Persistence in variable-yield nutrient-plankton models with nutrient recycling

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Abstract. Nutrient-phytoplankton-zooplankton models with general uptake functions in which only the internal nutrient concentration is capable of catalyzing cell growth and division for phytoplankton are proposed and analyzed. For the constant nutrient input model, it is shown that extinction or persistence of the population depends on its maximal growth rate relative to the total removal rate. The same biological conclusions hold for the periodic nutrient input model. However, while extinction and persistence are expressed in terms of convergence to steady states for the constant nutrient input model, these biological phenomena are exhibited in terms of asymptotic attraction to periodic solutions for the periodic nutrient input model.

Key words: cell quota – obligate predator – periodic system – uniform persistence – Poincaré map

1   Introduction

A system was proposed in the late 1940's by Riley et al. [24] for modeling the profiles of marine plankton. Since then numerious nutrient-plankton models have been constructed and studied by researchers in the area [1, 4, 5, 6, 9, 11, 13, 14, 17, 25, 29, 30, 34, 35]. The intensive investigation of nutrient-plankton interactions is motivated in large part by their important and fundamental role in the food webs.

One class of such models assumes spatial homogeneity and discusses asymptotic or transient behavior of the interaction between populations. In such models, it is frequently assumed that the growth rate of phytoplankton is constantly proportional to the nutrient uptake rate, that is, the growth

rate of the algae depends on the ambient nutrient available to the microorganism. Such systems are examples of using the classical Monod kinetics to model metabolism. However, experiments have demonstrated that algae can uptake nutrient in excess of its immediate needs, so that when the nutrient is depleted, the organism can still continue to grow and divide for some time until the internal reserves are exhausted. Ketchum [19] was among the first to document such a biological phenonemon.

One of the mathematical models that captures this biological observation is the Droop model, also called the variable-yield model [7, 8]. In this type of model it is assumed that a phytoplankton cell can store nutrient and that its growth rate depends on the amount of stored nutrient, called the cell quota. The cell quota may be viewed as the average amount of stored nutrient in each cell of the algae. The uptake rate of the organism is then dependent on the ambient nutrient concentration and perhaps the cell quota. Such models have been shown to provide good fits for the data observed in experiments [12, 20, 31].

Since the seminal work of Grover [13, 14] in the early 1990s, variable-yield plankton models have received considerable discussion. The first mathematical analysis was performed by Lange and Oyarzun [21], where they studied a single phytoplankton population in the chemostat with specific uptake and growth functions, and later extended their results to general growth and uptake functions [23]. Smith and Waltman analyzed a variable-yield model with two populations competing in the chemostat [26]. By using the competitive and cooperative properties of the system, they showed that competitive exclusion principal remains valid in the model. Smith also examined a single species variable-yield chemostat model with periodic nutrient input [28]. A threshold condition was obtained beyond which phytoplankton population can persist. Variable-yield nutrient-plankton models with specific grazing rates in closed ecological systems were investigated by Jang [17, 18].

In this manuscript we propose a general class of variable-yield nutrient-phytoplankton-zooplankton models to study the interaction between the nutrient and the organisms in an open ecological system. In these models, the two plankton levels are modeled in terms of their nutrient or nitrogen content, and it is assumed that there is no net nutrient loss due to physiological death or due to nutrient conversion. It is well known in population biology that zooplankton feeds on phytoplankton for survival. However, motivated by the consideration given in Ruan [25], we also discuss the case when the zooplankton population may feed on the nutrient so that the population may

be facultative.

Aside from the physiological death of the algae, phytoplankton may lose its nutrient content because of the exudation of organic substance. On the other hand, cell sinking is known as an important loss of phytoplankton. This is particularly true at the end of the spring bloom, which may drive the algal population out of the system such as being buried in deep sediments. Also, zooplankton mortality by higher predators can contribute to the death of the population, which is frequently not explicitly modeled in nutrient-plankton models due to intractibility of the analysis. The final destination of such dead zooplankton will be either as the form of ammonium, fecal pellets, or dead higher predators. Consequently, even under the assumption that there is no net nutrient loss due to physiological death and nutrient conversion, there are losses of nutrient or nitrogen content due to other causes so that the system is never closed. Furthermore, for natural nutrient-plankton systems there is usually a flux of nutrient in and out of the systems [6]. To incorporate these biological observations, we use a constant washout rate to model the losses amounting from various biological processes. For simplicity, the constant washout rate is assumed to be the same for the nutrient and the plankton populations.

We first present a general class of nutrient-plankton models with a constant limiting nutrient input. To incorporate day/night or seasonal cycles, nutrient-plankton models with a periodic limiting nutrient input will also be proposed. For these models, sufficient conditions for the extinction of phytoplankton, and zooplankton are derived. Persistent conditions for each of the populations are also given. Explicit criteria for the coexistence of both populations are obtained, where the notion of coexistence is captured by the concept of uniform persistence. For constant input nutrient models, persistence and extinction are characterized by the convergence to steady states, while for periodic nutrient input models, these biological consequences are expressed in terms of asymptotic attraction to periodic solutions.

In the following section, a general class of nutrient-plankton models with a constant limiting nutrient input is presented. The model with a periodic nutrient input is studied in Section 3. Section 4 demonstrates these analytical findings by numerical simulations. The final section provides a brief summary and discussion.

2 The model with constant nutrient input

We let $N(t), P(t)$ and $Z(t)$ denote the nutrient concentration, the concentration (or number of cells) of phytoplankton and zooplankton population at time t, respectively. Their units are nitrogen or nitrate per unit volume. It is assumed that the algal cell is capable of storing nutrient. Therefore there is a new state variable, $Q(t)$, the cell quota. It is the average amount of stored nutrient per algal cell at time t. As a result, $Q(t)$ is dimensionless. The growth rate of the phytoplankton depends on the cell quota, while the uptake rate depends on the ambient nutrient, and possibly on the cell quota. We let $u(Q)$ be the per-capita growth rate and $\rho(N, Q)$ the per-capita uptake rate of phytoplankton, respectively. Motivated by the explicit examples of functions u and ρ in the literature [7, 8, 13, 14, 21], we make the following assumptions [17, 23, 26, 27, 28].

(H1) There exists $Q_0 > 0$ such that $u(Q_0) = 0, u'(Q) > 0$ and $u'(Q)$ is continuous for $Q \geq Q_0$.

(H2) $\rho \in C^1(N, Q)$ for $N \geq 0, Q \geq Q_0; \rho(0, Q) = 0$ for $Q \geq Q_0; \dfrac{\partial \rho}{\partial N} > 0$ and $\dfrac{\partial \rho}{\partial Q} \leq 0$ for $N \geq 0, Q \geq Q_0$.

The quantity Q_0 is the minimum cell quota necessary to allow any cell division. We let parameters $\delta > 0$ and $\epsilon > 0$ denote the death rate of phytoplankton and zooplankton respectively. The constant washout rate $D > 0$ is assumed to be the same for the nutrient and both plankton populations. The zooplankton may also uptake nutrient. We use general functions $f(N)$ and $g(P)$ to describe the nutrient uptake and herbivore grazing for zooplankton respectively, which are assumed to satisfy the following hypotheses.

(H3) $f \in C^1([0, \infty))$, $f(0) = 0$, $f'(N) > 0$ for $N \geq 0$ and $\lim_{N \to \infty} f(N) = 1$.

(H4) $g \in C^1([0, \infty))$, $g(0) = 0$, $g'(P) > 0$ for $P \geq 0$ and $\lim_{P \to \infty} g(P) = 1$.

Therefore, zooplankton's uptakes increase with increasing food resource. The positive constant input nutrient concentration is denoted by N^0. Parameters $b \geq 0$ and $c > 0$ are the maximal nutrient uptake rate and ingestion rate of zooplankton respectively, while d is the fraction of zooplankton grazing conversion, $0 < d \leq 1$. Since the two plankton levels are modeled in terms of their nutrient content and there is no nutrient loss due to death and

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nutrient conversion, our model takes the following form.

$$
\begin{aligned}
\dot{N} &= D(N^0 - N) - P\rho(N, Q) + \delta PQ - bf(N)Z + c(1 - d)g(P)QZ + \epsilon Z, \\
\dot{P} &= P[u(Q) - \delta - D] - cg(P)Z, \\
\dot{Q} &= \rho(N, Q) - u(Q)Q, \\
\dot{Z} &= [bf(N) + dcg(P)Q - \epsilon - D]Z, \\
&\quad N(0) \geq 0, P(0) \geq 0, Q(0) \geq Q_0, Z(0) \geq 0.
\end{aligned}
\tag{2.1}
$$

Notice that when $b = 0$, there is no nutrient consumption by zooplankton. As a consequence, phytoplankton is the only resource contributing to the growth of zooplankton population and the population becomes obligate. Since $\dot{N}|_{N=0} > 0$, it follows that $N(t) > 0$ for $t > 0$. From (H1) and (H2) we see that $\dot{Q}|_{Q=Q_0} \geq 0$ and thus $Q(t) \geq Q_0$ for $t \geq 0$. Let $U = N^0 - N - PQ - Z$. It can be easily shown that $\dot{U} = -DU$ and we can rewrite system (2.1) as

$$
\begin{aligned}
\dot{U} &= -DU, \\
\dot{P} &= P[u(Q) - \delta - D] - cg(P)Z, \\
\dot{Q} &= \rho(N^0 - U - PQ - Z, Q) - u(Q)Q, \\
\dot{Z} &= [bf(N^0 - U - PQ - Z) + dcg(P)Q - \epsilon - D]Z, \\
&\quad P(0) \geq 0, Q(0) \geq Q_0, Z(0) \geq 0, U(0) + P(0)Q(0) + Z(0) \leq N^0.
\end{aligned}
\tag{2.2}
$$

Since $\lim_{t\to\infty} U(t) = 0$, the ω-limit set of (2.2) lies on the set $U = 0$. Restricted to the set $U = 0$, we have the limiting system of (2.2) given below.

$$
\begin{aligned}
\dot{P} &= P[u(Q) - \delta - D] - cg(P)Z, \\
\dot{Q} &= \rho(N^0 - PQ - Z, Q) - u(Q)Q, \\
\dot{Z} &= [bf(N^0 - PQ - Z) + dcg(P)Q - \epsilon - D]Z, \\
&\quad P(0) \geq 0, Q(0) \geq Q_0, Z(0) \geq 0, P(0)Q(0) + Z(0) \leq N^0.
\end{aligned}
\tag{2.3}
$$

Let $\Delta = \{(P, Q, Z) \in R_+^3 : Q \geq Q_0, PQ + Z \leq N^0\}$.

