

A THREE-TROPHIC-LEVEL MODEL OF PLANKTON DYNAMICS WITH NUTRIENT RECYCLING

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ABSTRACT. A three-trophic-level model of plankton dynamics with instantaneous nutrient recycling is considered. The model consists of autotrophic phytoplankton, herbivorous zooplankton, carnivorous zooplankton and dissolved limiting nutrient. Conditions are derived such that one or more components of the populations tend to extinction. Persistence criteria for the model are also obtained. As well, the bifurcation of periodic solutions from one of the coordinate plane into the positive cone is studied.

1. Introduction. To date several attempts to model nutrient plankton dynamics have been made. Early models tended to concentrate on the interaction of phytoplankton and zooplankton only. More recently, models have become more holistic by attempting to embrace a larger portion of our knowledge of the components of the ecosystem and the flow of materials between these components. Williams [41] provided the conceptual background for a plankton dynamics model incorporating bacteria, protozoans and dissolved organic matter. Evans and Parslow [13] presented a model of phytoplankton-zooplankton-nitrogen dynamics in a seasonably varying mixed layer. They showed how the seasonal recurrence of plankton cycles, in particular the spring bloom, is driven by the interaction of physical mixing with removal by grazers. DeAngelis, Bartell and Brenkert [9] studied the effects of nutrient recycling and food-chain length on resilience of a plankton model consisting of carnivore, herbivore, autotroph, detritus and nutrient. Fasham, Ducklow and McKelvie [14] constructed a simple but realistic model of plankton and nutrient dynamics of the oceanic mixed layer that includes the major plankton groups (plankton, zooplankton, bacteria) and the major forms of nitrogen (new and recycled inorganic forms, dissolved and particular organic forms).

An ecological system is virtually never totally closed to material fluxes from the outside; these are generally inputs of nutrients to the system,

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as well as losses from the system. Recently, Wroblewski, Sarmiento and Flierl [44] introduced a closed two-trophic-level food chain model which they used to study plankton densities in different ocean layers. Busenberg et al. [1] studied the stability of the model constructed by Wroblewski et al., and pursued the biological implications of the stability results and of the existence of stable oscillatory states. In [35], based on the model built by Wroblewski et al., we considered three open models consisting of phytoplankton, zooplankton and dissolved limiting nutrient with a constant input concentration of the limiting nutrient and different constant washout rates, a periodic input concentration and a constant washout rate, a constant input concentration and a periodic washout rate, respectively. Persistence and bifurcation were discussed.

In the present paper, we consider a three-trophic-level food chain model with instantaneous nutrient recycling, which consists of autotrophic phytoplankton, herbivorous zooplankton, carnivorous zooplankton and dissolved limiting nutrient. We suppose that the carnivorous zooplankton (Z_2) feeds on the herbivorous zooplankton (Z_1), in turn the herbivorous zooplankton feeds upon the autotrophic phytoplankton (P), and only phytoplankton takes nutrient (N) directly. All dead carnivorous zooplankton, herbivorous zooplankton and phytoplankton recycled back into nutrient. We will consider the question of extinction and persistence of the three trophic level model. It is also shown that coexistence of all components may occur in the form of bifurcating periodic solutions. Similar three-trophic-level chemostat type models have been studied by Butler, Hsu and Waltman [3], Keener [26], (see also Butler and Wolkowicz [6], Wolkowicz [43] and Waltman [40]).

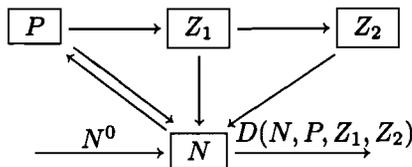


FIGURE 1. A three trophic level food chain for plankton dynamics with limit nutrient recycling. N^0 is the input rate of nutrient, D is the washout rate.

In our discussion, persistence is a central concept. We utilize the definitions of persistence developed by Butler, Freedman and Waltman [2] and Freedman and Moson [16]. A component $x(t)$ of a given system is said to be *persistent* if for any $x(0) > 0$ it follows that $\liminf_{t \rightarrow \infty} x(t) > 0$. If there exists $\delta > 0$ such that $\liminf_{t \rightarrow \infty} x(t) > \delta$, then $x(t)$ is said to be *uniformly persistent*. A system is (uniformly) persistent if each component is (uniformly) persistent. Persistence in biological systems has been discussed by many authors. We refer in particular to persistence in four-dimensional models, (see Butler and Wolkowicz [6], So and Freedman [37], Freedman, So and Waltman [19], Freedman and Rai [17], Kumar and Freedman [31], Kirlinger [27], Takeuchi [39] and Zaghrou [45]). For the existence of periodic solutions in the four-dimensional models, we refer to Butler, Hsu and Waltman [3], Keener [26], and Freedman, So and Waltman [19].

The paper is organized as follows. In the next section, we describe the model. In Section 3, we study questions of extinction and persistence. In Section 4 the bifurcation analysis is carried out. The final section contains a discussion.

2. The model. The compartmental model used for a food chain consisting of autotrophic phytoplankton (P), herbivorous zooplankton (Z_1), carnivorous zooplankton (Z_2) and dissolved limiting nutrient (N), is given by

$$\begin{aligned}
 \frac{dN}{dt} &= D(N^0 - N) - aP \frac{N}{k + N} + (1 - \delta)cZ_1(1 - e^{-\lambda P}) \\
 &\quad + (1 - \sigma)bZ_2 \frac{Z_1^2}{\ell + Z_1^2} + \gamma P + \varepsilon Z_1 + \mu Z_2 \\
 \frac{dP}{dt} &= aP \frac{N}{k + N} - cZ_1(1 - e^{-\lambda P}) - (\gamma + D)P \\
 (2.1) \quad \frac{dZ_1}{dt} &= Z_1[\delta c(1 - e^{-\lambda P}) - (\varepsilon + D)] - bZ_2 \frac{Z_1^2}{\ell + Z_1^2} \\
 \frac{dZ_2}{dt} &= Z_2[\sigma b \frac{Z_1^2}{\ell + Z_1^2} - (\mu + D)],
 \end{aligned}$$

$$N(0) \geq 0, \quad P(0) > 0, \quad Z_1(0) > 0, \quad Z_2(0) > 0,$$

where all parameters are positive and are interpreted as follows:

N^0 – input nutrient concentration rate

D – washout rate

a – maximal growth rate of the autotrophic phytoplankton

k – (Michaelis-Menten) half saturation constant

δ – herbivorous zooplankton resource conversion rate

σ – carnivorous zooplankton resource conversion rate

c – maximal herbivorous zooplankton ingestion rate

b – maximal carnivorous zooplankton ingestion rate

λ – rate at which saturation is achieved with decreasing phytoplankton level

ℓ – (Holling Type III) half saturation constant

γ – phytoplankton death rate

ε – herbivorous death rate

μ – carnivorous death rate.

