

# Nutrient-plankton models with nutrient recycling

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**Abstract.** 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 non-delayed 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.

**Keywords:** instantaneous nutrient recycling, delayed nutrient recycling, uniform persistence

## 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 diffusion model was proposed. The majority of these latter models are formulated in terms of ordinary differential equations [2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15]. However, models of partial differential equations arise when spatial inhomogeneity of either nutrient or plankton distribution is incorporated [16, 17, 18, 19, 20, 21, 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  $\gamma$  and  $\delta Z$  denote the per capita death rate of phytoplankton and zooplankton respectively. The quadratic mortality rate  $\delta Z^2$  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 functionals  $f$  and  $g$ , respectively, and our analysis is carried out for these general functions. However, we will use particular functional form for our numerical study in later section. The functional responses  $f$  and  $g$  are assumed to satisfy the following hypotheses.

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

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

In particular, Michaelis-Menten kinetics, Ivelov 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  $\alpha$  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 below.

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

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  $NZ$ -plane exists if  $f(N) = \frac{\gamma + D_1}{a}$  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  $P_1 = \frac{D(N^0 - N_1)}{\gamma + D_1 - \gamma_1} > 0$ . 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  $\delta Z^2$  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  $g(P) = \frac{D_2}{\alpha b}$ . After some straightforward calculations, it can be seen that  $\bar{N}$  satisfies

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

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  $a f(\bar{N}) - \gamma - D_1 > 0$ . 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 [7, 8, 9, 3, 5, 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.

$$\begin{aligned} \dot{N} &= D(N^0 - N) - a f(N)P + (1 - \alpha)bg(P)Z + \gamma_1 \int_{-\infty}^t F_1(t - s)P(s)ds \\ &\quad + c\delta \int_{-\infty}^t F_2(t - s)Z^2(s)ds \\ \dot{P} &= a f(N)P - \gamma P - bg(P)Z - D_1 P \\ \dot{Z} &= \alpha bg(P)Z - \delta Z^2 - D_2 Z \\ N(0) &\geq 0, P(x) = \phi(x), Z(x) = \psi(x), -\infty < x \leq 0, \end{aligned} \quad (3.1)$$

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.

**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

$$\begin{aligned} \dot{V} &= \dot{N} + \dot{P} + \dot{Z} + \gamma_1 \int_0^\infty [F_1(s)P(t) - F_1(s)P(t-s)]ds \\ &\quad + c\delta \int_0^\infty [F_2(s)Z^2(t) - F_2(s)Z^2(t-s)]ds \\ &= D(N^0 - N) + \gamma_1 P + c\delta Z^2 - \gamma P - \delta Z^2 - D_1 P - D_2 Z. \end{aligned}$$

Let  $\mathcal{S} = \{(N, P, Z) \in R_+^3 : DN^0 = DN + (\gamma - \gamma_1)P + (1 - c)\delta Z^2 + D_1 P + D_2 Z\}$ . Then  $\dot{V} < 0$  in the positive octant outside of the region bounded by the surface  $\mathcal{S}$ . 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

$$\begin{aligned} \dot{n} &= -Dn - af(N^0)p + \gamma_1 \int_{-\infty}^t F_1(t-s)p(s)ds \\ \dot{p} &= af(N^0)p - \gamma p - D_1 p \\ \dot{z} &= -D_2 z. \end{aligned} \tag{3.2}$$

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  $\lim_{t \rightarrow \infty} P(t) = 0$  and  $\lim_{t \rightarrow \infty} Z(t) = 0$  follows similarly as in the proof of Theorem 2.2. It is then

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 pure 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

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

Let the left hand side of the above equation be denoted by  $F(\beta i)$ . Since  $|\int_0^\infty e^{-\beta s i} F_1(s) ds| \leq 1$ , 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

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

Then  $G(0) = \frac{a^2 [f(N_1)]^2}{\gamma_1^2} > 1$  as  $a f(N_1) = \gamma + D_1 > \gamma_1$ , and  $G'(\beta) = \frac{4\beta^3 + 2\beta[(D + a f'(N_1) P_1)^2 - 2a^2 f'(N_1) f(N_1) P_1]}{a^2 [f'(N_1)]^2 P_1^2 \gamma_1^2}$ . Therefore if

$$[D + a f'(N_1) P_1]^2 \geq 2a^2 f'(N_1) f(N_1) P_1 \quad (3.5)$$

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

**Theorem 3.3** *If  $a f(N^0) > \gamma + D$ ,  $\alpha b g(P_1) < D_2$  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  $\alpha b g(P_1) > D_2$  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  $\liminf_{t \rightarrow \infty} N(t) \geq m$ ,  $\liminf_{t \rightarrow \infty} P(t) \geq m$ , 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  $a f(N^0) > \max\{\gamma + D_1 + D_2, \gamma + D\}$  and  $\alpha b g(P_1) > D_2$  hold. Then system (3.1) is uniformly persistent.*