Lemma 2.1 Δ *is positively invariant for (2.3) and solutions of (2.3) are bounded.*

Proof. Recall that $Q(t) \geq Q_0$ and $N(t) \geq 0$ for $t \geq 0$. Since $\dot{P}|_{P=0} = \dot{Z}|_{Z=0} = 0$, solutions of (2.3) satisfy $P(t), Z(t) \geq 0$ for $t \geq 0$. Moreover, $\frac{d}{dt}(PQ + Z)|_{PQ+Z=N^0} < 0$ and thus $P(t)Q(t) + Z(t) \leq N^0$ for $t \geq 0$. We

conclude that Δ is positively invariant for (2.3). Furthermore, since $\dot{Q} < 0$ for Q large, $Q(t)$ is bounded. Consequently, solutions of (2.3) are bounded. ∎

Once we show that populations do not grow unboundedly large, we turn to discuss steady state solutions. It's easy to see that the trivial steady state $E_0 = (0, Q^*, 0)$ always exists, where Q^* satisfies $\rho(N^0, Q) = u(Q)Q$. Since $\dot{Q} \leq \rho(N^0, Q) - u(Q)Q$, it follows that either $Q(t) \geq Q^*$ for $t \geq 0$ or $Q(t) \leq Q^*$ for all t large. If $Q(t) \geq Q^*$ for $t \geq 0$, then it is straightforward to show that $\lim_{t\to\infty} Q(t) = Q^*$. As a result, since $P(t) \leq N^0/Q_0$ and $Z(t) \leq N^0$ for $t \geq 0$, system (2.3) is dissipative.

To obtain steady states on the interior of the coordinate planes, we set $\dot{Z} = 0, \dot{P} = 0, \dot{Q} = 0$ and $P \neq 0$. Then $u(Q) = \delta + D$ and $\rho(N^0 - PQ, Q) = u(Q)Q$, and a steady state $E_1 = (P_1, Q_1, 0)$ exists if and only if $u(\infty) > \delta + D$ and $\rho(N^0, Q_1) > (\delta + D)Q_1$. Note that in this case $Q_1 < Q^*$ and steady state of this form is unique.

Similarly, setting $P = 0, \dot{Z} = 0, \dot{Q} = 0$ and $Z \neq 0$, we have $bf(N^0 - Z) = \epsilon + D$ and $\rho(N^0 - Z, Q) = u(Q)Q$. Hence a steady state $E_2 = (0, Q_2, Z_2)$ exists if and only if $bf(N^0) > \epsilon + D$. Furthermore, such a steady state on the interior of the positive Q-Z plane is unique if it exists, and also $Q_2 < Q^*$. On the other hand there is no steady state on the positive Q-Z plane if zooplankton is obligate. We further remark that Q^* in E_0 and Q_2 in E_2 are artificial as there are no phytoplankton populations present.

Our first result on the asymptotic behavior of (2.3) is given below.

Lemma 2.2 *If $u(Q^*) < \delta + D$, then $\lim_{t\to\infty} P(t) = 0$ for any solution $(P(t), Q(t), Z(t))$ of (2.3).*

Proof. If $Q(t) \leq Q^*$ for t large, then $\dot{P}(t) \leq P(t)[u(Q^*) - (\delta + D)] \leq 0$ for t large. Thus $\lim_{t\to\infty} P(t) = P^* \geq 0$ exists. If $P^* > 0$, then $\lim_{t\to\infty} \dot{P}(t) \neq 0$ and we obtain a contradiction. Hence $\lim_{t\to\infty} P(t) = 0$. On the other hand if $Q(t) \geq Q^*$ for $t \geq 0$, then $\lim_{t\to\infty} Q(t) = Q^*$. We choose $\eta > 0$ such that $Q(t) \leq Q^* + \eta$ for t large and $u(Q^* + \eta) < \delta + D$. A similar argument as above can be applied to show that $\lim_{t\to\infty} P(t) = 0$. ∎

Since $P(t) \leq N^0/Q_0$ for any solution of (2.3), the following lemma can be shown analogously to Lemma 2.2.

Lemma 2.3 *If $bf(N^0) + dcg(N^0/Q_0)Q^* < \epsilon + D$, then $\lim_{t\to\infty} Z(t) = 0$ for any solution $(P(t), Q(t), Z(t))$ of (2.3).*

Theorem 2.4 *If $u(Q^*) < \delta + D$ and $bf(N^0) < \epsilon + D$, then $E_0 = (0, Q^*, 0)$ is the only steady state for system (2.3) and solutions of (2.3) converge to E_0.*

Proof. If $u(\infty) \leq \delta + D$, then clearly E_1 doesn't exist. If $u(\infty) > \delta + D$ and Q_1 satisfies $u(Q_1) = \delta + D$, then $Q^* < Q_1$. Hence $\rho(N^0, Q_1) < (\delta + D)Q_1$ and E_1 doesn't exist. Furthermore, since $bf(N^0) < \epsilon + D$, E_2 doesn't exist and there is no positive steady state. Consequently, E_0 is the only steady state for (2.3).

Observe that $\lim_{t\to\infty} P(t) = 0$ by Lemma 2.2. If $Q(t) \leq Q^*$ for t large, we can find $\eta > 0$ such that $bf(N^0) + dcg(\eta)Q^* < \epsilon + D$ and $P(t) \leq \eta$ for t large. Accordingly, $\dot{Z}(t) \leq Z(t)[bf(N^0) + dcg(\eta)Q^* - \epsilon - D] \leq 0$ for t large and $\lim_{t\to\infty} Z(t) = z^* \geq 0$ exists. A contradiction to $\lim_{t\to\infty} \dot{Z}(t) = 0$ would be obtained if $z^* > 0$. Thus $\lim_{t\to\infty} Z(t) = 0$ and the ω-limit set of solutions of (2.3) lies on the Q-axis. Therefore, E_0 is globally asymptotically stable for (2.3). The case when $Q(t) \geq Q^*$ for $t \geq 0$ can be treated similarly. This completes the proof. ∎

Note that if zooplankton is obligate, the condition $bf(N^0) < \epsilon + D$ derived in Theorem 2.4 is trivially true. Therefore, it is more likely for both populations to become extinct if zooplankton is obligate.

Lemma 2.5 *If $u(Q^*) > \delta + D$, then steady state $E_1 = (P_1, Q_1, 0)$ exists and any solution $(P(t), Q(t), Z(t))$ of (2.3) with $P(0) > 0$ and $Z(0) = 0$ converges to E_1.*

Proof. Since $Q^* > Q_1$, $\rho(N^0, Q_1) > u(Q_1)Q_1$ and thus E_1 exists. We apply the Dulac criterion on the P-Q subsystem by letting $B(P, Q) = \dfrac{1}{P}$ for $P > 0, Q \geq Q_0$. As $\dfrac{\partial(\dot{P}B)}{\partial P} + \dfrac{\partial(\dot{Q}B)}{\partial Q} = -\dfrac{\partial\rho}{\partial N} + \dfrac{1}{P}\dfrac{\partial\rho}{\partial Q} - \dfrac{u'(Q)Q}{P} - \dfrac{u(Q)}{P} < 0$ for $P > 0, Q \geq Q_0$, system (2.3) has no nontrivial periodic solution on the positive P-Q plane and the conclusion follows. ∎

The following theorem provides a sufficient condition for the extinction of zooplankton population, whose proof is similar to that of Theorem 2.4.

Theorem 2.6 *If $u(Q^*) > \delta + D$ and $bf(N^0) + dcg(N^0/Q_0)Q^* < \epsilon + D$, then $E_0 = (0, Q^*, 0)$ and $E_1 = (P_1, Q_1, 0)$ are the only steady states for (2.3) and solutions $(P(t), Q(t), Z(t))$ of (2.3) with $P(0) > 0$ converge to E_1.*

In particular, if zooplankton is obligate, then the second inequality given

in Theorem 2.6 is easier to satisfy as $b = 0$. Consequently, the zooplankton population would be more likely to become extinct. The following results only valid when zooplankton is facultative and are parallel to Lemma 2.5 and Theorem 2.6. Their proofs are omitted.

Lemma 2.7 *If $bf(N^0) > \epsilon + D$, then steady state $E_2 = (0, Q_2, Z_2)$ exists and solution $(P(t), Q(t), Z(t))$ of (2.3) with $P(0) = 0, Z(0) > 0$ converges to E_2.*

Theorem 2.8 *If $bf(N^0) > \epsilon + D$ and $u(Q^*) < \delta + D$, then $E_0 = (0, Q^*, 0)$ and $E_2 = (0, Q_2, Z_2)$ are the only steady states for system (2.3) and solutions $(P(t), Q(t), Z(t))$ of (2.3) with $Z(0) > 0$ converge to E_2.*

We now assume $u(Q^*) > \delta + D$ and $bf(N^0) > \epsilon + D$ so that steady states $E_1 = (P_1, Q_1, 0)$ and $E_2 = (0, Q_2, Z_2)$ both exist. The case when zooplankton is obligate to phytoplankton can be treated similarly. A direct computation shows that the Jacobian matrix at $E_0 = (0, Q^*, 0)$ is

$$
J(E_0) = \begin{pmatrix} u(Q^*) - \delta - D & 0 & 0 \\ -Q^* \frac{\partial \rho}{\partial N} & \frac{\partial \rho}{\partial Q} - u'(Q^*)Q^* - u(Q^*) & -\frac{\partial \rho}{\partial N} \\ 0 & 0 & bf(N^0) - \epsilon - D \end{pmatrix},
$$

where $\frac{\partial \rho}{\partial N}$ and $\frac{\partial \rho}{\partial Q}$ are evaluated at (N^0, Q^*), and the Jacobian matrix at $E_1 = (P_1, Q_1, 0)$ is given as

$$
J(E_1) = \begin{pmatrix} 0 & P_1 u'(Q_1) & -cg(P_1) \\ -Q_1 \frac{\partial \rho}{\partial N} & a_{22} & -\frac{\partial \rho}{\partial N} \\ 0 & 0 & a_{33} \end{pmatrix},
$$

where $a_{22} = -P_1 \frac{\partial \rho}{\partial N} + \frac{\partial \rho}{\partial Q} - u'(Q_1)Q_1 - u(Q_1)$, $a_{33} = bf(N^0 - P_1 Q_1) + dcg(P_1)Q_1 - \epsilon - D$ and the arguments for $\frac{\partial \rho}{\partial N}$ and $\frac{\partial \rho}{\partial Q}$ are $(N^0 - P_1 Q_1, Q_1)$. Similarly, the Jacobian matrix at $E_2 = (0, Q_2, Z_2)$ is

$$
J(E_2) = \begin{pmatrix} u(Q_2) - \delta - D - cg'(0)Z_2 & 0 & 0 \\ -Q_2 \frac{\partial \rho}{\partial N} & c_{22} & -\frac{\partial \rho}{\partial N} \\ c_{31} & 0 & -bf'(N^0 - Z_2)Z_2 \end{pmatrix},
$$

where $c_{31} = -bQ_2 f'(N^0 - Z_2)Z_2 + dcg'(0)Q_2 Z_2$, $c_{22} = \frac{\partial \rho}{\partial Q} - u'(Q_2)Q_2 - u(Q_2)$ and $\frac{\partial \rho}{\partial N}$ and $\frac{\partial \rho}{\partial Q}$ are evaluated at $(N^0 - Z_2, Q_2)$.