We specify a constant input rate of dissolved limiting nutrient N^0 , as well as a loss rate D . The uptake kinetics of the limiting nutrient is described by a Michaelis-Menten function or Holling Type II functional response (see Holling [23])

$$\frac{N}{k + N},$$

where k is the Michaelis-Menten half-saturation constant. This uptake rate was proposed by Dugdale [11] and has been widely employed (see Busenberg et al. [1], Hallam [22] and Wroblewski et al. [44]). Various laboratory and field experiments indicate that this uptake response is reasonably appropriate for nitrate, ammonium and phosphate (see Rogers and McCarthy [34] and the references cited therein).

Marine copepods show an increasing ingestion rate as food concentrations increase. The functional form of this response has generally been assumed as the Michaelis-Menten or Holling Type II showing a saturation of the ingestion rate with high prey concentrations. Commonly, Ivlev's functional response formulation (see Ivlev [25])

$$1 - e^{-\lambda P}$$

is used to describe the herbivorous zooplankton grazing in curving-fitting and modelling (see Wroblewski et al. [44]), where λ is the rate

at which saturation is achieved with increasing phytoplankton level (per unit concentration).

The carnivorous zooplankton consumption of herbivorous zooplankton is modeled as Holling type III functional response (see Holling [23] and DeAngelis et al. [9])

$$\frac{Z_1^2}{\ell + Z_1^2},$$

where ℓ is a Holling type III half-saturation constant. The representation is appropriate for situations in which the rate of predation per capita prey tends to become smaller as the biomass of prey decreases, which may often occur if there are refuges for the prey.

During consumption, only fractions of phytoplankton and herbivorous zooplankton removed from the resource compartments, δ , $\delta \leq 1$, and σ , $\sigma \leq 1$, are assumed to be assimilated by the consumers herbivore and carnivore respectively, the remains go directly to the dissolved limiting nutrient. Two other losses of biotic components are also modeled: (1) direct losses from autotrophic phytoplankton, herbivorous zooplankton and carnivorous zooplankton with loss rates γ , ε and μ respectively, to the dissolved limiting nutrient; and (2) removal of biotic components from the system (DP , DZ_1 , and DZ_2) resulting from washout, harvesting or burial in deep sediments, for example.

Note that $E_1 = (N^0, 0, 0, 0)$ is always an equilibrium for system (2.1).

3. Extinction and persistence. In this section we change the variables in system (2.1) to nondimensional form. Let

$$\begin{aligned} \bar{N} &= \frac{N}{N^0}, & \bar{P} &= \frac{P}{N^0}, & \bar{Z}_1 &= \frac{Z_1}{N^0}, & \bar{Z}_2 &= \frac{Z_2}{N^0}, \\ \bar{k} &= \frac{k}{N^0}, & \bar{\ell} &= \frac{\ell}{N^0}, & \bar{a} &= \frac{a}{D}, & \bar{c} &= \frac{c}{D}, \\ \bar{b} &= \frac{b}{D}, & \bar{\gamma} &= \frac{\gamma}{D}, & \bar{\varepsilon} &= \frac{\varepsilon}{D}, & \bar{\mu} &= \frac{\mu}{D}, \\ & & \bar{t} &= Dt, & \bar{\lambda} &= \lambda N^0. \end{aligned}$$

After dropping the bars, system (2.1) becomes

$$\begin{aligned}
 \frac{dN}{dt} &= 1 - N - aP \frac{N}{k+N} + (1-\delta)cZ_1(1-e^{-\lambda P}) \\
 &\quad + (1-\sigma)bZ_2 \frac{Z_1^2}{\ell + Z_1^2} + \gamma P + \varepsilon Z_1 + \mu Z_2 \\
 \frac{dP}{dt} &= aP \frac{N}{k+N} - cZ_1(1-e^{-\lambda P}) - (\gamma+1)P \\
 \frac{dZ_1}{dt} &= Z_1[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)] - bZ_2 \frac{Z_1^2}{\ell + Z_1^2} \\
 \frac{dZ_2}{dt} &= Z_2[\sigma b \frac{Z_1^2}{\ell + Z_1^2} - (\mu+1)] \\
 N(0) &\geq 0, \quad P(0) > 0, \quad Z_1(0) > 0, \quad Z_2(0) > 0.
 \end{aligned}
 \tag{3.1}$$

Note that for system (3.1), the equilibrium E_1 assumes the form $E_1 = (1, 0, 0, 0)$.

Lemma 3.1. *The ω limit set of any solution of the initial value problem (3.1) lies in the hyperplane $N + P + Z_1 + Z_2 = 1$.*

Proof. Let $\Sigma(t) = N(t) + P(t) + Z_1(t) + Z_2(t)$, then

$$\frac{d\Sigma(t)}{dt} = 1 - \Sigma(t), \quad \Sigma(0) \geq 0,$$

and the lemma follows. \square

Note that the positive cone in (N, P, Z_1, Z_2) -plane is positively invariant. Lemma 3.1 implies the boundedness of solutions of system (3.1).

Put

$$\theta_1 = \frac{k}{\frac{a}{\gamma+1} - 1}, \quad \theta_2 = \frac{e^{-\lambda}}{1 - \frac{\varepsilon+1}{\delta c}}, \quad \theta_3 = \frac{\ell}{\frac{\sigma b}{\mu+1} - 1}.
 \tag{3.2}$$

In the following we give criteria for autotrophic phytoplankton or herbivorous zooplankton or carnivorous zooplankton or all of them to become extinct.

