

## DYNAMICS OF TWO PHYTOPLANKTON POPULATIONS UNDER PREDATION

JEAN-JACQUES KENGWOUNG-KEUMO

Department of Mathematical Sciences  
Cameron University  
2800 West Gore Boulevard  
Lawton, OK 73505, USA

(Communicated by Hermann J. Eberl)

**ABSTRACT.** The aim of this paper is to investigate the manner in which predation and single-nutrient competition affect the dynamics of a non-toxic and a toxic phytoplankton species in a homogeneous environment (such as a chemostat). We allow for the possibility that both species serve as prey for an herbivorous zooplankton species. We assume that the toxic phytoplankton species produces toxins that affect only its own growth (autotoxicity). The autotoxicity assumption is ecologically explained by the fact that the toxin-producing phytoplankton is not mature enough to produce toxins that will affect the growth of its nontoxic competitor. We show that, in the absence of phytotoxic interactions and nutrient recycling, our model exhibits uniform persistence. The removal rates are distinct and we use general response functions. Finally, numerical simulations are carried out to show consistency with theoretical analysis. Our model has similarities with other food-chain models. As such, our results may be relevant to a wider spectrum of population models, not just those focused on plankton. Some open problems are discussed at the end of this paper.

**1. Introduction.** The term “plankton” is used to describe freely-floating and weakly-swimming marine and freshwater organisms. Plankton are divided into broad functional groups, among them phytoplankton that live near the surface of the water where there is sufficient light to support photosynthesis just like plants on the land, and zooplankton that feed on other plankton. The microscopic and unicellular plants, phytoplankton, are consumed by zooplankton, the animals, which in turn are eaten by larger organisms. The highly diverse nature of phytoplankton communities seems to contradict the competitive exclusion principle, which states that when two species compete for the same resource, only one will survive. This is known as the paradox of plankton. Direct measurement of plankton biomass is difficult and expensive, so the modeling of plankton populations is an essential tool in improving our understanding of the physical and biological processes that contribute to the complexity of these systems.

Mathematical modeling of plankton populations goes back to Hallam[18, 19, 20]. He studied stability and persistence properties of a family of non-spatial plankton models. [16] investigated the bifurcational structure of a simple plankton model

---

2010 *Mathematics Subject Classification.* 91B74, 97M10, 62P12.

*Key words and phrases.* Plankton, phytoplankton, zooplankton, predation, chemostat, uniform persistence.

with zooplankton mortality modeled by  $-cZ^m$ ,  $1 \leq m \leq 2$ . They showed explicitly how cycles can persist for  $1 < m < 2$ . In addition,  $m = 2$  does not preclude the existence of cycles or chaos. [14] examined the behavior of two nutrient-phytoplankton-zooplankton-detritus models to help understand the factors that most influence the dynamics of such models. He further showed that the addition of a detritus compartment has little impact on the nature of the qualitative dynamics that were found for the corresponding nutrient-phytoplankton-zooplankton model. [32] examined nutrient-phytoplankton-zooplankton models with spatial heterogeneity. They proved that phytoplankton species with low diffusivity and zooplankton functional response with half-saturation constant can control algal blooms. [36] studied plankton nutrient models with both instantaneous and delayed nutrient recycling. He successively chose the nutrient input concentration and the maximal zooplankton ingestion rate as bifurcation parameters to show that the positive equilibrium loses its stability via a Hopf bifurcation as these parameters are varied through respective critical values. [25] explored nutrient-phytoplankton models with both instantaneous and delayed nutrient recycling and zooplankton mortality modeled by  $-cZ^2$ . Unlike other ecological models for which delays can destabilize the system (see for examples, [13], [36], and [4]), their numerical simulations suggested that delayed nutrient recycling can actually stabilize the nutrient-phytoplankton system. [10] proposed and analyzed four models of nutrient-phytoplankton-zooplankton populations to observe the dynamics of such models in the presence of additional food. Here the phytoplankton are toxic to the zooplankton species. [40] studied the growth dynamics of phytoplankton as a function of both time and concentration of nutrients. Their model helps understand the role of concentration of various explanatory variables (such as nutrients, temperature, light intensity, or combinations of such variables) in phytoplankton growth dynamics. [35] developed and analyzed a mathematical model describing the competition for a single growth-limiting nutrient between a non-toxic phytoplankton and a toxin-producing phytoplankton under allelopathic interactions.

With the use of mathematical models, the author (see [27]) generalized the work of [35] to demonstrate theoretically that the stable coexistence of two species competing for a single nutrient in a homogeneous medium would be possible provided (a) there is an allelopathic effect and (b) the input nutrient concentration is above a critical value given in [27]. The model in [27] is not uniformly persistent because of the simultaneous existence of one locally asymptotically stable interior equilibrium and one unstable interior equilibrium (saddle point), when the input nutrient concentration exceeds the critical value specified in [27]. The author further showed that predation in the presence of phytotoxic interactions and/or nutrient recycling would not make the resulting model uniformly persistent. The contents of the paper are largely devoted to extending the work in [27] to include predation. More specifically, we extend the nutrient-nontoxic phytoplankton-toxic phytoplankton model in [27], in the absence of phytotoxic interactions and nutrient recycling, to include predation of phytoplankton species by zooplankton and obtain a uniformly persistent model. Our findings are in favor that predation can be responsible for diversity in ecosystems (see [11]). [11] asserts that predation may promote, hinder or have no effect on interspecific competitive interactions. Our model represents a significant generalization of those previously analyzed ( see [8], [22], [17], and [29] among others).

The organization of this paper is as follows: The next section gives the description of the model. Section 3 contains preliminary results, existence and local stability of steady states. Section 4 gives ecological interpretations of stability inequalities. In Section 5, we study global stability results along with uniform persistence. In Section 6, numerical simulation results are provided to substantiate the analytical findings. The final section provides a brief summary and discussion.

**2. The model.** We analyze a model of two-species exploitative competition for a single growth-limiting, nonreproducing resource under predation in the culture vessel of a chemostat. The contents of the feed bottle are supplied to the growth chamber at a constant rate  $D$ , while the medium in the culture vessel is removed to the collection vessel at the same rate. Our model does not incorporate phytotoxic interactions and can be written

$$\begin{aligned} \frac{dN}{dt} &= (N_0 - N)D - \frac{1}{\gamma_1} f_1(N)P_1 - \frac{1}{\gamma_2} f_2(N)P_2, \\ \frac{dP_1}{dt} &= f_1(N)P_1 - \frac{1}{\eta_1} g_1(P_1)Z - m_1 P_1, \\ \frac{dP_2}{dt} &= f_2(N)P_2 - \frac{1}{\eta_2} g_2(P_2)Z - m_2 P_2, \\ \frac{dZ}{dt} &= (g_1(P_1) + g_2(P_2))Z - cZ, \\ N(0) &> 0, P_1(0) > 0, P_2(0) > 0, Z(0) > 0. \end{aligned} \tag{1}$$

Units of all variables and parameters in model (1) are given in Table 1. In these equations  $P_i(t)$  is the biomass of the  $i^{th}$  population of phytoplankton in the culture vessel at time  $t$ ,  $i = 1, 2$ . Population  $P_1$  is assumed to be nontoxic, while population  $P_2$  is assumed to be toxic. But we neglect the impact of toxins produced by  $P_2$  on the growth of  $P_1$ . The concentration of the nonreproducing resource in the culture vessel at time  $t$  is denoted by  $N(t)$ , while  $N_0$  is the concentration of resource  $N$  in the feed vessel.  $Z(t)$  is the biomass of zooplankton in the culture vessel at time  $t$ . We also neglect the impact of toxins on the growth of  $Z$ . Since perfect mixing of the culture vessel is assumed, nutrients, microorganisms and byproducts are removed in proportion to their concentration. The removal rate  $m_1$  of nontoxic phytoplankton  $P_1$  is the sum of washout rate  $D$  and the specific death rate  $\epsilon_1$ , so that  $m_1 = D + \epsilon_1$ . The removal rate  $m_2$  of toxic phytoplankton  $P_2$  is the sum of washout rate  $D$ , the specific death rate  $\epsilon_2$ , and the autotoxic coefficient  $a_2$ , so that  $m_2 = D + \epsilon_2 + a_2$  as per [38]. Finally, the removal rate  $c$  of zooplankton  $Z$  is the sum of washout rate  $D$  and the specific death rate  $\xi$ , so that  $c = D + \xi$ .

[39] show that a limiting cycle behavior exists when the zooplankton death rate is linear. [15] demonstrate numerically that this limiting cycle behavior disappears when a quadratic death rate for zooplankton is assumed to account for higher predation. We do not model higher predation in our model. We follow [39] and call the zooplankton loss term  $cZ$  the closure term because it closes the model at the top trophic level. For mathematical tractability of the model, we use a linear function to express the death of each organism.

