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Persistence and coexistence in zooplankton-phytoplankton-nutrient models with instantaneous nutrient recycling

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Abstract. We consider plankton-nutrient interaction models consisting of phytoplankton, herbivorous zooplankton and dissolved limiting nutrient with general nutrient uptake functions and instantaneous nutrient recycling. For the model with constant nutrient input and different constant washout rates, conditions for boundedness of the solutions, existence and stability of non-negative equilibria, as well as persistence are given. We also consider the zooplankton-phytoplankton-nutrient interaction models with a fluctuating nutrient input and with a periodic washout rate, respectively. It is shown that coexistence of the zooplankton and phytoplankton may arise due to positive bifurcating periodic solutions.

Key words: Persistence – Coexistence – Nutrient recycling – Bifurcation – Fluctuating nutrient input

1 Introduction

An early attempt to mathematically model profiles of marine plankton by Riley et al. [39] has been followed by models varying in complexity. A number of the later models were mainly concerned with phytoplankton-herbivore interactions (see Steele [43]). Recently, Evans and Parslow [17], Taylor [44], Wroblewski et al. [50] constructed models explicitly incorporating nutrient concentrations in the plankton-herbivore models.

The mathematical analysis of plankton models goes back to Hallam [27, 28, 29] who studied stability and persistence properties of a family of non-spatial plankton models, the so-called aquatic ecosystems or nutrient con-

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trolled plankton models. In [27], a threshold level for nutrient input required for persistence was given and hence, a necessary and sufficient condition for the persistence of an aquatic ecomodel was obtained. Arnold [1, 2], Arnold and Voss [3] also considered three component models made up of phytoplankton, zooplankton and organic phosphorus nutrient in a lake environment. Certain properties of the models such as the existence of limit cycles were discussed. In [24], Gard provided a simpler and sharper persistence criterion for a zooplankton-phytoplankton-nutrient model with general functional responses; he also showed how persistence criteria can be determined for nonautonomous type models in which the nutrient input rate may be time varying. In a recent article, Busenberg et al. [5] studied a model of a zooplankton-phytoplankton-nutrient interaction which was constructed by Wroblewski et al. [50]. It was shown in their paper that under certain conditions the coexistence of phytoplankton and zooplankton occurs in an orbitally stable oscillatory mode.

The zooplankton-phytoplankton-nutrient models describing lakes or oceans are different from the chemostat models (for chemostat models, cf. Waltman [46, 47] and the references therein), since lakes or oceans generally have a residence time of nutrient and sediments measured in years (see Powell and Richerson [37]). Hence the regeneration of nutrient due to bacterial decomposition of the dead biomass must be considered. Nisbet et al. [36] studied the effect of material recycling on ecosystem stability for closed systems. We regard nutrient recycling as an instantaneous term, thus neglecting the time required to regenerate nutrient from dead biomass by bacterial decomposition. For delay nutrient recycling in chemostat models, we refer to the recent articles by Beretta et al. [4], and Freedman and Xu [22].

Phytoplankton death is a gross parameterization of many processes including physiological death, exudation of organic substances and losses of phytoplankton due to sinking of cells through the bottom of the mixed layer (Wroblewski et al. [50]). Cell sinking can be an important loss especially at the end of the spring bloom when nutrients are depleted (Walsh [45]). Also, part of the zooplankton mortality representing the predation on zooplankton by higher predators are not explicitly modeled. The final destination of such dead zooplankton will be either ammonium, fecal pellets, or dead higher predators (Fasham et al. [18]). The fecal pellets and corpses of the higher predators will have high sinking rates and will therefore sink out from the mixed layer. Therefore in models of natural systems washout rate constants (or functions) which describe the removal of biotic components from the systems resulting from washout, harvesting, being buried in deep sediments (DeAngelis et al. [16]), soluble metabolic loss (Evans and Parslow [17]), or cell sinking (Wroblewski [49], Fasham et al. [18]) must be considered. Global dynamics of a chemostat model with differential death rates was recently studied by Wolkowicz and Lu [48].

In this paper, we consider three open systems which have three interacting components consisting of phytoplankton (P), herbivorous zooplankton (Z) and dissolved limiting nutrient (N). The two plankton levels are modeled in terms of their nitrogen, phosphorous or silicate content, N, which is assumed to be the nutrient primarily responsible for limiting phytoplankton reproduction.

In the first model (Fig. 1), based on the model constructed by Wroblewski et al. [50], we introduce a constant input concentration of the limiting nutrient, N^0, different constant washout rates D, D_1 and D_2 for the nutrient, phytoplankton and zooplankton respectively, to the model. We suppose the zooplankton

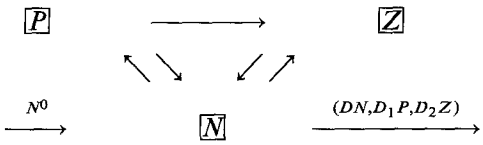

Fig. 1. The Z-P-N model with constant nutrient input (N^0) and different washout rates (D, D_1 and D_2). Arrows indicate nutrient flow pathways between phytoplankton (P), zooplankton (Z) and nutrient (N)

population feeds on both nutrient and phytoplankton (i.e., zooplankton is facultative or obligate), and only part of dead phytoplankton and zooplankton is recycled back into nutrients. We also use a general class of functions to describe nutrient uptake and functional response. Criteria for phytoplankton or zooplankton or both of them to become extinct, i.e., extinction thresholds, are derived. Boundedness of solutions is studied; this is essential for the model to be persistent. Existence of positive equilibria on both the N-P plane and the N-Z plane is considered which demonstrates that for the facultative predator model, the phytoplankton population can survive without zooplankton, and the zooplankton population too, can survive without phytoplankton. It is shown that subject to certain constraints, the system exhibits uniform persistence. In the case where the predator is obligate, we obtain criteria for persistence (and hence coexistence of both zooplankton and phytoplankton).

In the second model (Fig. 2), we consider the interaction involving nutrient with a periodic input. Similar cases for chemostat models have been studied by Hsu [31], Smith [42], Hale and Somolinos [26], Yang and Freedman [51]. We suppose that zooplankton does not take nutrient directly, i.e., the predator is obligate, and all dead zooplankton and phytoplankton are recycled back into nutrient. This model (as well as the next one) might be more applicable in laboratory aquaria or lakes than in oceanic regions. We show that there is an asymptotically stable periodic solution in the N-P plane, from which will bifurcate a continuum of positive solutions of the general system, hence coexistence of all population may occur.

In the third model (Fig. 3), we consider the interaction with periodic washout rate (cf. see Butler et al. [8]). We suppose that the predator is obligate, all phytoplankton ingested by zooplankton is utilized and all dead P and Z are recycled back into the nutrient. It is shown that coexistence exists for phytoplankton and zooplankton in the form of positive periodic solutions.

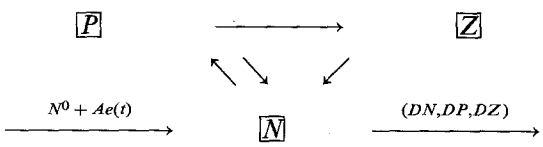

Fig. 2. The Z-P-N model with periodic nutrient input ($N^0 + Ae(t)$) and constant washout rate (D)

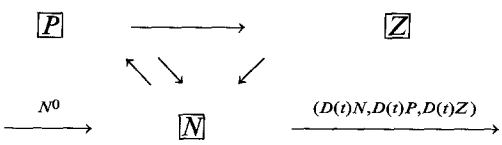

Fig. 3. The Z-P-N model with constant nutrient input (N^0) and periodic washout rate ($D(t)$)

Persistence in biological systems in a context related to this paper has been discussed by many authors. We utilize the definitions of persistence developed by Butler et al. [7], and Butler and Waltman [9], namely if $x(t)$ is such that $x(t) > 0$, we say that $x(t)$ persists if $\liminf_{t\to\infty} x(t) > 0$. Further, we say that $x(t)$ persists uniformly if there exists $\delta > 0$ such that $\liminf_{t\to\infty} x(t) \geqslant \delta$. Finally, a system persists (uniformly) if all components persist (uniformly).