Proposition 3.2. *If*

$$(3.3) \quad [\sigma b - (\mu + 1)](1 - \theta_3) \leq 0,$$

then $\lim_{t \rightarrow \infty} Z_2(t) = 0$.

Proof. From the fourth equation of system (3.1), we have that

$$\begin{aligned} \frac{dZ_2}{dt} &= Z_2 \left[\sigma b \frac{Z_1^2}{\ell + Z_1^2} - (\mu + 1) \right] \\ &= Z_2 \frac{\sigma b - (\mu + 1)}{\ell + Z_1^2} \left[Z_1^2 - \frac{\ell(\mu + 1)}{\sigma b - (\mu + 1)} \right] \\ &\leq Z_2 \frac{\sigma b - (\mu + 1)}{\ell + Z_1^2} (1 - \theta_3). \end{aligned}$$

Since there are no invariant sets such that $Z_2 > 0$ is constant, the conclusion follows. \square

If one of the inequalities $\sigma b \leq \mu + 1$ and $\theta_3 \geq 1$ holds, but not both, then (3.3) holds. Hence Proposition 3.2 indicates that if the growth rate of the carnivorous zooplankton is less than or equal to its loss rate, or if the parameter θ_3 is greater than or equal to one, then the carnivorous zooplankton population will die out.

Proposition 3.3. *If*

$$(3.4) \quad [\delta c - (\varepsilon + 1)](1 - \theta_2) \leq 0,$$

then $\lim_{t \rightarrow \infty} Z_1(t) = 0$ and consequently $\lim_{t \rightarrow \infty} Z_2(t) = 0$.

Proof. By the third equation of (3.1) we have

$$\frac{dZ_1}{dt} < Z_1[\delta c(1 - e^{-\lambda P}) - (\varepsilon + 1)]$$

$$\begin{aligned}
&= Z_1[\delta c - (\varepsilon + 1)] \left[1 - \frac{\delta c e^{-\lambda P}}{\delta c - (\varepsilon + 1)} \right] \\
&\leq Z_1[\delta c - (\varepsilon + 1)](1 - \theta_2).
\end{aligned}$$

Since there are no invariant sets such that $Z_1 > 0$ is constant, $Z_1(t) \rightarrow 0$ as $t \rightarrow \infty$. In view of the fourth equation of (3.1), $Z_1(t) \rightarrow 0$ implies $Z_2(t) \rightarrow 0$ as $t \rightarrow \infty$. This completes the proof. \square

Similarly, Proposition 3.3 shows that if the growth rate of the herbivorous zooplankton is less than or equal to its loss rate (death rate plus washout rate), or the parameter θ_2 is greater than or equal to one, than the herbivorous zooplankton population, and hence the carnivorous zooplankton population will become extinct.

Proposition 3.4. *If*

$$(3.5) \quad [a - (\gamma + 1)](1 - \theta_1) \leq 0,$$

then $\lim_{t \rightarrow \infty} P(t) = 0$ *and consequently* $\lim_{t \rightarrow \infty} Z_1(t) = \lim_{t \rightarrow \infty} Z_2(t) = 0$.

Proof. Similar to the proof of Proposition 3.3, we have

$$\begin{aligned}
\frac{dP}{dt} &< P \left[\frac{aN}{k + N} - (\gamma + 1) \right] \\
&\leq P \left[\frac{a}{1 + k} - (\gamma + 1) \right] \\
&= P \frac{a - (\gamma + 1)}{1 + k} \left[1 - \frac{k(\gamma + 1)}{a - (\gamma + 1)} \right] \\
&= P \frac{a - (\gamma + 1)}{1 + k} (1 - \theta_1),
\end{aligned}$$

which completes the proof. \square

This result demonstrates that if the maximum growth rate of phytoplankton is less than or equal to its loss rate, or the parameter θ_1 is

greater than or equal to one, then the phytoplankton, the herbivorous zooplankton and the carnivorous zooplankton will all become extinct.

From Proposition 3.4 we have the following

Proposition 3.5. *If (3.5) holds, then*

$$\lim_{t \rightarrow \infty} (N(t), P(t), Z_1(t), Z_2(t)) = E_1.$$

If any of the inequalities (3.3), (3.4) and (3.5) holds, persistence cannot occur in system (3.1). From now on, we always assume that the inverse inequalities of (3.3), (3.4) and (3.5) hold, i.e.

$$(A_1) \quad a > \gamma + 1 \text{ and } \theta_1 < 1.$$

$$(A_2) \quad \delta c > \varepsilon + 1 \text{ and } \theta_2 < 1.$$

$$(A_3) \quad \sigma b > \mu + 1 \text{ and } \theta_3 < 1.$$

Denote

$$\begin{aligned} H_1 &= \{(N, P, Z_1, Z_2) \in R_+^4 \mid P = Z_1 = Z_2 = 0\}, \\ H_{12} &= \{(N, P, Z_1, Z_2) \in R_+^4 \mid Z_1 = Z_2 = 0\}, \\ H_{123} &= \{(N, P, Z_1, Z_2) \in R_+^4 \mid Z_2 = 0\}. \end{aligned}$$

Clearly $E_1 = (1, 0, 0, 0)$ is globally asymptotically stable in $\text{Int } H_1$, which denotes the interior of H_1 , and E_1 is hyperbolic if (see Freedman and So [18, p. 80])

$$(3.6) \quad \frac{1}{k+1} > \frac{\gamma+1}{a}.$$

If the autotrophic phytoplankton is at the top trophic level, we have the subsystem

$$(3.7) \quad \begin{aligned} \frac{dN}{dt} &= 1 - N - aP \frac{N}{k+N} + \gamma P \\ \frac{dP}{dt} &= P \left[a \frac{N}{k+N} - (\gamma+1) \right]. \end{aligned}$$