It is interesting to note that the analysis of the model requires no assumptions on the signs of the  $\epsilon_i$ 's,  $\xi$  and  $a_2$ , provided the  $m_i$ 's and  $c$  all remain positive. This leaves the  $\epsilon_i$ 's,  $\xi$  and  $a_2$  open to other interpretations. For instance, when  $\epsilon_i$  is negative it means there is an additional food source for the  $i^{th}$  population of

phytoplankton. While a positive  $\epsilon_i$  accounts for a further deleterious effect on the  $i^{\text{th}}$  population of phytoplankton. Finally, a zero  $\epsilon_i$  means that there is no intrinsic death of the  $i^{\text{th}}$  population of phytoplankton. The interpretations of the sign of  $\xi$  are similar to those of the  $\epsilon_i$ 's. A negative, zero, and positive  $a_2$  indicate respectively stimulatory effects, no effects, and inhibitory effects of toxins produced by  $P_2$  on its own growth.

In system (1) the response functions  $f_i(N)$  represent the per capita rate of conversion of nutrient  $N$  to biomass of population  $P_i$  as a function of the concentration of nutrient  $N$ . We assume that the rate of conversion of nutrient to  $P_i$  biomass is proportional to the amount of nutrient consumed, so that the consumption rate of resource  $N$  per unit of population  $P_i$  is of the form  $\frac{1}{\gamma_i} f_i(N)$ , where  $\gamma_i$  is the growth yield constant (number of phytoplankton per unit of nutrient). We make the following assumptions concerning the response functions  $f_i$ :

$$f_i : \mathbf{R}_+ \longrightarrow \mathbf{R}_+, f_i \text{ is continuously differentiable,} \quad (2)$$

$$f_i(0) = 0, f_i'(N) > 0 \text{ for all } N \geq 0. \quad (3)$$

The break-even concentration for population  $P_i$  on nutrient  $N$  is obtained by setting  $\frac{dP_i}{dt} = 0 = f_i(N) - m_i$  and solving for  $N$ . By the monotonicity assumptions, the solution  $\lambda_i$  is a uniquely defined positive extended real number provided we assume  $\lambda_i = \infty$  if  $f_i(N) < m_i$  for all  $N \geq 0$ .

Note that the autotoxicity assumption on phytoplankton population  $P_2$  has a direct impact on the break-even concentration  $\lambda_2$ . Recall  $m_2 = D + \epsilon_2 + a_2$  (where  $a_2$  is the autotoxic coefficient) and  $\lambda_2$  is the unique positive solution of  $f_2(N) = m_2$ . This assumption is ecologically explained by the situation where toxic phytoplankton  $P_2$  is not mature enough to produce allelochemicals that will potentially affect the growth of its competitor  $P_1$  and the growth of its predator  $Z$ .

Let  $\mu_i$  denote the maximal growth rate of population  $P_i$  on resource  $N$ , so that

$$\lim_{N \rightarrow \infty} f_i(N) = \mu_i.$$

Lotka-Volterra kinetics (or Holling type I), Michaelis-Menten kinetics (or Holling type II), and sigmoidal kinetics (Holling type III or multiple saturation dynamics) are prototypes of response functions  $f_i$  found in the literature (see [2], [5], [14], [26], [31], [37], [42], [43] among others). The half-saturation constant  $K_i$  of the  $i^{\text{th}}$  phytoplankton species for nutrient is given by  $f_i(K_i) = \frac{\mu_i}{2}$  and represents the resource concentration supporting growth at half the maximal growth rate. Half-saturation constants and maximal growth rates can be measured experimentally (see [21]).

On the other hand, the response function  $g_i(P_i)$  represents the per capita rate of conversion of phytoplankton  $P_i$  to biomass of population  $Z$  as a function of the biomass of phytoplankton  $P_i$ . We assume that the rate of conversion of  $P_i$  biomass to  $Z$  biomass is proportional to the amount of phytoplankton consumed, so that the consumption rate of phytoplankton  $P_i$  per unit of population  $Z$  is of the form  $\frac{1}{\eta_i} g_i(P_i)$ , where  $\eta_i$  is a growth yield constant (number of zooplankton per unit of phytoplankton). Since  $P_1$  and  $P_2$  are perfectly substitutable resources for  $Z$  ([9], [28], [34], and [3]), the per-capita growth rate of zooplankton as a function of  $P_1$  and  $P_2$  takes the form  $G(P_1, P_2) = g_1(P_1) + g_2(P_2)$  for all  $P_1 \geq 0$  and  $P_2 \geq 0$ . Following [29], [37], [42] and others, we make the following assumptions concerning the response functions  $g_i$ :

$$g_i : \mathbf{R}_+ \longrightarrow \mathbf{R}_+, g_i \text{ is continuously differentiable,} \quad (4)$$

$$g_i(0) = 0, g'_i(P_i) > 0, \lim_{P_i \rightarrow \infty} g_i(P_i) = \omega_i, \text{ for all } P_i \geq 0, \tag{5}$$

where  $\omega_i$  denotes the maximal growth rate of zooplankton  $Z$  on phytoplankton  $P_i$ .

It will also be convenient to express  $g_i(P_i)$  as

$$g_i(P_i) = P_i h_i(P_i), \tag{6}$$

where  $h_i(P_i)$  is some positive and differentiable function. Since  $g_i$  is continuously differentiable it follows that

$$\lim_{P_i \rightarrow 0} h_i(P_i) = g'_i(0), \tag{7}$$

and so we define

$$h_i(0) = g'_i(0). \tag{8}$$

The breakeven concentration for population  $Z$  on phytoplankton  $P_i$  is obtained by setting  $\frac{dZ}{dt} = 0 = g_i(P_i) - c$  and solving for  $P_i$ . By the monotonicity assumptions, the solution  $\Lambda_i$  is a uniquely defined positive extended real number as long as we assume  $\Lambda_i = \infty$  if  $g_i(P_i) < c$  for all  $P_i \geq 0$ .

Prototypes of response functions  $g_i$  often found in the literature (see [1], [2], [5], [14], [26], [31], [37], [42], [43]) include:

- Lotka-Volterra kinetics (or Holling type I):  $g_i(P_i) = \frac{c}{\Lambda_i} P_i$  when  $\Lambda_i$  is finite.
- Michaelis-Menten kinetics (or Holling type II):  $g_i(P_i) = \frac{\omega_i P_i}{\Lambda_i (\frac{\omega_i}{c} - 1) + P_i}$ , where  $\Lambda_i$  is finite.
- Sigmoidal kinetics (Holling type III or multiple saturation dynamics):  $g_i(P_i) = \frac{\omega_i P_i^2}{(\Lambda_i (\frac{\omega_i}{c} - 1) + P_i)(B_i + P_i)}$ , where  $B_i = \Lambda_i(\omega_i - 1)$  when  $\Lambda_i$  is finite.
- Usually, Ivlev's functional response formulation (see [24]),  $g_i(P_i) = \omega_i [1 - \exp(-\alpha_i P_i)]$ , is appropriate to describe the zooplankton grazing, where  $\alpha_i$  is the rate at which saturation is achieved with increasing  $i^{th}$  phytoplankton population levels.

The half-saturation constant  $L_i$  of zooplankton for the  $i^{th}$  phytoplankton population is given by  $g_i(L_i) = \frac{\omega_i}{2}$  and represents the phytoplankton biomass  $P_i$  supporting growth at half the maximal growth rate.

System (1) was considered by [8] under the assumptions that specific death rates are insignificant compared to the washout rate  $D$  ( $\epsilon_i = 0, i = 1, 2, \xi = 0$ ) and  $Z$  feeds only on one phytoplankton population  $P_i$ . [22] studied system (1) under linearity of the nutrient-dependent species growth function and the predator functional response. They proposed simple rules (based on equilibrium nutrient concentration and herbivore density) that govern competitive outcomes. Motivated by the rich dynamics of nonlinear growth of species, [17] relaxed the linearity assumptions in [22] and used the type I and II functional responses. Their local analytical results and numerical results are in line with the results we provide in this paper. System (1) was also considered by [29] under the assumption that one of the  $P_i$ 's is absent. As such, our model represents a significant generalization of those previously analyzed.

In the system (1), the toxic phytoplankton population  $P_2$  is either the green alga, *Enteromorphs linza*, or the unicellular green alga, *Chlorella vulgaris* provided the species has no phytotoxic interactions on the growth of its nontoxic competitor  $P_1$ . *Enteromorphs linza* releases allelochemicals which are auto-stimulatory to the growth of *Enteromorpha* species. *Chlorella vulgaris* produces an autotoxin which has the ability to regulate the growth of its own population and also inhibits the

TABLE 1. Units of variables and parameters in the description of model (1) (see [15] and references therein). Here  $1 \text{ } Cg = 20 \text{ } mg$ , where  $C$  is carbon. A hyphen  $-$  means dimensionless while  $d$  stands for day.