Suppose that the equations governing interacting populations are of the form $\dot{x}_i = f_i(t, x_1, \cdots, x_n), 1 \le i \le n$. Then the system is said to be *persistent* if $\liminf_{t \to \infty} x_i(t) > 0$ for any population with $x_i(0) > 0, 1 \le i \le n$. The system is said to be *uniformly persistent* if there exists a positive constant k_0 such that $\liminf_{t \to \infty} x_i(t) \ge k_0$ for $1 \le i \le n$ for every trajectory with positive initial condition. The explicit Jacobian matrices given above enable us to obtain the following sufficient condition for population coexistence.

Theorem 2.9 *Let $u(Q^*) > \delta + D$ and $bf(N^0) > \epsilon + D$. If*

$$bf(N^0 - P_1 Q_1) + dcg(P_1)Q_1 > \epsilon + D \qquad (2.4)$$

and

$$u(Q_2) - cg'(0)Z_2 > \delta + D \qquad (2.5)$$

hold, then system (2.3) is uniformly persistent and (2.3) has an interior equilibrium $E_3 = (\bar{P}, \bar{Q}, \bar{Z})$.

Proof. Since $u(Q^*) > \delta + D$ and $bf(N^0) > \epsilon + D$, steady states E_1 and E_2 both exist. Therefore, the left hand sides of (2.4) and (2.5) are well defined. From the Jacobian matrix at E_0, we see that E_0 is a saddle point with stable manifold lying in the Q-axis. It's easy to see that E_1 is also a saddle point which is globally asymptotically stable in the positive P-Q plane and is unstable in the positive direction orthogonal to the P-Q plane by the Jacobian matrix at E_1. Similary, E_2 is a saddle point which is globally asymptotically stable in the positive Q-Z plane and is unstable in the positive direction orthogonal to the Q-Z plane. Therefore, system (2.3) is persistent by [10]. As a result, since (2.3) is dissipative, (2.3) is uniformly persistent by [33]. Finally, we apply Corollary of [3] and conclude that (2.3) has an interior equilibrium $E_3 = (\bar{P}, \bar{Q}, \bar{Z})$ with $\bar{P}, \bar{Z} > 0$ and $\bar{Q} > Q_0$. ■

When zooplankton is obligate, by using the same argument as we did for the proof of Theorem 2.9, it can be shown that system (2.3) is uniformly persistent and also has an interior equilibrium if $u(Q^*) > \delta + D$ and (2.4) holds for $b = 0$. We now exploit the extinction, persistence and coexistence results on the limiting system to discuss the dynamics of the original system (2.1). Since E_0, E_1 and E_2 are hyperbolic for system (2.3) when they exist and (2.3) possesses no cycle of steady states, using system (2.2) and a result of Thieme [27, 32], the dynamics of (2.1) can be described below.

Theorem 2.10 *The dynamics of system (2.1) are summarized as the following.*

(1) If $u(Q^*) < \delta + D$ and $bf(N^0) < \epsilon + D$, then $E_0^* = (N^0, 0, Q^*, 0)$ is the only steady state for (2.1) and solutions of (2.1) converge to E_0^*.

(2) If $u(Q^*) > \delta + D$ and $bf(N^0) + dcg(N_0/Q_0)Q^* < \epsilon + D$, then E_0^* and $E_1^* = (N_1, P_1, Q_1, 0)$ are the only steady states for (2.1) and solutions of (2.1) with $P(0) > 0$ converge to E_1^*, where $N_1 = N^0 - P_1 Q_1$.

(3) If $u(Q^*) < \delta + D$ and $bf(N^0) > \epsilon + D$, then E_0^* and $E_2^* = (N_2, 0, Q_2, Z_2)$ are the only steady states for (2.1) and solutions of (2.1) with $Z(0) > 0$ converge to E_2^*, where $N_2 = N^0 - Z_2$.

(4) If $u(Q^*) > \delta + D$, $bf(N^0) > \epsilon + D$, and (2.4) and (2.5) are satisfied, then there exists $\hat{\delta} > 0$ such that $\liminf_{t\to\infty} P(t) \geq \hat{\delta}$ and $\liminf_{t\to\infty} Z(t) \geq \hat{\delta}$ for any solutions of (2.1) with $P(0), Z(0) > 0$. Moreover, (2.1) has an interior equilibrium $E_3^* = (\bar{N}, \bar{P}, \bar{Q}, \bar{Z})$, where $\bar{N} = N^0 - \bar{P}\bar{Q} - \bar{Z}$.

Recall that $\lim_{t\to\infty}(N(t) + P(t)Q(t) + Z(t)) = N^0$ for any solution of (2.1), and thus $\limsup_{t\to\infty} N(t) \leq N^0$. Consequently, N^0 can be viewed as the maximal long time sustainable nutrient concentration available to the populations. Since Q^* solves $\rho(N^0, Q) - u(Q)Q = 0$, Q^* is the maximal cell quota for phytoplankton and $u(Q^*)$ becomes the maximal growth rate of the algae. In addition to predation by zooplankton, phytoplankton population experiences losses due to its death and washout. Therefore, if the maximal growth rate $u(Q^*)$ is less than the sum of death and washout rates, i.e., $u(Q^*) < \delta + D$, then phytoplankton becomes extinct. Similarly, $bf(N^0)$ can be interpreted as the maximal growth rate of zooplankton from nutrient consumption. Therefore if $u(Q^*) < \delta + D$ and $bf(N^0) < \epsilon + D$, since phytoplankton cannot survive and the available nutrient also cannot sustain the zooplankton population, both populations inevitably become extinct.

On the other hand, as the maximal phytoplankton population for the model is N^0/Q_0, the maximal growth rate of zooplankton from consumption of algae is $dcg(N^0/Q_0)Q^*$. Hence $bf(N^0) + dcg(N^0/Q_0)Q^*$ is the maximal growth rate for zooplankton from consumption of both the nutrient and algae. It follows that the zooplankton population becomes extinct if this maximal growth rate is less than the total removal rate $\epsilon + D$. Consequently, phytoplankton population persists if the maximal growth rate $u(Q^*)$ of the population exceeds its total removal rate $\delta + D$. This persistent phenomenon is denoted by the convergence to a steady state as demonstrated in Theorem

2.10 (2). Similar biological interpretations can be made for Theorem 2.10 (3) if zooplankton is facultative.

Notice that when $u(Q^*) > \delta + D$ and $bf(N^0) > \epsilon + D$, each individual population can survive under the condition that there is no other species present, i.e., we have two steady states E_1 and E_2 such that each of E_1 and E_2 is globally asymptotically stable on the positive P-Q and positive Q-Z plane, respectively. This is possible because zooplankton also feeds on the nutrient. Theorem 2.10 (4) states that under this circumstance both populations can coexist if the maximal growth rate of each of the populations exceeds its total removal rate when the population is near the steady state for which the other population is absent.

We remark that when zooplankton is obligate, i.e., when $b = 0$, the condition $bf(N^0) > \epsilon + D$ derived in Theorem 2.10 (3) can never be satisfied. Therefore it is impossible for the zooplankton population to survive without the presence of the algal population. However, it is straightforward to show that both populations can coexist with each other if we set $b = 0$ in inequality (2.4) and ignore $bf(N^0) > \epsilon + D$ and inequality (2.5) in Theorem 2.10 (4). Consequently, these conditions become a set of sufficient conditions for coexistence when zooplankton is obligate to phyplankton. Similar biological interpretations can be made for Theorem 2.10 (1) and (2) when $b = 0$.

3   The model with periodic nutrient input

To simulate the seasonal or day/night variations of the nutrient in a natural environment, we assume that the input concentration of the limiting nutrient varies 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 $|e(t)| \leq 1$. We let $< h(t) >= \frac{1}{\tau} \int_0^\tau h(t)dt$ denote the mean value of a τ-periodic function h. Model (2.1) with fluctuating nutrient input takes the following form.

$$
\begin{aligned}
\dot{N} &= D(N^0 + ae(t) - N) - P\rho(N,Q) + \delta PQ - bf(N)Z + c(1-d)g(P)QZ + \epsilon Z, \\
\dot{P} &= P[u(Q) - \delta - D] - cg(P)Z, \\
\dot{Q} &= \rho(N,Q) - u(Q)Q, \\
\dot{Z} &= [bf(N) + dcg(P)Q - \epsilon - D]Z, \\
&\quad N(0) \geq 0, P(0) \geq 0, Q(0) \geq Q_0, Z(0) \geq 0.
\end{aligned}
\tag{3.1}
$$

We begin by considering the τ-periodic equation

$$\dot{N} = D(N^0 + ae(t) - N). \tag{3.2}$$

It is straightforward to show that (3.2) has a unique τ-periodic solution $N^*(t) = \dfrac{De^{-Dt}}{e^{D\tau} - 1} \displaystyle\int_t^{t+\tau} e^{Dr}(N^0 + ae(r))dr$ and every solution of (3.2) can be written as $N(t) = N^*(t) + (N(0) - N^*(0))e^{-Dt}$. Thus $\lim_{t\to\infty}(N(t) - N^*(t)) = 0$, where $N^0 - a \leq N^*(t) \leq N^0 + a$ for $t \geq 0$.

