



Nutrient-Plankton Models with Nutrient Recycling

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Abstract—In this paper, nutrient-phytoplankton-zooplankton interaction with general uptake functions in which nutrient recycling is either instantaneous or delayed is considered. To account for higher predation, zooplankton's death rate is modeled by a quadratic term instead of the usual linear function. Persistence conditions for each of the delayed and nondelayed models are derived. Numerical simulations with data from the existing literature are explored to compare the two models. It is demonstrated numerically that increasing zooplankton death rate can eliminate periodic solutions of the system in both the instantaneous and the delayed nutrient recycling models. However, the delayed nutrient recycling can actually stabilize the nutrient-plankton interaction. © 2005 Elsevier Ltd. All rights reserved.

Keywords—Instantaneous nutrient recycling, Delayed nutrient recycling, Uniform persistence.

NOMENCLATURE

N^0	constant input nutrient concentration	γ_1	phytoplankton recycling rate, $0 < \gamma_1 \leq \gamma$
D	nutrient input and washout rate	δ	zooplankton death rate
D_1	phytoplankton washout rate	c	zooplankton recycling rate, $0 < c \leq 1$
D_2	zooplankton washout rate	b	maximal zooplankton ingestion rate of phytoplankton
a	maximal nutrient uptake rate by phytoplankton	α	zooplankton conversion rate, $0 < \alpha \leq 1$
γ	phytoplankton death rate		

1. INTRODUCTION

Deterministic mathematical models of nutrient-plankton interaction with different complexity have been constructed and analyzed since the pioneering work of Riley *et al.* [1] in which a simple

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diffusion model was proposed. The majority of these latter models are formulated in terms of ordinary differential equations [2–15]. However, models of partial differential equations arise when spatial inhomogeneity of either nutrient or plankton distribution is incorporated [16–22].

The importance of nutrient recycling has been well documented [23] and extensively investigated for closed ecological systems. Nutrient recycling in many of these studies is usually assumed to be instantaneous. In other words, the time that is required to regenerate nutrient from dead plankton via bacterial decomposition is neglected in the model formulation. The consideration of delayed nutrient recycling dates back to Beretta *et al.* [24,25] in the early 1990s, where they modeled an open chemostat system with a single species of phytoplankton feeding upon a limiting nutrient and only past dead phytoplankton is partially recycled into the nutrient concentration. They examined the effect of delayed nutrient recycling upon the stability of the interior steady state. In a more recent study by Ruan [11], both the instantaneous and the delayed nutrient recycling were considered for an open nutrient-phytoplankton-zooplankton system. Ruan's numerical simulations demonstrated that the delayed nutrient recycling model exhibits more oscillations than the instantaneous nutrient recycling model [11].

Following the work of Lotka-Volterra, the death rate of an organism in most of the mathematical models is usually modeled by a linear functional, i.e., the per capita mortality rate of a biological population is a constant. The simplicity of this assumption makes the model mathematically tractable. The choice of zooplankton's mortality is biologically controversial and it has a significant impact on the dynamics of the resulting system. A quadratic term used to model zooplankton death rate was initiated by Edwards and Brindley [5]. They demonstrated numerically that the limiting cycle behavior for which a linear death rate was considered disappeared when a quadratic death rate for zooplankton was assumed.

The purpose of this study is to investigate nutrient-plankton interaction in an open ecological system with both the instantaneous and delayed nutrient recycling, where we use a quadratic term to model zooplankton mortality. Parameter values cited in the existing literature are numerically simulated to make our comparison. For each of these models, explicit conditions are derived for population persistence. Unlike other ecological models for which delays can destabilize the system, our numerical simulations presented here suggest that delayed nutrient recycling can actually stabilize the nutrient-plankton system. Moreover, the periodic solution of the system disappeared as we increase zooplankton's mortality rate, and this finding is the same as that of the result obtained by Edwards and Brindley [5].

The remaining manuscript is organized as follows. The nutrient-plankton model with instantaneous nutrient recycling is presented in the next section. Section 3 studies the model with delayed nutrient recycling. Numerical examples and simulations are given in Section 4. The final section provides a brief summary and discussion.

2. THE MODEL WITH INSTANTANEOUS NUTRIENT RECYCLING

Let $N(t)$, $P(t)$, and $Z(t)$ be the nutrient concentration, the phytoplankton population, and zooplankton population at time t , respectively. The two plankton levels are modeled in terms of nutrient content and therefore their units are nitrogen or nitrate per unit volume. We let γ and δZ denote the per capita death rate of phytoplankton and zooplankton, respectively. The quadratic mortality rate δZ^2 is used to model higher predation by invertebrate upon zooplankton. In a natural nutrient-plankton system, waters flowing into the system bring input of fluxes of nutrients and outflows also carry out nutrients [23]. We assume that the input nutrient concentration is a constant and is denoted by N^0 . The rate of the waters flowing in and out of the system is assumed to be a constant D . However, we use D_1 and D_2 for phytoplankton population and zooplankton population washout rate respectively, where D , D_1 , and D_2 may be different to account for other physical consideration such as sinking of phytoplankton.

The phytoplankton nutrient uptake and zooplankton grazing are modeled by general functions f and g , respectively, and our analysis is carried out for these general functions. However, we will use particular functional forms for our numerical study in later section. The functional responses f and g are assumed to satisfy the following hypotheses.

- (H1) $f \in C^1([0, \infty))$, $f(0) = 0$, $f'(x) > 0$, for $x \geq 0$ and $\lim_{x \rightarrow \infty} f(x) = 1$.
 (H2) $g \in C^1([0, \infty))$, $g(0) = 0$, $g'(x) > 0$, for $x \geq 0$ and $\lim_{x \rightarrow \infty} g(x) = 1$.

In particular, Michaelis-Menten kinetics, Ivellev and Holling type III satisfy both hypotheses. Let parameter a be the maximal nutrient uptake rate of phytoplankton and b be the maximal zooplankton ingestion rate. Parameters α and c are the fraction of zooplankton grazing conversion and nutrient recycling, respectively.