Variable or parameter	Units
$t$ time	$d$
$N(t)$ concentration of nutrient at time $t$	$gCm^{-3}$
$P_1(t)$ biomass of phytoplankton species 1 at time $t$	$gCm^{-3}$
$P_2(t)$ biomass of phytoplankton species 2 at time $t$	$gCm^{-3}$
$Z(t)$ biomass of zooplankton species at time $t$	$gCm^{-3}$
$N_0$ input nutrient concentration	$gCm^{-3}$
$D$ washout rate	$d^{-1}$
$m_i$ removal rate of phytoplankton species $i$ ( $i = 1, 2$ )	$d^{-1}$
$c$ removal rate of zooplankton species	$d^{-1}$
$\gamma_i$ growth yield constant of phytoplankton $P_i$ on nutrient $N$	$-$
$\eta_i$ growth yield constant of zooplankton on phytoplankton $P_i$	$-$
$\mu_i$ maximal growth rate of phytoplankton $P_i$ on nutrient $N$	$d^{-1}$
$\omega_i$ maximal growth rate of zooplankton on phytoplankton $P_i$	$d^{-1}$
$K_i$ half saturation constant for phytoplankton $P_i$	$d^{-1}$
$L_i$ half saturation constant of zooplankton for phytoplankton $P_i$	$d^{-1}$
$\lambda_i$ and $\Lambda_i$ breakeven concentration of species	$gCm^{-3}$

growth of *Asterionella formosa* and *Nitzschia frustulum*. Nontoxic phytoplankton  $P_1$  can be either *Enteromorpha*, or *Asterionella formosa* or *Nitzschia frustulum*. Table 1 in [17] summarizes more possible species pairs  $(P_1, P_2)$ . The nutrient  $N$  can be a source of vitamin  $B_{12}$ , phosphorus (see for example, [17]), or nitrogen and the zooplankton population  $Z$  is *Daphnia* species (see for example, [17]).

**3. Some preliminary results.** The Fundamental Existence-Uniqueness Theorem (see, for example, [33]) ensures that solutions of (1) exist uniquely for all time. The first lemma is a statement that solutions of (1) are positive and bounded. These are minimal requirements for a reasonable population model.

**Lemma 3.1.** *Solutions of model (1) are (a) positive and (b) bounded.*

*Proof. Proof of (a).* Suppose that there exists a first time  $\bar{t}_0 > 0$  such that  $N(\bar{t}_0) = 0$ , that is  $N(t) > 0$  for all  $0 \leq t \leq \bar{t}_0$  and  $N(\bar{t}_0) = 0$ . Then  $\frac{dN}{dt}(t_0) \leq 0$ . However,  $\frac{dN}{dt}(t_0) = N_0 D > 0$  by the first equation of model (1), a contradiction.

Suppose now that  $Z(0) > 0$ , then  $\frac{dZ}{dt} = (g_1(P_1) + g_2(P_2))Z - cZ$  yields  $Z(t) = Z(0) \exp(\int_0^t h(s) ds) > 0$ , where  $h(s) = g_1(P_1(s)) + g_2(P_2(s)) - c$ .

We now show that  $P_i(t) > 0$  for all  $t$ ,  $i \in \{1, 2\}$ . For a fixed  $i \in \{1, 2\}$ , let  $\bar{t}_i = \min \{t > 0 : P_i(t) = 0\}$  and define

$$B_i = \min \left\{ f_i(N(t)) - m_i - \frac{1}{\eta_i} h_i(P_i(t)) Z(t), 0 \leq t \leq \bar{t}_i \right\}.$$

Then for  $t \in [0, \bar{t}_i]$  we have  $\frac{dP_i(t)}{dt} \geq B_i P_i(t)$ , so that  $P_1(t) \geq P_i(0) \exp(B_i t) > 0$ . In particular,  $P_1(\bar{t}_i) \geq P_i(0) \exp(B_i \bar{t}_i)$ , a contradiction.

*Proof of (b).* Define  $T(t) = N(t) + \frac{1}{\gamma_1} P_1(t) + \frac{1}{\gamma_2} P_2(t) + Z(t)$ . From (1) we have  $\frac{dT}{dt} \leq N_0 D - D_0 T$ , where  $D_0 = \min(D, m_1, m_2, c)$ . By Gronwall's lemma,  $T(t) \leq \frac{N_0 D}{D_0} + (T(0) - \frac{N_0 D}{D_0}) \exp(-D_0 t)$ . So  $N(t) + \frac{1}{\gamma_1} P_1(t) + \frac{1}{\gamma_2} P_2(t) + Z(t) \leq \frac{N_0 D}{D_0}$  if  $T(0) < \frac{N_0 D}{D_0}$  and  $N(t) + \frac{1}{\gamma_1} P_1(t) + \frac{1}{\gamma_2} P_2(t) + Z(t) \leq T(0)$  otherwise. Thus, by (a) all solutions of (1) are bounded.  $\square$

**Proposition 3.1.** *Given any  $\delta > 0$ , for all solutions  $N(t)$  of (1),  $N(t) \leq N_0 + \delta$  for all sufficiently large  $t$ .*

*Proof.* Let  $\delta > 0$  be given. From the first equation of (1) we have

$$\frac{dN}{dt} = (N_0 - N)D - \frac{1}{\gamma_1} f_1(N)P_1 - \frac{1}{\gamma_2} f_2(N)P_2 \leq (N_0 - N)D. \tag{9}$$

Hence,  $N(t) \leq N_0 + [N(0) - N_0] \exp(-tD)$  for all  $t$ . Since  $[N(0) - N_0] \exp(-tD)$  approaches 0 as  $t$  tends to infinity,  $N(t) \leq N_0 + \delta$  for all sufficiently large  $t$ .  $\square$

**Proposition 3.2.** *If there exists a  $t_0 \geq 0$  such that  $N(t_0) \leq N_0$ , then  $N(t) < N_0$  for all  $t \geq t_0$ .*

*Proof.* Suppose there exists a first time  $\tilde{t} > t_0$  such that  $N(\tilde{t}) = N_0$  and  $N(t) < N_0$  for all  $t_0 \leq t < \tilde{t}$ . Then  $\frac{dN}{dt}(\tilde{t}) \geq 0$ . However, from the first equation of (1),  $\frac{dN}{dt}(\tilde{t}) \leq -\sum_{i=1}^2 \frac{P_i(\tilde{t})}{\gamma_i} f_i(N(\tilde{t})) < 0$ , a contradiction.  $\square$

The following Lemma 3.2 will be used to define some of the steady states in the next section. The proof uses the assumptions on the  $f_i$ 's and the Intermediate Value Theorem.

**Lemma 3.2.** *For  $i \in \{1, 2\}$  fixed, there exists a unique  $\bar{N}_i > 0$  solution of  $\gamma_i(N_0 - N)D = \Lambda_i f_i(N)$  when  $\Lambda_i$  is finite.*

*Proof.* Fix  $i \in \{1, 2\}$  and, assume  $\Lambda_i$  is finite. Define

$$u_i : [0, +\infty) \rightarrow \mathbf{R}_+, u_i(N) = \Lambda_i f_i(N) - \gamma_i(N_0 - N)D$$

It is straightforward to check that  $u_i$  is well-defined and continuous on  $[0, +\infty)$  with  $u_i(0) = -\gamma_i N_0 D$  and  $\lim_{N \rightarrow +\infty} u_i(N) = +\infty$ . Moreover,  $u_i$  is differentiable on  $[0, +\infty)$  with  $\frac{du_i(N)}{dN} = \Lambda_i f'_i(N) + \gamma_i D > 0$  if  $\Lambda_i$  is finite. Hence by the Intermediate Value Theorem and the bijectivity of  $u_i$ , there exists a unique  $N_i \in (0, +\infty)$  such that  $u_i(N_i) = 0$ ; that is,  $\gamma_i(N_0 - N_i)D = \Lambda_i f_i(N_i)$  whenever  $\Lambda_i$  is finite. Take  $\bar{N}_i = N_i$  to complete the proof.  $\square$

**4. Steady states: Existence and local stability.** Equilibria of model (1) are given by the solutions of:

$$\frac{dN}{dt} = \frac{dP_1}{dt} = \frac{dP_2}{dt} = \frac{dZ}{dt} = 0.$$

Five of the equilibria are readily identified and are given by  $E_0 = (N_0, 0, 0, 0)$ ,  $E_{\lambda_1} = (\lambda_1, \bar{P}_1, 0, 0)$ ,  $E_{\lambda_2} = (\lambda_2, 0, \bar{P}_2, 0)$ ,  $E_{\Lambda_1} = (\bar{N}_1, \Lambda_1, 0, \bar{Z}_1)$ , and  $E_{\Lambda_2} = (\bar{N}_2, 0, \Lambda_2, \bar{Z}_2)$ ;



where  $\bar{P}_i = \frac{\gamma_i(N_0 - \lambda_i)D}{m_i}$ ,  $\bar{N}_i$  is defined in Lemma 3.2, and  $\bar{Z}_i = \frac{\Lambda_i(f_i(\bar{N}_i) - m_i)}{h_i(\Lambda_i)}$ , for  $i = 1, 2$ .

We do not have any equilibrium point of the form  $(N, 0, 0, Z)$ , with  $N$  and  $Z$  positive. We prove later that there exists at least one interior equilibrium point.