*Proof.* We need to construct a Liapunov-like function. Define  $\rho(N, P, Z) = NPZ$ . Then  $\rho$  is continuous on  $R_+^3$ ,  $\rho(N, P, Z) = 0$  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]. ■

## 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,  $f(N) = \frac{N}{k + N}$ , 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  $g(P) = \frac{P}{m + P}$ , where  $m$  has the same range as that of  $k$ . This range was within the parameter region given in [5], which was collected from different research articles using these functional forms. The model for the instantaneous nutrient recycling is given below.

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

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

$$\begin{aligned}
\dot{N} &= D(N^0 - N) - \frac{aNP}{k+N} + (1-\alpha)\frac{bPZ}{m+P} + 0.02\gamma_1 \int_{-\infty}^t e^{-0.02(t-s)}P(s)ds \\
&\quad + 0.01c\delta \int_{-\infty}^t e^{-0.01(t-s)}Z^2(s)ds \\
\dot{P} &= \frac{aNP}{k+N} - \gamma P - \frac{bPZ}{m+P} - D_1P \\
\dot{Z} &= \alpha\frac{bPZ}{m+P} - \delta Z^2 - D_2Z \\
&\quad N(0), P(0), Z(0) > 0.
\end{aligned} \tag{4.2}$$

Specific parameter values are  $D = D_1 = D_2 = 0.01$ ,  $N^0 = 1.0$ ,  $a = b = c = 0.6$ ,  $k = m = 0.2$ ,  $\gamma = 0.2$ ,  $\gamma_1 = 0.15$  and  $\alpha = 0.25$ . 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  $af(N^0) = 0.5 > \gamma + D_1 = 0.21$  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. This is also true for the delayed model (4.2). As we increase  $\delta$ , the positive periodic solution disappeared and there exists a unique positive steady state. Simulations also demonstrate that solutions of (4.1) and respectively (4.2) with positive initial conditions converge to the positive steady state. From the plot we can see that the solution converges to the positive steady state with initial condition  $N(0) = 0.1$   $P(0) = 0.4$  and  $Z(0) = 0.2$ . However, convergence of solutions of (4.2) to the steady state are faster than convergence of solutions of (4.1)

**Put Figure 1 here**

Bifurcation diagrams using  $\delta$  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  $\delta$ , where  $\delta_0$  is the smallest  $\delta$  value for which the positive steady

state is non-hyperbolic. From these numerical simulations for both delayed and non-delayed 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  $\delta_0$  for model (4.2) are smaller than those  $\delta_0$ 's' values for the non-delayed 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.

**Put Figure 2 here**

We now change  $D$ 's values but keep other parameter values fixed except  $\delta$ . 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 true for system (4.2).

We next change phytoplankton uptake rate  $f(N)$  to  $f(N) = \frac{N^2}{k + N^2}$ , with the same  $k$  value as models (4.1) and (4.2),  $k = 0.2$ . 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  $D = D_1 = D_2 = 0.01$ .