Since phytoplankton uptakes nutrient and zooplankton preys on the phytoplankton, there are minus terms $-af(N)P$ and $-bg(P)Z$ in the equations for \dot{N} and \dot{P} , respectively. Positive feed back terms $\gamma_1 P$, $c\delta Z^2$, and $(1 - \alpha)bg(P)Z$ will appear in the equation \dot{N} due to recycling. Our model with the above biological assumptions can be written as the following three-dimensional ordinary differential equations,

$$\begin{aligned}\dot{N} &= D(N^0 - N) - af(N)P + \gamma_1 P + c\delta Z^2 + (1 - \alpha)bg(P)Z, \\ \dot{P} &= af(N)P - \gamma P - bg(P)Z - D_1 P, \\ \dot{Z} &= \alpha bg(P)Z - \delta Z^2 - D_2 Z, \\ N(0), P(0), Z(0) &\geq 0,\end{aligned}\tag{2.1}$$

where $0 < \gamma_1 \leq \gamma$, $0 < \alpha$, $c \leq 1$, and $D, N^0, a, b, D_1, D_2, \delta > 0$.

The parameters in system (2.1) and their biological meanings are summarized in the nomenclature at the beginning of the paper.

Clearly, solutions of (2.1) exist for all positive time. If $N(0) = 0$, then, $\dot{N}(0) > 0$ implies $N(t) > 0$, for $t > 0$ sufficiently small. On the other hand, if there exists $t_0 > 0$, such that $N(t_0) = 0$ and $N(t) > 0$, for $0 \leq t < t_0$, then, $\dot{N}(t_0) > 0$, and we obtain a contradiction. This shows that $N(t) > 0$, for $t > 0$. Similar arguments can be shown that $P(t)$ and $Z(t)$ remain nonnegative for all positive time. Let $T = N + P + Z$. Then, $\dot{T} \leq D(N^0 - N) - D_1 P - D_2 Z \leq DN^0 - D_0 T$, where $D_0 = \min\{D, D_1, D_2\}$. Thus,

$$\limsup_{t \rightarrow \infty} (N(t) + P(t) + Z(t)) \leq \frac{DN^0}{D_0},$$

and we conclude the following lemma.

LEMMA 2.1. *Solutions of (2.1) are nonnegative and bounded.*

Our next step is to find simple solutions of (2.1). The trivial equilibrium $E_0 = (N^0, 0, 0)$ always exists for (2.1). A steady state on the interior of NP -plane exists if $f(N) = \gamma + D_1/a$ has a solution N_1 and $N_1 < N^0$. In this case, the steady state is unique and is denoted by $E_1 = (N_1, P_1, 0)$, where $P_1 = (D(N^0 - N_1))/(\gamma + D_1 - \gamma_1) > 0$. Clearly, there is no interior steady state on the NZ -coordinate plane due to the fact that zooplankton is obligate to phytoplankton. The existence of an interior steady state is difficult to derive analytically due to the quadratic term δZ^2 in (2.1) and its uniqueness is also not clear either. However, if $(\bar{N}, \bar{P}, \bar{Z})$ is a positive steady state, then, $\bar{N} > N_1$ by the second equation of (2.1).

From the Jacobian matrix associated with system (2.1), we can conclude that E_0 is locally asymptotically stable if $af(N^0) < \gamma + D_1$ and E_1 is locally asymptotically stable if $\alpha bg(P_1) < D_2$. In particular, E_0 is locally asymptotically stable if $a \leq \gamma + D_1$. In the following, we show that E_0 is globally asymptotically stable if the inequality is true.

THEOREM 2.2. *If $a \leq \gamma + D_1$, then, E_0 is the only equilibrium and solutions of (2.1) converge to E_0 .*

PROOF. The uniqueness of the steady state E_0 is trivial. Note $\dot{P} < (a - D_1 - \gamma)P$ implies $\lim_{t \rightarrow \infty} P(t) = \hat{p}$ exists. By using $\lim_{t \rightarrow \infty} \dot{P}(t) = 0$, we have $\hat{p} = 0$. Thus, for any $\epsilon > 0$, there exists $t_0 > 0$, such that $P(t) < \epsilon$, for $t \geq t_0$. We choose $\epsilon > 0$, such that $\alpha bg(\epsilon) - D_2 < 0$. Hence, $\dot{Z}(t) \leq [\alpha bg(\epsilon) - D_2]Z(t)$, for $t \geq t_0$ implies $\lim_{t \rightarrow \infty} Z(t) = 0$. Consequently, for any $\epsilon > 0$, there exists $t_1 > 0$, such that $P(t), Z(t) < \epsilon$, for $t \geq t_1$. Therefore, $\dot{N}(t) \leq D(N^0 - N) + \gamma_1\epsilon + c\delta\epsilon^2 + (1 - \alpha)bg(\epsilon)\epsilon$, if $t \geq t_1$, and hence,

$$\limsup_{t \rightarrow \infty} N(t) \leq \frac{DN^0 + \gamma_1\epsilon + c\delta\epsilon^2 + (1 - \alpha)bg(\epsilon)\epsilon}{D}.$$

Letting $\epsilon \rightarrow 0^+$, we have $\limsup_{t \rightarrow \infty} N(t) \leq N^0$. Similarly, since there exists $M > 0$, such that $N(t) \leq M$, for $t \geq 0$, we have

$$\dot{N} \geq D(N^0 - N) - af(M)\epsilon,$$

for $t \geq t_1$ and it can be shown that $\liminf_{t \rightarrow \infty} N(t) \geq N^0$. Thus, $\lim_{t \rightarrow \infty} N(t) = N^0$ and E_0 is globally asymptotically stable. ■

THEOREM 2.3. *If $af(N^0) > \gamma + D_1$, then, steady states $E_0 = (N^0, 0, 0)$ and $E_1 = (N_1, P_1, 0)$ both exist for (2.1), where E_0 is unstable and E_1 is globally asymptotically stable on the positive NP -plane. In addition,*