We now let $V = N^*(t) - N - PQ - Z$. Then $\dot{V} = -DV$ and system (3.1) can be rewritten as

$$
\begin{aligned}
\dot{V} &= -DV, \\
\dot{P} &= P[u(Q) - \delta - D] - cg(P)Z, \\
\dot{Q} &= \rho(N^*(t) - V - PQ - Z, Q) - u(Q)Q, \\
\dot{Z} &= [bf(N^*(t) - V - PQ - Z) + dcg(P)Q - \epsilon - D]Z.
\end{aligned} \tag{3.3}
$$

Observe that the ω-limit set of (3.3) lies to the set $V = 0$. Restricted to $V = 0$, we have the following limiting system for (3.1).

$$
\begin{aligned}
\dot{P} &= P[u(Q) - \delta - D] - cg(P)Z, \\
\dot{Q} &= \rho(N^*(t) - PQ - Z, Q) - u(Q)Q, \\
\dot{Z} &= [bf(N^*(t) - PQ - Z) + dcg(P)Q - \epsilon - D]Z, \\
&\quad P(0) \geq 0, Q(0) \geq Q_0, P(0)Q(0) + Z(0) \leq N^*(0).
\end{aligned} \tag{3.4}
$$

It follows that solutions of (3.4) satisfy $P(t) \geq 0, Q(t) \geq Q_0, Z(t) \geq 0$, $P(t)Q(t) + Z(t) \leq N^*(t) \leq N^0 + a$ for $t \geq 0$, and system (3.4) is dissipative.

A variable-yield single species chemostat model with periodic nutrient input was studied by Smith [28]. Let $\Gamma = \{(P, Q, Z) \in R_+^3 : Q \geq Q_0, PQ + Z \leq N^*(0)\}$. It is useful to consider the Poincaré map T induced by (3.4); that is, $T : \Gamma \to \Gamma$ by $T(P(0), Q(0), Z(0)) = (P(\tau), Q(\tau), Z(\tau))$, where $(P(t), Q(t), Z(t))$ is the solution of (3.4) with initial condition $(P(0), Q(0), Z(0))$. Since (3.4) is dissipative, T is also dissipative. Moreover, T has a global attractor, that is, T has a maximal compact invariant subset X of Γ such that $\lim_{n\to\infty} T^n x \in X$ for any $x \in \Gamma$.

To understand the dynamics of (3.4), it is natural to first discuss the trivial τ-periodic equation

$$
\begin{aligned}
\dot{Q} &= \rho(N^*(t), Q) - u(Q)Q, \\
&\quad Q(0) \geq Q_0.
\end{aligned} \tag{3.5}
$$

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It follows from Smith [28] that (3.5) has a unique τ-periodic solution $Q^*(t)$ which is moreover globally asymptotically attracting for (3.5). Consequently, (3.4) always has a trivial τ-periodic solution $(0, Q^*(t), 0)$. However, similar to the autonomous system presented in the previous section, $Q^*(t)$ is biological irrelevent as there is no phytoplankton present.

Lemma 3.1 *If $< u(Q^*(t)) >< \delta + D$, then $\lim_{t \to \infty} P(t) = 0$ for any solution of (3.4).*

Proof. Since $\dot{Q} \leq \rho(N^*(t), Q) - u(Q)Q$, it follows that $Q(t) \leq \hat{Q}(t)$ for $t \geq 0$, where $\hat{Q}(t)$ is the solution of (3.5) with $\hat{Q}(0) = Q(0)$. By using $\hat{Q}(t) - Q^*(t) \to 0$ as $t \to \infty$, the first equation in (3.4) yields

$$P(t+\tau) \leq P(t) e^{\tau/2} < u(Q^*(t)) - \delta - D >$$

for t large. Thus $\lim_{t \to \infty} P(t) = 0$. ∎

Note that as $P(t)Q(t) \leq N^*(t) \leq N^0 + a$ and $Q(t) \geq Q_0$, then $P(t) \leq \dfrac{N^0 + a}{Q_0}$ for all solutions of (3.4). The following lemma can be proved similarly as Lemma 3.1.

Lemma 3.2 *If $< bf(N^*(t)) + dcg(\frac{N^0+a}{Q_0})Q^*(t) >< \epsilon + D$, then $\lim_{t \to \infty} Z(t) = 0$ for any solution of (3.4).*

The following theorem provides a sufficient condition for the extinction of both populations on the ω-limit set of (3.1).

Theorem 3.3 *If $< u(Q^*(t)) >< \delta + D$ and $< bf(N^*(t)) >< \epsilon + D$, then $\lim_{t \to \infty} P(t) = \lim_{t \to \infty} Z(t) = 0$ and $\lim_{t \to \infty}(Q(t) - Q^*(t)) = 0$ for any solution of (3.4), i.e., $(0, Q^*(t), 0)$ is globally attracting for system (3.4).*

Proof. Since $< u(Q^*(t)) >< \delta + D$, then $\lim_{t \to \infty} P(t) = 0$ by Lemma 3.1. Thus for every $\xi > 0$, there exists $t_0 > 0$ such that $P(t) \leq \xi$ for $t \geq t_0$. We choose $\xi > 0$ such that $< bf(N^*(t)) + dcg(\xi)Q^*(t) >< \epsilon + D$. By a similar argument as in Lemma 3.2 we can show that $\lim_{t \to \infty} Z(t) = 0$.

We now use the Poincaré map T introduced earlier. Since $\lim_{t \to \infty} P(t) = \lim_{t \to \infty} Z(t) = 0$ and T has a global attractor X, X lies on the Q-axis. Restricted to the Q-axis, $T^n(0, Q(0), 0) = (0, T_1^n(Q(0)), 0)$, where T_1 is the Poincaré map generated by (3.5). Since T_1 has a unique fixed point $Q^*(0)$ which is moreover globally asymptotically stable for T_1, it follows that T has a unique fixed point $(0, Q^*(0), 0)$ which is globally asymptotically stable

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for T. This shows that the trivial τ-periodic solution $(0, Q^*(t), 0)$ is globally attracting for (3.4). ∎

Therefore both popultions are more likey to become extinct if zooplankton is obligate to phytoplankton. Motivated by the observation that there would be no zooplankton population at any future time if its initial population is zero, we discuss the P-Q subsystem of (3.4).

$$
\begin{aligned}
\dot{P} &= P[u(Q) - \delta - D], \\
\dot{Q} &= \rho(N^*(t) - PQ, Q) - u(Q)Q, \\
& Q(0) \geq Q_0, P(0) \geq 0, P(0)Q(0) \leq N^*(0).
\end{aligned}
\tag{3.6}
$$

By introducing a new state variable, (3.6) can be transformed into a competitive system. Exploiting the competitive properties, Smith [28] obtained the following result for system (3.6).

Lemma 3.4 *If $< u(Q^*(t)) >> \delta + D$, then system (3.6) has a unique τ-periodic solution $(\bar{P}(t), \bar{Q}(t))$ with $\bar{P}(t) > 0$ and $\bar{Q}(t) > Q_0$. Moreover, solution $(P(t), Q(t))$ of (3.6) with $P(0) > 0$ satisfies $(P(t), Q(t)) \to (\bar{P}(t), \bar{Q}(t))$ as $t \to \infty$.*

As a consequence of Lemma 3.4, system (3.4) has a unique τ-periodic solution of the form $(\bar{P}(t), \bar{Q}(t), 0)$ if $< u(Q^*(t)) >> \delta + D$, where $\bar{P}(t) > 0$ and $\bar{Q}(t) > Q_0$. The linearization of (3.4) corresponding to $(0, Q^*(t), 0)$ gives the linear periodic system $\dot{X} = A(t)X$, with $A(t)$ giving by

$$
\begin{pmatrix}
u(Q^*(t)) - \delta - D & 0 & 0 \\
-Q^*(t)\frac{\partial\rho}{\partial N} & \frac{\partial\rho}{\partial Q} - u'(Q^*(t))Q^*(t) - u(Q^*(t)) & -\frac{\partial\rho}{\partial N} \\
0 & 0 & bf(N^*(t)) - \epsilon - D
\end{pmatrix},
$$

where the arguments for $\frac{\partial\rho}{\partial N}$ and $\frac{\partial\rho}{\partial Q}$ are $(N^*(t), Q^*(t))$. From this we see that the Floquet multipliers for the trivial τ-periodic solution $(0, Q^*(t), 0)$ are $e^{\tau<u(Q^*(t))-\delta-D>}$, $e^{\tau<\frac{\partial\rho}{\partial Q}-u'(Q^*(t))Q^*(t)-u(Q^*(t))>} < 1$ and $e^{\tau<bf(N^*(t))-\epsilon-D>}$. Consequently, these multipliers can be used to show the following theorem whose proof is postponed in the Appendix.

Theorem 3.5 *If $< u(Q^*(t)) >> \delta + D$ and $< bf(N^*(t)) + dcg((N^0 + a)/Q_0)Q^*(t) >< \epsilon + D$, then solution $(P(t), Q(t), Z(t))$ of (3.4) with $P(0) > 0$ satisfies $(P(t), Q(t), Z(t)) \to (\bar{P}(t), \bar{Q}(t), 0)$ as $t \to \infty$.*

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If the zooplankton population is obligate, i.e., if $b = 0$, then the population cannot survive without the algae. However, when zooplankton is faculative, the population may persist by consuming nutrient alone. Therefore, since the positive Q-Z plane is invariant, we consider the Q-Z subsystem of (3.4).

$$
\begin{aligned}
\dot{Q} &= \rho(N^*(t) - Z, Q) - u(Q)Q, \\
\dot{Z} &= [bf(N^*(t) - Z) - \epsilon - D]Z, \\
& Q(0) \geq Q_0, 0 \leq Z(0) \leq N^*(0).
\end{aligned} \tag{3.7}
$$

We are able to show the existence of a unique τ-periodic solution in the interior of positive QZ-plane which is moreover globablly attracting for system (3.7). Its proof is presented in the Appendix.