## 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 Figures 5-7 and 14-16 with  $\delta > 0$  very 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,  $\delta_0$  in the delayed model is smaller than  $\delta_0$  in the non-delayed 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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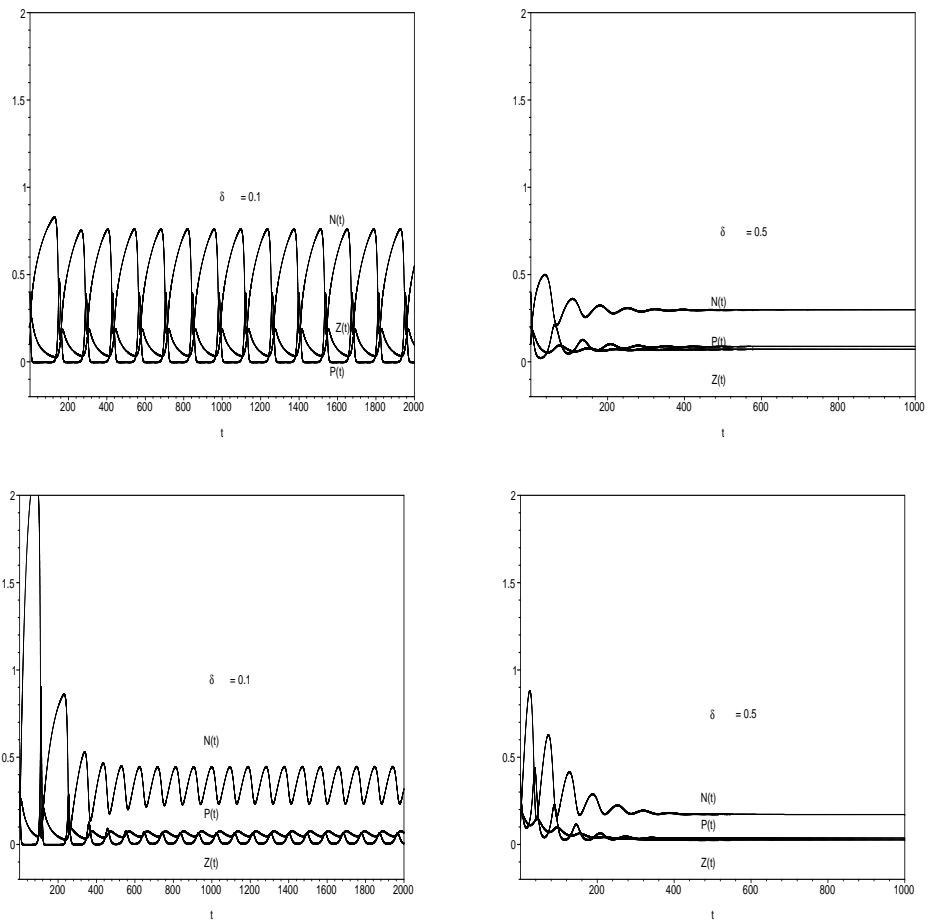


Figure 1: The top two figures are for system (4.1) while the bottom figures are for system (4.2). Solutions with initial condition  $N(0) = 0.1$ ,  $P(0) = 0.4$  and  $Z(0) = 0.2$  are plotted.