- (a) *if $\alpha bg(P_1) < D_2$, then, (2.1) has no positive steady state and E_1 is locally asymptotically stable;*
- (b) *if $\alpha bg(P_1) > D_2$, then, E_1 is unstable and system (2.1) is uniformly persistent.*

PROOF. Since $af(N^0) > \gamma + D_1$ and (H1) holds, $af(N) = \gamma + D_1$ has a solution $N_1 < N^0$. Thus, steady state E_1 exists and E_0 is unstable. We apply the Dulac criterion to eliminate the existence of a nontrivial periodic solution in the NP -plane by choosing $B(N, P) = 1/P$, for $N \geq 0, P > 0$. Then,

$$\frac{\partial}{\partial N}(B\dot{N}) + \frac{\partial}{\partial P}(B\dot{P}) = -D/P - af'(N) < 0,$$

for $N \geq 0, P > 0$. Therefore, E_1 is globally asymptotically stable on the NP plane by the Poincaré-Bendixson theorem.

(a) Suppose now $\alpha bg(P_1) < D_2$. It's clear that E_1 is locally asymptotically stable by the Jacobian matrix $J(E_1)$. We prove that (2.1) has no positive steady state. Suppose on the contrary that (2.1) has a positive steady state $E_2 = (\bar{N}, \bar{P}, \bar{Z})$. Then, $\alpha bg(\bar{P}) = \delta\bar{Z} + D_2 > D_2$, and thus, $\bar{P} > P_1$. On the other hand, $D(N^0 - \bar{N}) = (\gamma + D_1 - \gamma_1)\bar{P} + D_2\bar{Z} + (1 - c)\delta\bar{Z}^2$ and $D(N^0 - N_1) = (\gamma + D_1 - \gamma_1)P_1 < (\gamma + D_1 - \gamma_1)\bar{P} < D(N^0 - \bar{N})$ imply $N_1 > \bar{N}$. This contradicts an earlier observation that $N_1 < \bar{N}$. Hence, (2.1) has no interior steady state.

(b) Since $\alpha bg(P_1) > D_2$, it follows from the Jacobian matrix at E_1 that E_1 is unstable. Moreover, since (2.1) is dissipative, the remaining assertion follows from the standard techniques of uniform persistence theory. Indeed, since E_1 is globally asymptotically stable on the positive NP plane, unstable in the positive direction orthogonal to the NP plane, and E_0 is globally asymptotically stable on the positive NZ plane and unstable in the direction orthogonal to the NZ plane, (2.1) is weakly persistent and thus uniformly persistent [26]. ■

Notice that system (2.1) may not have a positive steady state $(\bar{N}, \bar{P}, \bar{Z})$ even when $af(N^0) > \gamma + D_1$ and $\alpha bg(P_1) > D_2$. We illustrate this point by considering the case when $\delta = 0$. It follows from the third equation of (2.1) that \bar{P} must solve $g(P) = D_2/\alpha b$. After some straightforward calculations, it can be seen that \bar{N} satisfies

$$D(N^0 - N) + \gamma_1\bar{P} - \alpha af(N)\bar{P} - (\gamma + D_1)(1 - \alpha)\bar{P} = 0. \tag{2.2}$$

Since the derivative of the left-hand side of (2.2) with respect to N is negative, a positive solution \bar{N} exists if

$$DN^0 + \gamma_1 \bar{P} > (1 - \alpha)(\gamma + D_1) \bar{P}.$$

If the above inequality is satisfied, then, a unique positive steady state $(\bar{N}, \bar{P}, \bar{Z})$ exists if in addition $af(\bar{N}) - \gamma - D_1 > 0$. Therefore, the positive steady state may not always exist even when both boundary steady states are unstable. This conclusion is very different from previous plankton models studied by many authors [3,5,7-9,14,15] for which a positive steady state is guaranteed to exist if the boundary steady states are unstable. Numerical simulations in Section 4 will illustrate the observation made here.

3. THE MODEL WITH DELAYED NUTRIENT RECYCLING

In this section, we incorporate delayed nutrient recycling into model (2.1). The model now takes the following form.

$$\begin{aligned} \dot{N} &= D(N^0 - N) - af(N)P + (1 - \alpha)bg(P)Z + \gamma_1 \int_{-\infty}^t F_1(t - s)P(s) ds \\ &\quad + c\delta \int_{-\infty}^t F_2(t - s)Z^2(s) ds, \\ \dot{P} &= af(N)P - \gamma P - bg(P)Z - D_1P, \\ \dot{Z} &= \alpha bg(P)Z - \delta Z^2 - D_2Z, \\ N(0) &\geq 0, \quad P(x) = \phi(x), \quad Z(x) = \psi(x), \quad -\infty < x \leq 0, \end{aligned} \tag{3.1}$$

where $\phi, \psi : (-\infty, 0] \rightarrow [0, \infty)$ are bounded and continuous, and the delay kernels $F_i : [0, \infty) \rightarrow [0, \infty)$ are continuous, bounded and satisfy $\int_0^\infty F_i(s) ds = 1$, for $i = 1, 2$. The assumptions about f and g are given in (H1) and (H2), respectively.

Our first step in studying system (3.1) is to prove that the system is biologically meaningful, i.e., we show that solutions of (3.1) remain nonnegative and are bounded.

LEMMA 3.1. *Solutions of (3.1) are nonnegative and bounded.*

PROOF. Let $(N(t), P(t), Z(t))$ be a solution of (3.1). Clearly, if $P(t_0) = 0$, for some $t_0 \geq 0$, then, $P(t) = 0$, for $t \geq t_0$. The same is true for $Z(t)$. If $N(0) = 0$, then, $\dot{N}(0) > 0$ implies $N(t) > 0$, for $t > 0$ sufficiently small. Suppose on the other hand there exists $t_1 > 0$, such that $N(t_1) = 0$ and $N(t) > 0$, for $0 < t < t_1$. Then, we must have $\dot{N}(t_1) \leq 0$, but it follows from the first equation of (3.1) that $\dot{N}(t_1) \geq DN^0 > 0$. We obtain a contradiction. Hence, we conclude that solutions of (3.1) are nonnegative.

