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THE EFFECT OF DELAYS ON STABILITY AND PERSISTENCE IN PLANKTON MODELS †

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1. INTRODUCTION

Recently, Beretta *et al.* [1] studied a chemostat-type model to simulate the growth of planktonic communities of unicellular algae in lakes, where the plankton feeds on a limiting nutrient supplied at a constant rate. They supposed that the limiting nutrient is partially recycled after the death of the organisms and they used a distributed delay to model the nutrient recycling in order to study its effect on the stability of the positive equilibrium. In [2], Bischi investigated the effects of the time delay involved in nutrient recycling on resilience, that is, the rate at which a system returns to a stable steady state following a perturbation. Their results show that when a system is characterized by oscillatory behavior, an increase in the distributed time delay can have a stabilizing effect. This is a counter-intuitive result, because in general it has been found that the introduction of time delays is a destabilizing process, in the sense that increasing the time delay could cause a stable equilibrium to become unstable and/or cause the populations to fluctuate (see Cushing [3], Freedman and Rao [4], Gopalsamy and Aggarwala [5] and MacDonald [6]).

The mathematical analysis of chemostat-type models has been studied by many authors. In the case of instantaneous dynamics, we refer to a recent survey paper by Waltman [7] and the references cited therein. Chemostat-type models incorporating discrete delays have been investigated by Freedman *et al.* [8]. We refer to Cushing [3], MacDonald [6], Gopalsamy [9, 10] and Kuang [11] for further references to delayed models in population biology.

In this paper, we introduce a discrete time delay term to the model of Beretta *et al.* [1], this term may be considered as delay due to gestation, and we also allow the washout rates for nutrient and plankton to be different. By using the “linear chain trick technique” of MacDonald [6], we can transform the two dimensional integrodifferential system into a three dimensional one with a discrete time delay. Using the discrete time delay as a bifurcation parameter, we show that the model undergoes a Hopf bifurcation. We also consider the question of persistence. It is shown that conditions for uniform persistence are the same as those for the instantaneous case. Hence, both the discrete time delay and the distributed time delay are “harmless” (a term coined by Gopalsamy [9]) in our model.

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We now recall the definitions of persistence given in Butler *et al.* [12]. A component $x(t)$ of a given ODE system is said to be *persistent* if for any $x(0) > 0$ it follows that $x(t) > 0$, $t > 0$ and $\liminf_{t \rightarrow \infty} x(t) > 0$. If there exists $\delta > 0$ (independent of $x(0)$) such that $x(t)$ is persistent and $\liminf_{t \rightarrow \infty} x(t) > \delta$, then $x(t)$ is said to be *uniformly persistent*. For a FDE system, a component $x(t)$ is persistent if for any $\phi(s) > 0$, $-\infty < s < t_0$, it follows that $x(t) > 0$, $t > 0$ and $\liminf_{t \rightarrow \infty} x(t) > 0$. If there exists $\delta > 0$ (independent of $\phi(t)$) such that $x(t)$ is persistent and $\liminf_{t \rightarrow \infty} x(t) > \delta$, then $x(t)$ is said to be *uniformly persistent*. A system is uniformly persistent if each component is uniformly persistent.

A system is dissipative if for any solution $y(t)$, there is a positive number M such that $\limsup_{t \rightarrow \infty} |y(t)| < M$. To verify this property for a given system, usually Liapunov functions (functionals) and differential inequalities are employed. We refer readers interested in appropriate techniques to Haddock *et al.* [13] and Zhang [14] on functional differential equations with infinite delay.

The rest of this paper is organized as follows. In Section 2 the integrodifferential model with a discrete time delay and a distributed time delay is described. We will review some previous results on some special cases of our model in Section 3. In Section 4 we prove that the system is dissipative and that a Hopf bifurcation occurs at the positive equilibrium if the discrete delay is increased past a critical value. Persistence is also discussed in this section. Finally, some concluding remarks and discussions are given in Section 5.

2. AN INTEGRODIFFERENTIAL MODEL

We consider the following integrodifferential system as a model of plankton–nutrient interaction with a discrete time delay due to gestation and a distributed time delay involved in nutrient recycling

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 \int_{-\infty}^t F(t-s)P(s) ds \\ \frac{dP}{dt} &= P[a_1 u(N(t-\tau)) - (\gamma + D_1)] \end{aligned} \quad (2.1)$$

with initial conditions

$$\begin{aligned} N(s) &= \phi(s), & s \in [-\tau, 0], \\ P(s) &= \psi(s), & s \in (-\infty, t_0], \end{aligned}$$

where N is the concentration of a limiting nutrient and P is a measure of plankton population.