2 *Z-P-N* model with constant nutrient input and washout rates

The instantaneous zooplankton-phytoplankton-nutrient (Z-P-N) model consisting of three interacting components, herbivorous zooplankton (Z), phytoplankton (P) and dissolved limiting nutrient (N), is given by the following set of ordinary differential equations

$$\begin{aligned}
\frac{dN}{dt} &= D(N^0 - N) - aPu(N) - bZv(N) + (1-\delta)cZw(P) + \gamma_1 P + \varepsilon_1 Z \\
\frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D_1)P \\
\frac{dZ}{dt} &= Z[bv(N) + \delta cw(P) - (\varepsilon + D_2)].
\end{aligned} \tag{2.1}$$

We assume that all parameters are non-negative and are interpreted as follows:

a –maximal nutrient uptake rate for the phytoplankton
b –maximal nutrient uptake rate for the zooplankton
c –maximal zooplankton ingestion rate
N^0 –input concentration of the nutrient
D –washout rate of the nutrient
D_1 –washout rate of the phytoplankton
D_2 –washout rate of the zooplankton
γ –phytoplankton mortality rate
ε –zooplankton death rate
γ_1 –nutrient recycle rate after the death of the phytoplankton, $\gamma_1 \leqslant \gamma$
ε_1 –nutrient recycle rate after the death of the zooplankton, $\varepsilon_1 \leqslant \varepsilon$
δ –the fraction of zooplankton nutrient conversion, $0 < \delta \leqslant 1$.

Functions $u(N)$ and $v(N)$ describe the nutrient uptake rates of phytoplankton and zooplankton, respectively. We assume the following general hypotheses on the nutrient uptake functions (Hale and Somolinos [26]).

(i) The functions are non-negative, increasing and vanish when there is no nutrient.

(ii) There is a saturation effect when the nutrient is very abundant.

That is, we assume that $u(N)$ and $v(N)$ are continuous functions defined on $[0, \infty)$, and satisfy

$$u(0) = 0, \quad \frac{du}{dN} > 0 \quad \text{and} \quad \lim_{N\to\infty} u(N) = 1, \tag{2.2}$$

$$v(0) = 0, \quad \frac{dv}{dN} > 0 \quad \text{and} \quad \lim_{N\to\infty} v(N) = 1. \tag{2.3}$$

In particular, these kinds of functions include the Michaelis–Menten functions (Caperon [11]), Wroblewski et al. [50], Busenberg et al. [5])

$$u(N) = \frac{N}{k_1 + N}, \qquad v(N) = \frac{N}{k_2 + N},$$

where k_1 and k_2 are the half-saturation constants or Michaelis–Menten constants.

$w(P)$ represents the response function describing herbivore grazing. It is also assumed that $w(P)$ is continuous on $[0, \infty)$ and satisfies

$$w(0) = 0, \qquad \frac{dw}{dP} > 0 \quad \text{and} \quad \lim_{P \to \infty} w(P) = 1. \tag{2.4}$$

Usually, Ivlev's functional response formulation [32]

$$w(P) = 1 - e^{-\lambda P}$$

is used to describe the zooplankton grazing, where λ is the rate at which saturation is achieved with increasing phytoplankton levels (per unit concentration).

We assume that only a fraction of the dead phytoplankton, γ_1 ($\gamma_1 \leqslant \gamma$), is recycled into dissolved nutrient. The zooplankton dynamics includes growth as assimilated ingested ration and a loss rate of ε due to high level predation, physiological death, etc. Also, we assume that only a fraction, ε_1 ($\varepsilon_1 \leqslant \varepsilon$) of the dead zooplankton is recycled into dissolved nutrient within the mixed layer.

During consumption only a fraction of the phytoplankton removed through zooplankton predation, δ ($\delta \leqslant 1$), is assumed to be assimilated by zooplankton, the remainder goes directly to the available nitrate.

D, D_1 and D_2 are washout rates (or removal rates, diffusive rates) of biotic components from the system resulting from washout, diffusion, harvesting, being buried in deep sediments, soluble metabolic loss or cell sinking, for example. Those processes in general do not take place at the same time, so we suppose that D, D_1 and D_2 are different.

Note that $E_0 = (N^0, 0, 0)$ is always an equilibrium for system (2.1). We first give criteria for phytoplankton or zooplankton or both of them to become extinct.

Theorem 2.1 *Let the inequality*

$$a \leqslant \gamma + D_1 \tag{2.5}$$

hold. Then $\lim_{t \to \infty} P(t) = 0$.

Proof. From system (2.1), we have that

$$\begin{aligned} \frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D_1)P \\ &\leqslant P[au(N) - (\gamma + D_1)] \\ &\leqslant P[a - (\gamma + D_1)] \\ &\leqslant 0 \quad \text{by (2.5).} \end{aligned}$$

Since there is no invariant set such that $P > 0$ is constant, the theorem follows. □

Theorem 2.1 demonstrates that if the maximal nutrient uptake rate is less than or equal to the loss rate, then the phytoplankton population is eliminated.

Similarly, we can prove the following theorem.

Theorem 2.2 *Let the inequality*

$$b + \delta c \leqslant \varepsilon + D_2 \tag{2.6}$$

hold. Then $\lim_{t \to \infty} Z(t) = 0$.

This result shows that the zooplankton population cannot exist if the summation of its maximal nutrient uptake rate and its net ingestion rate is less than or equal to its loss rate.

Corollary 2.3 *If* (2.5) *and* (2.6) *hold, then* $\lim_{t \to \infty} (N(t), P(t), Z(t)) = E_0$.

By Corollary 2.3, if (2.5) and (2.6) hold, then both of the phytoplankton population and zooplankton population become extinct. In this case, it is not feasible for persistence of system (2.1).

If phytoplankton is the top trophic level, and zooplankton is set at zero, then we have the subsystem

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 P \\ \frac{dP}{dt} &= P[au(N) - (\gamma + D_1)]. \end{aligned} \tag{2.7}$$

System (2.7) has an interior equilibrium (N_1, P_1), where

$$N_1 = u^{-1}\left(\frac{\gamma + D_1}{a}\right), \qquad P_1 = \frac{D\left(N^0 - u^{-1}\left(\frac{\gamma + D_1}{a}\right)\right)}{\gamma + D_1 - \gamma_1}$$

provided

$$\gamma + D_1 < a \tag{2.8}$$

and

$$u^{-1}\left(\frac{\gamma + D_1}{a}\right) < N^0. \tag{2.9}$$

So we have the following theorem.

Theorem 2.4 *If the inequalities* (2.8) *and* (2.9) *hold, then system* (2.1) *has a non-negative equilibrium* $E_1 = (N_1, P_1, 0)$ *where* N_1 *and* P_1 *are defined as above.*

Similarly, we have

Theorem 2.5 *If the inequalities*

$$\varepsilon + D_2 < b \tag{2.10}$$

and

$$v^{-1}\left(\frac{\varepsilon + D_2}{b}\right) < N^0 \tag{2.11}$$

hold, then system (2.1) *has a non-negative equilibrium* $E_2 = (N_2, 0, Z_2)$ *where*

$$N_2 = v^{-1}\left(\frac{\varepsilon + D_2}{b}\right), \qquad Z_2 = \frac{D\left(N^0 - v^{-1}\left(\frac{\varepsilon + D_2}{b}\right)\right)}{\varepsilon + D_2 - \varepsilon_1}.$$

Theorem 2.4 indicates that if (2.8) and (2.9) hold, then the phytoplankton population can survive on the nutrient, while Theorem 2.5 demonstrates that the predator zooplankton may be able to survive on the nutrient without the prey phytoplankton if (2.10) and (2.11) hold. This is not true if (2.11) fails, and the equilibrium E_2 does not exist.