To show solutions of (3.1) are bounded, we construct a Liapunov function as follows. Let $V : R_+^3 \rightarrow R_+$ be defined by

$$V = N + P + Z + \gamma_1 \int_0^\infty \int_{t-s}^t F_1(s)P(u) du ds + c\delta \int_0^\infty \int_{t-s}^t F_2(s)Z^2(u) du ds.$$

Then, $V \geq 0$, $V \rightarrow \infty$ as $\|(N, P, Z)\| \rightarrow \infty$ and the time derivative of V along the trajectories of (3.1) is

$$\begin{aligned} \dot{V} &= \dot{N} + \dot{P} + \dot{Z} + \gamma_1 \int_0^\infty [F_1(s)P(t) - F_1(s)P(t - s)] ds \\ &\quad + c\delta \int_0^\infty [F_2(s)Z^2(t) - F_2(s)Z^2(t - s)] ds \\ &= D(N^0 - N) + \gamma_1 P + c\delta Z^2 - \gamma P - \delta Z^2 - D_1P - D_2Z. \end{aligned}$$

Let $S = \{(N, P, Z) \in R_+^3 : DN^0 = DN + (\gamma - \gamma_1)P + (1 - c)\delta Z^2 + D_1P + D_2Z\}$. Then, $\dot{V} < 0$ in the positive octant outside of the region bounded by the surface S . As a result, solutions of (3.1) are bounded by [27]. ■

Since the delay kernels are normalized to one, it is straightforward to see that system (3.1) always has steady state $E_0 = (N^0, 0, 0)$, and the existence of boundary steady state $E_1 = (N_1, P_1, 0)$ is the same as system (2.1). Let $n = N - N^0$, $p = P$, and $z = Z$. The linearization [28,29] of (3.1) with respect to E_0 yields the following system,

$$\begin{aligned} \dot{n} &= -Dn - af(N^0)p + \gamma_1 \int_{-\infty}^t F_1(t-s)p(s) ds, \\ \dot{p} &= af(N^0)p - \gamma p - D_1p, \\ \dot{z} &= -D_2z. \end{aligned} \tag{3.2}$$

Let $B^*(\lambda)$ denote the Laplace transform of F_1 , i.e., $B^*(\lambda) = \int_0^\infty e^{-\lambda s} F_1(s) ds$. The roots of the characteristic equation associated with E_0 are the zeros of the determinant of the following matrix,

$$\begin{pmatrix} \lambda + D & af(N^0) - \gamma_1 B^*(\lambda) & 0 \\ 0 & \lambda - af(N^0) + \gamma + D_1 & 0 \\ 0 & 0 & \lambda + D_2 \end{pmatrix}.$$

It follows that the roots of the characteristic equation are $-D, -D_2$, and $af(N^0) - \gamma - D_1$. Therefore, E_0 is locally asymptotically stable for (3.1) if $af(N^0) < \gamma + D_1$. In the following, we show that E_0 is globally asymptotically stable if $a \leq \gamma + D_1$.

THEOREM 3.2. *If $a \leq \gamma + D_1$, then, $E_0 = (N^0, 0, 0)$ is globally asymptotically stable for (3.1).*

PROOF. Let $(N(t), P(t), Z(t))$ be a solution of (3.1). The proof of

$$\lim_{t \rightarrow \infty} P(t) = 0 \quad \text{and} \quad \lim_{t \rightarrow \infty} Z(t) = 0$$

follows similarly as in the proof of Theorem 2.2. Then, it is straightforward to show that

$$\int_{-\infty}^t F_1(t-s)P(s) ds = 0.$$

Indeed, for any $\epsilon > 0$ there exists $t_0 > 0$, such that $P(t) < \epsilon$, for $t \geq t_0$. Since solutions of (3.1) are bounded, there exists $K > 0$, such that $K = \sup_{-\infty < t < \infty} P(t) < \infty$. Thus,

$$\begin{aligned} \int_{-\infty}^t F_1(t-s)P(s) ds &= \int_{-\infty}^{t_0} F_1(t-s)P(s) ds + \int_{t_0}^t F_1(t-s)P(s) ds \\ &= \int_{t-t_0}^\infty F_1(s)P(t-s) ds + \int_{t_0}^t F_1(t-s)P(s) ds \\ &\leq K \int_{t-t_0}^\infty F_1(s) ds + \epsilon, \\ &\rightarrow \epsilon \text{ as } t \rightarrow \infty. \end{aligned}$$

Since $\epsilon > 0$ is arbitrary, this completes the claim. Similarly since $\lim_{t \rightarrow \infty} Z(t) = 0$, we can prove that $\lim_{t \rightarrow \infty} \int_{-\infty}^t F_2(t-s)Z^2(s) ds = 0$. It follows from the first equation of (3.1) that $\lim_{t \rightarrow \infty} N(t) = N^0$ and E_0 is globally asymptotically stable. ■

We remark that the proof of Theorem 3.2 can be carried over to the case when $P(0) = 0$ without the assumption $a \leq \gamma + D_1$ as zooplankton feeds upon phytoplankton alone. Therefore, E_0 is always globally asymptotically stable on the NZ -plane. If $af(N^0) > \gamma + D$, then, E_0 is unstable

and there exists a steady state $E_1 = (N_1, P_1, 0)$, where N_1, P_1 are defined as in Section 2. Let $n = N - N_1$, $p = P - P_1$, and $z = Z$. The linearization of system (3.1) at E_1 yields the following system,

$$\begin{aligned} \dot{n} &= -Dn - af'(N_1)P_1n - af(N_1)p + (1 - \alpha)bg(P_1)z + \gamma_1 \int_{-\infty}^t F_1(t - s)p(s) ds, \\ \dot{p} &= af'(N_1)P_1n - bg(P_1)z, \\ \dot{z} &= \alpha bg(P_1)z - D_2z. \end{aligned} \tag{3.3}$$