In system (2.1), all parameters are positive constants. D is the washout rate of nutrient, $1/D$ has the physical dimension of time and represents the average time that nutrient and waste products spend in the system (see Smith [15]). D_1 is the washout rate of plankton, and we assume that $D \neq D_1$ (see Wolkowicz and Lu [16] and Ruan [17]). N^0 is the input concentration of the limiting nutrient, a is the maximum uptake rate of nutrient and $a_1 (\leq a)$ is the maximum specific growth rate of plankton, γ is the death rate of plankton and $\gamma_1 (\leq \gamma)$ is the nutrient recycle rate after the death of plankton. There is a delay of time τ due to gestation, which we model following Bush and Cook [18].

The function $u(N)$ describes the nutrient uptake rate of plankton. We assume the following general hypotheses on $u(N)$ (see Hale and Somolinos [19]):

- (i) $u(N)$ is nonnegative, 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 continuous function defined on $[0, \infty)$ and

$$u(0) = 0, \quad \frac{du}{dN} > 0, \quad \lim_{N \rightarrow \infty} u(N) = 1.$$

In particular, these hypotheses are satisfied by the Michaelis–Menten function (Caperon [20])

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

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

The delay kernel $F(s)$ is a nonnegative 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 kernels such that

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

According to MacDonald [6], we define the average time lag as

$$T = \int_0^\infty sF(s) ds. \tag{2.3}$$

In particular, the exponential kernel

$$F(s) = \alpha e^{-\alpha s}, \quad \alpha > 0 \tag{2.4}$$

is usually used (see Cushing [3], Cunningham and Nisbet [21]); the average time lag is

$$T = \int_0^\infty s e^{-\alpha s} ds = \frac{1}{\alpha}.$$

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

$$\gamma + D_1 < a_1 \quad \text{and} \quad u^{-1}\left(\frac{\gamma + D_1}{a_1}\right) < N^0, \tag{2.5}$$

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

$$N^* = u^{-1}\left(\frac{\gamma + D_1}{a_1}\right), \quad P^* = \frac{a_1 D(N^0 - N^*)}{a(\gamma + D_1) - a_1 \gamma_1}. \tag{2.6}$$

3. SOME SPECIAL CASES

In this section we consider some special cases of system (2.1).

Case 1. $\tau = 0, F(s) = \delta(s)$. When the time delays are neglected, that is, the discrete delay $\tau = 0$ and the delay kernel is a delta function $F(s) = \delta(s)$, we get the following instantaneous

model

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 P \\ \frac{dP}{dt} &= P[a_1 u(N) - (\gamma + D_1)].\end{aligned}\tag{3.1}$$

Model (3.1) was studied by Beretta *et al.* [1] and Ruan [17]. According to theorem 2.6 of [17], we first have the following proposition.

PROPOSITION 3.1. System (3.1) is dissipative.

System (3.1) has the same equilibria E_0 and E^* as system (2.1). By theorem 3.1 of [1], we have the following proposition.

PROPOSITION 3.2. If $u(N^0) < (\gamma + D_1)/a_1$, then $\lim_{t \rightarrow \infty} (N(t), P(t)) = E^0$.

This result indicates that if the maximum growth rate of the plankton population is less than or equal to its loss rate, i.e. $a_1 \leq \gamma + D_1$, or the plankton population does not have enough nutrient, i.e. $a_1 > \gamma + D_1$ but $u(N^0) < (\gamma + D_1)/a_1$, then the plankton population becomes extinct.

By theorem 3.2 of [1], we have the following proposition.

PROPOSITION 3.3. If the positive equilibrium E^* exists, it is globally asymptotically stable in R_+^2 .

Comparing the results in chemostat models in Waltman [22], we can see that the nutrient recycling term plays a stabilizing role for the positive equilibrium. Since possessing a globally asymptotically stable equilibrium is sufficient for persistence, we have the following proposition.

PROPOSITION 3.4. If the inequalities in (2.5) hold, then system (3.1) is uniformly persistent.

Propositions 3.3 and 3.4 show that if the maximum growth rate of plankton is greater than its loss rate and plankton has enough nutrient, then the plankton population can survive in the long term.

