)} \quad \text{for } s \geqq t > 0 . \qquad (4.11)$$

It follows from (4.11) that

$$P^*\left[\int_t^{t+\tau} e^{x_2(s)}\,ds + \tau e^{x_2(t+\tau)}\right] = \int_t^{t+\tau} P(s)\,ds + \tau P(t+\tau)$$

$$\leqq P(t)\left[\int_t^{t+\tau} e^{\gamma_1(s-t)}\,ds + \tau e^{\gamma_1\tau}\right]$$

$$= \left[\frac{1}{\gamma_1}(e^{\gamma_1\tau}-1) + \tau e^{\gamma_1\tau}\right]P(t)\,. \qquad (4.12)$$

By using (2.17), (4.12), we obtain

$$\dot{V} \leqq -Dx_1(t)\xi(x_1(t)) - aP(t)\xi^2(x_1(t))$$

$$+ \left\{\frac{1}{2}c\left[aU(N^*) - b\gamma + b\gamma\int_t^\infty f(s)\,ds\right]\right.$$

$$\times\left[\frac{1}{\gamma_1}(e^{\gamma_1\tau}-1) + \tau e^{\gamma_1\tau}\right]$$

$$+ \frac{bc\gamma}{2}[T_f^* + T_f e^{\gamma_1\tau}]\right\}P(t)\xi^2(x_1(t))$$

$$+ b\gamma\left[\sup_{-\infty < s \leqq 0} P(s) + P^*\right]\int_t^\infty f(s)\,ds\,. \qquad (4.13)$$

Note that $\lim_{t\to\infty} b\gamma\int_t^\infty f(s)\,ds = 0$ and $\int_0^t\int_t^\infty f(s)\,ds\,du \leqq \int_0^\infty sf(s)\,ds = T_f < \infty$. Then, using (4.13) and the same argument used in the proof of Theorem 2.1, one can show that the positive equilibrium of (4.1) is global attractive. This completes the proof. $\qquad\square$

Remark 4.2. Obviously, when $\tau = 0$, Theorem 4.1 reduces to Theorem 2.1 and Remark 2.2.

A special case of system (4.1) is that when the kernel f is a Delta function, that is, the nutrient recycling is instantaneous. The model now has the form

$$\dot{N} = D(N^0 - N) - aU(N)P + b\gamma P,$$
$$\dot{P} = P[-(\gamma + D) + cU(N(t-\tau))]. \qquad (4.14)$$

System (4.14) was briefly discussed in [26]. It was found that the delay has an effect on stability of the positive equilibrium. However, by Theorem 4.1, we have the following result on the global attractivity of the positive equilibrium of system (4.14).

Corollary 4.3. *Assume that*
   (a) *the inequalities in (2.4) holds;*
   (b) *the delay $\tau > 0$ satisfies*

$$T_\tau < a\,. \qquad (4.15)$$

Then the positive equilibrium E^* of (4.14) is globally attractive.

Remark 4.4. If $\tau = 0$, (4.15) is automatically satisfied. This is Theorem 3.2 of Beretta et al. [1] or Theorem 2.7 of Ruan [25], that is, if the positive equilibrium exists, it is globally attractive. Theorem 4.3 indicates that if the delay τ is sufficient small, then the positive equilibrium E^* is still globally attractive.

5 Discussion

In this paper, we have discussed global attractivity of the positive equilibrium of plankton-nutrient models with delayed nutrient recycling. We supposed that there is a delay in the growth response of plankton to nutrient uptake. We also considered the case where the delay describing nutrient recycling is a constant or variable discrete delay.

In the first model, system (2.1), we supposed that the limit nutrient is partially recycled after the death of plankton due to bacterial decomposition and used a distributed delay to model nutrient recycling. Recall that the sufficient conditions we obtained for global attractivity of the positive equilibrium E^* are as follows:

$$\gamma + D < c, \qquad U^{-1}\left(\frac{\gamma + D}{c}\right) < N^0 \tag{2.4}$$

and

$$\gamma[T_f^* + T_f] < \frac{2a}{bc}, \tag{2.6}$$

where T_f is the average time delay defined in (2.3) and T_f^* is defined in Theorem 2.1 and is somehow similar to the average time delay. The first inequality in (2.4) indicates that c, the maximum specific growth rate of plankton, must be greater than $\gamma + D$, the total loss rate of plankton and the second inequality in (2.4) means that there must be enough nutrient input concentration. Notice that the inequalities in (2.4) are required throughtout the paper to gurantee the existence of the positive equilibrium and when the delays are absent, they are exactly the global stability conditions. Condition (2.6) demonstrates that the positive equilibrium is still globally attractive if the average time delay involved in nutrient recycling is relatively small, in other words, if the process of recycling is relatively short.

The results in Sect. 3 show that if the delay describing nutrient recycling is a constant or variable discrete delay, one can still have global attractivity of the positive equilibrium as long as the delay is sufficient small.

In Sect. 4, we introduced a discrete delay in the planktonic growth response term. It has been found (see Ruan [26]) that this delay has a distabilizing effect on stability of the positive equilibrium. In Theorem 4.2, we showed that if the inequalities in (2.4) hold and if

$$T_\tau + T_{\tau,f} < a, \tag{4.2}$$

then the positive equilibrium E^* of (4.1) is globally attractive, where T_τ depends on the discrete delay τ and $T_{\tau,f}$ depends on both the discrete delay τ and the distributed delay kernel f. Inequality (4.2) thus gives us an estimate for the delays: when the delays are sufficiently small such that (4.2) holds, then the equilibrium is globally attractive; when the delays are increased and (4.2) is invalid, the equilibrium may lose its stability and a Hopf bifurcation may occur (see Ruan [26]).

The results in this paper indicate that in order to have global attractivity, delays must be relatively small. These results justify the common belief that "small delays are negligible in some modelling processes as far as stabilities are concerned".

It should be pointed out that our method can be used to analyze models with two or more various delays appearing in the first equation. In fact, the global asymptotic stability of the chemostat-type competition models (Freedman and Xu [12]) has been studied by us (see Ruan and He [27]). It would be interesting to investigate the global stability of the predator-prey models (see Ruan and Wolkowicz [28]). Also, as suggested by the referee, it would be very interesting to consider the Droop model with delays. We leave this for future study.

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