Lemma 3.6 *If* $< bf(N^*(t)) >> \epsilon + D$, *then system (3.7) has a unique τ-periodic solution* $(\hat{Q}(t), \hat{Z}(t))$ *with* $\hat{Z}(t) > 0$ *and* $\hat{Q}(t) > Q_0$. *Moreover, solutions of (3.7) with* $Z(0) > 0$ *satisfy* $(Q(t), Z(t)) \to (\hat{Q}(t), \hat{Z}(t))$ *as* $t \to \infty$.

It follows from Lemma 3.6 that system (3.4) has a unique τ-periodic solution of the form $(0, \hat{Q}(t), \hat{Z}(t))$ if $< bf(N^*(t)) >> \epsilon + D$, where $\hat{Z}(t) > 0$ and $\hat{Q}(t) > Q_0$. The following theorem can be proved similarly as Theorem 3.5 and the proof is omitted.

Theorem 3.7 *If* $< u(Q^*(t)) >< \delta + D$ *and* $< bf(N^*(t)) >> \epsilon + D$, *then solution* $(P(t), Q(t), Z(t))$ *of (3.4) with* $Z(0) > 0$ *satisfies* $(P(t), Q(t), Z(t)) \to (0, \hat{Q}(t), \hat{Z}(t))$ *as* $t \to \infty$.

We now assume $< u(Q^*(t)) >> \delta + D$ and $< bf(N^*(t)) >> \epsilon + D$ so that both τ-periodic solutions $(\bar{P}(t), \bar{Q}(t), 0)$ and $(0, \hat{Q}(t), \hat{Z}(t))$ exist. When $b = 0$, there is no periodic solution of the form $(0, \hat{Q}(t), \hat{Z}(t))$. However, the same analysis given below can be used to treat the case.

The linearization of (3.4) with respect to $(\bar{P}(t), \bar{Q}(t), 0)$ produces the linear system $\dot{X} = B(t)X$, with $B(t)$ equal to

$$
\begin{pmatrix}
u(\bar{Q}(t)) - \delta - D & \bar{P}(t)u'(\bar{Q}(t)) & -cg(\bar{P}(t)) \\
-\bar{Q}(t)\frac{\partial \rho}{\partial N} & a_{22}(t) & -\frac{\partial \rho}{\partial N} \\
0 & 0 & a_{33}(t)
\end{pmatrix},
$$

where $a_{22}(t) = -\bar{P}(t)\frac{\partial \rho}{\partial N} + \frac{\partial \rho}{\partial Q} - u'(\bar{Q}(t))\bar{Q}(t) - u(\bar{Q}(t))$, $a_{33}(t) = bf(N^*(t) - \bar{P}(t)\bar{Q}(t)) + dcg(\bar{P}(t))\bar{Q}(t) - \epsilon - D$, and $\frac{\partial \rho}{\partial N}$ and $\frac{\partial \rho}{\partial Q}$ are evaluated at $(N^*(t) -$

$\bar{P}(t)\bar{Q}(t), \bar{Q}(t))$. It follows from Lemma 3.4 that the Floquet multipliers ρ_1, ρ_2 for $(\bar{P}(t), \bar{Q}(t))$ are less than 1 in modulus. We apply Lemma 6.4 of [27, chapter 3] and conclude that the Floquet multipliers for $(\bar{P}(t), \bar{Q}(t), 0)$ are ρ_1, ρ_2 and $e^{\tau < a_{33}(t) >}$.

Similarly, the linearization of (3.4) corresponding to $(0, \hat{Q}(t), \hat{Z}(t))$ gives the linear periodic system $\dot{X} = C(t)X$, where $C(t)$ is

$$\begin{pmatrix} u(\hat{Q}(t)) - \delta - D - cg'(0)\hat{Z}(t) & 0 & 0 \\ -\hat{Q}(t)\frac{\partial\rho}{\partial N} & \frac{\partial\rho}{\partial Q} - u'(\hat{Q}(t))\hat{Q}(t) - u(\hat{Q}(t)) & -\frac{\partial\rho}{\partial N} \\ b_{31}(t) & 0 & b_{33}(t) \end{pmatrix},$$

with $b_{31}(t) = -b\hat{Q}(t)f'(N^*(t) - \hat{Z}(t))\hat{Z}(t) + dcg'(0)\hat{Q}(t)\hat{Z}(t)$, $b_{33}(t) = bf(N^*(t) - \hat{Z}(t)) - \epsilon - D - bf'(N^*(t) - \hat{Z}(t))\hat{Z}(t)$ and the arguments for $\frac{\partial\rho}{\partial N}$ and $\frac{\partial\rho}{\partial Q}$ are $(N^*(t) - \hat{Z}(t), \hat{Q}(t))$. Analogous to Lemma 6.4 of [27, chapter 3], it can be shown that the Floquet multipliers of $(0, \hat{Q}(t), \hat{Z}(t))$ are s_1, s_2 and $e^{\tau < u(\hat{Q}(t)) - \delta - D - cg'(0)\hat{Z}(t) >}$, where s_1, s_2 are the Floquet multipliers of $(\hat{Q}(t), \hat{Z}(t))$ for the subsystem (3.7) with $|s_1|, |s_2| < 1$ by Lemma 3.6.

By using these linear periodic systems and the associated Floquet multipliers, we obtain a sufficient condition for the persistence of both populations on the ω-limit set of system (3.1). The proof is given in Appendix.

Theorem 3.8 *Let* $< u(Q^*(t)) >> \delta + D$ *and* $< bf(N^*(t)) >> \epsilon + D$. *If*

$$< bf(N^*(t) - \bar{P}(t)\bar{Q}(t)) + dcg(\bar{P}(t))\bar{Q}(t) >> \epsilon + D \qquad (3.8)$$

and

$$< u(\hat{Q}(t)) - cg'(0)\hat{Z}(t) >> \delta + D \qquad (3.9)$$

hold, then system (3.4) is uniformly persistent and (3.4) has a positive τ-periodic solution $(P^0(t), Q^0(t), Z^0(t))$, where $P^0(t), Z^0(t) > 0$ and $Q^0(t) > Q_0$.

When zooplankton is obligate to phytoplankton, by using similar arguments as in the proof of Theorem 3.8, it can be shown that system (3.4) is uniformly persistent and possesses a positive τ-periodic solution if $< u(Q^*(t)) >> \delta + D$ and (3.8) is satisfied for $b = 0$. Once the dynamics of (3.4) are well understood, we are ready to discuss the dynamics of the original system (3.1). One way to carry over the analysis to the full system is by considering the

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Poincaré map as we did for the proof of Theorem 3.5. For simplicity, we take a different approach here. We consider the equivalent system of (3.1), (3.2). Clearly, (3.2) is dissipative. We rewrite system (3.4) as $\dot{\mathbf{Y}} = F(\mathbf{Y}, t)$ and system (3.2) as $\dot{\mathbf{X}} = F(\mathbf{X}, t) + R(\mathbf{X}, t)$. Then it is straightforward to show that there exist $C > 0$ and $\xi > 0$ such that $|R(\mathbf{X}, t)| \leq Ce^{-\xi t}$ for $t \geq 0$ for every solution $\mathbf{X}(t)$. Consequently, Lemma A.4 of Hale and Somolinos [15] implies that the asymptotics of (3.2) and thus of (3.1) are the same as its limiting system (3.4). Therefore, the dynamics of system (3.1) can be stated below.

Theorem 3.9 *The dynamics of (3.1) are summarized as the following.*

(1) *If $< u(Q^*(t)) >< \delta + D$ and $< bf(N^*(t)) >< \epsilon + D$, then $\lim_{t \to \infty}(N(t) - N^*(t)) = \lim_{t \to \infty} P(t) = \lim_{t \to \infty} Z(t) = \lim_{t \to \infty}(Q(t) - Q^*(t)) = 0$ for any solution $(N(t), P(t), Q(t), Z(t))$ of (3.1), i.e., the τ-periodic solution $(N^*(t), 0, Q^*(t), 0)$ is globally attracting for (3.1).*

(2) *If $< u(Q^*(t)) >> \delta + D$ and $< bf(N^*(t)) + dcg((N^0 + a)/Q_0)Q^*(t) >< \epsilon + D$, then (3.1) has a τ-periodic solution $(\bar{N}(t), \bar{P}(t), \bar{Q}(t), 0)$ with $\bar{N}(t), \bar{P}(t) > 0, \bar{Q}(t) > Q_0$, and solutions $(N(t), P(t), Q(t), Z(t))$ of (3.1) with $P(0) > 0$ satisfy $(N(t), P(t), Q(t), Z(t)) \to (\bar{N}(t), \bar{P}(t), \bar{Q}(t), 0)$ as $t \to \infty$.*

(3) *If $< u(Q^*(t)) >< \delta + D$ and $< bf(N^*(t)) >> \epsilon + D$, then (3.1) has a τ-periodic solution $(\hat{N}(t), 0, \hat{Q}(t), \hat{Z}(t))$, where $\hat{N}(t), \hat{Z}(t) > 0$ and $\hat{Q}(t) > Q_0$ such that solutions $(N(t), P(t), Q(t), Z(t))$ of (3.1) with $Z(0) > 0$ satisfy $(N(t), P(t), Q(t), Z(t)) \to (\hat{N}(t), 0, \hat{Q}(t), \hat{Z}(t))$ as $t \to \infty$.*

(4) *If $< u(Q^*(t)) >> \delta + D$ and $< bf(N^*(t)) >> \epsilon + D$, and (3.8) and (3.9) are satisfied, then there exists $\kappa > 0$ such that $\liminf_{t \to \infty} P(t) \geq \kappa$ and $\liminf_{t \to \infty} Z(t) \geq \kappa$ for any solution of (3.1) with $P(0) > 0, Z(0) > 0$. Moreover, system (3.1) has a positive τ-periodic solution $(N^0(t), P^0(t), Q^0(t), Z^0(t))$, where $N^0(t), P^0(t), Z^0(t) > 0$ and $Q^0(t) > Q_0$.*

If we let $T(t)$ denote the total nutrient concentration at time t, i.e., $T(t) = N(t) + P(t)Q(t) + Z(t)$, then $\dot{T} = D(N^0 + ae(t) - T)$ and thus $\lim_{t \to \infty}(T(t) - N^*(t)) = 0$. Therefore, the possible maximal nutrient concentration available to the populations at any given time t is $N^*(t)$. Since

$Q^*(t) > Q_0$ is the unique τ-periodic solution of (3.5) to which each solution attracts, $< u(Q^*(t)) >$ can be viewed as the maximal average growth rate for the phytoplankton population. Thus, the phytoplankton population goes extinct if this maximal average growth rate is less than the total removal rate $\delta + D$ for the population. Consequently, $< bf(N^*(t)) >$ is the maximal average growth rate of zooplankton and both populations become extinct if this maximal average growth rate is less than its total removal rate $\epsilon + D$. In particular, the condition $< bf(N^*(t)) > < \epsilon + D$ is trivially true if zooplankton is obligate.