We say that a steady state does not exist if any one of its components is negative.  $E_0$  always exists, whereas a necessary and sufficient condition on the parameters for feasibility of  $E_{\lambda_i}$  is  $N_0 > \lambda_i$  for  $i = 1, 2$ . In other words, if the maximum growth rate  $\mu_i$  of the  $i^{th}$  phytoplankton species is less than the loss rate or if there is inadequate nutrient supply for the  $i^{th}$  phytoplankton species,  $E_{\lambda_i}$  is not biologically relevant. Similarly  $N_0 - \frac{\Lambda_i m_i}{\gamma_i D} > \bar{N}_i > \lambda_i$  and  $f_i(\bar{N}_i) > m_i$  are the necessary and sufficient conditions for feasibilities of  $E_{\Lambda_i}$ ,  $i = 1, 2$ . That is, if the growth of the  $i^{th}$  phytoplankton species at the  $\bar{N}_i$ -level of nutrient is less than its removal rate or if the growth of zooplankton  $Z$  at the  $\Lambda_i$ -level of phytoplankton is less than its removal rate, then  $E_{\Lambda_1}$  and  $E_{\Lambda_2}$  are biologically irrelevant.

The local stability properties of (1) through an examination of the linearized system about the equilibria  $E_0$ ,  $E_{\lambda_1}$ , and  $E_{\lambda_2}$  are omitted because they are straightforward and follow from the characteristic equation of the variational matrix of (1) evaluated at each of these equilibria and the Routh-Hurwitz criterion (see for example, [12]). We will just investigate the local stability properties of (1) through an examination of the linearized system about the equilibria  $E_{\Lambda_1}$  and  $E_{\Lambda_2}$ .

We assume that  $N_0 - \frac{\Lambda_2 m_2}{\gamma_2 D} > \bar{N}_2 > \lambda_2$  and  $f_2(\bar{N}_2) > m_2$ , so that  $E_{\Lambda_2}$  exists. We examine the local stability properties of  $E_{\Lambda_2}$ . The Jacobian matrix of (1) evaluated at  $E_{\Lambda_2}$ , is given by

$$\begin{pmatrix} -D - \frac{\Lambda_2 f_2'(\bar{N}_2)}{\gamma_2} & -\frac{f_1(\bar{N}_2)}{\gamma_1} & -\frac{f_2(\bar{N}_2)}{\gamma_2} & 0 \\ 0 & f_1(\bar{N}_2) - m_1 - \frac{\bar{Z}_2}{\eta_1} g_1'(0) & 0 & 0 \\ \Lambda_2 f_2'(\bar{N}_2) & 0 & f_2(\bar{N}_2) - m_2 - \frac{\bar{Z}_2}{\eta_2} g_2'(\Lambda_2) & -\frac{c}{\eta_2} \\ 0 & \bar{Z}_2 g_1'(0) & \bar{Z}_2 g_2'(\Lambda_2) & 0 \end{pmatrix}.$$

The corresponding characteristic polynomial is given by

$$p(\alpha) = (\alpha - f_1(\bar{N}_2) + m_1 + \frac{\bar{Z}_2}{\eta_1} g_1'(0))(\alpha^3 + A\alpha^2 + B\alpha + C),$$

where

$$A = -f_2(\bar{N}_2) + m_2 + \frac{\bar{Z}_2}{\eta_2} g_2'(\Lambda_2) + D + \frac{\Lambda_2 f_2'(\bar{N}_2)}{\gamma_2}, \tag{10a}$$

$$B = (D + \frac{\Lambda_2 f_2'(\bar{N}_2)}{\gamma_2})(-f_2(\bar{N}_2) + m_2 + \frac{\bar{Z}_2}{\eta_2} g_2'(\Lambda_2)) + g_2'(\Lambda_2) \bar{Z}_2 \frac{c}{\eta_2} + \Lambda_2 f_2'(\bar{N}_2) \frac{f_2(\bar{N}_2)}{\eta_2}, \tag{10b}$$

$$C = \bar{Z}_2 g_2'(\Lambda_2) \frac{c}{\eta_2} (D + \frac{\Lambda_2 f_2'(\bar{N}_2)}{\gamma_2}) > 0. \tag{10c}$$

The monotonicity of  $f_2(N)$  and  $g_2(P_2)$ , the positivity of  $\bar{N}_2$ ,  $\Lambda_2$ , and  $\bar{Z}_2$ , together with the Routh-Hurwitz criterion, ensure that the roots of the cubic factor have negative real parts if and only if  $A > 0$  and  $AB > C$ . Hence,  $E_{\Lambda_2}$  is locally asymptotically stable if and only if  $f_1(\bar{N}_2) < \frac{\bar{Z}_2}{\eta_1} g_1'(0) + m_1$ ,  $A > 0$  and  $AB > C$ .

The local stability analysis of  $E_{\Lambda_1} = (\bar{N}_1, \Lambda_1, 0, \bar{Z}_1)$  is symmetrical to the analysis for  $E_{\Lambda_2}$ . It is straightforward to show that the coefficients of the cubic factor of the



corresponding characteristic polynomial are given by

$$\hat{A} = -f_1(\bar{N}_1) + m_1 + \frac{\bar{Z}_1}{\eta_1}g'_1(\Lambda_1) + D + \frac{\Lambda_1 f'_1(\bar{N}_1)}{\gamma_1}, \tag{11a}$$

$$\begin{aligned} \hat{B} = (D + \frac{\Lambda_1 f'_1(\bar{N}_1)}{\gamma_1})(-f_1(\bar{N}_1) + m_1 + \frac{\bar{Z}_1}{\eta_1}g'_1(\Lambda_1)) + g'_1(\Lambda_1)\bar{Z}_1 \frac{c}{\eta_1} \\ + \Lambda_1 f'_1(\bar{N}_1) \frac{f_1(\bar{N}_1)}{\eta_1}, \end{aligned} \tag{11b}$$

$$\hat{C} = \bar{Z}_1 g'_1(\Lambda_1) \frac{c}{\eta_1} (D + \frac{\Lambda_1 f'_1(\bar{N}_1)}{\gamma_1}) > 0. \tag{11c}$$

We summarize the results of this section in the following theorem.

**Theorem 4.1.** 1.  $E_0$  always exists. It is locally asymptotically stable for (1) if and only if  $N_0 < \lambda_i$  (so that  $f_i(N_0) < m_i$ ) for  $i = 1, 2$ .  
 2. Suppose  $\lambda_1 < N_0$ , so that  $E_{\lambda_1}$  exists.  $E_{\lambda_1}$  is locally asymptotically stable if and only if  $\lambda_1 < \lambda_2$  (so that  $f_2(\lambda_1) < m_2$ ) and  $g_1(\frac{\gamma_1(N_0 - \lambda_1)D}{m_1}) < c$ .  
 3. Suppose  $\lambda_2 < N_0$ , so that  $E_{\lambda_2}$  exists.  $E_{\lambda_2}$  is locally asymptotically stable if and only if  $\lambda_2 < \lambda_1$  (so that  $f_1(\lambda_2) < m_1$ ) and  $g_2(\frac{\gamma_2(N_0 - \lambda_2)D}{m_2}) < c$ .  
 4. Suppose  $N_0 - \frac{\Lambda_2 m_2}{\gamma_2 D} > \bar{N}_2 > \lambda_2$  and  $f_2(\bar{N}_2) > m_2$ , so that  $E_{\Lambda_2}$  exists. It is locally asymptotically stable for (1) if and only if  $f_1(\bar{N}_2) < m_1 + \frac{\eta_2 \Lambda_2 (f_2(\bar{N}_2) - m_2)}{c \eta_1} g'_2(0)$ ,  $A > 0$ , and  $AB > C$ ; where  $A, B$  and  $C$  are defined in 10a–10c.  
 5. Similarly, suppose  $N_0 - \frac{\Lambda_1 m_1}{\gamma_1 D} > \bar{N}_1 > \lambda_1$  and  $f_1(\bar{N}_1) > m_1$ , so that  $E_{\Lambda_1}$  exists. It is locally asymptotically stable for (1) if and only if  $f_2(\bar{N}_1) < m_2 + \frac{\eta_1 \Lambda_1 (f_1(\bar{N}_1) - m_1)}{c \eta_2} g'_2(0)$ ,  $\hat{A} > 0$ , and  $\hat{A}\hat{B} > \hat{C}$ ; where  $\hat{A}, \hat{B}$  and  $\hat{C}$  are defined in 11a–11c.

**5. Ecological interpretations of inequalities.** This section gives ecological interpretations of inequalities resulting from the local stability results for model (1).

By statement 1 of Theorem 4.1, the species-free steady state  $E_0$  is locally asymptotically stable if and only if  $f_i(N_0) < m_i$ , for  $i = 1, 2$ . That is, the growth of phytoplankton  $P_i$  at the  $N_0$ -level of nutrient is strictly less than its removal rate  $m_i$ . Thus neither  $P_1$  nor  $P_2$  can survive at this level of nutrient. Since  $P_1$  and  $P_2$  are the only resources for zooplankton  $Z$ , it readily follows that  $Z$  also goes extinct.