Theorem 2.6 *All solutions of system* (2.1) *are bounded.*

Proof. We have

$$\begin{aligned}\frac{d}{dt}(N + P + Z) &= DN^0 - DN + \gamma_1 P + \varepsilon_1 Z - \gamma P - D_1 P - \varepsilon Z - D_2 Z \\ &\leqslant -D_0(N + P + Z) + DN^0,\end{aligned}$$

where $D_0 = \min\{D, D_1, D_2\}$. The theorem follows. □

Theorem 2.7 *If the non-negative equilibria* E_1 *and* E_2 *exist, then* (N_1, P_1) *and* (N_2, Z_2) *are globally asymptotically stable in the N-P plane and N-Z plane, respectively.*

Proof. We only prove the global asymptotic stability of (N_1, P_1) in the N-P plane; the stability of (N_2, P_2) in the N-Z plane can be proved similarly. Define a Liapunov function (cf. Harrison [30])

$$V(N, P) = \int_{N_1}^{N} \frac{u(x) - u(N_1)}{u(x)}\,dx + \frac{au(N_1) - \gamma_1}{au(N_1)} \int_{P_1}^{P} \frac{x - P_1}{x}\,dx. \tag{2.12}$$

Then, if (2.8) holds, $u(N_1) - \gamma_1 > 0$, $V(N, P) = 0$ if and only if $N = N_1$, $P = P_1$ and $V(N, P) \geqslant 0$ in the N-P plane. The time derivative of V along the trajectories of the subsystem (2.7) is

$$\begin{aligned}\frac{dV}{dt} &= \frac{u(N) - u(N_1)}{u(N)}[D(N^0 - N) - aPu(N) + \gamma_1 P] \\ &\quad + \frac{au(N_1) - \gamma_1}{au(N_1)}(P - P_1)[au(N) - (\gamma + D_1)] \\ &= (u(N) - u(N_1))\left[\frac{D(N^0 - N)}{u(N)} - \left(a - \frac{\gamma_1}{u(N)}\right)P\right. \\ &\quad \left. - \frac{D(N^0 - N_1)}{u(N_1)} + \left(a - \frac{\gamma_1}{u(N_1)}\right)P_1\right] \\ &\quad + \left(a - \frac{\gamma_1}{u(N_1)}\right)(P - P_1)[u(N) - u(N_1)] \\ &= (u(N) - u(N_1))\left[-\frac{D(N^0 - N_1) + \gamma_1 P}{u(N)u(N_1)}(u(N) - u(N_1)) - \frac{D(N - N_1)}{u(N)}\right] \\ &= -\frac{D(N^0 - N_1) + \gamma_1 P}{u(N)u(N_1)}[u(N) - u(N_1)]^2 - \frac{D}{u(N)}(N - N_1)(u(N) - u(N_1)).\end{aligned}$$

Since $N_1 < N^0$, the first term is negative. The second term is negative because $u(N)$ is an increasing function. Thus, $dV/dt \leqslant 0$ and $dV/dt = 0$ if and only if $N = N_1$. The largest invariant subset of the set of the point where $dV/dt = 0$ is (N_1, P_1). Therefore by LaSalle's theorem (LaSalle and Lefschetz [34]), (N_1, P_1) is globally asymptotically stable in the N-P plane. □

Theorem 2.8 *If the inequalities* (2.8)–(2.11) *hold and*

$$bv(N_1) + \delta cw(P_1) - (\varepsilon + D_2) > 0 \tag{2.13}$$

$$au(N_2) - cZ_2 w'(0) - (\gamma + D_1) > 0, \tag{2.14}$$

then system (2.1) *is persistent.*

Proof. By Theorems 2.4 and 2.5, there are three equilibria on all the coordinate planes, i.e., $E_0 = (N^0, 0, 0)$, $E_1 = (N_1, P_1, 0)$ and $E_2 = (N_2, 0, Z_2)$. We first show that all equilibria are saddle points.

For $E_0 = (N^0, 0, 0)$, the variational matrix of system (2.1) at E_0 is

$$\begin{bmatrix} -D & -au(N^0) + \gamma_1 & -bv(N^0) + \varepsilon_1 \\ 0 & au(N^0) - (\gamma + D_1) & 0 \\ 0 & 0 & bv(N^0) - (\varepsilon + D_2) \end{bmatrix}.$$

By inequalities (2.9) and (2.11), the eigenvalues of the variational matrix are $\lambda_1 = -D < 0$, $\lambda_2 = au(N^0) - (\gamma + D_1) > 0$, $\lambda_3 = bv(N^0) - (\varepsilon + D_2) > 0$, so E_0 is a saddle point.

The variational matrix of system (2.1) at $E_1 = (N_1, P_1, 0)$ has the form

$$\begin{bmatrix} -D - aP_1 u'(N_1) & -au(N_1) + \gamma_1 & -bv(N_1) + (1-\delta)cw(P_1) + \varepsilon_1 \\ aP_1 u'(N_1) & 0 & -cw(P_1) \\ 0 & 0 & bv(N_1) + \delta cw(P_1) - (\varepsilon + D_2) \end{bmatrix},$$

and the eigenvalues of the variational matrix are λ_1, λ_2 which are the roots of the equation

$$\lambda^2 + (D + aP_1 u'(N_1))\lambda + aP_1 u'(N_1)(au(N_1) - \gamma_1) = 0$$

and

$$\lambda_3 = bv(N_1) + \delta cw(P_1) - (\varepsilon + D_2).$$

Clearly, λ_1 and λ_2 have negative real parts, and $\lambda_3 > 0$ by condition (2.13). Therefore E_1 is a saddle point, and since $\lambda_3 > 0$, E_1 is unstable in the direction orthogonal to the N-P coordinate plane.

The variational matrix of system (2.1) at $E_2 = (N_2, 0, Z_2)$ has the form

$$\begin{bmatrix} -D - bZ_2 v'(N_2) & -au(N_2) + (1-\delta)cZ_2 w'(0) + \gamma_1 & -bv(N_2) + \varepsilon_1 \\ 0 & au(N_2) - (\gamma + D_1) - cZ_2 w'(0) & 0 \\ -bZ_2 v'(N_2) & \delta cZ_2 w'(0) & 0 \end{bmatrix}.$$

By analogous arguments to those analyzing E_1 and condition (2.14), we can prove that E_2 is a saddle point, and it is unstable in the direction orthogonal to the N-Z coordinate plane.

Now let

$$G(N, P, Z) = au(N) - \frac{cZw(P)}{P} - (\gamma + D_1),$$

$$H(N, P, Z) = bv(N) + \delta cw(P) - (\varepsilon + D_2).$$

We have that

$$H(N_1, P_1, 0) = bv(N_1) + \delta cw(P_1) - (\varepsilon + D_2) > 0$$

$$G(N_2, 0, Z_2) = au(N_2) - cZ_2 w'(0) - (\gamma + D_1) > 0.$$

According to Theorem 5.1 of Freedman and Waltman [20], system (2.1) is persistent. This completes the proof. □

Condition (2.13) in Theorem 2.8 means that near the positive equilibrium (N_1, P_1) in the N-P plane, the growth rate of the zooplankton population is positive, and condition (2.14) means that near the positive equilibrium (N_2, Z_2) in the N-Z plane, the growth rate of the phytoplankton population is positive. Theorem 2.8 shows that if inequalities (2.8)–(2.11) hold (which guarantee the existence of (N_1, P_1) and (N_2, Z_2)), then the positive growth rates of zooplankton and phytoplankton near (N_1, P_1) and (N_2, Z_2) respectively, imply the survival of all three components.

In model (2.1), since the predator zooplankton is facultative, competition for the nutrient between phytoplankton and zooplankton exists in some sense, but Theorem 2.8 shows that competitive exclusion does not occur in the Z-P-N models.

Note that from the theorem of Butler et al. [7] we can obtain uniform persistence for our system. We now are able to state criteria which guarantee the existence of an interior equilibrium, by the corollary of [7].

Theorem 2.9 *Suppose the hypotheses of Theorem* 2.8 *hold. Then system* (2.1) *has an interior equilibrium* $E^* = (N^*, P^*, Z^*)$.