Since $N^*(t) \leq N^0 + a$ for all t, $(N^0 + a)/Q_0$ is the maximal possible phytoplankton population in the model. Accordingly, $< dcg((N^0 + a)/Q_0)Q^*(t) >$ is the maximal average growth rate of zooplankton from ingestion of the algal population. As a result, the second inequality given in Theorem 3.9 (2) becomes the maximal average growth rate of zooplankton by consumpton of both nutrient and algae. If this growth rate is less than the total removal rate $\epsilon + D$, then zooplankton population becomes extinct. Therefore under this circumstance, the phytoplankton population can persist in a periodic fashion if its maximal average growth rate $< u(Q^*(t)) >$ from consumption of nutrient exceeds its total removal rate $\delta + D$. Similar biological interpretaions can be made for Theorem 3.9 (3) if the zooplankton population is assumed to be facultative.

Parallel to Theorem 2.10 (4), Theorem 3.9 (4) provides a criterion for coexistence of both populations. Conditions (3.8) and (3.9) given in the theorem require that the maximal average growth rate of each of the populations exceeds its total removal rate near the periodic solution for which the other species is absent. When zooplankton is obligate, i.e., when $b = 0$, it is also straightforward to show that both populations can coexist with each other by applying the same idea as in the proof of Theorem 3.8 and the remark stated before Theorem 3.9. However, the second inequality and (3.9) presented in Theroem 3.9 (4) are omitted and b is zero in (3.8) as in this situation zooplankton can never survive without the phytoplankton.

4 Numerical simulations

In this section we use numerical examples to illustrate our analytical results derived in the previous sections. In particular, we restrict to the case when zooplankton population is obligate to phytoplankton. Consequently, we as-

sume $b = 0$ in this section.

We adopt growth rate u and uptake rate ρ taken from Grover [13, 14]

$$u(Q) \;=\; u_{max}\frac{(Q - Q_{min})_+}{k + (Q - Q_{min})_+}, \tag{4.1}$$

$$\rho(N, Q) \;=\; \rho_{max}(Q)\frac{N}{N + 4}, \tag{4.2}$$

where $\rho_{max}(Q) = \rho_{max}^{high} - (\rho_{max}^{high} - \rho_{max}^{low})\frac{(Q - Q_{min})_+}{Q_{max} - Q_{min}}$ and $(Q - Q_{min})_+$ denotes the positive part of $Q - Q_{min}$. Specific parameter values are $\rho_{max}^{high} = 15, \rho_{max}^{low} = 0.9, Q_{min} = 3, Q_{max} = 30, u_{max} = 2.16$ and $k = 2$. The zooplankton's grazing rate is modeled by the function $g(P) = 1 - e^{-0.5P}$.

Limiting system (2.3) with above functional forms becomes

$$
\begin{aligned}
\dot{P} &= P[2.16\frac{(Q - 3)_+}{2 + (Q - 3)_+} - \delta - D] - c(1 - e^{-0.5P})Z, \\
\dot{Q} &= [15 - 0.522(Q - 3)_+]\frac{N^0 - PQ - Z}{N^0 - PQ - Z + 4} - 2.16\frac{(Q - 3)_+Q}{2 + (Q - 3)_+}, \tag{4.3} \\
\dot{Z} &= [dc(1 - e^{-0.5P})Q - \epsilon - D]Z, \\
&\quad P(0) \geq 0, Q(0) \geq 3, Z(0) \geq 0, P(0)Q(0) + Z(0) \leq N^0.
\end{aligned}
$$

When $N^0 = 3.75, D = 0.4, \delta = 0.7, c = 2, \epsilon = 0.1$ and $d = 0.7$, conditions given in Theorem 2.10 (4) are satisfied. As a result, the full system is uniformly persistent. Simulated numerically, system (4.3) has two steady states on the PQ coordinate plane: $E_0 = (0, 5.510033752, 0)$, $E_1 = (0.2108343004, 5.075471698, 0)$, and a unique positive steady state $E_3 = (0.1420430870, 5.209340229, 0.03492216781)$. We plot solution $(N(t), P(t), Z(t))$ for the full system with initial condition $P(0) = 0.5$, $Q(0) = 3$ and $Z(0) = 1$ in Figure 1. The solution stabilizes to the positive steady state very rapidly. Similar qualitative behavior for $(N(t), P(t), Z(t))$ is obtained with different initial conditions. Therefore, numerical simulations suggest that E_3 is globally asymptotically stable for the parameters given.

For periodic nutrient input model, we use $N^0 = 3.75$ as given above and let $a = 3$. We choose the periodic function $e(t) = \sin(\pi/10t)$. Therefore, the period is 20 for our example. We can calculate $N^*(t)$ explicitly as given in

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Section 3. The limiting system (3.4) now takes the following form.

$$
\begin{aligned}
\dot{P} &= P[2.16\frac{(Q-3)_+}{2+(Q-3)_+} - \delta - D] - c(1 - e^{-0.5P})Z, \\
\dot{Q} &= [15 - 0.522(Q-3)_+]\frac{N^*(t) - PQ - Z}{N^*(t) - PQ - Z + 4} - 2.16\frac{(Q-3)_+Q}{2+(Q-3)_+}, \quad (4.4) \\
\dot{Z} &= [dc(1 - e^{-0.5P})Q - \epsilon - D]Z, \\
&\quad P(0) \geq 0, Q(0) \geq 3, Z(0) \geq 0, P(0)Q(0) + Z(0) \leq 3.75.
\end{aligned}
$$