System (3.7) has an interior equilibrium (\bar{N}, \bar{P}) , where

$$\bar{N} = \frac{k(\gamma+1)}{a-(\gamma+1)}, \quad \bar{P} = \frac{a-(k+1)(\gamma+1)}{a-(\gamma+1)}$$

provided $a > \gamma + 1$. Choosing a Liapunov function $V_1(N, P)$ as follows

$$V_1(N, P) = \int_{\bar{N}}^N \frac{x}{k+x} \frac{\gamma+1}{x} \frac{1}{a} dx + \frac{1}{\gamma+1} \int_{\bar{P}}^P \frac{y-\bar{P}}{y} dy,$$

it is not difficult to prove that (\bar{N}, \bar{P}) is globally asymptotically stable in the $N-P$ plane (see Ruan [33]), that is, system (3.1) has an equilibrium $E_2 = (\bar{N}, \bar{P}, 0, 0)$ which is globally asymptotically stable with respect to $\text{Int } H_{12}$, and E_2 is hyperbolic if

$$(3.8) \quad 1 - e^{-\lambda \bar{P}} > \frac{(\varepsilon + 1)}{\delta c}.$$

If the herbivorous zooplankton Z_1 is at the highest trophic level, we have the following subsystem

$$(3.9) \quad \begin{aligned} \frac{dN}{dt} &= 1 - N - aP \frac{N}{k+N} + (1-\delta)cZ_1(1-e^{-\lambda P}) + \gamma P + \varepsilon Z_1 \\ \frac{dP}{dt} &= aP \frac{N}{k+N} - cZ_1(1-e^{-\lambda P}) - (\gamma+1)P \\ \frac{dZ_1}{dt} &= Z_1[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)]. \end{aligned}$$

System (3.9) has an interior equilibrium $(\tilde{N}, \tilde{P}, \tilde{Z}_1)$ if $\delta c > \varepsilon + 1$, where

$$\tilde{P} = \frac{1}{\lambda} \ln \frac{\delta c}{\delta c - (\varepsilon + 1)},$$

\tilde{Z}_1 is the positive solution, satisfies $\tilde{Z}_1 < 1 - \tilde{P}$, of the quadratic equation

$$(3.10) \quad \begin{aligned} Z_1^2 - \left[\left(\frac{\delta(a-\gamma-1)}{\varepsilon+1} - 1 \right) \tilde{P} + k + 1 \right] Z_1 \\ + \tilde{P} \frac{\delta}{\varepsilon+1} [(a-\gamma-1)(1-\tilde{P}) - k(\gamma+1)] = 0, \end{aligned}$$

and $\tilde{N} = 1 - \tilde{P} - \tilde{Z}_1$. Hence system (3.1) has an equilibrium $E_3 = (\tilde{N}, \tilde{P}, \tilde{Z}_1, 0)$. Define a Liapunov function

$$V_2(N, P, Z_1) = \int_{\tilde{N}}^N \frac{x - \tilde{N}}{x} dx + \int_{\tilde{P}}^P \frac{\delta c(1 - e^{-\lambda y}) - (\epsilon + 1)}{1 - e^{-\lambda y}} dy + \int_{\tilde{Z}_1}^{Z_1} \frac{z - \tilde{Z}_1}{z} dz.$$

The derivative of V along trajectories of (3.9) is

$$\begin{aligned} \frac{dV_2}{dt} &= \frac{N - \tilde{N}}{N} \left(1 - N - aP \frac{N}{k + N} + (1 + \delta)cZ_1(1 - e^{-\lambda P}) + \gamma P + \epsilon Z_1 \right) \\ &\quad + [\delta c(1 - e^{-\lambda P}) - (\epsilon + 1)] \left\{ \frac{P}{1 - e^{-\lambda P}} \left[a \frac{\tilde{N}}{k + \tilde{N}} - (\gamma + 1) \right] - c\tilde{Z}_1 \right\} \\ &\quad + \frac{aP}{1 - e^{-\lambda P}} [\delta c(1 - e^{-\lambda P}) - (\epsilon + 1)] \left[\frac{N}{k + N} - \frac{\tilde{N}}{k + \tilde{N}} \right]. \end{aligned}$$

Define $\phi_1(N)$, $\phi_2(P)$ and $\psi_2(P)$ as follows

$$\phi_1(N) = \frac{k}{(k + \xi_1 N)^2}, \quad 0 < \xi_1 < 1,$$

$$\phi_2(P) = \lambda e^{-\lambda \xi_2 P}, \quad 0 < \xi_2 < 1,$$

$$\psi_2(P) = - \left[\frac{a\tilde{N}}{k + \tilde{N}} - (\gamma + 1) \right] \frac{(1 + \lambda \xi_3 P)e^{-\lambda \xi_3 P} - 1}{(1 - e^{-\lambda \xi_3 P})^2}, \quad 0 < \xi_3 < 1,$$

such that

$$\frac{N}{k + N} - \frac{\tilde{N}}{k + \tilde{N}} = \phi_1(N)(N - \tilde{N}),$$

$$\delta c(1 - e^{-\lambda P}) - (\epsilon + 1) = \delta c \phi_2(P)(P - \tilde{P}),$$

$$\frac{P}{1 - e^{-\lambda P}} \left[\frac{a\tilde{N}}{k + \tilde{N}} - (\gamma + 1) \right] - c\tilde{Z}_1 = \psi_2(P)(P - \tilde{P}).$$

Then

$$\frac{dV_2}{dt} = -\frac{1}{N} (1 + a\tilde{P}\phi_1(N))(N - \tilde{N})^2$$

$$\begin{aligned}
 & + \left[\frac{\gamma}{N} + (1-\delta)c\tilde{Z}_1 \frac{\phi_2(P)}{N} + a\delta c\phi_1(N) \frac{P\phi_2(P)}{1-e^{-\lambda\tilde{P}}} \right. \\
 & \qquad \qquad \qquad \left. - \frac{a}{k+N} \right] \cdot (N-\tilde{N})(P-\tilde{P}) \\
 & + \frac{1}{N}[\varepsilon + (1-\delta)c(1-e^{-\lambda\tilde{P}})](N-\tilde{N})(Z_1-\tilde{Z}_1) \\
 & - \delta c\phi_2(P)\psi_2(P)(P-\tilde{P})^2 \\
 & + (1-\delta)c \frac{N-\tilde{N}}{N} \phi_2(P)(P-\tilde{P})(Z_1-\tilde{Z}_1) \\
 & = WSW^T,
 \end{aligned}$$