Statement 2 biologically means that  $E_{\lambda_1}$  is locally asymptotically stable provided (a) there is adequate nutrient supply for phytoplankton  $P_1$ , (b) the growth of phytoplankton  $P_2$  at the  $\lambda_1$ -level of nutrient is strictly less than its removal (washout, intrinsic death, and autotoxicity) rate and (c) the growth of animal plankton  $Z$  at the  $\frac{\gamma_1(N_0 - \lambda_1)D}{m_1}$ -level of phytoplankton  $P_1$  is strictly less than its removal rate. These three conditions explain why only phytoplankton  $P_1$  avoids extinction.

A biological interpretation of statement 3 parallels that of statement 2, and therefore is omitted.

The first conditions on statements 4 and 5 are ecologically more complex. Let us rewrite the first condition of statement 4,

$$f_1(\bar{N}_2) < \frac{\eta_2 \Lambda_2 (f_2(\bar{N}_2) - m_2)}{c \eta_1} g'_1(0) + m_1. \tag{12}$$

Recall that when  $P_1 = 0$ , the only removal incurred by phytoplankton  $P_1$  comes from washout and intrinsic death at rate  $m_1$  because  $g_1(0) = 0$ . Since the system

(1) is being considered near the  $E_{\Lambda_2}$  steady state, the quantity  $\frac{\eta_2 \Lambda_2 (f_2(\bar{N}_2) - m_2)}{c \eta_1} g'_1(0)$  is very small. This gives us an idea of how phytoplankton  $P_1$  is slightly being suppressed from the system (1) due to (a) competition pressure by phytoplankton  $P_2$ , and (b) predation by zooplankton  $Z$  in a small neighborhood of  $E_{\Lambda_2}$ . Therefore inequality (12) means that the growth of phytoplankton  $P_1$  at the  $\bar{N}_2$ -level of nutrient is strictly less than the rate at which  $P_1$  is being removed from the system (1) in a small neighborhood of  $E_{\Lambda_2}$ . Phytoplankton population  $P_2$  depresses nutrient availability to the lowest level  $\bar{N}_2$  and sustains the higher predator density. This is referred to as the  $R^*$  and  $P^*$  rules (see for example, [22]).

An ecological interpretation of inequality

$$f_2(\bar{N}_1) < m_2 + \frac{\eta_1 \Lambda_1 (f_1(\bar{N}_1) - m_1)}{c \eta_2} g'_2(0)$$

in statement 5 parallels that of the first condition of statement 4, and is therefore omitted.

**6. Transfer of Local stability and bifurcation.** This section deals with the hierarchy of steady states. It is shown that under certain conditions local stability transfers from one steady state to another as the input nutrient concentration  $N_0$  is increased. It is straightforward to prove that whenever a new steady state coalesces with an existing one, a transcritical bifurcation occurs. For the sake of exposition, we assume that  $\lambda_1 < \lambda_2$  (so that species  $P_1$  is the stronger competitor).

When  $N_0 < \lambda_1$ , only the washout equilibrium  $E_0$  exists and is stable. For  $N_0 = \lambda_1$ ,  $E_{\lambda_1}$  becomes feasible through a transcritical bifurcation at  $E_0$ . Then  $E_{\lambda_1}$  is a saddle. When  $\lambda_1 < N_0 < \lambda_2$ ,  $E_{\lambda_1}$  is stable and at some point (that is, when  $N_0 - \frac{\Lambda_1 m_1}{\gamma_1 D} > \bar{N}_1 > \lambda_1$ )  $E_{\Lambda_1}$  becomes feasible via a transcritical bifurcation at  $E_{\lambda_1}$ . The washout equilibrium  $E_0$  loses another degree of stability at  $N_0 = \lambda_2$  where  $E_{\lambda_2}$  becomes feasible through  $E_0$ . Henceforth,  $E_0$ ,  $E_{\lambda_1}$  and  $E_{\lambda_2}$  are unstable while  $E_{\Lambda_1}$  is already in the nonnegative cone of  $\mathbf{R}_+^4$ . Finally, for  $\lambda_2 < N_0$ ,  $E_{\Lambda_2}$  undergoes a transcritical bifurcation at  $E_{\lambda_2}$  and becomes feasible.

At some point (that is, when  $N_0 - \frac{\Lambda_2 m_2}{\gamma_2 D} > \bar{N}_2 > \lambda_2$ ) all the boundary equilibria  $E_0$ ,  $E_{\lambda_1}$ ,  $E_{\lambda_2}$ ,  $E_{\Lambda_1}$  and  $E_{\Lambda_2}$  exist in the nonnegative cone of  $\mathbf{R}_+^4$ . The stabilities of  $E_{\Lambda_1}$  and  $E_{\Lambda_2}$  follow from the facts that the  $\bar{N}_i$ 's depend continuously on the input concentration  $N_0$ , and their stability criteria are continuous functions of the  $\bar{N}_i$ . Given that  $E_{\Lambda_1}$  and  $E_{\Lambda_2}$  are born from  $E_{\lambda_1}$  and  $E_{\lambda_2}$ , respectively, increasing the  $\bar{N}_i$ 's slightly will not change the directions of the inequalities in statements 4 and 5 of Theorem 4.1.

**7. Global results.** In this section we investigate global properties of system (1). We first establish the competition-independent extinction of  $P_i$  (due to inadequate nutrient supply). The proof uses the following result due to [30]

**Lemma 7.1.** (*Miller's Lemma*) Let  $\omega(t) \in C^2(t_0, \infty)$ ,  $\omega(t) \geq 0$  and  $K > 0$ .

(a) If  $\omega'(t) \geq 0$ ,  $\omega(t)$  is bounded and  $\omega''(t) \leq K$  for all  $t \geq t_0$  then  $\omega'(t) \rightarrow 0$  as  $t \rightarrow \infty$ .

(b) If  $\omega'(t) \leq 0$ ,  $\omega''(t) \leq -K$  for all  $t \geq t_0$  then  $\omega'(t) \rightarrow 0$  as  $t \rightarrow \infty$ .

**Lemma 7.2.** If  $\lambda_i > N_0$ , then  $P_i(t) \rightarrow 0$  as  $t \rightarrow \infty$  in (1).

*Proof of Lemma 7.2.* Choose  $\delta > 0$  so that  $N_0 + \delta < \lambda_i$ . By Proposition 3.1,  $N(t) < N_0 + \delta$  for all sufficiently large  $t$ . From the second and third equations of system (1), and by monotonicity properties of uptake functions  $f_i$  and  $g_i$ , we have

$$\frac{dP_i(t)}{dt} \leq P_i(t)[f_i(N(t)) - m_i] \leq P_i(t)[f_i(N_0 + \delta) - m_i] \tag{13}$$

for all sufficiently large  $t$ . Hence by the definition of  $\lambda_i$  (that is,  $f_i(\lambda_i) = m_i$ ),  $\frac{dP_i(t)}{dt} < 0$  for all sufficiently large  $t$ . Also,  $P_i''(t)$  is bounded below. It follows from Lemma 7.1 that  $P_i'(t) \rightarrow 0$  as  $t \rightarrow \infty$ . However,  $\limsup_{t \rightarrow \infty} f_i(N(t)) < f_i(N_0 + \delta) < m_i$  so that the only possibility is that  $P_i(t) \rightarrow 0$  as  $t \rightarrow \infty$ .  $\square$

The next result states that  $E_0$  is a global attractor if it is the only steady state (i.e. when there is inadequate nutrient supply for both phytoplankton populations). Under the conditions of this theorem, the food chain under investigation crashes.

**Theorem 7.1.** *If  $N_0 < \lambda_i$  for  $i = 1, 2$ , then the species-free steady state  $E_0$  is globally asymptotically stable for (1).*

*Proof.* Since  $N_0 < \lambda_i$  for  $i = 1, 2$ , by Lemma 7.2 we obtain  $P_i(t) \rightarrow 0$  as  $t \rightarrow \infty$  in (1). Take

$$Q \in \{(N, P_1, P_2, Z) \in \mathbf{R}_+^4 : N > 0, P_1 > 0, P_2 > 0, Z > 0\}.$$

Let  $\Omega(Q)$  denote the omega limit set of the orbit through  $Q$ . Then it follows that any  $P = (N, P_1, P_2, Z) \in \Omega(Q)$  satisfies  $P_1 = 0, P_2 = 0$ . On  $\{(N, 0, 0, Z) \in \mathbf{R}_+^4\}$  the system reduces to

$$\begin{aligned} N'(t) &= (N_0 - N(t))D, \\ Z'(t) &= -cZ \end{aligned} \tag{14}$$

and hence  $N(t) \rightarrow N_0$  and  $Z(t) \rightarrow 0$  as  $t \rightarrow \infty$ . Therefore,  $\{E_0\} \in \Omega(Q)$ . Since all solutions are positive and bounded (see Lemma 3.1),  $\Omega(Q)$  is a nonempty compact subset of  $\mathbf{R}_+^4$ . If  $P \in \Omega(Q)$  then the entire trajectory through  $P$  is in  $\Omega(Q)$ . Hence,  $E_0$  is the only candidate. Thus,  $E_0$  is globally asymptotically stable for (1).  $\square$

We now provide conditions under which  $E_{\lambda_i}$  is globally asymptotically stable.