Case 2. $F(s) = \delta(s)$. When the distributed time delay in the nutrient recycling term is neglected, i.e. $F(s) = \delta(s)$, model (2.1) becomes

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 P \\ \frac{dP}{dt} &= P[a_1 u(N(t - \tau)) - (\gamma + D_1)].\end{aligned}\tag{3.2}$$

This model also has the same equilibria E_0 and E^* as system (2.1) if the inequalities in (2.5) hold. A similar chemostat type model was studied by Freedman *et al.* [8]. Analogous to the procedures in [8], one can prove the following results.

PROPOSITION 3.5. System (3.2) is dissipative.

PROPOSITION 3.6. There exists $\tau_0 > 0$ such that a family of periodic solutions of system (3.2) bifurcates from E^* for τ near τ_0 .

Similarly to the proof of theorem 5.5 of Zhao [23], we can prove the following persistence result about the discrete delay model.

PROPOSITION 3.7. If the inequalities in (2.5) hold, then system (3.2) is uniformly persistent.

Case 3. $\tau = 0$. When the discrete time delay due to gestation is neglected, i.e. $\tau = 0$, the model has the following form

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 \int_{-\infty}^t F(t-s)P(s) ds \\ \frac{dP}{dt} &= P[a_1u(N) - (\gamma + D_1)]. \end{aligned} \tag{3.3}$$

Again system (3.3) has the same equilibria E_0 and E^* as system (2.1) provided the inequalities in (2.5) are satisfied. System (3.3) was studied by Beretta *et al.* [1] and Bischi [2]. By theorem 2.1 of [1] or theorem 1 of [2], we have the following proposition.

PROPOSITION 3.8. System (3.3) is dissipative.

Similarly to theorems 4.1 and 4.2 in [1], we have the following stability criteria independent of the value of distributed time delay.

PROPOSITION 3.9. If $(D + aP^*u'(N^*))^2 \geq 2aP^*u'(N^*)(\gamma + D_1)$, then the positive equilibrium E^* of system (3.3) is locally asymptotically stable. In particular, if $F(s) = \alpha e^{-\alpha s}$, then E^* is always asymptotically stable.

If $F(s) = \alpha e^{-\alpha s}$, then model (3.3) is a special case of model (4.1) in Section 4 when $\tau = 0$. Hence, by theorem 4.3 in Section 4, we have the following proposition.

PROPOSITION 3.10. If $F(s) = \alpha e^{-\alpha s}$ and the inequalities in (2.5) are satisfied, then system (3.3) is uniformly persistent.

4. THE GENERAL CASE

From now on, we suppose $F(s) = \alpha e^{-\alpha s}$ for $\alpha > 0$, i.e. we consider the following model

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 \int_{-\infty}^t \alpha e^{-\alpha(t-s)}P(s) ds \\ \frac{dP}{dt} &= P[a_1u(N(t-\tau)) - (\gamma + D_1)]. \end{aligned} \tag{4.1}$$

The following result shows that solutions of system (4.1) are bounded and, hence, lie in a compact set and are continuable for all positive time.

THEOREM 4.1. System (4.1) is dissipative.

Proof. We choose

$$V(t, N(t), P(\cdot)) = N(t) + \frac{a}{a_1} P(t) + \gamma_1 \int_{-\infty}^t \int_{t-s}^{\infty} \alpha e^{-\alpha \xi} d\xi P(s) ds.$$

The derivative of V along the trajectories of (4.1) is

$$\begin{aligned} \frac{dV}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 \int_{-\infty}^t \alpha e^{-\alpha(t-s)} P(s) ds \\ &\quad + aPu(N(t - \tau)) - \frac{a(\gamma + D_1)}{a_1} P \\ &\quad + \gamma_1 P \int_0^{\infty} \alpha e^{-\alpha \xi} d\xi - \gamma_1 \int_{-\infty}^t \alpha e^{-\alpha(t-s)} P(s) ds \\ &= D(N^0 - N) - \frac{a(\gamma + D_1) - \gamma_1 a_1}{a_1} P \\ &\quad - aP[u(N(t)) - u(N(t - \tau))] \\ &\leq -DN - \frac{a(\gamma + D_1) - \gamma_1 a_1}{a_1} P + DN^0 \end{aligned}$$

if $N(\xi) \leq N(t)$ for $t - \tau \leq \xi \leq t$. By a classical Liapunov-Razumikhin theorem about boundedness (see, Zhang [14]), we know that system (4.1) is dissipative. This completes the proof.