where $W = (N - \tilde{N}, P - \tilde{P}, Z_1 - \tilde{Z}_1)$ and the matrix $S = (s_{ij})_{3 \times 3}$ is defined as

$$s_{11} = -\frac{1}{N}(1 + a\tilde{P}\phi_1(N)),$$

$$s_{22} = -\delta c\phi_2(P)\psi_2(P),$$

$$s_{33} = 0,$$

$$s_{12} = s_{21} = \frac{1}{2} \left[\frac{\gamma}{N} + (1-\delta)c\tilde{Z}_1 \frac{\phi_2(P)}{N} + a\delta c\phi_1(N) \frac{P\phi_2(P)}{1-e^{-\lambda\tilde{P}}} - \frac{a}{k+N} \right],$$

$$s_{13} = s_{31} = \frac{1}{2N}[\varepsilon + (1-\delta)c(1-e^{-\lambda\tilde{P}})],$$

$$s_{23} = s_{32} = \frac{1}{2}(1-\delta)c \frac{N-\tilde{N}}{N} \phi_2(P).$$

If S is negative definite for all $(N, P, Z_1) \in H_{123}$, then E_3 is globally asymptotically stable with respect to H_{123} (see Freedman and So [18]). Now we introduce the following assumption

(A₄) The equilibrium $E_3 = (\tilde{N}, \tilde{P}, \tilde{Z}_1, 0)$ is globally asymptotically stable with respect to H_{123} .

Similarly, if the inequality

$$(3.11) \quad \frac{\tilde{Z}_1^2}{\ell + \tilde{Z}_1^2} > \frac{\mu + 1}{\sigma b}$$

holds, E_3 is hyperbolic.

Remark. Inequalities (3.6), (3.8) and (3.11) imply the inequalities $a > \gamma + 1$, $\delta c > \varepsilon + 1$ and $\sigma b > \mu + 1$, respectively.

Now we state the main result of this section.

Theorem 3.6. *Suppose that assumptions (A_1) – (A_4) and inequalities (3.6), (3.8) and (3.11) hold. Then system (3.1) exhibits uniform persistence.*

Proof. By Lemma 3.1, the system (3.1) is dissipative. Now $\mathcal{M} = \{E_1, E_2, E_3\}$ is an isolated covering. Inequality (3.6) implies that E_1 is hyperbolic, so E_1 is a saddle point. Since E_1 is globally asymptotically stable with respect to H_1 , it follows that $H_1 \subset W^+(E_1)$ (the stable set of E_1), hence $W^+(E_1) \cap R_+^4 = \emptyset$.

E_2 is also a saddle point and is globally asymptotically stable with respect to H_{12} , and it has a one-dimensional unstable manifold whose direction is out of the plane H_{12} , hence $W^+(E_2) \cap R_+^4 = \emptyset$. Similar statements apply to E_3 .

The global asymptotic stability of E_1, E_2 and E_3 with respect to H_1, H_{12} and H_{123} respectively also implies that the boundary flow is isolated and acyclic with \mathcal{M} . Therefore, by Theorem 3.1 of Butler and Waltman [5], uniform persistence follows. \square

Theorem 3.6 shows that if near the boundary equilibria E_1 , E_2 and E_3 , the growth rates of phytoplankton, herbivorous zooplankton and carnivorous zooplankton are positive, respectively, and all the parameters θ_1, θ_2 and θ_3 are less than one, then all components have long term survival.

By Theorem 5 of Hutson [24], we have the following result.

Theorem 3.7. *Under the hypothesis of Theorem 3.6, the system (3.1) has an interior equilibrium $E^* = (N^*, P^*, Z_1^*, Z_2^*)$.*

4. Coexistence. We can use Lemma 3.1 to eliminate one variable from system (3.1).

$$\begin{aligned}
 \frac{dP}{dt} &= aP \left[\frac{a(1-P-Z_1-Z_2)}{1+k-P-Z_1-Z_2} - (\gamma+1) \right] - cZ_1(1-e^{-\lambda P}) \\
 (4.1) \quad \frac{dZ_1}{dt} &= Z_1[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)] - bZ_2 \frac{Z_1^2}{\ell+Z_1^2} \\
 \frac{dZ_2}{dt} &= Z_2[\sigma b \frac{Z_1^2}{\ell+Z_1^2} - (\mu+1)].
 \end{aligned}$$

Since every trajectory is asymptotic to its ω limit set, it is sufficient to analyze the system (4.1). Lemma 3.1 implies that trajectories which form the positive ω limit set of any solution of (3.1) are solutions of (4.1) satisfying $0 \leq P, Z_1, Z_2 \leq 1$.

Now we consider subsystem (3.9), the special case $Z_2 \equiv 0$ in (3.1). After dropping subscripts we have

$$\begin{aligned}
 \frac{dN}{dt} &= 1 - N - ap \frac{N}{k+N} + (1-\delta)cZ(1-e^{-\lambda P}) + \gamma P + \varepsilon Z \\
 (4.2) \quad \frac{dP}{dt} &= aP \frac{N}{k+N} - cZ(1-e^{-\lambda P}) - (\gamma+1)P \\
 \frac{dZ}{dt} &= Z[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)], \\
 N(0) &\geq 0, \quad P(0) > 0, \quad Z(0) > 0.
 \end{aligned}$$

System (4.2) inherits from the larger system (3.1) the properties that the positive octant is positively invariant, that $a \leq \gamma+1$ or $\theta_1 \geq 1$ forces $\lim_{t \rightarrow \infty} P(t) = 0$ (and hence $\lim_{t \rightarrow \infty} Z(t) = 0$) that $\delta c \leq \varepsilon+1$ or $\theta_2 \leq 1$ forces $\lim_{t \rightarrow \infty} Z(t) = 0$, and that the ω limit set of any solution of (4.2) lies in the set $\Delta_1 = \{(N, P, Z) | N+P+Z=1, N \geq 0, P \geq 0, Z \geq 0\}$. Hence, it suffices to analyze the system

$$\begin{aligned}
 (4.3) \quad \frac{dP}{dt} &= P \left[\frac{a(1-P-Z)}{1+k-P-Z} - (\gamma+1) \right] - cZ(1-e^{-\lambda P}) \\
 \frac{dZ}{dt} &= Z[\delta c(1-e^{-\lambda P}) - (\varepsilon+1)].
 \end{aligned}$$