The characteristic equation satisfies

$$[\lambda - \alpha bg(P_1) + D_2] \{ \lambda^2 + [D + af'(N_1)P_1]\lambda + af'(N_1)P_1 [af(N_1) - \gamma_1 B^*(\lambda)] \} = 0.$$

Clearly, one solution is $\lambda = \alpha bg(P_1) - D_2$, which is real. The remaining solutions satisfy

$$\lambda^2 + [D + af'(N_1)P_1]\lambda + af'(N_1)P_1 [af(N_1) - \gamma_1 B^*(\lambda)] = 0. \tag{3.4}$$

Notice that $\lambda = 0$ cannot be a solution of (3.4) as $B^*(0) = 1$ and $af(N_1) = \gamma + D_1 > \gamma_1$. Moreover, (3.4) is also the characteristic equation of the NP subsystem of (3.1) at steady state (N_1, P_1) . We derive a sufficient condition, such that solutions of (3.4) lie on the left half complex plane and thus, we can conclude that (N_1, P_1) is locally asymptotically stable for the NP subsystem of (3.1). Our argument given here is similar to that of MacDonald [30].

Since solutions of (3.4) are continuous functions of the coefficients and it is known from Section 2 that (N_1, P_1) is globally asymptotically stable for the NP subsystem when there is no delay, it is sufficient to examine the case when solutions of (3.4) are purely imaginary. Observe that if $\lambda = \beta i$ is a solution, then, $\lambda = -\beta i$ is also a solution. Thus, letting $\lambda = \beta i$, $\beta > 0$, (3.4) becomes

$$\frac{-\beta^2 + [D + af'(N_1)P_1]\beta i + a^2 f'(N_1)P_1 f(N_1)}{af'(N_1)P_1 \gamma_1} = \int_0^\infty e^{-\beta si} F_1(s) ds.$$

Let the left-hand side of the above equation be denoted by $F(\beta i)$. Since $|\int_0^\infty e^{-\beta si} F_1(s) ds| \leq 1$, a necessary condition for $z = \beta i$ to be a solution of (3.4) is $|F(\beta i)| \leq 1$. We shall impose a condition on the parameters so that the necessary condition $|F(\beta i)| \leq 1$ is violated and consequently, we will be able to conclude that solutions of (3.4) have negative real parts.

Let

$$G(\beta) = |F(\beta i)|^2 = \frac{[a^2 f'(N_1) f(N_1) P_1 - \beta^2]^2}{a^2 [f'(N_1)]^2 P_1^2 \gamma_1^2} + \frac{\beta^2 [D + af'(N_1)P_1]^2}{a^2 [f'(N_1)]^2 P_1^2 \gamma_1^2}.$$

Then,

$$G(0) = \frac{a^2 [f(N_1)]^2}{\gamma_1^2} > 1, \quad \text{as } af(N_1) = \gamma + D_1 > \gamma_1,$$

and

$$G'(\beta) = \frac{4\beta^3 + 2\beta [(D + af'(N_1)P_1)^2 - 2a^2 f'(N_1) f(N_1) P_1]}{a^2 [f'(N_1)]^2 P_1^2 \gamma_1^2}.$$

Therefore, if

$$[D + af'(N_1)P_1]^2 \geq 2a^2 f'(N_1) f(N_1) P_1, \tag{3.5}$$

then, $G'(\beta) > 0$, for $\beta > 0$. Hence, $|F(\beta i)| > 1$, for all $\beta > 0$. Consequently, the real parts of λ of solutions of (3.4) are negative if (3.5) is satisfied. We summarize our results into the following.

THEOREM 3.3. *If $af(N^0) > \gamma + D$, $\alpha bg(P_1) < D_2$ and (3.5) holds, then, $E_1 = (N_1, P_1, 0)$ is locally asymptotically stable for (3.1).*

Therefore, as long as local asymptotic stability of E_1 is concerned, delayed-nutrient recycling model can destabilize the system. Suppose now $\alpha bg(P_1) > D_2$, so that E_1 is unstable. Similar to Section 2, we adopt the concept of persistence to show long term survival of the populations. Specifically, system (3.1) is said to be *uniformly persistent* if there exists $m > 0$, such that

$$\begin{aligned}\liminf_{t \rightarrow \infty} N(t) &\geq m, \\ \liminf_{t \rightarrow \infty} P(t) &\geq m,\end{aligned}$$

and

$$\liminf_{t \rightarrow \infty} Z(t) \geq m,$$

for any solution of (3.1) with $N(0) > 0$, $\phi(x) > 0$, and $\psi(x) > 0$, for $-\infty < x \leq 0$. In the following, we apply Theorem 3.3 of Ruan and Wolkowicz [31] to provide a set of sufficient conditions for which system (3.1) is uniformly persistent.

THEOREM 3.4. *Suppose $af(N^0) > \max\{\gamma + D_1 + D_2, \gamma + D\}$ and $\alpha bg(P_1) > D_2$ hold. Then, system (3.1) is uniformly persistent.*

PROOF. We need to construct a Liapunov-like function. Define $\rho(N, P, Z) = NPZ$. Then, ρ is continuous on \mathbb{R}_+^3 , $\rho(N, P, Z) = 0$ if and only if either $N = 0$, $P = 0$, or $Z = 0$. Moreover,

$$\begin{aligned}\psi(N, P, Z) &= \frac{\dot{\rho}(N, P, Z)}{\rho(N, P, Z)} \\ &= D \left(\frac{N^0}{N} - 1 \right) - af(N)P/N + (1 - \alpha)bg(P)Z/N \\ &\quad + \gamma_1/N \int_{-\infty}^t F_1(t-s)P(s)ds + \alpha bg(P) - \delta Z - D_2 \\ &\quad + c\delta/N \int_{-\infty}^t F_2(t-s)Z^2(s)ds + af(N) - \gamma - bg(P)Z/P - D_1,\end{aligned}$$

where $\psi(N^0, 0, 0) = af(N^0) - \gamma - D_1 - D_2 > 0$ and $\psi(N_1, P_1, 0) = 1/N_1[D(N^0 - N_1) - af(N_1)P_1 + \gamma_1 P_1] + \alpha bg(P_1) - D_2 = \alpha bg(P_1) - D_2 > 0$, i.e., $\psi(N, P, Z) > 0$ at E_0 and E_1 . Thus, (3.1) is uniformly persistent by [31]. \blacksquare