We use the same parameter values as in the constant nutrient input model with the exception that $\delta = 0.65$. With these parameters, conditions given in Theorem 3.9 (4) are satisfied. Therefore, the corresponding full system is uniformly persistent and has a positive periodic solution. Figure 2 plots a positive periodic solution. Numerical simulations with different initial conditions suggest that the positive periodic solution is globally attracting. Figure 3 plots trajectories $(N(t), P(t), Z(t))$ with initial condition $P(0) = 0.5, Q(0) = 3$ and $Z(0) = 1$.
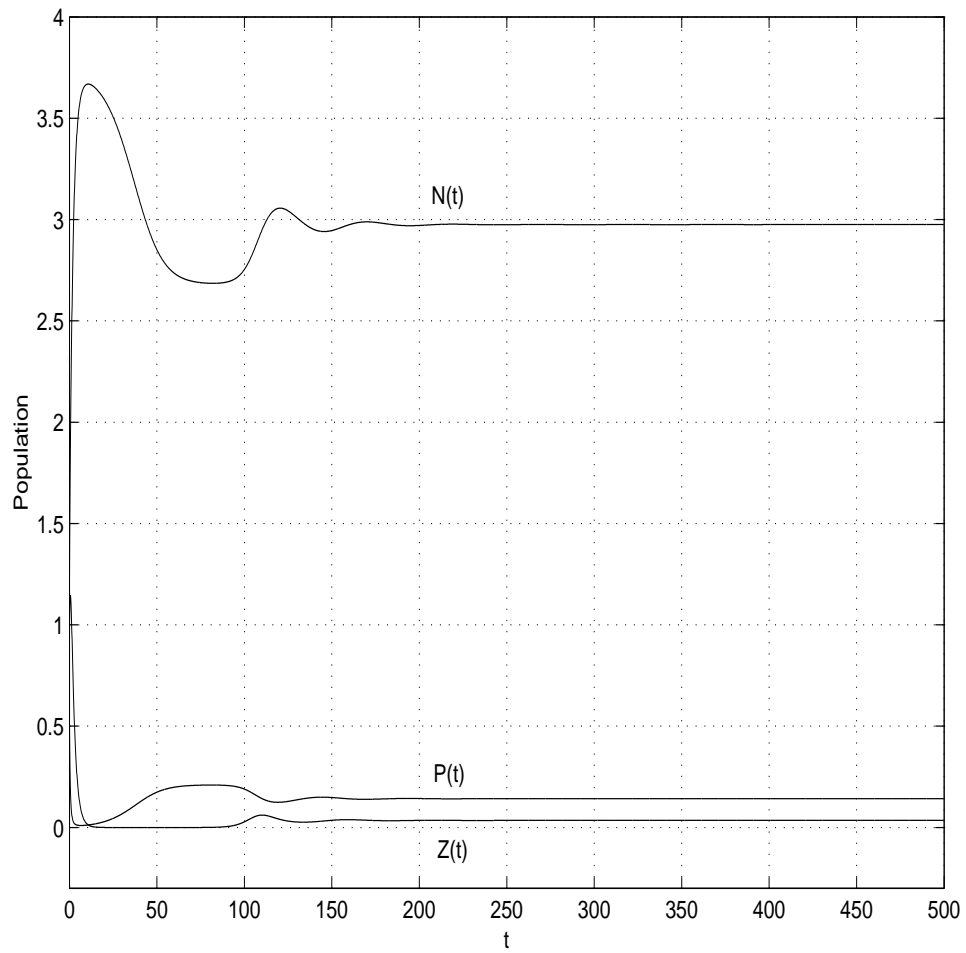
Figure 1: Solution $(N(t), P(t), Z(t))$ is plotted. The solution quickly stabilizes in a positive steady state fasion.
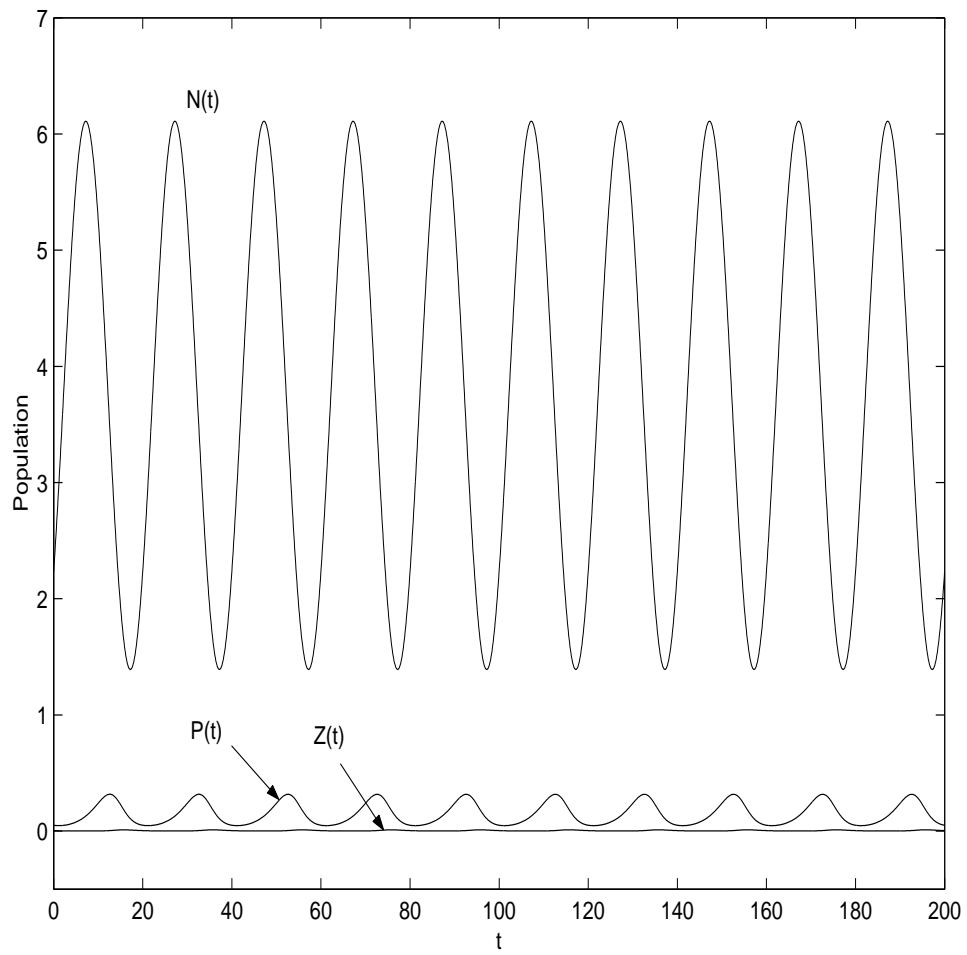
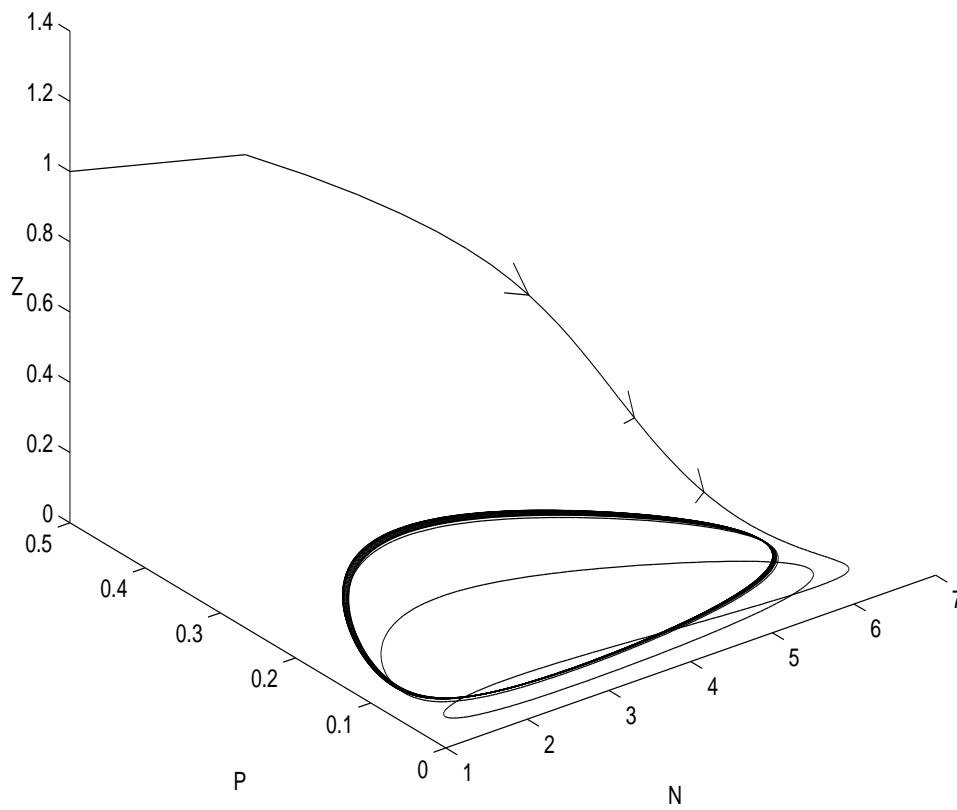Figure 2: A positive periodic solution $(N(t), P(t), Z(t))$ is plotted with time as the horizontal axis.

Figure 3: A 3-dimensional plot for the solution $(N(t), P(t), Z(t))$ with initial condition $(1.25, 0.5, 1)$.

5 Discussion

Nutrient-phytoplankton-zooplankton models with many different biological assumptions and complexity have been studied by numerious researchers. The purpose of theoretical studies of such a model aims either to capture the essence of some general feature of the system or to encompass the whole system.

In the open ocean, plankton communities inhabit an environment which is constantly changing, both as a result of predictible seasonal variations and unpredictiable influences. In this manuscript we ignore the spatial distribution of both plankton populations and the nutrient concentration and propose simple nutrient-phytoplankton-zooplankton models with general uptake functions to study nutrient-plankton interaction in open ecological systems. The two plankton levels are modeled in terms of their nutrient content. We assume that there is no nutrient loss due to physiological death or nutrient conversion. For natural systems, however, there are always losses because of other biological reasons. We use a constant washout rate to model the loss of nutrient and both plankton populations amounting from various biological processes other than physiological death and nutrient conversion. In section 2 we studied the system with a constant limiting nutrient input. We also investigated a model with a periodic nutrient input in section 3 to account for seasonal or day/night variations. The zooplankton population in both of these environments may be obligate or facultative.

The nutrient-plankton models discussed here separate the nutrient concentration in the internal nutrient pool from the external nutrient concentration and only the internal nutrient concentration is capable of catalyzing cell growth for phytoplankton. Explicitly we adopt the Droop model mechanism for phytoplankton. Threshold conditions are then derived for population extinction, persistence, and coexistence.

The dynamics of the constant limiting nutrient input model (2.1) were shown to depend on the maximal growth rates of the populations. If the total removal rate of phytoplankton exceeds its maximal growth rate, then phytoplankton becomes extinct, and as a result $bf(N^0)$ becomes the maximal growth rate of the zooplankton. Therefore, both populations go extinct if the maximal growth rate of zooplankton is also less than its total removal rate. This conclusion is independent of whether zooplankton is obligate or facultative. When phytoplankton's maximal growth rate exceeds its total removal rate, then phytoplankton can survive and thus $bf(N^0) + dcg(N_0/Q_0)Q^*$ be-

comes the maximal growth rate of the zooplankton. Zooplankton becomes extinct if its total removal rate exceeds this maximal growth rate, and as a result only phytoplankton persists. When the maximal growth rate of phytoplankton exceeds its total removal rate and zooplankton is obligate, then both populations can coexist with each other if in addition the maximal growth rate of zooplankton is greather than its removal rate when the population is near the steady state for which phytoplankton popoulation is present. Similar biological interpretations can be drawn when zooplankton is facultative.

The dynamics of the nutrient-plankton model (3.1) with a periodic nutrient input were also shown to depend on the maximal average growth rates of the populations. We can make the same biological conclusions as we did for the constant nutrient input model (2.1). However, due to the periodicity of the environment, the expression of survivability of each of the individual populations is captured by asymptotically attracting to periodic functions instead of converging to steady states.

A   Appendix

Proof of Theorem 3.5 We consider the Poincaré map $T : \Gamma \to \Gamma$ defined earlier. Since $\lim_{t\to\infty} Z(t) = 0$ by Lemma 3.2 and T has a global attractor X, X lies on the P-Q plane. Restricted to the P-Q coordinate plane, $T^n(P(0), Q(0), 0) = (S^n(P(0), Q(0)), 0)$, where S is the Poincaré map induced by system (3.6). Consequently, T has two fixed points $(0, Q^*(0), 0)$ and $(\bar{P}(0), \bar{Q}(0), 0)$. It remains to be shown that $\lim_{n\to\infty} T^n(P(0), Q(0), Z(0)) = (\bar{P}(0), \bar{Q}(0), 0)$ if $P(0) > 0$. Our analysis given here is similar to that used in [28]. Let $A = \{(P, Q, Z) \in \Gamma : P = 0\}$. Then A is a closed subset of Γ. Our assumption implies that the maximal compact invariant subset of A is $M = \{(0, Q^*(0), 0)\}$ which is moreover isolated in the P-Q plane. The Jacobian derivative J of T at $(0, Q^*(0), 0)$ is given by $\Phi(\tau)$, where $\Phi(t)$ is the fundamental matrix solution of $\dot{X} = A(t)X$. It follows that the stable set $W^s(M)$ of M, $\{x \in \Gamma : \lim_{t\to\infty} T^n x \in M\}$, lies on A. Therefore, T is uniformly persistent with respect to A by Theorem 4.1 of Hofbauer and So [16], i.e., there exists $\eta > 0$ such that $\liminf_{n\to\infty} d(T^n(P(0), Q(0), Z(0)), A) > \eta$ for any $(P(0), Q(0), Z(0)) \in \Gamma$ with $P(0) > 0$. Accordingly, any subsequential limit of T has the form $(P, Q, 0)$ with $P > \eta$. Consequently, $T^n(P(0), Q(0), Z(0)) \to (\bar{P}(0), \bar{Q}(0), 0)$ as $n \to \infty$ if $P(0) > 0$ and the proof

is now complete. ∎

Proof of Lemma 3.6 Note that $\dot{Z}$ can be decoupled from $\dot{Q}$ in (3.7) as given below:

$$\dot{Z} = [bf(N^*(t) - Z) - \epsilon - D]Z, \qquad (A.1)$$
$$0 \leq Z(0) \leq N^*(0).$$