As an example, we consider the following model

$$\begin{aligned}
\frac{dN}{dt} &= D(N^0 - N) - \frac{aNP}{k_1 + N} - \frac{bNZ}{k_2 + N} + (1-\delta)cZ(1 - e^{-\lambda P}) + \gamma_1 P + \varepsilon_1 Z \\
\frac{dP}{dt} &= \frac{aNP}{k_1 + N} - cZ(1 - e^{-\lambda P}) - (\gamma + D_1)P \\
\frac{dZ}{dt} &= Z\left[\frac{bN}{k_2 + N} + \delta c(1 - e^{-\lambda P}) - (\varepsilon + D_2)\right],
\end{aligned} \tag{2.15}$$

where all parameters are positive. Now inequalities (2.8) and (2.9) become

$$\frac{\gamma + D_1}{a} < \frac{N^0}{k_1 + N^0}, \tag{2.16}$$

and inequalities (2.10) and (2.12) become

$$\frac{\varepsilon + D_2}{b} < \frac{N^0}{k_2 + N^0}. \tag{2.17}$$

System (2.15) has the following equilibria

$$E_0 = (N^0, 0, 0), \qquad E_1 = \left(\frac{k_1 \alpha}{1-\alpha}, \frac{D\left(N^0 - \frac{\alpha}{1-\alpha} k_1\right)}{\gamma + D_1 - \gamma_1}, 0\right)$$

and

$$E_2 = \left(\frac{k_2\beta}{1-\beta}, 0, \frac{D\left(N^0 - \frac{\beta}{1-\beta}k_2\right)}{\varepsilon + D_2 - \varepsilon_1} \right)$$

on the coordinate planes where $\alpha = (\gamma + D_1)/a$, $\beta = (\varepsilon + D_2)/b$. By Theorem 2.8, we have

Theorem 2.10 *Suppose inequalities* (2.16) *and* (2.17) *hold, if*

$$\frac{k_1\alpha}{k_2 + (k_1 - k_2)\alpha} + \frac{\delta c}{b}\left\{1 - \exp\left[-\frac{\lambda D\left(N^0 - \frac{\alpha}{1-\alpha}k_1\right)}{\gamma + D_1 - \gamma_1} \right]\right\} > \beta,$$

$$\frac{k_2\beta}{k_1 + (k_2 - k_1)\beta} - \frac{\frac{c\lambda D}{a}\left(N^0 - \frac{\beta}{1-\beta}k_2\right)}{\varepsilon + D_2 - \varepsilon_1} > \alpha.$$

Then system (2.15) *is persistent.*

In Theorem 2.8, persistence criteria are given when the predator is facultative ($bv(N^0) > \varepsilon + D_2$); in that case the zooplankton population can survive without the phytoplankton population. Actually, if the predator is obligate ($bv(N^0) < \varepsilon + D_2$), even though zooplankton cannot survive without phytoplankton, persistence may occur. In the following we consider the case where the predator is obligate.

If we suppose that the zooplankton population does not take nutrient directly, i.e., $b = 0$, then system (2.1) takes the following form

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + (1-\delta)cZw(P) + \gamma_1 P + \varepsilon_1 Z \\ \frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D_1)P \\ \frac{dZ}{dt} &= Z[\delta cw(P) - (\varepsilon + D_2)]. \end{aligned} \tag{2.18}$$

If $\delta c \leqslant \varepsilon + D_2$, then the zooplankton population cannot exist; if $a \leqslant \gamma + D_1$, then phytoplankton and hence zooplankton cannot exist. Hence system (2.18) does not persist if any of the above inequalities holds. In the following, we suppose that the inverse direction inequalities, i.e. (2.8) and

$$\varepsilon + D_2 < \delta c \tag{2.19}$$

hold.

Notice that $E_0 = (N^0, 0, 0)$ is an equilibrium for system (2.18) and is globally asymptotically stable in N-axis direction. If (2.8) and (2.9) hold, then $E_1 = (N_1, P_1, 0)$ given by Theorem 2.4 is also an equilibrium of (2.18) and is globally asymptotically stable with respect to the N-P plane. Also all solutions of system (2.18) are bounded.

If (2.19) holds, then E_0 is a saddle point and is unstable in the direction orthogonal to the N-Z plane. If the inequality

$$w(P_1) > \frac{\varepsilon + D_2}{\delta c} \tag{2.20}$$

holds, then E_1 is a saddle point and is unstable in the direction orthogonal to the N-P plane. Hence by Butler–McGehee lemma (cf. [21]), inequality (2.20) implies the persistence of system (2.18). It is known that persistence of the Z component is equivalent to entire system persistence (Gard and Hallam [25]) for models of the form (2.18). Following the similar arguments by Hallam [27, 28] and Gard [24], we know that condition (2.20) is also necessary for persistence in system (2.18). The result in [7] implies that system (2.18) processes an interior equilibrium $E^* = (N^*, P^*, Z^*)$ with

$$P^* = w^{-1}\left(\frac{\varepsilon + D_2}{\delta c}\right). \tag{2.21}$$

Theorem 2.11 *Assume* (2.8), (2.9) *and* (2.19) *hold. Then system* (2.18) *persists if and only if* (2.20) *holds. Furthermore, under* (2.20) *system* (2.18) *has a positive interior equilibrium.*

This result indicates that solutions of system (2.18) are uniformly ultimately bounded and have components which do not tend to zero under certain conditions. Condition (2.20) means that near the positive equilibrium (N_1, P_1) in the N-P plane, the growth rate of zooplankton is positive.

Notice also that the right hand side of inequality (2.20) is the value of the function $w(P)$ at P^* by (2.21). So condition (2.20) is equivalent to $w(P_1) > w(P^*)$. Since $w(P)$ is increasing by (2.4), it is also equivalent to $P_1 > P^*$.

Now we consider (2.15) with $b = 0, k_1 = k$, namely

$$\begin{aligned}
\frac{dN}{dt} &= D(N^0 - N) - \frac{aNP}{k+N} + (1-\delta)cZ(1 - e^{-\lambda P}) + \gamma_1 P + \varepsilon_1 Z \\
\frac{dP}{dt} &= \frac{aNP}{k+N} - cZ(1 - e^{-\lambda P}) - (\gamma + D_1)P \\
\frac{dZ}{dt} &= Z[\delta c(1 - e^{-\lambda P}) - (\varepsilon + D_2)].
\end{aligned} \tag{2.22}$$

System (2.22) has two equilibria on the boundary,

$$E_0 = (N^0, 0, 0) \quad \text{and} \quad E_1 = \left(\frac{\alpha}{1-\alpha}k, \frac{D\left(N^0 - \frac{\alpha}{1-\alpha}k\right)}{\gamma + D_1 - \gamma_1}, 0\right)$$

provided (2.16) holds, where $\alpha = (\gamma + D_1)/a$. The persistence condition (2.20) becomes

$$1 - \exp\left[-\frac{\lambda D\left(N^0 - \frac{\alpha}{1-\alpha}k\right)}{\gamma + D_1 - \gamma_1}\right] > \frac{\varepsilon + D_2}{\delta c} \tag{2.23}$$

and the positive interior equilibrium $E^* = (N^*, P^*, Z^*)$ is given by

$$\begin{aligned}
P^* &= \frac{1}{\lambda}\ln\frac{\delta c}{\delta c - (\varepsilon + D_2)}, \\
Z^* &= \frac{\delta P^*}{\varepsilon + D_2}\left[a\frac{N^*}{k+N^*} - (\gamma + D_1)\right],
\end{aligned}$$

and N^* is the positive root of

$$DN^{*2} + BN^* - C = 0, \tag{2.24}$$

where

$$B = D(k - N^0) + \left[(\gamma + D_1 - \gamma_1) + \delta(a - \gamma - D_1)\left(1 - \frac{\varepsilon_1}{\varepsilon + D_2}\right)\right]P^*,$$

$$C = k\left\{DN^0 + \left[\delta(\gamma + D_1)\left(1 - \frac{\varepsilon_1}{\varepsilon + D_2}\right) - (\gamma + D_1 - \gamma_1)\right]P^*\right\}.$$

Therefore, we have the following result.