Note that we may restrict our attention to the triangular region $\Delta_2 = \{(P, Z) | 0 \leq P, Z, P + Z \leq 1\}$. The critical points on the boundary of Δ_1 for (4.3) are

$$C_1 = (0, 0), \quad C_2 = (1 - \theta_1, 0).$$

The variational matrix of (4.2) takes the form

$$M = \begin{pmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{pmatrix},$$

where

$$m_{11} = \frac{a(1 - P - Z)}{1 + k - P - Z} - \frac{akP}{(1 + k - P - Z)^2} - (\gamma + 1) - c\lambda Z e^{-\lambda P},$$

$$m_{12} = - \frac{akP}{(1 + k - P - Z)^2} - c(1 - e^{-\lambda P}),$$

$$m_{21} = \delta c \lambda Z e^{-\lambda P},$$

$$m_{22} = \delta c(1 - e^{-\lambda P}) - (\varepsilon + 1).$$

At $C_1 = (0, 0)$, the variational matrix has the form

$$M_1 = \begin{pmatrix} \frac{[a - (\gamma + 1)](1 - \theta_1)}{1 + k} & 0 \\ 0 & -(\varepsilon + 1) \end{pmatrix}.$$

Thus, if $a < \gamma + 1$ or $\theta_1 > 1$, C_1 is an asymptotically stable critical point, and if $a > \gamma + 1$ and $\theta_1 < 1$ (which we are assuming), then C_1 is a saddle point.

At $C_2 = (1 - \theta_1, 0)$, M takes the form

$$M_2 = \begin{pmatrix} - \frac{ak(1 - \theta_1)}{(k + \theta_1)^2} & - \frac{ak(1 - \theta_1)}{(k + \theta_1)^2} - c(1 - e^{-\lambda(1 - \theta_1)}) \\ 0 & [\delta c - (\varepsilon + 1)](1 - \theta_2 e^{\lambda \theta_1}) \end{pmatrix}.$$

For C_2 to be biologically meaningful, i.e., to be in the positive quadrant, it must be the case that $0 < \theta_1 < 1$. So if $\theta_2 e^{\lambda \theta_1} > 1$, C_2 is an

asymptotically stable critical point, if $0 < \theta_2 e^{\lambda \theta_1} < 1$, C_2 is a saddle point.

Let (P_c, Z_c) be a critical point in the interior of Δ_2 , i.e.

$$(4.4) \quad P_c \left[\frac{a(1 - P_c - Z_c)}{1 + k - P_c - Z_c} - (\gamma + 1) \right] - cZ_c(1 - e^{-\lambda P_c}) = 0,$$

$$(4.5) \quad \delta c(1 - e^{-\lambda P}) - (\varepsilon + 1) = 0.$$

From (4.5) we have that

$$(4.6) \quad P_c = 1 - \frac{1}{\lambda} \ln \frac{1}{\theta_2}, \quad \text{if } \theta_2 < 1,$$

so we are assuming that $Z_c > 0$ satisfies (4.4) and it may be rewritten as the following

$$\lambda \delta k(\gamma + 1) \left(\frac{1}{\lambda} \ln \frac{1}{\theta_2} - \theta_1 - Z_c \right) = \left[(\lambda k - a)Z_c - \frac{a}{\lambda} \ln \frac{1}{\theta_2} \right] (\varepsilon + 1)\theta_1.$$

If $\theta_1 > (1/\lambda) \ln(1/\theta_2)$, i.e. $\theta_2 e^{\lambda \theta_1} > 1$, (4.4) has no positive solution. Thus if C_2 is asymptotically stable, there is no interior critical point. If $\theta_2 e^{\lambda \theta_1} < 1$, then (4.4) has precisely one positive solution Z_c .

The variational matrix at (P_c, Z_c) has the form

$$M_3 = \begin{pmatrix} \frac{Z_c[(\varepsilon + 1)\theta_2 e^\lambda - c\lambda\delta + c\delta \ln \frac{1}{\theta_2}]}{\theta_2 \delta e^\lambda (1 - \frac{1}{\lambda} \ln \frac{1}{\theta_2})} & & \\ -\frac{ak(1 - \frac{1}{\lambda} \ln \frac{1}{\theta_2})}{(k + \frac{1}{\lambda} \ln \frac{1}{\theta_2} - Z_c)^2} & -\frac{ak(1 - \frac{1}{\lambda} \ln \frac{1}{\theta_2})}{(k + \frac{1}{\lambda} \ln \frac{1}{\theta_2} - Z_c)^2} - \frac{\varepsilon + 1}{\delta} & \\ \frac{\delta c \lambda Z_c}{\theta_2 e^\lambda} & 0 & \end{pmatrix}.$$

If $\theta_2 > e^{-\lambda}$, i.e. $1 - (1/\lambda) \ln(1/\theta_2) > 0$, the determinant of M_3 is positive, then the stability of (P_c, Z_c) depends on the trace of M_3 , i.e., if

$$(4.7) \quad \frac{Z_c[(\varepsilon + 1)\theta_2 e^\lambda - c\lambda\delta + c\delta \ln \frac{1}{\theta_2}]}{\theta_2 \delta e^\lambda (1 - \frac{1}{\lambda} \ln \frac{1}{\theta_2})^2} < \frac{ak}{(k + \frac{1}{\lambda} \ln \frac{1}{\theta_2} - Z_c)^2},$$

(P_c, Z_c) is asymptotically stable.

System (4.3) is different from the Gause-type predator-prey systems described by Kuang and Freedman [30], and the chemostat type systems investigated by Cheng [7], Liou and Cheng [32], Ding [10] and Kuang [28]. The uniqueness theorems about the limit cycle and the methods utilized there do not seem to work for system (4.3). However, by a result of Erle [12], we know that system (4.3) has at most a finite number of limit cycles and if (P_c, Z_c) is unstable, (4.3) must have at least one asymptotically stable limit cycle. We make the following assumption (see Butler, Hsu and Waltman [3] and Freedman, So and Waltman [19]).

(A₅) There exists a limit cycle for system (4.3) which has a Floquet multiplier strictly less than one.