Consider the Poincaré map $R : [0, N^*(0)] \to [0, N^*(0)]$ by $Rz_0 = Z(\tau, z_0)$, where $Z(t, z_0)$ is the solution of (A.1) with $Z(0, z_0) = z_0$. Clearly $R0 = 0$ and $\dot{R}z_0 = \dfrac{\partial Z(\tau, z_0)}{\partial z_0} = v(\tau)$, where $v(t)$ satisfies

$$\dot{v} = [bf(N^*(t) - Z) - \epsilon - D - bf'(N^*(t) - Z)Z]v$$
$$v(0) = 1.$$

Since

$$v(t) = e^{\int_0^t [bf(N^*(s) - Z(s, z_0)) - \epsilon - D - bf'(N^*(s) - Z(s, z_0))Z(s, z_0)]ds},$$

we have $\dot{R}z_0 = v(\tau) > 0$ for $0 \leq z_0 \leq N^*(0)$. Hence R is strictly increasing on $[0, N^*(0)]$. In particular, $\dot{R}0 > 1$ by our hypothesis. Since $RN^*(0) < N^*(0)$, R has at least one positive fixed point $\hat{Z}(0)$, where $\hat{Z}(0) < N^*(0)$. Observe from (A.1) that a periodic solution $Z(t)$ satisfies $< bf(N^*(t) - Z(t)) > = \epsilon + D$. Thus if (A.1) has two positive τ-periodic solutions $\bar{Z}(t)$ and $\hat{Z}(t)$, then there exists $t_0 \in (0, \tau)$ such that $\bar{Z}(t_0) = \hat{Z}(t_0)$ and consequently $\bar{Z}(t) = \hat{Z}(t)$ for all t. We conclude that the positive fixed point $\hat{Z}(0)$ of R is unique. It is then straightforward to show that $\lim_{n \to \infty} R^n z_0 = \hat{Z}(0)$ if $z_0 \in (0, N^*(0)]$. Indeed, $Rz_0 > z_0$ if $z_0 \in (0, \hat{Z}(0))$ and thus $\{R^n z_0\}_{n=0}^{\infty}$ is an increasing sequence which is moreover bounded above by $\hat{Z}(0)$. Therefore, $R^n z_0$ must converge to a positive fixed point of R. Since the positive fixed point is unique, this shows that $\lim_{n \to \infty} R^n z_0 = \hat{Z}(0)$. The argument for $z_0 \in (\hat{Z}(0), N^*(0)]$ is similar. We conclude that (A.1) has a unique τ-periodic solution $\hat{Z}(t)$ with $0 < \hat{Z}(t) < N^*(t)$ which is globally attracting for (A.1) in $(0, N^*(0)]$.

We now discuss system (3.7). If (3.7) has two τ-periodic solutions $(Q_i(t), Z_i(t))$ with $Z_i(t) > 0$ and $Q_i(t) > Q_0$, $i = 1, 2$, then since $Z_i(t)$ is a τ-periodic solution of (A.1) it follows that $Z_1(t) = Z_2(t)$ for all t. It follows from the first equation of (3.7) that there exists $t_0 \in (0, \tau)$ such that

$$\frac{\rho(N^*(t_0) - Z_1(t_0), Q_1(t_0))}{Q_1(t_0)} - u(Q_1(t_0)) = \frac{\rho(N^*(t_0) - Z_2(t_0), Q_2(t_0))}{Q_2(t_0)} - u(Q_2(t_0)).$$

If $Q_1(t_0) < Q_2(t_0)$, then the left hand side of the above equality is greater than the right hand side of the equality and vice versa if $Q_1(t_0) > Q_2(t_0)$. Therefore we conclude that $Q_1(t_0) = Q_2(t_0)$ and (3.7) has at most one positive τ-periodic solution. We next show the existence of such a periodic solution. We consider the τ-periodic equation

$$
\begin{aligned}
\dot{Q} &= \rho(N^*(t) - \hat{Z}(t), Q) - u(Q)Q, \\
& Q(0) \geq Q_0,
\end{aligned}
\tag{A.2}
$$

where $N^*(t) - \hat{Z}(t) > 0$ and is τ-periodic. We define the Poincaré map $F : [Q_0, \infty) \to [Q_0, \infty)$ by $F(q_0) = Q(\tau, q_0)$, where $Q(t, q_0)$ is the solution of (A.2) with $Q(0, q_0) = q_0$. By a similar argument as for R, we can show that F is strictly increasing, $F(Q_0) > Q_0$, and $F(Q) < Q$ for all Q large. Therefore, it can be shown that (A.2) has a unique τ-periodic solution $\hat{Q}(t)$, $Q_0 < \hat{Q}(t)$, and as a result (3.7) has a unique τ-periodic solution $(\hat{Q}(t), \hat{Z}(t))$ with $\hat{Z}(t) > 0$ and $\hat{Q}(t) > Q_0$. Consequently, (3.7) has two τ-periodic solutions $(Q^*(t), 0)$ and $(\hat{Q}(t), \hat{Z}(t))$. Since (3.7) is competitive, every solution of (3.7) is asymptotic to a τ-periodic solution [27]. Therefore the result follows as every solution $Z(t)$ of (A.1) with $Z(0) > 0$ attracts to $\hat{Z}(t)$. $\blacksquare$

Proof of Theorem 3.8 Since $< u(Q^*(t)) >> \delta + D$ and $< bf(N^*(t)) >> \epsilon + D$, the τ-periodic solutions $(\bar{P}(t), \bar{Q}(t), 0)$ and $(0, \hat{Q}(t), \hat{Z}(t))$ both exist. Therefore the left hand sides of (3.8) and (3.9) are well defined. We apply Theorem 3.1 of Butler and Waltman [2] to show uniform persistence of (3.4). Let $\mathcal{F}$ be the continuous flow generated by (3.4) and $\partial\mathcal{F}$ be $\mathcal{F}$ restricted to the boundary $\partial\Gamma$. We first claim that $\partial\mathcal{F}$ is isolated and acyclic. Let $M_0 = \{(0, Q^*(t), 0)|0 \leq t \leq \tau\}$, $M_1 = \{(\bar{P}(t), \bar{Q}(t), 0)|0 \leq t \leq \tau\}$, $M_2 = \{(0, \hat{Q}(t), \hat{Z}(t))|0 \leq t \leq \tau\}$, and let $\Lambda^+(x)$ denote the ω-limit set of x. Then the invariant set of $\partial\mathcal{F}$, $\Omega(\partial\mathcal{F}) = \cup_{x \in \partial\Gamma}\Lambda^+(x)$, is $\{M_0, M_1, M_2\}$. Clearly $\partial\mathcal{F}$ is acyclic as M_0, M_1 and M_2 are globally attracting on the positive Q-axis, the positive P-Q plane and the positive Q-Z plane respectively so that no subset of $\{M_0, M_1, M_2\}$ forms a cycle. It remains to be shown that each M_i is isolated for $\partial\mathcal{F}$ and for $\mathcal{F}$, respectively, for $i = 0, 1, 2$. We only claim that M_0 is isolated for $\mathcal{F}$ as the remaining assertion can be shown similarly.

Let $\hat{c} = \max_{P \in [0, (N^0+a)/Q_0]}g'(P)$. Since $< u(Q^*(t)) >> \delta + D$, we choose $\rho > 0$ such that

$$
1/\tau \int_0^\tau [u(Q^*(t) - \rho) - (\delta + D + c\hat{c}\rho)]dt > 0.
$$

Let $\mathcal{N} = \{(P, Q, Z) \in \Gamma : d((P, Q, Z), M_0) < \rho\}$, where d is the usual Euclidean metric on R^3. We show that $\mathcal{N}$ is an isolating neighborhood of M_0 in Γ, i.e., M_0 is the maximal invariant set in $\mathcal{N}$. If not, then there exists an invariant set V in Γ such that $M_0 \subset V \subset \mathcal{N}$ and $V \setminus M_0 \neq \emptyset$. Since M_1 and M_2 are globally attracting in the positive P-Q and Q-Z planes respectively, we can find $x(0) = (P(0), Q(0), Z(0)) \in V \setminus M_0$ such that $P(0), Z(0) > 0$. Then $x(t) \in V$ for all t. But $V \subset \mathcal{N}$ implies

$$
\begin{aligned}
\frac{\dot{P}}{P} &= u(Q) - \delta - D - \frac{cg(P)}{P}Z \\
&\geq u(Q^*(t) - \rho) - \delta - D - c\hat{c}\rho
\end{aligned}
$$

and thus

$$
P(t) \geq P(0)e^{\int_0^t [u(Q^*(s) - \rho) - \delta - D - c\hat{c}\rho]ds}.
$$

As a consequence, $P(t) \to \infty$ as $t \to \infty$. We obtain a contradiction and conclude that M_0 is isolated for $\mathcal{F}$. Therefore, $\partial\mathcal{F}$ is isolated. Let $\overset{\circ}{\Gamma}$ denote the interior of Γ. It follows from (3.8), (3.9) and the Floquet multipliers of the τ-periodic solutions $(0, Q^*(t), 0), (\bar{P}(t), \bar{Q}(t), 0)$ and $(0, \hat{Q}(t), \hat{Z}(t))$ that $W^+(M_i) \cap \overset{\circ}{\Gamma} = \emptyset$ for $i = 0, 1, 2$, where $W^+(M_i)$ denotes the stable set of M_i. We apply Theorem 3.1 of [2] and conclude that (3.4) is uniformly persistent. Since (3.4) is also dissipative, Theorem 4.11 of Yang and Freedman [36] implies that (3.4) has a τ-periodic solution in $\overset{\circ}{\Gamma}$. Accordingly, (3.4) has a positive τ-periodic solution. ∎

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