4. NUMERICAL SIMULATIONS

In this section, we will use numerical simulations to study systems (2.1) and (3.1). Michaelis-Menton functions as nutrient uptake rate for phytoplankton are frequently adopted by many researchers. We will first use Michaelis-Menton forms to simulate our models. Specifically, $f(N) = N/(k + N)$, where the half-saturation constant k varies from 0.02 to 0.25. The zooplankton grazing rate is also modeled by a Michaelis-Menton function $g(P) = P/(m + P)$, where m has the same range as that of k . This range is within the parameter region given in [5], where the data in [5] were collected from different research articles using these functional forms. The model for the instantaneous nutrient recycling is given below.

$$\begin{aligned}\dot{N} &= D(N^0 - N) - \frac{aNP}{k + N} + c\delta Z^2 + (1 - \alpha)\frac{bPZ}{m + P} + \gamma_1 P, \\ \dot{P} &= \frac{aNP}{k + N} - \gamma P - \frac{bPZ}{m + P} - D_1 P, \\ \dot{Z} &= \alpha\frac{bPZ}{m + P} - \delta Z^2 - D_2 Z,\end{aligned}\tag{4.1}$$

$N(0), P(0), Z(0) > 0.$

For the delayed model, we choose delay kernels $F_1(t - s) = 0.02e^{-0.02(t-s)}$ and $F_2(t - s) = 0.01e^{-0.01(t-s)}$. Consequently, model (3.1) becomes

$$\begin{aligned} \dot{N} &= D(N^0 - N) - \frac{aNP}{k + N} + (1 - \alpha) \frac{bPZ}{m + P} + 0.02\gamma_1 \int_{-\infty}^t e^{-0.02(t-s)} P(s) ds, \\ &\quad + 0.01c\delta \int_{-\infty}^t e^{-0.01(t-s)} Z^2(s) ds, \\ \dot{P} &= \frac{aNP}{k + N} - \gamma P - \frac{bPZ}{m + P} - D_1 P, \\ \dot{Z} &= \alpha \frac{bPZ}{m + P} - \delta Z^2 - D_2 Z \end{aligned} \tag{4.2}$$

$N(0), P(0), Z(0) > 0.$

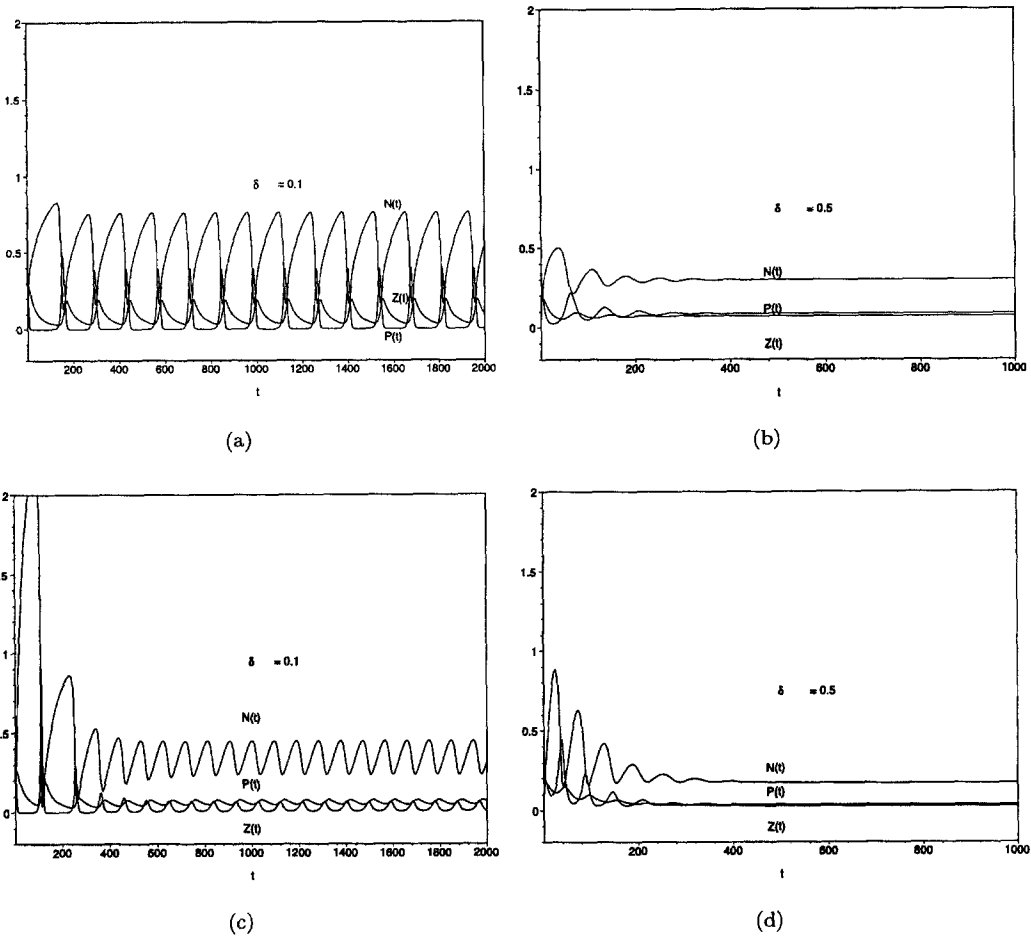


Figure 1. The top two figures are for system (4.1) while the bottom figures are for system (4.2). Solutions with initial condition $N(0) = 0.1, P(0) = 0.4,$ and $Z(0) = 0.2$ are plotted.