Now we define a new variable

$$Y(t) = \int_{-\infty}^t \alpha e^{-\alpha(t-s)} P(s) ds, \quad (4.2)$$

then by the linear chain trick technique (MacDonald [6]), the two dimensional integro-differential system (4.1) can be transformed into an equivalent three dimensional one with a discrete delay

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 Y \\ \frac{dP}{dt} &= P[a_1 u(N(t - \tau)) - (\gamma + D_1)] \\ \frac{dY}{dt} &= \alpha P - \alpha Y, \end{aligned} \quad (4.3)$$

where the variable $Y(t)$ can be interpreted as an intermediate component which causes the delay, such as the dead plankton in the sediments.

System (4.3) has two equilibria provided the inequalities in (2.5) hold. If confusion does not arise, they are still denoted by $E_0 = (N^0, 0, 0)$ and $E^* = (N^*, P^*, Y^*)$ with $P^* = Y^*$.

The linearized system of (4.3) at the equilibrium E^* has the form

$$\begin{aligned} \frac{dn(t)}{dt} &= -(D + aP^*u'(N^*))n(t) - au(N^*)p(t) + \gamma_1y(t) \\ \frac{dp(t)}{dt} &= a_1P^*u'(N^*)n(t - \tau) \\ \frac{dy(t)}{dt} &= \alpha p(t) - \alpha y(t), \end{aligned} \tag{4.4}$$

where $n(t) = N(t) - N^*$, $p(t) = P(t) - P^*$ and $y(t) = Y(t) - Y^*$. This leads to the characteristic equation

$$\lambda^3 + \rho\lambda^2 + \beta\lambda = \delta e^{-\lambda\tau} + \eta\lambda e^{-\lambda\tau}, \tag{4.5}$$

where

$$\begin{aligned} \rho &= \alpha + D + aP^*u'(N^*) > 0, \\ \beta &= \alpha(D + aP^*u'(N^*)) > 0, \\ \delta &= -\alpha a_1P^*u'(N^*)(au(N^*) - \gamma_1) < 0, \\ \eta &= -aa_1P^*u(N^*)u'(N^*) < 0. \end{aligned}$$

The stability of E^* can be determined according to the sign of the real parts of the solutions λ of equation (4.5). Let $\lambda = \mu + iv$, we consider λ and, hence, μ and v as functions of the delay τ . Substituting into (4.5), we obtain the following equations

$$\begin{aligned} \mu^3 - 3\mu v^2 + \rho(\mu^2 - v^2) + \beta\mu &= [(\delta + \eta\mu) \cos \tau v + \eta v \sin \tau v] e^{-\tau\mu}, \\ -v^3 + 3\mu^2 v + 2\rho\mu v + \beta v &= [\eta v \cos \tau v - (\delta + \eta\mu) \sin \tau v] e^{-\tau\mu}. \end{aligned} \tag{4.6}$$

A necessary condition for a stability change of E^* is that the characteristic equation has a pure imaginary solution $\lambda = iv$. Let $\hat{\tau}$ be such that $\mu(\hat{\tau}) = 0$. Then we can reduce equations (4.6) to (where $\hat{v} = v(\hat{\tau})$)

$$\begin{aligned} -\rho\hat{v}^2 &= \delta \cos \hat{\tau}\hat{v} + \eta\hat{v} \sin \hat{\tau}\hat{v}, \\ -\hat{v}^3 + \beta\hat{v} &= \eta\hat{v} \cos \hat{\tau}\hat{v} - \delta \sin \hat{\tau}\hat{v}. \end{aligned} \tag{4.7}$$

Equations (4.7) give an equation in \hat{v} of the form

$$\Phi(\hat{v}^2) = \hat{v}^6 + (\rho^2 - 2\beta)\hat{v}^4 + (\beta^2 - \eta^2)\hat{v}^2 - \delta^2 = 0. \tag{4.8}$$

Since when $\hat{v} = 0$, $\Phi(0) < 0$ and for sufficiently large values of \hat{v} , $\Phi > 0$, hence, the cubic equation (4.8) has one or more real roots \hat{v}^2 . From equations (4.7), we can solve for $\hat{\tau}$, which is

$$\hat{\tau}_n = \frac{1}{\hat{v}} \arcsin \frac{\hat{v}^3(\delta - \rho\eta) - \hat{v}\beta\delta}{\eta^2\hat{v}^2 + \delta^2} + \frac{2n\pi}{\hat{v}}, \quad n = 0, 1, 2, \dots \tag{4.9}$$