Theorem 2.12 *If* (2.16) *and* (2.19) *hold, then system* (2.22) *persists if and only if* (2.23) *holds. Furthermore, under* (2.23), *system* (2.22) *has a unique positive interior equilibrium* $E^* = (N^*, P^*, Z^*)$ *where* N^*, P^* *and* Z^* *are defined as above.*

For the Michaelis–Menten function $u(N) = N/(k + N)$ and the Ivlev function $w(P) = 1 - e^{-\lambda P}$, we proved in Theorem 2.12 that system (2.22) has a unique positive interior equilibrium; we conjecture uniqueness is also true in Theorem 2.11 and Theorem 2.8.

The numerical analysis by Busenberg et al. [5] is very interesting. Using the parameter values reported by Wroblewski et al. [50],

$$a = 2.0, \quad k = 0.2 \quad \gamma = 0.1, \quad \varepsilon = 0.2,$$
$$\lambda = 0.5, \quad c = 0.5, \quad \delta = 0.7,$$

they showed numerically that for a special case of our model (2.22) when $D = D_1 = D_2 = 0$, $\gamma_1 = \gamma$, $\varepsilon_1 = \varepsilon$, there is a periodic oscillatory coexistence state.

For our model (2.22), if we use the above parameter values reported by Wroblewski et al. [50] and the following values

$$D = 0.4, \quad D_1 = 0.3, \quad D_2 = 0.1,$$
$$N^0 = 3.75, \quad \gamma_1 = 0.08, \quad \varepsilon_1 = 0.15,$$

then all conditions of Theorem 1.12 are satisfied, hence system (2.22) with the above parameter values is persistent, and has a unique positive interior equilibrium $E^* = (0.38, 3.89, 8.17)$ which is unstable.

3 *Z-P-N* model with fluctuating nutrient input

To simulate seasons or day/night cycles in a natural environment, we assume that the input concentration of the limiting nutrient is allowed to vary periodically around a mean value $N^0 > 0$, with an amplitude A, $A < N^0$, and period τ; that is, according to the law $N^0 + Ae(t)$, where $e(t)$ is a τ-periodic function of mean value zero and $|e(t)| \leqslant 1$. Though the following technique works for the case when the predator is facultative, a mathematical simplification arises if we assume that the predator is obligate, i.e., $b = 0$. We also assume that $\gamma_1 = \gamma$, $\varepsilon_1 = \varepsilon$ and $D = D_1 = D_2$; the latter assumption often appears in chemostat models (cf. Waltman [47]).

We consider the Z-P-N model with periodic nutrient input

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 + Ae(t) - N) - aPu(N) + (1-\delta)cZw(P) + \gamma P + \varepsilon Z\\ \frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D)P\\ \frac{dZ}{dt} &= Z[\delta cw(P) - (\varepsilon + D)],\end{aligned} \tag{3.1}$$

where functions $u(N)$ and $w(P)$, parameters D, N^0, a, c, δ, γ and ε are the same as in Sect. 2.

This system describes conditions for plankton growth in lakes where the limiting nutrients such as silica nitrate and phosphate are supplied from streams draining the watershed. As seasons change, stream drainage patterns change causing variations in the supply of nutrients.

Let $N^*(t)$ be the unique τ-periodic solution of the equation

$$\frac{dN}{dt} = -DN + D(N^0 + Ae(t)), \tag{3.2}$$

that is,

$$N^*(t) = \frac{D}{e^{D\tau} - 1}\int_0^\tau e^{Dr}(N^0 + Ae(t+r))\,dr. \tag{3.3}$$

It is easy to verify that $N^*(t)$ is globally exponentially stable, and moreover, every solution $N(t)$ of (3.2) can be written as

$$N(t) = N^*(t) + C\,e^{-Dt},$$

where $C = N(0) - N^*(0)$. Suppose

$$e_1 = \min_{0 \leqslant t \leqslant \tau} e(t), \qquad e_2 = \max_{0 \leqslant t \leqslant \tau} e(t).$$

Then all solutions $N(t)$ eventually enter the interval $[N^0 + Ae_1, N^0 + Ae_2]$ and remain there for all future time.

Definition 3.1 A system of ordinary differential equations $dy/dt = f(t, y)$ defined in a domain Ω is *dissipative* if there exists a B such that all solutions $y(t)$ with $y(t) \in \Omega$ for all t satisfy $\limsup_{t \to \infty} |y(t)| \leqslant B$.

Theorem 3.2 *Each solution* $(N(t), P(t), Z(t))$ *of system* (3.1) *with initial value in* R^3_+ *will remain in* R^3_+ *for all* $t \geqslant 0$, *and the system is dissipative in* R^3_+.

Proof. It is obvious that solutions $(N(t), P(t), Z(t))$ of (3.1) with initial data (N_0, P_0, Z_0) in R^3_+ remain in R^3_+ for all $t \geqslant 0$. Let

$$S(t) = N(t) + P(t) + Z(t) - N^*(t). \tag{3.4}$$

We have that

$$\frac{dS}{dt} = -DN - DP - DZ + DN^* = -DS.$$

It follows that for some B_1 and $t \geqslant 0$,

$$S(t) = S(0)\,e^{-Dt} \leqslant B_1.$$

Thus, for $t \geqslant 0$

$$N(t) + P(t) + Z(t) \leqslant N^*(t) + B_1.$$

Since $N^*(t)$ is a globally exponentially stable periodic solution of (3.2), there is a B such that

$$\limsup_{t \to \infty} [N(t) + P(t) + Z(t)] \leqslant B, \tag{3.5}$$

that is, system (3.2) is dissipative in R^3. □

We know that in an Euclidean space $\mathscr{E}$, a periodic ordinary differential equation is equivalent to a dynamical system $\pi(x, t)$ on a cylinder $E = \mathscr{E} \times \mathscr{Q}$ with a flow $\mathscr{F}$, where $\mathscr{Q} = [0, \tau]/\{0, \tau\}$ is a quotient space of $[0, \tau]$ by identifying 0 and τ, or $\mathscr{Q}$ can be regarded as a nontrivial circle on the plane. We think of E as a subset of $\mathscr{E} \times R^2$. In fact, for system (3.1), $\mathscr{E} = R \times R^3_+$. To study the asymptotic behavior of solutions of (3.1), we only need to study the Ω-limit sets of trajectories of a dynamical system π with flow $\mathscr{F}$ on E.

For each point $x \in E$, we denote it by $x = (N, P, Z, Q)$, where $Q \in \mathscr{Q}$. Let $\partial E_P = \{(N, P, Z, Q) \in E \mid P = 0\}$, $\partial E_Z = \{(N, P, Z, Q) \in E \mid Z = 0\}$. We denote the restrictions of flow $\mathscr{F}$ to ∂E_P and ∂E_Z by $\partial \mathscr{F}_P$ and $\partial \mathscr{F}_Z$, respectively. $\Lambda^+(x)$ denotes the omega limit of the orbit through x.

Definition 3.3 *An isolated invariant set* M for the flow $\mathscr{F}$ is a nonempty invariant set which is the maximal invariant set in some neighbourhood of itself. Note that if M is a compact, isolated invariant set, one may always choose a compact isolating neighbourhood.