Specific parameter values are

$$\begin{aligned} D &= D_1 = D_2 = 0.01, \\ N^0 &= 1.0, \\ a &= b = c = 0.6, \\ k &= m = 0.2, \end{aligned}$$

$$\gamma = 0.2,$$

$$\gamma_1 = 0.15,$$

and

$$\alpha = 0.25.$$

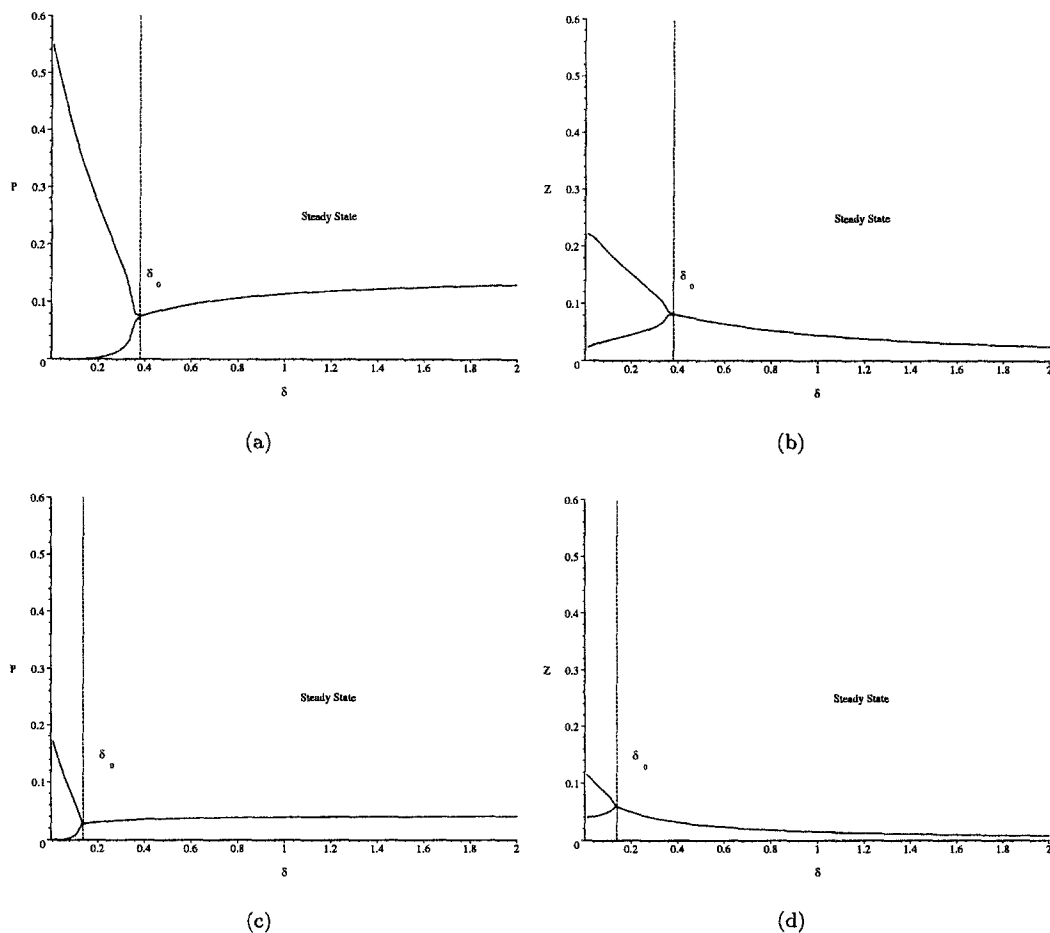


Figure 2. When D , D_1 , and D_2 are increased to 0.1, both systems (4.1) and (4.2) have a unique positive steady state even when δ is very small as shown by the top two figures for systems (4.1) and (4.2), respectively. The bottom two figures used Holling-III (4.3) as phytoplankton nutrient uptake rate. All the other parameters used are the same as that of Figure 1.

These parameter values are within the range of the values investigated by [5]. Note that, in this case, $N_1 = 0.1077$ and $P_1 = 0.1487$. Also, $af(N^0) = 0.5 > \gamma + D_1 + D_2 = 0.22$ and $abg(P_1) = 0.064 > D_2 = 0.01$. Therefore, it follows from Theorems 2.2 and 3.4 that systems (4.1) and (4.2) are uniformly persistent. However, simulations suggest that there exists no positive steady state when $\delta > 0$ is small. When $\delta = 0.1$, numerical simulations indicate that there is a unique positive periodic solution and solutions of (4.1) with positive initial conditions are asymptotic to this positive periodic solution. The same is also found for the delayed model (4.2). As we increase δ , the positive periodic solution disappeared and there exists a unique positive steady state for both systems. Simulations also demonstrate that solutions of (4.1) and respectively, (4.2) with positive initial conditions converge to the positive steady state. The top two plots of Figure 1 plot the

solution of system (4.1) with initial condition $N(0) = 0.1$, $P(0) = 0.4$, and $Z(0) = 0.2$. The bottom two plots are for the delayed model (4.2). From these figures, we see that the solution converges to the positive steady state when $\delta = 0.5$. However, convergence of solutions of (4.2) to the steady state are faster than convergence of solutions of (4.1).

Bifurcation diagrams using δ as our bifurcation parameter are given here, where we plot the minimum and maximum values of the components of the positive periodic solution when it exists. As shown on these figures, positive periodic solutions occur first and then followed by positive steady state as we increase δ , where δ_0 is the smallest δ value for which the positive steady state is nonhyperbolic. From these numerical simulations for both delayed and nondelayed models, we conclude that the predation by higher predator upon the zooplankton can stabilize the system, i.e., the quadratic death rate of zooplankton can eliminate periodic solution. This conclusion is similar to the one obtained in [3] for which the method of numerical simulation was explored. Moreover, from these plots, we see that the values of δ_0 for model (4.2) are smaller than those δ_0 values for the nondelayed model (4.1). Therefore, we can conclude that the delayed model can stabilize the system. This numerical finding is very different from the common belief that delay can destabilize the system.