Let $(P(t), Z_1(t))$ be a periodic solution of period τ of system (4.3) which is given by (A₅) for the parameters $a, k, \gamma, c, \lambda, \delta$ and ε . Then $(P(t), Z_1(t), 0)$ is a solution of system (4.1) for any choice of parameters b, σ, ℓ and μ . Now fix b, σ and μ and define

$$h(\ell) = \frac{\sigma b}{\tau} \int_0^\tau \frac{Z_1^2(\xi)}{\ell + Z_1^2(\xi)} d\xi,$$

where ℓ will be treated as a bifurcation parameter.

Let Γ be the orbit corresponding to the solution $(P(t), Z_1(t), 0)$. Let Ω be a two-dimensional local transverse section of Γ , let W_0 and W_1 be open subsets of Ω . For each value of ℓ , the Poincaré map $T : W_0 \rightarrow W_1$ exists. For a given periodic orbit, the linearization about the periodic orbit and the linearization of the Poincaré map about the fixed point corresponding to Γ are related, which is precisely made in the following statement.

Lemma 4.1. *The spectrum of the linearization of the Poincaré map union $\{1\}$ is equal to the spectrum of the linearization of the solution map defined by*

$$\Phi(P^0, Z_1^0, Z_2^0) = (P(\tau), Z_1(\tau), Z_2(\tau)),$$

where

$$P(0) = P^0, \quad Z_1(0) = Z_1^0, \quad Z_2(0) = Z_2^0$$

and τ is the period of the periodic solution map.

As a consequence, to show that one Floquet multiplier passes from inside to outside the unit circle is equivalent to show that an eigenvalue of the linearization of the Poincaré map passes from inside to the outside the unit circle. For this, we need the following bifurcation theorem in Marsden and McCracken [33] (see also [8]).

Lemma 4.2. *Let W be an open neighborhood of $0 \in R^2$ and I be an open interval about $0 \in R$. Let $\Phi_v : W \rightarrow R^n$ be such that the map $(v, x) \rightarrow \Phi_v(x)$ is a C^k map ($k \geq 1$) from $I \times W$ to R^2 , and such that $\Phi_v(0) = 0$ for all $v \in I$. Define L_v to be the differential map $d\Phi_v(0)$ and suppose that all eigenvalues of L_v lie inside the unit circle of the complex plane for $v < 0$. Assume that there is a real, simple eigenvalue $\ell(v)$ of L_v such that $\ell(0) = 1$ and $(d\ell/dv)(0) > 0$. Let v_0 be the eigenvector corresponding to $\ell(0)$. Then there is a C^{k-1} curve C of fixed points of $\Phi : (v, x) \rightarrow (v, \Phi_v(x))$ near $(0, 0)$ in $I \times R^2$ which together with the points $(v, 0)$ are the only fixed points of Φ near $(0, 0)$. The curve C is tangent to v_0 at $(0, 0)$ in $I \times R^2$.*

The following theorem is the main result of this section.

Theorem 4.3. *Let $a, k, \gamma, c, \lambda, \delta, \varepsilon, b, \sigma$ and μ be fixed so that (A_1) , (A_2) , the first inequality of (A_3) , and (A_5) hold. Then there exists a number ℓ^* such that for $\ell < \ell^*$, $|\ell^* - \ell|$ sufficiently small, system (3.1) has a periodic orbit in R_+^4 arbitrarily near the plane $N + P + Z_1 = 1$, $Z_2 = 0$.*

Proof. The proof is heavily dependent upon the techniques used by Butler, Hsu and Waltman [3] and Freedman, So and Waltman [19]. Let $(P(t), Z_1(t))$ be the unique periodic solution of (4.3), the Floquet exponents are 0 and $-\alpha < 0$. Let ℓ^* be an undetermined constant, and let $v = \ell^* - \ell$. Let Γ be the orbit associated with the periodic solution $(P(t), Z_1(t), 0)$ when $\ell = \ell^*$. Fix a point $x_0 \in \Gamma$ and let Ω be the transverse section to Γ at x_0 , identifying x_0 with $0 \in R^2$. Let Φ_v be the Poincaré map associated with the periodic solution $(P(t), Z_1(t), 0)$ from v near 0. From the analytic dependence of the vector field defined by (4.3) on its parameters, it follows that the solutions are analytic in parameters and initial conditions, and so is the Poincaré map. Hence

there is a neighborhood W_0 of x_0 in Ω such that for all v sufficiently close to zero, Φ_v is defined on W_0 .

Now we study the spectrum of $L_v = d\Phi_v(0)$ by examining the Floquet multipliers of the corresponding system of differential equations. The variational matrix associated with the linearization of (4.1) takes the form

$$\begin{pmatrix} f_P(P(t), Z_1(t), 0) & f_{Z_1}(P(t), Z_1(t), 0) & f_{Z_2}(P(t), Z_1(t), 0) \\ \delta c \lambda Z e^{-\lambda P(t)} & \delta c(1 - e^{-\lambda P}) - (\varepsilon + 1) & -\frac{bZ_1^2}{\ell + Z_1^2} \\ 0 & 0 & \frac{\sigma b Z_1^2}{\ell + Z_1^2} - (\mu + 1) \end{pmatrix},$$

where $dP/dt = f(P, Z_1, Z_2)$ in (4.1). The two-dimensional system

$$\frac{d}{dt} \begin{pmatrix} P(t) \\ Z_1(t) \end{pmatrix} = A(t) \begin{pmatrix} P(t) \\ Z_1(t) \end{pmatrix}$$

has one Floquet multiplier equal to 1 since $(P(t), Z_1(t))^T$ is a periodic solution and one multiplier inside the unit circle, call it $e^{-\alpha}$, by the hypothesis (A₅). The third Floquet multiplier of the full system has the form $\exp[h(\ell) - (\mu + 1)]$.