For an isolated invariant set $M \subset E$, we define

$$W^+_w(M) = \{x \in E \mid \Lambda^+(x) \cap M \neq \varnothing\}$$

as the *weak stable set* and

$$W^+(M) = \{x \in E \mid \Lambda^+(x) \neq \varnothing \text{ and } \Lambda^+(x) \subset M\}$$

as the *stable set*, and we denote

$$\Omega(M) = \bigcup_{x \in M} \Lambda^+(x).$$

Define $M = \{(N^*(t), 0, 0, Q) \in E \mid Q \in \mathscr{Q}\}$, then M is a compact invariant set for $\mathscr{F}$. It is easy to verify that the boundaries ∂E_P, ∂E_Z and hence $\partial E = \partial E_P \cup \partial E_Z$ are invariant. Moreover, we have

Lemma 3.4 $\partial E_P \subset W^+(M)$ *such that if* $x \in \partial E_P \backslash M$, *then*

$$\|\pi(x, t)\| \to \infty \quad \text{as } t \to -\infty.$$

Proof. Since $Z(t) = Z(0)\, e^{-(\varepsilon + D)t}$ whenever $x = (N_0, 0, Z_0, 0) \in \partial E_P$, we have $\pi(x, t) = (N(t), 0, Z(t), t \bmod(\tau)) \to (N^*(Q(t)), 0, 0, Q(t))$ as $t \to \infty$, $Q \in [0, \tau]$, i.e., $\partial E_P \subset W^+(E)$. On the other hand, for $x \in \partial E_P \backslash M$, since $N(t) = N^*(t) + C\, e^{-Dt}$ for some constant $C \neq 0$ whenever $N(t_0) \neq N^*(t_0)$ for any $t_0 \in [0, \tau]$, then $N(t) \neq N^*(t)$. Therefore $\|\pi(x, t)\| \to \infty$ as $t \to -\infty$. □

Let $B(\tau)$ denote the Banach space of continuous τ-periodic real valued functions $x : R \to R$ under the supremum norm

$$|x|_0 = \sup_{0 \leqslant t \leqslant \tau} |x(t)|.$$

Let $B_+(\tau) = \{x \in B(\tau) \mid x(t) > 0 \text{ for all } t\}$ and

$$\langle x(t) \rangle = \frac{1}{\tau} \int_0^\tau x(t)\, dt.$$

The following result indicates that if the phytoplankton population has positive growth rate near the stable periodic solution $N^*(t)$ of (3.2), then it is persistent.

Theorem 3.5 *If*

$$\sigma_0 = a\langle u(N^*(t)) \rangle - (\gamma + D) > 0, \tag{3.6}$$

then

$$\liminf_{t \to \infty} P(t) > 0.$$

Proof. First we prove that M is isolated. Since $\sigma_0 > 0$ and $u(N)$ is continuous, there is $\Delta_0 > 0$ such that for some $\alpha > 0$

$$a\langle u(N^*(t+\alpha) - \Delta_0) \rangle - (\gamma + D + \Delta_0) \geqslant \frac{\sigma_0}{2} > 0. \tag{3.7}$$

Since $\mathscr{F}$ is dissipative, we can find $\xi > 0$ and $t_0 \geqslant 0$ such that $0 \leqslant P(t) \leqslant \xi$ for all $t \geqslant t_0$. Define

$$L = c \max_{0 \leqslant P(t) \leqslant \xi} w(P) > 0 \quad \text{and} \quad \Delta = \frac{\Delta_0}{L} > 0.$$

Then $\mathscr{N}_\Delta = \{x \in E | \varrho(x, M) < \Delta\}$ is an isolating neighbourhood of M, where ϱ is the metric of E. Otherwise, there is an invariant set G containing M in $\mathscr{N}_\Delta$ with $G \backslash M \neq \varnothing$. Lemma 3.3 implies that $(G \backslash M) \cap \partial E_P = \varnothing$. Therefore for any $x \in G \backslash M$, then $x \notin \partial E_P$, i.e., $P_0 > 0$. Since G is invariant, $\gamma^+(x) \subset G \subset \mathscr{N}_\Delta$ where $\gamma^+(x)$ is the positive semiorbit through x. Now we have

$$\frac{d}{dt}[\ln P(t)] \geqslant au(N^*(t) - \Delta_0) - (\gamma + D + \Delta_0) \quad \text{in } \mathscr{N}_\Delta.$$

From (3.7) it follows that

$$P(n\tau) \geqslant P_0 \exp\left(\frac{\sigma_0}{2} n\tau\right) \to \infty \quad \text{as } n \to \infty,$$

a contradiction to $\pi(x, n\tau) \in G$ for all $n \geqslant 0$. So M is isolated.

Now for any $x \in E$ and $\pi(x, t) = (N_x(t), P_x(t), Z_x(t), t \bmod(\tau))$, if $\liminf_{t \to \infty} P_x(t) = 0$, then $\Lambda^+(x) \cap \partial E_P \neq \varnothing$, and hence $M \subset \Lambda^+(x)$, so $W_w^+(M) = \{x \in E \mid \liminf_{t \to \infty} P_x(t) = 0\}$. We claim that for any $x \in E \backslash \partial E_P$, if $\Lambda^+(x) \in M$, then there exists $\alpha > 0$ such that

$$|N_x(t) - N^*(t+\alpha)| \to 0 \quad \text{as } t \to \infty.$$

In fact, if $\Lambda^+(x) \subset M$, then $P_x(t)$ and $Z_x(t)$ tend to zero as $t \to \infty$, which implies $N_x(t) - N^*(t+\alpha)$ tends to zero for some $\alpha > 0$. Hence

$$\lim_{t \to \infty} [a\langle u(N(t)) \rangle - (\gamma + D)] = \sigma_0 > 0$$

and $\liminf_{t \to \infty} P_x(t) > 0$, a contradiction to $\Lambda^+(x) \cap \partial E_P \neq \varnothing$, i.e., $x \notin W^+(M)$, by Lemma 3.4 we have $W^+(M) = \partial E_P$, so $x \in W_w^+(M) \backslash W^+(M)$. Hence by Theorem 4.1 of Butler and Waltman [9], $\Lambda^+(x) \cap (W^+(M) \backslash M) \neq \varnothing$. It follows from

Lemma 3.4 that $\Lambda^+(x)$ is unbounded, a contradiction to the dissipativeness of $\mathscr{F}$. Hence $\Lambda^+(x) \cap \partial E_P = \varnothing$, and $\Lambda^+(x)$ is compact, so $\varrho(\Lambda^+(x), \partial E_P) > 0$, i.e., $\liminf_{t \to \infty} P(t) > 0$. □

Theorem 3.6 *If $\sigma_0 > 0$, then there exists a nontrivial asymptotically stable τ-periodic orbit on ∂E_Z.*

Proof. Define a Poincaré map T from P-Z plane to itself by $T(N_0, P_0) = (N(\tau), P(\tau))$. By Theorem 3.5 and the dissipativity for each (N_0, P_0) in the interior of R^2_+, $\{T^n(N_0, P_0)\}$ has a convergent subsequence. So by Massera's fixed point theorem (see Sansone and Conti [41]), there exists a fixed point $(\bar{N}, \bar{P})$ of T in the interior of R^2_+, which gives a nontrivial periodic orbit on ∂E_Z.

We observe that $v(N, P, t) = N + P$ is a solution of the initial-boundary value problem

$$\begin{cases} v_t + [D(N^0 + Ae(t) - N) - (au(N) - \gamma)P]v_N \\ \quad + [(au(N) - (\gamma + D)P]u_P + Du = D(N^0 + Ae(t)) \\ v(N, 0, t) = N^*(t), \quad v(N, P, 0) = v(N, P, \tau), \quad t \in [0, \tau], N \geqslant 0, P \geqslant 0. \end{cases}$$

By Theorems 3.7 and 3.8 of Yang and Freedman [51], the nontrivial τ-periodic orbit on ∂E_Z is asymptotically stable. This completes the proof. □

Let $(\bar{N}, \bar{P})$ be the asymptotically stable τ-periodic solution of the reduced system

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 + Ae(t) - N) - aPu(N) + \gamma P \\ \frac{dP}{dt} &= P[au(N) - (\gamma + D)] \end{aligned} \tag{3.8}$$

in Theorem 3.6. We will show in the following that this solution of (3.8) yields a solution $(N, P, Z) = (\bar{N}, \bar{P}, 0) \in B^3_+(\tau)$ of system (3.1) from which will bifurcate a continuum of positive solutions of (3.1) using ε as the bifurcating parameter.

To do this by means of Theorem 1 of Cushing [14], it is necessary that the solution $(\bar{N}, \bar{P})$ of the reduced system (3.8) be *noncritical*; i.e., that the linearized system of (3.8) at $(\bar{N}, \bar{P})$ have no Floquet exponents with zero real part. We assume throughout that $(\bar{N}, \bar{P})$ is stably noncritical, i.e., that these Floquet exponents have negative real parts.