**Theorem 7.2.** (a) *Suppose  $\lambda_1 < N_0 < \lambda_2$  and  $\omega_1 < c$ . Then  $E_{\lambda_1}$  is globally asymptotically stable for (1).*

(b) *Suppose  $\lambda_2 < N_0 < \lambda_1$  and  $\omega_2 < c$ . Then  $E_{\lambda_2}$  is globally asymptotically stable for (1).*

*Proof.* We prove only (a) as the proof of (b) is symmetrical. Take

$$Q \in \{(N, P_1, P_2, Z) \in \mathbf{R}_+^4 : N > 0, P_1 > 0, P_2 > 0, Z > 0\}.$$

Let  $\Omega(Q)$  denote the omega limit set of the orbit through  $Q$ . Then it follows from Lemma 7.2 that any  $P = (N, P_1, P_2, Z) \in \Omega(Q)$  satisfies  $P_2 = 0$ . On  $\{(N, P_1, 0, Z) \in \mathbf{R}_+^4\}$  the system reduces to

$$\begin{aligned} N'(t) &= (N_0 - N(t))D - \frac{P_1(t)}{\gamma_1} f_1(N(t)), \\ P_1'(t) &= P_1(t)(f_1(N(t)) - m_1) - \frac{g_1(P_1)Z}{\eta_1}, \\ Z'(t) &= (g_1(P_1(t)) - c)Z(t). \end{aligned} \tag{15}$$

The third equation of (15) gives us

$$Z'(t) = (g_1(P_1(t)) - c)Z(t) < (\omega_1 - c)Z(t) \tag{16}$$

for all sufficiently large  $t$ . Hence,  $Z(t) \leq Z(0) \exp((\omega_1 - c)t) \rightarrow 0$  as  $t \rightarrow \infty$  (because  $\omega_1 < c$ ). By Lemma 3.1  $Z(t) > 0$  and so  $Z(t) \rightarrow 0$  in (1). On  $\{(N, P_1, 0, 0) \in \mathbf{R}_+^4\}$  system (15) reduces to

$$\begin{aligned} N'(t) &= (N_0 - N(t))D - \frac{P_1(t)}{\gamma_1} f_1(N(t)), \\ P_1'(t) &= P_1(t)(f_1(N(t)) - m_1). \end{aligned} \tag{17}$$

By an argument comparable to that given in [23],  $N(t) \rightarrow \lambda_1$  and  $P_1(t) \rightarrow \bar{P}_1 = \frac{\gamma_1(N_0 - \lambda_1)D}{m_1}$ . Therefore,  $\{E_{\lambda_1}\} \in \Omega(Q)$ . Since (17) has no periodic orbits and the boundary is acyclic, it follows from Lemma 4.3 in [41] that  $E_{\lambda_1}$  is globally asymptotically stable for (1).  $\square$

The limitations of asymptotic stability are local behavior of the system in a neighborhood of the equilibrium under investigation, eventual coexistence of species on cyclical or chaotic orbits when there is an unstable equilibrium, and possibility of most orbits (trajectories) to tend to extinction states (see for example, [1]).

Persistence applies to those cases where none of the components of the ecosystem goes extinct. Most importantly, to end this section we state a uniform persistence result to derive the existence of at least one interior equilibrium. The proof uses Theorem 3.1 in [7] (see Appendix), which is a slightly modified version of the main result of [6] on uniformly persistent systems.

**Theorem 7.3.** *Suppose the following conditions hold:*

1.  $E_{\lambda_i}$  exists and is globally asymptotically stable for (1) with initial conditions in  $\{(N, P_1, P_2, 0) : N \geq 0, P_i > 0, P_j = 0, i \neq j\}$ ,
2.  $f_i(\lambda_j) > m_i$  and  $g_j(\bar{P}_j) > c$  for  $i \neq j$ ,
3.  $E_{\Lambda_i}$  exists and is globally asymptotically stable for (1) with initial conditions in  $\{(N, P_1, 0, Z) : N \geq 0, P_i > 0, P_j = 0, Z > 0\}$ ,
4.  $f_i(\bar{N}_j) > \frac{\bar{Z}_j}{\eta_j} g_i'(0) + m_i, i \neq j$ .

Then system (1) is uniformly persistent.

*Proof.* See Appendix  $\square$

It follows from Theorem 7.3 that model (1) has at least one interior equilibrium. Extensive simulations (given in the next section) indicate that this interior equilibrium point may be unique and attracts all solutions of (1) regardless of initial conditions in the positive cone  $Int(\mathbf{R}_+^4)$ . The analytical part of this result is left for future investigation.

**8. Example.** In the figures of this section, each of the outcomes previously described analytically is illustrated. We ran simulations using Matlab. The timeframe for our simulations was 0 to 25000 days. Only the first 60 days are shown in the figures below. A very large grid of initial conditions  $(N(0), P_1(0), P_2(0), Z(0))$  in the positive cone  $Int(\mathbf{R}_+^4)$  was considered to ensure convergence of all solutions of system (1) to the indicated equilibrium. For illustration, in all figures, we choose  $(N(0), P_1(0), P_2(0), Z(0)) = (0.1, 0.7, 0.7, 0.8)$ .

We consider the system (1) with  $D = m_i = \gamma_i = \eta_i = 1, i = 1, 2, c = 1.1, \mu_1 = 8.5, \mu_2 = 6, K_1 = 0.6, K_2 = 0.7, \omega_1 = 8.4, \omega_2 = 5.9, L_1 = 0.9,$  and

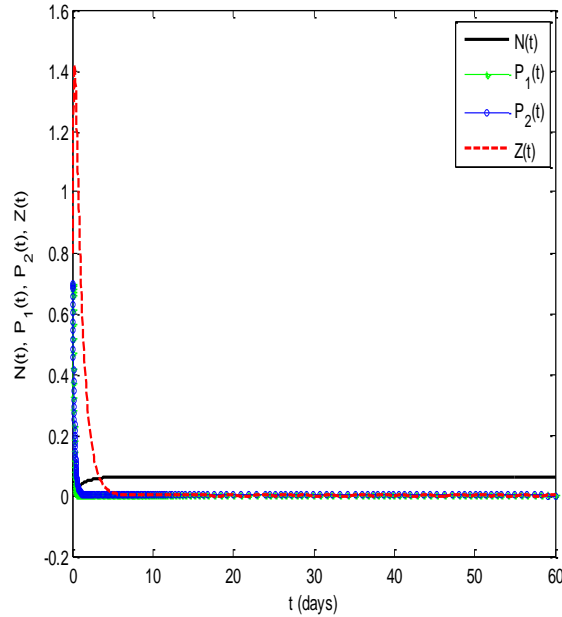


FIGURE 1. Plots of  $N(t)$ ,  $P_1(t)$ ,  $P_2(t)$ , and  $Z(t)$  when the input nutrient concentration  $N_0 = 0.06$  satisfies  $N_0 < \lambda_1 < \lambda_2$  and  $(N(0), P_1(0), P_2(0), Z(0)) = (0.1, 0.7, 0.7, 0.8)$ . By Theorem 7.1, the species-free equilibrium  $E_0$  is globally asymptotically stable for model (1).

$L_2 = 1.8$ . The consumption functions  $f_i$  and  $g_i$  follow Michaelis-Menten kinetics, so that  $f_1(N) = \frac{8.5N}{0.6+N}$ ,  $f_2(N) = \frac{6N}{0.7+N}$ ,  $g_1(P_1) = \frac{8.4P_1}{0.9+P_1}$ , and  $g_2(N) = \frac{5.9P_2}{1.8+P_2}$ . It is straightforward to check that  $\lambda_1 = 0.07$  and  $\lambda_2 = 0.14$ . Some of these parameters values are borrowed from [29] and references therein.

We first take  $N_0 = 0.06$ , so that  $N_0 < \lambda_1 < \lambda_2$ . By Theorem 7.1, the species-free steady state  $E_0$  is globally asymptotically stable: all solutions of (1) tend to  $E_0$  regardless of initial condition. One such solution is depicted in Figure 1.

We then increase  $N_0$  to 0.12, so that  $\lambda_1 < N_0 < \lambda_2$ . In addition,  $c = 1.1 < \omega_1$ . By Theorem 7.2,  $E_{\lambda_1}$  is globally asymptotically stable for (1): all solutions of system (1) tend  $E_{\lambda_1}$  regardless of initial condition. One such solution is depicted in Figure 2.

We further increase  $N_0$  to 0.7, so that  $\lambda_1 < \lambda_2 < N_0$ . It can be shown that all of the hypotheses of Theorem 7.3 are satisfied so that system (1) is uniformly persistent. Thus, all components of solutions of model (1) are bounded away from zero (independent of initial data) after a sufficiently long time. One such solution is depicted in Figure 3. Note that uniform persistence implies immediately that there is at least one interior equilibrium. Extensive numerics indicate that this equilibrium might be unique.