We now change D values but keep other parameter values fixed except δ . Specifically, we use $D = D_1 = D_2 = 0.1$ and $\delta = 0.001$. Simulations suggest that the system now has a unique positive steady state and solutions of system (4.1) with positive initial conditions all converge to this steady state. The same is also true for system (4.2). The top two figures in Figure 2 plot solutions of systems (4.1) and (4.2) respectively, with initial condition $(N(0), P(0), Z(0)) = (0.1, 0.4, 0.2)$. The figure on the left is for system (4.1) while the plot on the right is for system (4.2).

We next use all the same parameter values as that for Figure 1 but change phytoplankton uptake rate $f(N)$ to

$$f(N) = \frac{N^2}{k + N^2}, \quad (4.3)$$

with $k = 0.2$. Clearly, this functional form satisfies (H1) and is often referred to as a Holling-III functional response. Simulations show that similar numerical results are obtained when $D = D_1 = D_2 = 0.01$. The bottom two figures in Figure 2 plot the solution of both nondelayed and delayed systems with the same initial condition as Figure 1, respectively.

5. DISCUSSION

Nutrient-plankton interaction with different complexities have been intensively investigated. In addition to its central role in the global carbon cycle, planktonic communities comprise a wide diversity of organisms that form the basis of marine food webs. A recent paper by Grover [32] used a stoichiometry approach with several nutrients to investigate plankton interaction. In this manuscript, we studied nutrient-phytoplankton-zooplankton models with a single nutrient in a natural open system. The per capita death rate of zooplankton is modeled by a linear function of the zooplankton population instead of a constant. This assumption takes into account the higher level predation upon zooplankton. The consideration was first incorporated and investigated by [4]. They showed numerically that a quadratic zooplankton death rate can eliminate the periodic solutions for which a linear death rate was used.

Our analysis showed that the mortality rate of zooplankton plays no role in the system for persistence of both plankton populations. This observation is illustrated in Theorem 2.3(b) and Theorem 3.4. Moreover, local stability of the boundary steady states for either the instantaneous or delayed nutrient recycling model is also independent of the zooplankton death rate. However, our numerical simulations in this study suggest that zooplankton's quadratic death rate can eliminate the existence of periodic solutions for which a linear zooplankton mortality was employed. This is demonstrated by the bifurcation diagrams given in Figure 3 with $\delta > 0$ very

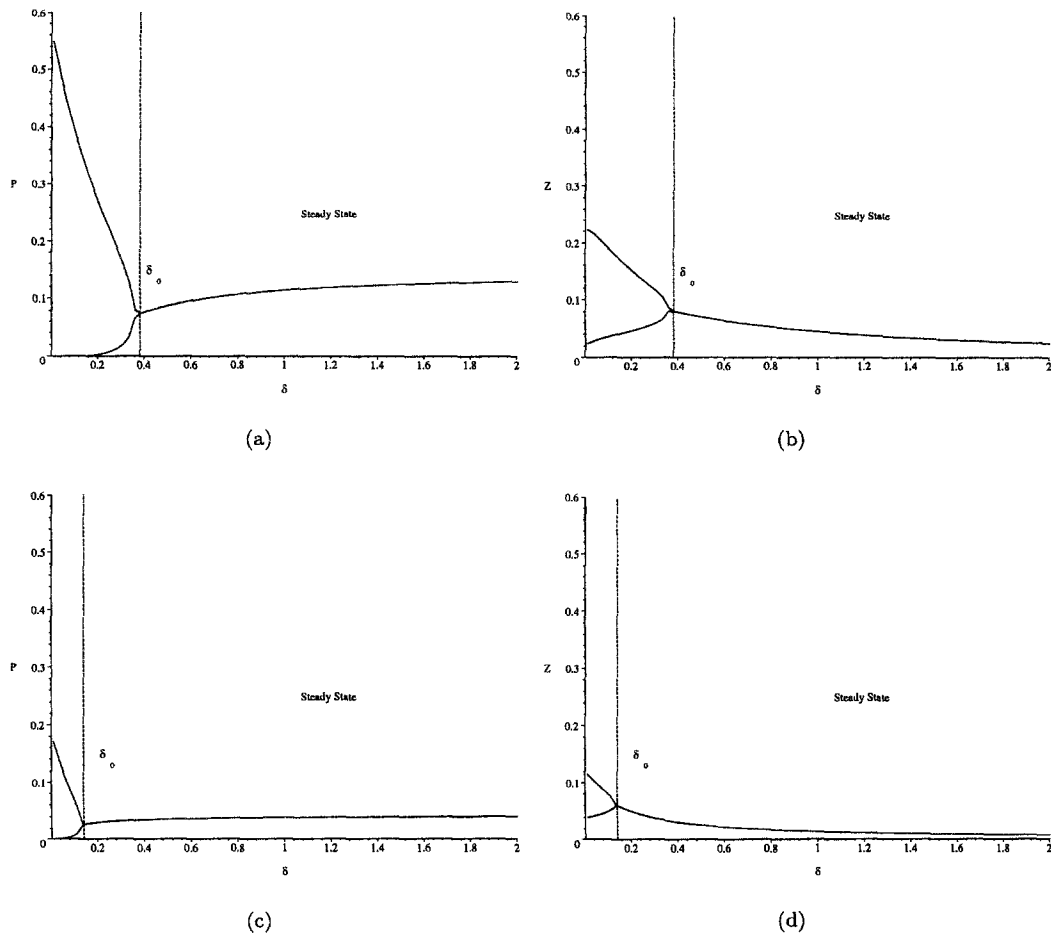


Figure 3. Bifurcation diagrams are given here. The top figures are for system (4.1) and the bottom figures are for system (4.2). We only plot the P and Z components.

small. With the same parameter values given in both the instantaneous and delayed nutrient recycling models, we see from these bifurcation diagrams that the delayed model can actually stabilize the system. That is, δ_0 in the delayed model is smaller than δ_0 in the nondelayed model. This numerical result is very different from the common belief that delay can destabilize the system. On the other hand, natural systems are in general stable. This study provides valuable finding that delay may not destabilize the system if the system incorporates more complex and more realistic assumptions within the model.

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