Since $h(0) = \sigma b > (\mu + 1)$ by assumption (A₃) and

$$h(\ell) \leq \frac{\sigma b}{\ell \tau} \int_0^\tau x^2(\zeta) d\zeta,$$

if ℓ is sufficiently large, $h(\ell)$ is arbitrarily small. Note that $h(\ell)$ is continuous and decreasing with ℓ , there is a unique value ℓ^* such that $h(\ell^*) = \mu + 1$. Note also that

$$\frac{dh}{d\ell} = -\frac{\sigma b}{\tau} \int_0^\tau \frac{x^2(\zeta)}{(\ell + x^2(\zeta))^2} d\zeta < 0,$$

in particular, when r passes through 0, i.e., ℓ passes through ℓ^* , $h(\ell)$ crosses the value $\mu + 1$ non-tangentially, and

$$\frac{\partial e^r}{\partial \ell}(\ell^*) = \frac{dh}{d\ell}(\ell^*) \cdot e^{h(\ell^*) - (\mu + 1)} < 0$$

as $r = h(\ell) - (\mu + 1)$ passes through zero. Thus $(\partial e^r / \partial v)(0) > 0$ (where $v = \ell^* - \ell$), so the Floquet multiplier passes through the unit circle transversally.

We know that the Poincaré map is analytic in parameter and initial conditions, so $(v, x) \rightarrow \Phi_v(x)$ is analytic from $I \times W$, $\Phi_v(0) = 0$ for all $v \in I$ and $L_v = d\Phi_v(0)$ has eigenvalues $e^{-\alpha}$ and e^r , and crosses the unit circle non-tangentially as r passes through zero.

Applying Lemma 4.2, we obtain a C^1 curve \mathcal{C} of fixed points of $\Phi : (v, x) \rightarrow (v, \Phi_v(x))$ bifurcating from $(v, 0)$ at $(0, 0)$. For such (v, x) , we have $x = \Phi_v(x)$, so x is a fixed point of the Poincaré map Φ_v , therefore \mathcal{C} correspond to a 1-parameter family of periodic solutions of (4.1) hence (3.1). Since \mathcal{C} is tangent to the eigenvector associated with the eigenvalue 1 of $L_v = d\Phi(0)$, the direction of v_0 is transverse to the $P\text{-}Z_1$ plane, so \mathcal{C} is transverse to the $P\text{-}Z_1$ plane. It follows that there is a branch of periodic solutions of (3.1) in the positive octant if $|\ell - \ell^*| = |v|$ is sufficiently small. This completes the proof. \square

5. Discussion. We have considered a three-trophic-level model of plankton dynamics with instantaneous nutrient recycling, which consists of autotrophic phytoplankton, herbivorous zooplankton, carnivorous zooplankton and dissolved limiting nutrient. We suppose that there are a constant input concentration to the system, and a constant washout rate from the system.

Firstly we have given criteria for autotrophic phytoplankton or herbivorous zooplankton or carnivorous zooplankton or all of them to become extinct. Next we have studied the question of persistence, sufficient conditions are obtained which guarantee the survival of all elements of the population, which also imply the existence of an interior equilibrium in the positive cone.

If we interpret the persistence conditions in terms of their counterparts for the unscaled model, we gain insight into the biology of the situation. Conditions (A₁) and (3.6) can be interpreted as follows

$$(5.1) \quad a > \gamma + D, \quad \theta_1 = \frac{k}{N^0 \left(\frac{a}{\gamma + D} - 1 \right)} < 1$$

and

$$(5.2) \quad \frac{N^0}{k + N^0} > \frac{\gamma + D}{a}.$$

Conditions (5.1) and (5.2) can be achieved either by increasing N^0 , the input nutrient concentration rate, by increasing a , the growth rate of the autotrophic phytoplankton or by decreasing γ and D , the death rate and washout rate of phytoplankton, by decreasing k , the saturation constant of phytoplankton. Conditions (A₂) and (3.8) can be interpreted as

$$(5.3) \quad \delta c > \varepsilon + D, \quad \theta_2 = \frac{e^{-\lambda N^0}}{1 - \frac{\varepsilon + D}{\delta c}} < 1$$

and

$$(5.4) \quad 1 - e^{-\lambda \bar{P}} > \frac{\varepsilon + D}{\delta c}.$$

These conditions can be achieved either by increasing N^0 , the input nutrient concentration rate, by increasing c , the herbivore ingestion rate, by increasing δ , the herbivore resource conversion rate, by increasing λ , the saturation rate of herbivore or by decreasing ε and D , the herbivorous death rate and washout rate. While conditions (A₃) and (3.11) can be interpreted as

$$(5.5) \quad \sigma b > \mu + D, \quad \theta_3 = \frac{\ell}{N^0 \left(\frac{\sigma b}{\mu + D} - 1 \right)} < 1$$

and

$$(5.6) \quad \frac{N^0 \widetilde{Z}_1^2}{\ell + N^0 \widetilde{Z}_1^2} > \frac{\mu + D}{\sigma b}.$$

Similarly, these conditions can be achieved either by increasing N^0 , the input nutrient concentration rate, by increasing b , the carnivore ingestion rate, by increasing σ , the carnivore resource conversion rate or by decreasing μ and D , the carnivorous death rate and washout rate, by decreasing ℓ , the saturation constant of carnivore.

According to the predictions of this model, there are a number of ways to influence the outcome of the plankton-nutrient interactions. Increasing the input nutrient concentration rate and decreasing the loss rate are essential to ensure persistence. It is interesting that for the persistence conditions to be achieved, k and ℓ , the saturation constants of phytoplankton and carnivorous zooplankton, must be decreased while λ , the saturation rate of herbivorous zooplankton, must be increased. This is because that the herbivore is the intermediate population that feeds upon the phytoplankton and is in turn fed by carnivore. A reasonable increase of the saturation rate for the herbivore is necessary to balance the food chain such that the whole system exhibits persistence. As Proposition 3.3 shows, if λ is too small so that $\theta_2 \geq 1$, then not only the herbivore, but also the carnivore will become extinct.

The extinction results imply that bifurcation can occur. Since predator-prey system can have an oscillatory tendency, it is natural to seek oscillatory coexistence of all components of the population. Finally, under appropriate circumstance, we have shown that coexistence of the autotroph, herbivore and carnivore occurs in the form of bifurcating periodic orbit.

It would be of great interest to investigate the homogeneous Neumann problem and Dirichlet problem for reaction-diffusion models of plankton nutrient dynamics, we propose to do this in a future paper.

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