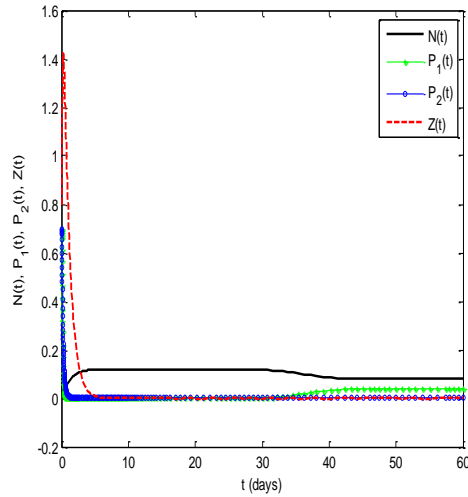


FIGURE 2. Plots of  $N(t)$ ,  $P_1(t)$ ,  $P_2(t)$ , and  $Z(t)$  when the input nutrient concentration  $N_0 = 0.12$  satisfies  $\lambda_1 < N_0 < \lambda_2$ ,  $c = 1.1 < \omega_1$  and  $(N(0), P_1(0), P_2(0), Z(0)) = (0.1, 0.7, 0.7, 0.8)$ . By Theorem 7.2, the boundary equilibrium  $E_{\lambda_1}$  is globally asymptotically stable for model (1).

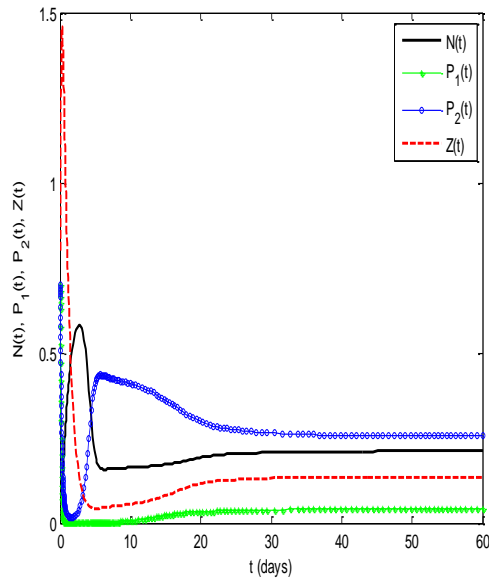


FIGURE 3. Plots of  $N(t)$ ,  $P_1(t)$ ,  $P_2(t)$ , and  $Z(t)$  when the input nutrient concentration  $N_0 = 0.7$  satisfies  $\lambda_1 < \lambda_2 < N_0$  and  $(N(0), P_1(0), P_2(0), Z(0)) = (0.1, 0.7, 0.7, 0.8)$ . By Theorem 7.3 the system (1) is uniformly persistent: all components of solutions of (1) are bounded away from zero (independent of initial data) after a sufficiently long time.

**9. Concluding remarks.** In this paper, we extended the main model in [27] to include the effects of predation on the ecosystem structure in the absence of phytotoxic effects. The resulting model is a significant generalization of the works of [8], [22], [17] and [29] among others. Using the input nutrient concentration as the bifurcation parameter, we described the evolution of equilibria into the nonnegative cone of  $\mathbf{R}_+^4$ , provided conditions for the existence and stability of equilibria, and conditions under which all species persist. Ecological interpretations of the stability conditions are given. Numerical simulations support our analytical findings. The model in [27] lacks uniform persistence features because of the simultaneous existence of two interior equilibrium points of opposite stabilities. Model (1) extends the main model in [27] and exhibits uniform persistence. Our findings are in line with the statement that predation can be responsible for diversity in ecosystems (see for example, [11]).

In the case of uniform persistence, extensive simulations indicate that all solutions of model (1) converge to a unique interior steady state regardless of initial conditions in the the positive cone  $Int(\mathbf{R}_+^4)$ . The analytical part of this global result will complete the global results of this paper and is left for future investigation. Model (1) in the presence of phytotoxic interactions is not uniformly persistent. Since the model in [27] is not uniformly persistent, we will show in future work that adding predation by zooplankton  $Z$  increases the number of boundary equilibria without making the resulting model uniformly persistent. Finally, while we have assumed a spatially homogeneous environment on the system (1), we could further consider the possibility of studying the impact of diffusion on model (1).

The model (1) has similarities with other food-chain models. As such, the results of this paper may be relevant to a wider spectrum of population models, not just those focused on plankton.

**Acknowledgments.** The author would like to thank the editor and both referees for their helpful suggestions on improving the manuscript. Also, the author would like to thank Mrs. P. Wyatt for proofreading the manuscript and Dr. E. Ncheuguim for helping with the resolution of figures.

**Appendix.** We paraphrase a Lemma and a Theorem that underlie the proof of Theorem 7.3.

**Lemma 9.1.** *Consider the system of differential equations*

$$\dot{x} = f(x), \quad (18)$$

where the vector-valued function  $f$  is continuous on an open set  $G \subseteq \mathbf{R}^n \rightarrow \mathbf{R}^n$ .

If the solution  $\phi(t, x^0)$  of (18) remains in a compact set  $K$  for all  $0 \leq t < \infty$ , then its positive limit set  $\Omega(C^+)$  is a nonempty, compact, and invariant set with respect to (18). Moreover,  $\phi(t, x^0)$  approaches the set  $\Omega(C^+)$  as  $t \rightarrow \infty$  (i.e., for every  $\epsilon > 0$  there exists a  $T > 0$  such that for every  $t > T$  there exists a point  $a \in \mathbf{R}^n$  (possibly depending on  $t$ ) such that  $|\phi(t, x^0) - a| < \epsilon$ ).

**Theorem 9.1.** (Theorem 3.1, [7]) *Let  $\Phi_t$  be a continuous flow on a locally compact metric space  $E$  with invariant boundary. Assume that the flow  $\Phi_t$  is dissipative and the boundary flow is isolated and is acyclic with acyclic covering  $\mathcal{M}$ . Then  $\Phi_t$  is uniformly persistent if and only if*

$$\Omega(M_j^+) \cap Int(E) = \emptyset,$$

for each  $M_j \in \mathcal{M}$ .



*Proof of Theorem 7.3.* We prove Theorem 7.3 in five steps. Let  $C^+$  denote the positive cone in  $(\mathbf{R}^4, \rho)$  where for  $X = (\bar{N}, \bar{P}_1, \bar{P}_2, \bar{Z})^T$  and  $Y = (N, P_1, P_2, Z)^T$ ,  $\rho(X, Y) = \sum_{k=1}^4 |Y_k - X_k|$ .  $(C^+, \rho)$  is a locally compact metric space. Denote by  $\mathcal{F} = (C^+, \mathbf{R}, \pi)$  the continuous flow of model (1),  $\gamma^+(X)$  the positive semiorbit of  $\mathcal{F}$  through  $X$ ,  $\Lambda^+(X)$  the omega limit set of  $\gamma^+(X)$ , and  $W^+(M)$  the stable manifold of an isolated invariant set  $M$  for the flow  $\mathcal{F}$ .

**Step 1.** The flow  $\mathcal{F}$  is dissipative, that is for each  $X \in C^+$ ,  $\Lambda^+(X)$  is nonempty and the invariant set  $\Omega(\mathcal{F}) = \bigcup_{X \in C^+} \Lambda^+(X)$  has compact closure.

In fact, if there is an  $\bar{X} \in C^+$  such that  $\Lambda^+(\bar{X}) = \emptyset$ , then no positive semiorbit of  $\mathcal{F}$  passes through  $\bar{X}$ . This contradicts the statement that for any set of initial conditions in  $C^+$ , there is a unique trajectory solution to model (1). It readily follows that  $\Lambda^+(X) \neq \emptyset$  for each  $X \in C^+$ . To complete the proof of step 1, let us observe that  $\overline{\Omega(\mathcal{F})} = \bigcap_{X \in C^+} \overline{\Lambda^+(X)}$ . Let  $X_0$  be an initial condition in  $C^+$  and  $\pi(t, X_0)$  be a solution of model (1). By Lemma 3.1,  $\pi(t, X_0)$  remains positive and bounded for all  $0 \leq t < \infty$ . That is, for any  $0 \leq t < \infty$ ,  $\overline{\pi(t, X_0)}$  remains in a closed and bounded (compact) subset  $K$  of  $\mathbf{R}^4$ . Therefore,  $\overline{\Omega(\mathcal{F})}$  is not empty, compact and invariant with respect to (1) by Lemma 9.1. Thus  $\mathcal{F}$  is dissipative.

**Step 2.**  $\partial\mathcal{F}$  is acyclic. The stable manifold structures of  $E_0, E_{\lambda_1}, E_{\lambda_2}, E_{\Lambda_1}$ , and  $E_{\Lambda_2}$  imply that they are not cyclically chained to each other on the boundary  $\partial\mathcal{F}$ . In addition the steady states form a covering of invariant subsets of  $\partial\mathcal{F}$  with respect to (1). Thus,  $\partial\mathcal{F}$  is acyclic.

**Step 3.**  $\partial\mathcal{F}$  is isolated.  $E_0, E_{\lambda_1}, E_{\lambda_2}, E_{\Lambda_1}$ , and  $E_{\Lambda_2}$  are the invariant sets on  $\partial\mathcal{F}$ . These five equilibrium points constitute a finite covering  $\mathcal{M}$  of  $\Omega(\partial\mathcal{F})$ . They are pairwise-disjoint, compact and isolated for both  $\partial\mathcal{F}$  and  $\mathcal{F}$ . Hence,  $\partial\mathcal{F}$  is isolated by definition.