In order to establish Hopf bifurcation at $\tau = \hat{\tau}$, we need to show that $(d/d\tau)\mu(\hat{\tau}) \neq 0$. From (4.6), differentiating with respect to τ and setting $\tau = \hat{\tau}$, $\nu = \hat{\nu}$, $\mu = 0$, and solving for $d\mu/d\tau$ and $dv/d\tau$, we get

$$\frac{d\mu(\hat{\tau})}{d\tau} = \frac{AC - BD}{A^2 + B^2}, \quad (4.10)$$

where

$$A = 3\hat{\nu}^2 - \beta - \eta\hat{\tau}\hat{\nu} \sin \hat{\tau}\hat{\nu} + (\eta - \delta\hat{\tau}) \cos \hat{\tau}\hat{\nu},$$

$$B = 2\rho\hat{\nu} + (\eta - \delta\hat{\tau}) \sin \hat{\tau}\hat{\nu} + \eta\hat{\tau}\hat{\nu} \cos \hat{\tau}\hat{\nu},$$

$$C = \delta\hat{\tau} \sin \hat{\tau}\hat{\nu} - \eta\hat{\nu}^2 \cos \hat{\tau}\hat{\nu},$$

$$D = \eta\hat{\nu}^2 \sin \hat{\tau}\hat{\nu} + \delta\hat{\nu} \cos \hat{\tau}\hat{\nu}.$$

Using (4.7), we have

$$\begin{aligned} AC - BD &= \hat{\nu}^2[3\hat{\nu}^4 + 2(\rho^2 - 2\beta)\hat{\nu}^2 + (\beta^2 - \eta^2)] \\ &= \hat{\nu}^2 \frac{d\Phi}{d\hat{\nu}^2}. \end{aligned}$$

Hence, if $\hat{\nu}_0$ is the first positive root of (4.8), we have

$$\frac{d\mu(\hat{\tau}_0)}{d\tau} = \frac{\hat{\nu}_0^2}{A^2 + B^2} \frac{d\Phi}{d\hat{\nu}^2}(\hat{\nu}_0^2) > 0,$$

where

$$\hat{\tau}_0 = \frac{1}{\hat{\nu}_0} \arcsin \frac{\hat{\nu}_0^3(\delta - \rho\eta) - \hat{\nu}_0\beta\delta}{\eta^2\hat{\nu}_0^2 + \delta^2}.$$

By the Hopf Bifurcation theorem (see [24, 25]), we have the following theorem.

THEOREM 4.2. A Hopf bifurcation occurs from E^* for τ near $\hat{\tau}_0$.

As an example, let $u(N)$ be the Michaelis-Menten uptake function. We consider the system

$$\frac{dN}{dt} = 0.1(20 - N) - \frac{10NP}{6 + N} + 3.2 \int_{-\infty}^t 0.2 e^{-0.2(t-s)} P(s) ds \quad (4.11)$$

$$\frac{dP}{dt} = P \left[\frac{9N(t - \tau)}{6 + N(t - \tau)} - 4.1 \right].$$

If $\tau = 0$, with the same parameters the numerical simulations of Beretta *et al.* [1] suggest that the positive equilibrium is ‘‘practically’’ globally stable (Fig. 1).

By theorem 4.2, we can find that $\hat{\tau}_0 = 0.39$. Thus the positive equilibrium loses its stability and a family of periodic solutions bifurcates from it as τ passes through $\hat{\tau}_0 = 0.39$. A trajectory of model (4.11) when $\tau = 0.41$, is depicted in Fig. 2.

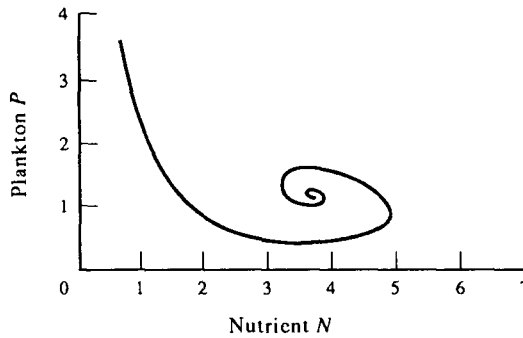


Fig. 1. When $\tau = 0$, E^* is stable (see [1]).