Theorem 3.7 *Assume $\sigma_0 > 0$ and that $(\bar{N}, \bar{P}) \in B^2_+(\tau)$ is a stably noncritical solution of* (3.8). *Then there exists a set $\Pi^+ = \{(N, P, Z, \mu) \in B^3_+(\tau) \times R\}$ with $(N, P, Z) > 0$ solving* (3.1), *the closure of Π^+ is a continuum which connects $(\bar{N}, \bar{P}, 0, \bar{\mu}) \in B^3(\tau) \times R$, $\bar{\mu} = -\langle cw(\bar{P})\rangle$, to a solution of the form $(\tilde{N}, \tilde{P}, 0, \tilde{\mu}) \in B^3(\tau) \times R$, where $(\tilde{N}, \tilde{P}, 0, \tilde{\mu}) \neq (\bar{N}, \bar{P}, 0, \bar{\mu})$, $\tilde{N} > 0$ and $\tilde{P} > 0$.*

Proof. Define $\Omega^3 = \{(N, P, Z) \in R^3 \mid N > 0\}$, by Theorem 1 of Cushing [14] with $d_2(t) = -\mu = -(\varepsilon + D)$, there is a continuum $C^+ \subset B^3(\tau) \times R$ of solutions of (3.1) which contains the bifurcating point $(\bar{N}, \bar{P}, 0, \bar{\mu})$ and which connects to the boundary of the set $\Omega^3_\tau \times R \subset B^3(\tau) \times R$, where $\Omega^3_\tau = \{(N, P, Z) \in B^3(\tau) \mid N + \bar{N} > 0\}$. And in an open neighborhood of $(\bar{N}, \bar{P}, 0, \bar{\mu})$, the set $C^+/\{(\bar{N}, \bar{P}, 0, \bar{\mu})\}$ consists of positive solutions of (3.1). The continuum C^+ cannot

consist entirely of positive solutions, otherwise, in order to connect to the boundary of $\Omega_\tau^3 \times R$, C^+ would have to be unbounded which would contradict Theorem 3.2. Thus C^+ must leave the positive cone $B_+^3(\tau) \times R$ at a point other than the bifurcating point.

Denote by C_0^+ the maximal subcontinuum of C^+ which connects $(\bar{N}, \bar{P}, 0, \bar{\mu})$ to the boundary of $B_+^3(\tau) \times R$ and define $\Pi^+ = C_0^+ \cap (B_+^3(\tau) \times R)$. Then the closure of Π^+ is a continuum which connects $(\bar{N}, \bar{P}, 0, \bar{\mu})$ to the boundary of $B_+^3(\tau) \times R$, i.e., the closure of Π^+ contains $(\bar{N}, \bar{P}, 0, \bar{\mu})$ and a point $(\tilde{N}, \tilde{P}, 0, \tilde{\mu}) \neq (\bar{N}, \bar{P}, 0, \bar{\mu})$ where $\tilde{N} \geqslant 0$ and $\tilde{P} \geqslant 0$.

Let $(N_n, P_n, 0, \mu_n) \in \Pi^+$ be a sequence which converges in $B^3(\tau) \times R$ to $(\tilde{N}, \tilde{P}, 0, \tilde{\mu})$. If $(N, P, Z) = (\tilde{N}, \tilde{P}, 0)$, dividing the second equation of (3.1) by $P_n > 0$ and taking average, we obtain

$$\langle au(N_n) \rangle = \gamma + D. \tag{3.9}$$

If $\tilde{N} \equiv 0$, let $n \to \infty$ in (3.9), then we get a contradiction to $\gamma + D > 0$. Hence it must be the case $\tilde{N} > 0$.

If $\tilde{P} \equiv 0$, then from the first equation of (3.1) in the limit as $n \to \infty$, we see that $\tilde{N} \in B_+(\tau)$ solves the periodic equation (3.2) and hence $\tilde{N} = N^*$. From (3.9), it follows that $\langle au(N^*) \rangle = \gamma + D$, a contradiction to $\sigma_0 > 0$. Hence $\tilde{N} > 0$ and $\tilde{P} > 0$. □

Since $\sigma_0 > 0$ is the persistence condition for the phytoplankton population by Theorem 3.5, Theorem 3.7 demonstrates that coexistence of all components could occur if phytoplankton is persistent and if the death rate of zooplankton is reasonably low. This is reminiscent of a similar phenomenon for the chemostat models in a periodic environment studied by Smith [42] and Cushing [15]. For the Michaelis–Menten function $u(N) = N/(k + N)$ and the Ivlev function $w(P) = 1 - e^{-\lambda P}$, one can determine the stability of the bifurcating solutions in Theorem 3.7, following the procedures by Smith [42], Cushing [15] or Keener [33].

4 *Z-P-N* model with periodic washout rate

Consider the zooplankton-phytoplankton-nutrient model with periodic washout rate

$$\begin{aligned} \frac{dN}{dt} &= D(t)(N^0 - N) - aPu(N) + \gamma P + \varepsilon Z \\ \frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D(t))P \\ \frac{dZ}{dt} &= Z[cw(P) - (\varepsilon + D(t))], \end{aligned} \tag{4.1}$$

where the periodic washout rate $D(t)$ is a positive, continuous function with period τ, all parameters and other functions are same as in Sect. 2. It is convenient to scale time by the mean value of $D(t)$, i.e.,

$$\langle D(t) \rangle = \frac{1}{\tau} \int_0^\tau D(t)\, dt.$$

We assume that all the phytoplankton removed through zooplankton predation is assimilated by zooplankton, and all dead phytoplankton and zooplankton are

recycled to nutrient completely, i.e., $\delta = 1$, $\gamma_1 = \gamma$, $\varepsilon_1 = \varepsilon$. Similar to the procedure in Sect. 3, we know that the positive cone and the boundaries ∂E_P, ∂E_Z are invariant, and the system is dissipative, i.e., we have

$$\lim_{t \to \infty} [N(t) + P(t) + Z(t)] = N^0,$$

where the convergence is exponential.

Firstly we consider the two dimensional system

$$\begin{aligned} \frac{dN}{dt} &= D(t)(N^0 - N) - aPu(N) + \gamma P \\ \frac{dP}{dt} &= P[au(N) - (\gamma + D(t))]. \end{aligned} \tag{4.2}$$

For any solution of (4.2), $N(t) + P(t) = N^0 + R(t)$ where $R(t) = O(e^{-\alpha t})$ as $t \to \infty$ for some $\alpha > 0$. Then $P(t)$ is a solution of

$$\frac{dx(t)}{dt} = x(t)[au(N^0 - x(t)) - (\gamma + D(t))] + r(t), \tag{4.3}$$

where $r(t) = O(e^{-\alpha t})$ as $t \to \infty$ and $\alpha > 0$. In turn, (4.3) is a perturbation of

$$\frac{dy(t)}{dt} = y(t)[au(N^0 - y(t)) - (\gamma + D(t))]. \tag{4.4}$$

It was shown by Butler and Freedman [6] using Massera's theorem that Eq. (4.4) has a unique positive τ-periodic solution $\varphi(t)$ which is globally asymptotically stable. It is not difficult to show that $\varphi(t)$ is exponentially asymptotically stable. A simple Gronwall's inequality argument shows that if $x(t)$ is any solution of (4.3), then $x(t) = \varphi(t) + O(e^{-\beta t})$ for some $\beta > 0$. Note that $\varphi(t)$ is independent of the choice of $P(t)$, although (4.3) is not; in particular, $P(t)$ converges exponentially to $\varphi(t)$ as $t \to \infty$. Define $\psi(t) = N^0 - \varphi(t)$. Then $N(t)$ converges exponentially to $\psi(t)$ as $t \to \infty$. And

$$\frac{d\varphi(t)}{dt} = \varphi(t)[au(N^0 - \varphi(t)) - (\gamma + D(t))] = \varphi(t)[au(\psi(t)) - (\gamma + D(t))],$$

$$\frac{d\psi(t)}{dt} = -\frac{d\varphi(t)}{dt} = -a\varphi(t)u(\psi(t)) + (N^0 - \psi(t))(\gamma + D(t)).$$

Thus $(\psi(t), \varphi(t))$ is a solution of (4.2) and is globally exponentially stable.

Referring back to Theorems 2.1 and 2.2, since $\langle D \rangle = 1$ we need $a > \gamma + 1$ and $c > \varepsilon + 1$. Hence we have the following result.