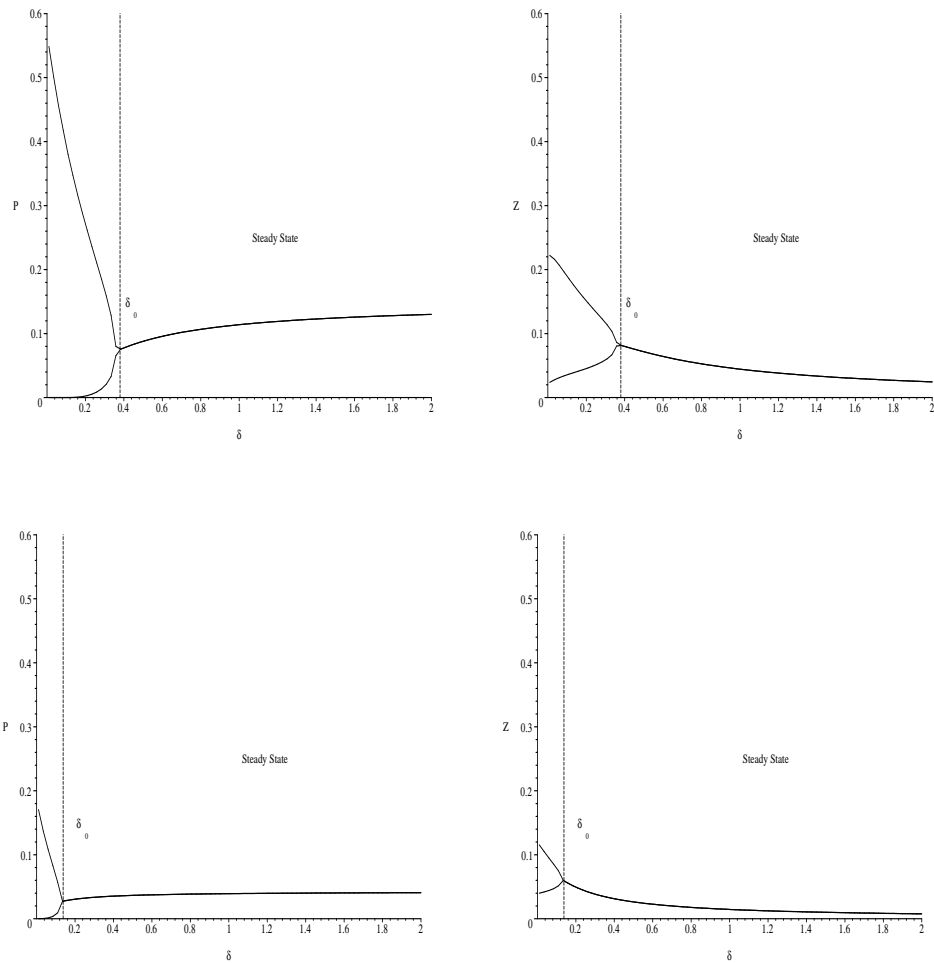


Figure 2: Bifurcation diagrams are given here. The top figures are for system (4.1) and the bottom figures are for system (4.2).

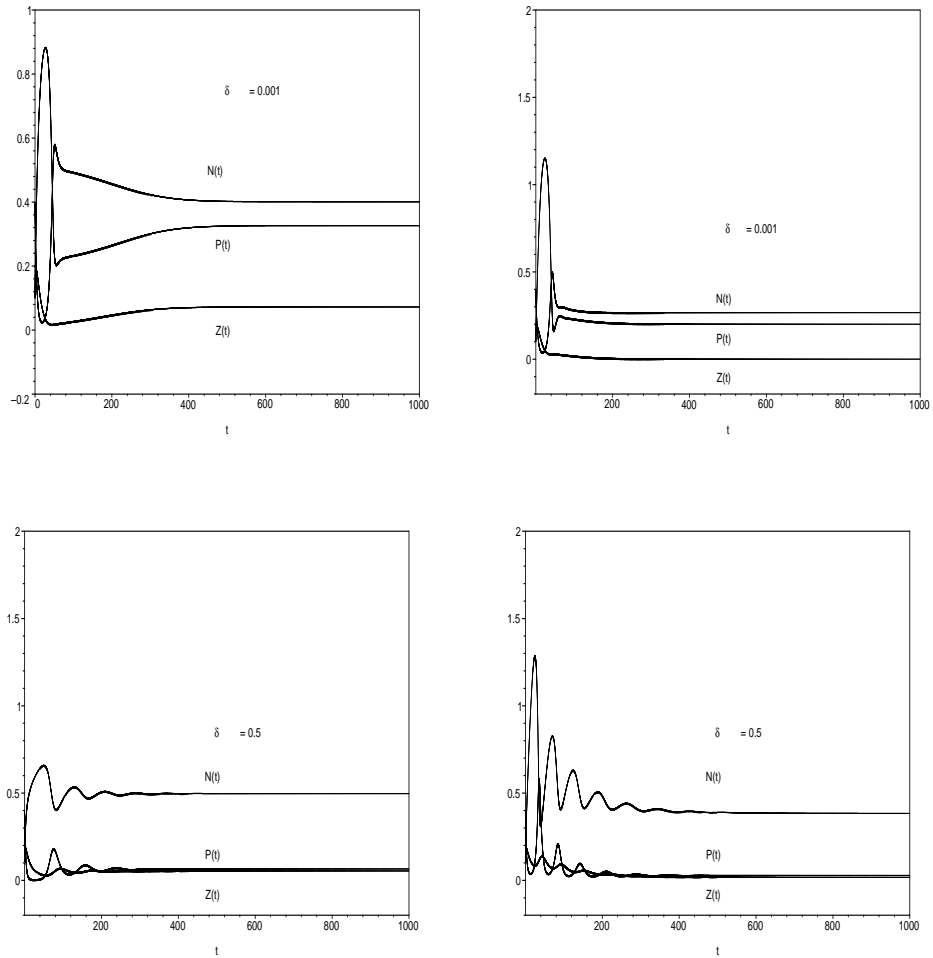


Figure 3: When  $D$ ,  $D_1$  and  $D_2$  are increased to 0.1, both systems (4.1) and (4.2) have a unique positive steady state even when  $\delta$  is very small as shown by the top two figures for systems (4.1) and (4.2), respectively. The bottom two figures use Holling-III as phytoplankton nutrient uptake rate.