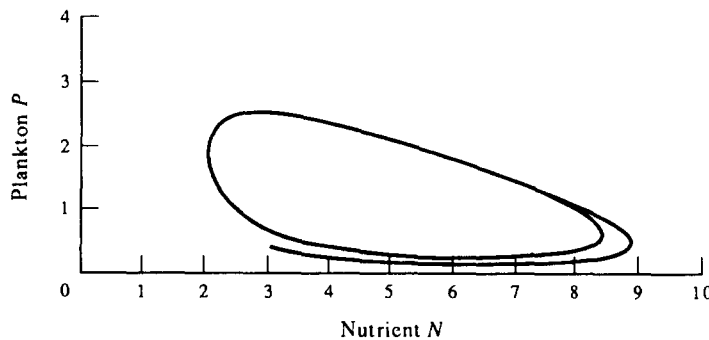


Fig. 2. A trajectory of model (4.11) with $\tau = 0.41$.

We know that E_0 is the only boundary equilibrium of system (4.3). At E_0 the characteristic equation has the form

$$(\lambda + D)(\lambda + \alpha)[\lambda - (a_1 u(N^0) - (\gamma_1 + D_1))] = 0. \tag{4.12}$$

It follows that two of the eigenvalues $\lambda_1 = -D$ and $\lambda_2 = -\alpha$ are negative. If the inequalities in (2.5) hold, then the third eigenvalue $\lambda_3 = a_1 u(N^0) - (\gamma_1 + D_1)$ is positive. Also, in a sufficiently small half-disc neighbourhood of E^0 , dP/dt is positive by the second equation of system (4.3), so there is no trajectory approaching E_0 from the P direction. Hence, E_0 is locally stable in the N and Y directions and is locally unstable in the P direction, that is, E_0 is a saddle point. Solutions initiating on the N -axis tend to E_0 and the stable set of E_0 does not intersect the positive cone. Hence, E_0 is the only compact invariant set on the boundary, and there are no cycles in the boundary.

Therefore, according to the main theorem of Hale and Waltman [26], we have the following result.

THEOREM 4.3. If the inequalities in (2.5) hold, then system (4.3) and, hence, system (4.1) is uniformly persistent.

Note that by proposition 3.4 the inequalities in (2.5) are also persistence conditions for the instantaneous model (3.1).

Table 1. The effects of delays

	Dissipativity	Stability of E^*	Uniform persistence
$\tau = 0$ $F(s) = \delta(s)$	True (proposition 3.1)	Global asymptotic stability (proposition 3.3)	True under (2.5) (proposition 3.4)
$\tau \neq 0$ $F(s) = \delta(s)$	True (proposition 3.5)	Hopf bifurcation (proposition 3.6)	True under (2.5) (proposition 3.7)
$\tau = 0$ $F(s) = \alpha e^{-\alpha s}$	True (proposition 3.8)	Local asymptotic stability (proposition 3.9)	True under (2.5) (proposition 3.10)
$\tau \neq 0$ $F(s) = \alpha e^{-\alpha s}$	True (theorem 4.1)	Hopf bifurcation (theorem 4.2)	True under (2.5) (theorem 4.3)

5. DISCUSSION

We have considered a plankton–nutrient model with a discrete time delay and a distributed time delay. The discrete time delay is regarded as the lag due to gestation and the distributed time delay is used to describe the nutrient recycling.

We have studied the boundedness of solutions of the model. By choosing the discrete delay as a bifurcation parameter, we have shown that a Hopf bifurcation may occur when the discrete delay passes its critical value. This is parallel to the case with only a discrete time delay (proposition 3.6). Note that in the case with only a distributed time delay, Hopf bifurcation does not occur (Beretta *et al.* [1]). Our result shows that the effect of the discrete time delay on the model is somehow stronger than that of the distributed time delay.

We have also investigated persistence of the model. It is interesting that the conditions for uniform persistence are the same as that for the instantaneous model (proposition 3.4 and theorem 4.3), which are also the same conditions for existence of a positive equilibrium. The first equivalent can be explained as that both the discrete time delay and the distributed time delay are “harmless” for persistence in our model. Similar phenomena have been observed by Wang and Ma [27] for models with discrete time delay, and by Burton and Hutson [28] for models with continuous (infinite) delay. Even though the stability of the interior equilibrium cannot be determined in our model, our result shows that existence conditions of the interior equilibrium are enough to ensure uniform persistence of the model.

The effect of both the discrete delay and the distributed delay on dissipativity, stability of the interior equilibrium and persistence are summarized in Table 1.

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