Theorem 4.1 *Assume that $a > \gamma + 1$. There are positive τ-periodic functions $N(t)$ and $\varphi(t)$, such that the solution $(N(t), \varphi(t))$ of* (4.2) *is exponentially stable for* (4.2), *and $\varphi(t)$ is globally asymptotically stable for* (4.4).

Now for the three dimensional system (4.1), there may be two periodic solutions on the boundary of the non-negative cone, the constant solution $E_0 = (N^0, 0, 0)$ and solution $E_1 = (N(t), \varphi(t), 0)$.

Our main purpose in this section is to prove the following theorem.

Theorem 4.2 *Let a and γ be given such that $a > \gamma + 1$. If there exists $\alpha = \alpha(a, \gamma)$ such that for any $c > \alpha$, the bifurcation parameter ε can be chosen such that $\langle w(\varphi(t)) \rangle > (\varepsilon + 1)/c$, where $\varphi(t)$ is the positive τ-periodic solution of* (4.4), *then system* (4.1) *possesses a positive τ-periodic solution $(N(t), P(t), Z(t))$ near E_1 and bifurcating from E_1.*

Proof. We may restrict our attention to the invariant triangle $\triangle: N+P+Z=N_0, N, P, Z \geqslant 0$. Eliminating N from (4.1) restricted to $\triangle$, we have the equations

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 f_1(t, x_1, x_2) \\ \frac{dx_2}{dt} &= x_2 f_2(t, x_1, x_2), \end{aligned} \tag{4.5}$$

where

$$f_1(t, x_1, x_2) = au(N^0 - x_1 - x_2) - cx_2 \frac{w(x_1)}{x_1} - (\gamma + D(t)),$$

$$f_2(t, x_1, x_2) = cw(x_1) - (\varepsilon + D(t)).$$

System (4.5) is a predator-prey model with periodic coefficients. We verify that conditions of Theorem 2.2 of Butler and Freedman [6] are satisfied.

(H$_1$) $f_{11} = \dfrac{df_1}{\partial x_1} = -au' - cx_2 \dfrac{w'(x_1)}{x_1} + cx_2 \dfrac{w(x_1)}{x_1}$,

$$f_{12} = \frac{\partial f_1}{\partial x_2} = -au' - c\frac{w(x_1)}{x_1}, \quad f_{21} = \frac{\partial f_2}{\partial x_1} = cw'(x_1), \quad f_{22} = \frac{\partial f_2}{\partial x_2} = 0.$$

Hence $f_{ij}(i, j = 1, 2)$ exist and are continuous for $(t, x_1, x_2) \in R \times R_+^2$, where $R_+^2 = \{(x_1, x_2) \in R^2, x_1 \geqslant 0, x_2 \geqslant 0\}$.

(H$_2$) In the absence of predator, there is a seasonally varying carrying capacity for the prey, say the function $K_1^*(t)$, such that $[x_1 - K_1^*(t)]f_1(t, x_1, 0) = [x_1 - K_1^*(t)][au(N^0 - x_1) - (\gamma + D(t))] < 0$ for all $x_1 > 0$ and $x_1 \neq K_1^*(t)$.

(H$_3$) There exists a critical population density for the predator, say $K_2^*(t)$, above which it cannot survive in the absence of prey, such that

$$[x_2 - K_2^*(f)]f_1(t, 0, x_2) = [x_2 - K_2^*(t)][au(N^0 - x_2) - cx_2 w'(0) - (\gamma + D(t)] < 0$$

for all $x_2 \geqslant 0$ and $x_2 \neq K_2^*(t)$.

(H$_4$) $f_{12} = -au' - c\dfrac{w(x_1)}{x_1} < 0$ for all $(t, x_1, x_2) \in R \times R_+^2$.

(H$_5$) $x_1 f_{11} + x_2 f_{22} = -a(x_1 + x_2)u' - cx_2 w'(x_1) < 0$ for all $(t, x_1, x_2) \in R \times R_+^2$.

(H$_6$) There is a minimum level for the prey population, say $\hat{K}_1(t)$, at which the predator can survive when its own population density is at a low level, this $\hat{K}_1(t)$ is such that $[x_1 - \hat{K}_1(t)]f_2(t, x_1, 0) = [x_1 - \hat{K}_1(t)][cw(x_1) - (\varepsilon + D(t))] > 0$ for all $x_1 \geqslant 0$ and $x_1 \neq \hat{K}_1(t)$.

(H$_7$) $f_{22} = 0$ for all $(t, x_1, x_2) \in R \times R_+^2$.

(H$_8$) $x_1 f_{21} + x_2 f_{22} = cx_1 w'(x_1) > 0$ for all $(t, x_1, x_2) \in R \times R_+^2$.

And we have

$$\langle f_2(t, 0, 0)\rangle = \langle -(\varepsilon + D(t))\rangle = -\varepsilon - 1 \leqslant 0,$$

$$\langle f_2(t, \varphi(t), 0)\rangle = \langle cw(\varphi(t))\rangle - (\varepsilon + D(t)) = c\langle w(\varphi(t))\rangle - (\varepsilon + 1) > 0.$$

By Theorem 2.2 of Butler and Freedman [6], system (4.5) has a periodic solution $(\psi_1(t), \psi_2(t))$ with $\psi_1(t) > 0$ and $\psi_2(t) > 0$. As in [6], $\langle f_2(t, 0, 0)\rangle = -\varepsilon - 1$, so ε

can be chosen as a bifurcation parameter such that system (4.1) has a positive τ-periodic solution $(N(t), P(t), Z(t))$ near E_1 and which bifurcates from E_1. This completes the proof. □

This result indicates that if the growth rate of phytoplankton is positive and the death rate of zooplankton is relatively low, then a positive periodic solution in the three dimensional space will bifurcate from the asymptotically stable periodic solution in the N-P plane, hence predator-prey coexistence could occur.

5 Discussion

In this paper we have discussed several zooplankton-phytoplankton-nutrient models with general uptake functions and instantaneous nutrient recycling terms. Different from the model studied by Wroblewski et al. [50] and Busenberg et al. [5], we introduce nutrient concentration input and washout rates to the plankton-nutrient interacting models.

Firstly, we have considered a model with a constant nutrient input and different constant washout rates, the zooplankton population could be facultative or obligate. We have given conditions for boundedness of solutions, existence and stability of the equilibria and persistent criteria for the system. Competition for the nutrient exists in some sense if zooplankton is facultative, but competitive exclusion does not happen. For the case where zooplankton is obligate, persistence has been studied.

As a consequence of the persistence Theorem 2.11, we note that model (2.18) has a dynamic persistence threshold; that is, there exists a number above which the system persists, below which it does not. From persistence condition (2.20) we get the non-dimensional persistence threshold in terms of the nutrient input concentration

$$N^0 > u^{-1}\left(\frac{\gamma + D_1}{a}\right) + \frac{\gamma + D_1 - \gamma_1}{D} w^{-1}\left(\frac{\varepsilon + D_2}{\delta c}\right). \tag{5.1}$$

This inequality demonstrates that the model is nutrient controlled (Hallam [28]). Persistence occurs more likely if the nutrient input concentration (N^0) is increased or the death rate of the zooplankton population (ε) is relatively low. Since enriching the environment may destablize the system, that is, "enrichment paradox" may happen (see Busenberg et al. [5], also Ruan and Freedman [40] and Freedman and Ruan [20]), it is natural to seek oscillatory coexistence of all components.

Next we have considered the plankton-nutrient interacting models with periodic nutrient input and periodic washout rate, respectively. The persistence inequality (5.1) is not always true for the two periodic models (3.1) and (4.1), hence we cannot get persistence. However, it is shown that in both cases, there are positive periodic solutions in the three dimensional spaces bifurcating from stable periodic solutions in the N-P plane with the death rate of zooplankton used as the bifurcating parameter. Therefore, as in (5.1), if the death rate of zooplankton is relatively low, coexistence of all three components could occur.

The discrete delay due to ingestion and the distributed delay in the nutrient recycling can be introduced to the above zooplankton-phytoplankton-nutrient models. We leave this to future study.

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