**Step 4.** The covering  $\mathcal{M}$  built in step 3 is acyclic and satisfies:

$$\forall M_i \in \mathcal{M}, W^+(M_i) \cap \text{Int}(C^+) = \emptyset. \quad (19)$$

The acyclicity of  $\mathcal{M}$  follows from step 2. The  $M_i$ 's are boundary steady states of model (1) and the hypotheses of Theorem 7.3 guarantee that each of them is a saddle in  $\mathbf{R}^4$ . The stable manifold of  $M_i \in \mathcal{M}$  is given by  $W^+(M_i) = \{X \in C^+ : \Lambda^+(X) \neq \emptyset, \Lambda^+(X) \subset M_i\}$  and has an empty intersection with the interior of the positive cone  $C^+$ .

**Step 5.** Conclusion. By Theorem 3.1 of [7], we conclude that  $\mathcal{F}$  is uniformly persistent. This completes the proof of Theorem 7.3.  $\square$

## REFERENCES

- [1] H. M. Anderson, V. Hutson and R. Law, On the conditions for persistence of species in ecological communities, *Amer. Natur.*, **139** (1992), 663–668.
- [2] R. Aris and A. E. Humphrey, Dynamics of a chemostat in which two organisms compete for a common substrate, *Biotechnol. Bioeng.*, **19** (1977), 1375–1386.
- [3] M. M. Ballyk and G. S. K. Wolkowicz, Exploitative competition in the chemostat for two perfectly substitutable resources, *Math. Biosci.*, **118** (1993), 127–180.
- [4] E. Beretta, G. Bischi and F. Solimano, Stability in chemostat equations with delayed nutrient recycling, *J. Math. Biol.*, **28** (1990), 99–111.
- [5] B. Boon and H. Laudelout, Kinetics of nitrite oxidation by *Nitrobacter winogradskyi*, *Biochem. J.*, **85** (1962), 440–447.
- [6] G. Butler, H. I. Freedman and P. Waltman, Uniform persistent systems, *Proc. Amer. Math. Soc.*, **96** (1986), 425–430.

- [7] G. Butler and P. Waltman, [Persistence in dynamical systems](#), *J. Diff. Equ.*, **63** (1986), 255–263.
- [8] G. J. Butler and G. S. K. Wolkowicz, [Predator-mediated competition in the chemostat](#), *J. Math. Biol.*, **24** (1986), 167–191.
- [9] G. J. Butler and G. S. K. Wolkowicz, [Exploitative competition in a chemostat for two complementary, and possibly inhibitory, resources](#), *Math. Biosci.*, **83** (1987), 1–48.
- [10] S. Chakraborty and J. Chattopadhyay, [Nutrient-phytoplankton-zooplankton dynamics in the presence of additional food source—A mathematical study](#), *J. Biol. Syst.*, **16** (2008), 547–564.
- [11] P. Chesson, J. M. Chase, P. A. Abrams, J. P. Grover, S. Diehl, R. D. Holt, S. A. Richards, R. M. Nisbet and T. J. Case, The interaction between predation and competition: A review and synthesis, *Eco. Let.*, **5** (2002), 302–315.
- [12] W. A. Coppel, *Stability and Asymptotic Behavior of Differential Equations*, Heath, Boston, 1965.
- [13] J. M. Cushing, *Integrodifferential Equations and Delay Models in Population Dynamics*, Heidelberg, Springer-Verlag, 1977.
- [14] A. M. Edwards, [Adding detritus to a nutrient-phytoplankton-zooplankton model: A dynamical-systems approach](#), *J. Plankton Res.*, **23** (2001), 389–413.
- [15] A. M. Edwards and J. Brindley, [Oscillatory behaviour in a three-component plankton population model](#), *Dyna. Stabi. Syst.*, **11** (1996), 347–370.
- [16] A. M. Edwards and J. Brindley, [Zooplankton mortality and the dynamical behaviour of plankton population models](#), *Bull. Math. Biol.*, **61** (1999), 303–339.
- [17] J. P. Grover and R. D. Holt, [Disentangling resource and apparent competition: Realistic models for plant-herbivore communities](#), *J. Theor. Biol.*, **191** (1998), 353–376.
- [18] T. G. Hallam, On persistence of aquatic ecosystems. in *Ocean. Sound Scat. Predic.* (eds. N. R. Anderson and B. G. Zahuranc), Plenum, New York, 1977, 749–765.
- [19] T. G. Hallam, Controlled persistence in rudimentary plankton models, in *Proceedings of the First International Conference on Mathematical Modeling* (eds. J. R. Avula), Vol. IV, University of Missouri Press, Rolla, 1977, 2081–2088.
- [20] T. G. Hallam, [Structural Sensitivity of grazing formulation in nutrient controlled plankton models](#), *J. Math. Biol.*, **5** (1978), 261–280.
- [21] S. R. Hansen and S. P. Hubbell, [Single-nutrient microbial competition: Qualitative agreement between experimental and theoretical forecast outcomes](#), *Sci.*, **207** (1980), 1491–1493.
- [22] R. D. Holt, J. Grover and D. Tilman, [Simple rules for interspecific dominance in systems with exploitative and apparent competition](#), *Amer. Natur.*, **144** (1994), 741–771.
- [23] S. B. Hsu, [Limiting behavior for competing species](#), *SIAM J. Appl. Math.*, **34** (1978), 760–763.
- [24] J. P. Ivlev, *Experimental Ecology of the Feeding of Fishes*, Yale University Press, New Haven, 1961.
- [25] S. R. J. Jang and J. Baglama, [Nutrient-plankton models with nutrient recycling](#), *Comput. Math. Appl.*, **49** (2005), 375–378.
- [26] J. L. Jost, S. F. Drake, A. G. Fredrickson and M. Tsuchiya, Interaction of tetrahymena pyriformis, escherichia, coli, azotobacter vinelandii and glucose in a minimal medium, *J. Bacteriol.*, **113** (1976), 834–840.
- [27] J.-J. Kengwoung-Keumo, *Competition Between Two Phytoplankton Species Under Predation and Allelopathic Effects*, Ph.D. dissertation, New Mexico State University, Las Cruces, New Mexico, U.S.A., 2012.
- [28] J. A. León and D. B. Tumpson, Competition between two species for two complementary or substitutable resources, *J. Theor. Biol.*, **50** (1975), 185–201.
- [29] B. Li and Y. Kuang, [Simple Food Chain in a Chemostat with Distinct Removal Rates](#), *J. Math. Anal. and Appl.*, **242** (2000), 75–92.
- [30] R. K. Miller, *Nonlinear Volterra Equation*, W. A. Benjamin, N.Y., 1971.
- [31] J. Monod, *Recherche sur la Croissance des Cultures Bacteriennes*, Hermann et Cie, Paris, 1942.
- [32] B. Mukhopadhyay and R. Bhattacharyya, [Modelling phytoplankton allelopathy in a nutrient-plankton model with spatial heterogeneity](#), *Ecol. Model.*, **198** (2006), 163–173.
- [33] L. Perko, *Differential Equations and Dynamical Systems*, Third edition, Springer, 2001.
- [34] D. Rapport, [An optimization model of food selection](#), *Amer. Natur.*, **105** (1971), 575–587.
- [35] S. Roy, [The coevolution of two phytoplankton species on a single resource: Allelopathy as a pseudo-mixotrophy](#), *Theor. Popul. Biol.*, **75** (2009), 68–75.
- [36] S. Ruan, Oscillations in plankton models with recycling, *J. Theor. Biol.*, **208** (2001), 15–26.

- [37] S. Ruan, Persistence and coexistence in zooplankton-phytoplankton-nutrient models with instantaneous nutrient recycling, *J. Math. Biol.*, **31** (1993), 633–654.
- [38] A. Sinkkonen, Modelling the effect of autotoxicity on density-dependent phytotoxicity, *J. Theor. Biol.*, **244** (2007), 218–227.
- [39] J. H. Steele and E. W. Henderson, The role of predation in plankton models, *J. Plankton Res.*, **14** (1992), 157–172.
- [40] M. A. Tabatabai, W. M. Eby, S. Bae and K. P. Singh, A flexible multivariable model for phytoplankton growth, *Math. Biosci. Eng.*, **10** (2013), 913–923.
- [41] H. R. Thieme, Convergence results and a Poincaré-Bendixson trichotomy for asymptotically autonomous differential equations, *J. Math. Biol.*, **30** (1992), 755–763.
- [42] G. S. K. Wolkowicz and Z. Lu, Global dynamics of a mathematical model of competition in the chemostat: General response functions and differential death rates, *J. Appl. Math.*, **52** (1992), 222–233.
- [43] R. D. Yang and A. E. Humphrey, Dynamics and steady state studies of phenol biodegradation in pure and mixed cultures, *Biotechnol. Bioeng.*, **17** (1975), 1211–1235.

Received December 26, 2013; Accepted May 09, 2014.

*E-mail address:* [jkengwou@cameron.edu](mailto:jkengwou@cameron.edu)