Droop models of nutrient-plankton interaction with intratrophic predation

S. R.-J. Jang[1], J. Baglama[2]

1. Department of Mathematics, University of Louisiana at Lafayette, Lafayette, LA 70504-1010
2. Department of Mathematics, University of Rhode Island, Kingston, RI 02881-0816

Abstract. Droop models of nutrient-phytoplankton-zooplankton interaction with intratrophic predation of zooplankton are introduced and investigated. The models proposed in this study are open ecosystems which include both a constant and a periodic input nutrient models. A simple stochastic model mimics a randomly varying nutrient input is also presented. For the deterministic models it is shown analytically that intratrophic predation has no effect on the global asymptotic dynamics of the systems if either one of the populations has a negative growth rate. Numerical simulations are also used to investigate the effects of intratrophic predation. Unlike the deterministic models for which both populations can coexist with each other if populations' net growth rates are positive, plankton populations can become extinct if the input nutrient concentration is modeled randomly.

Key words: cell quota – intratrophic predation – uniform persistence – Poincaŕe maps – Wiener process

1 Introduction

Classical deterministic prey-predator models have been exploited to study and interpret nutrient-plankton interactions very successfully. Intratrophic predation on the other hand has received only limited attention. Its discussion was initiated by Polis [17], who showed that cannibalism is an important and frequently occurred mechanism in population dynamics. In addition to cannibalism, intratrophic predation may include broader biological phenomena. For example, instead of modeling each species under study explicitly to

produce a large system, one may build models for which a population consisting of several species of organisms and one or more species may prey on others. This is particularly true for nutrient-plankton interactions as there are many species of zooplankton and some of the larger species of zooplankton do prey on the smaller species.

Kohmeier and Ebenhoh [13] were among the first to propose a mathematical model to study intratrophic predation between predator and prey interaction. The model was extended and analyzed by Pitchford and Brindley [16]. Motivated by the consideration of zooplankton, Jang and Baglama [10] proposed a nutrient-phytoplankton-zooplankton model with a constant nutrient input to investigate intratrophic predation. The model was generalized to a periodic nutrient input system by Jang et al. [12]. The biological conclusions obtained in [10] indicate that intratrophic predation can increase phytoplankton population level and decrease zooplankton population level for the coexisting steady state and it can also stabilize the system. For the periodic input nutrient model [12], it was found that intratrophic predation has no impact on the asymptotic dynamics of the system if the maximal average growth rates of both plankton populations are less than one. Moreover, numerical simulations performed in [12] suggest that the mechanism can eliminate the chaotic behavior of the system.

The above mentioned models assume that growth rate of phytoplankton is constantly proportional to its nutrient uptake rate. Consequently, the growth rate is directly related to the ambient nutrient available to the population. It is known that phytoplankton can uptake nutrient in excess of its immediate needs. Experiments performed by Ketchum [24] have demonstrated that algae can continue to grow and divide for quite some time even when the ambient nutrient is depleted. Several models have been formulated to incorporate this observation. Our main objective in this manuscript is to study intratrophic predation by taking this phenomena into consideration. Specially, we will use the Droop model [3] developed by Droop to study nutrient-plankton interaction with intratrophic predation.

Following that of [10, 11, 13, 16] we assume that the food resource available to the zooplankton is a weighted sum of phytoplankton and zooplankton. In addition, it is assumed that the nutrient concentration is separated into internal and external nutrient concentration and only the internal nutrient concentration is capable of catalyzing cell growth for phytoplankton. That is, we adopt the Droop model mechanism for phytoplankton growth [3, 4]. Such a model is also refereed to as a variable-yield model.

When the input nutrient concentration is a constant, the dynamics of the system depend on the maximal growth rates of the plankton populations relative to the total removal rates. Intratrophic predation has no effect on the dynamics of the model if phytoplankton's net growth rate, i.e., the maximal growth rate minus the total removal rate, is negative. The same is true for the periodic nutrient input model. When the net growth rates of both populations are positive, numerical techniques are then employed to further our investigation. The simulations suggest that intratrophic predation can eliminate the chaotic behavior of the system when the input nutrient is modeled periodically. Unlike the deterministic models for which both populations can persist when the maximum growth rates of both populations are positive, numerical simulations with the functional forms and parameter values chosen suggest that it is possible for both populations to become extinct when a white noise is added to the system.

In the next section, model derivation and analysis for the constant nutrient input are presented. Section 3 studies a periodic system with a fluctuating nutrient input. Numerical simulations are given in section 4. The last section provides a brief summary.

2 A model with constant nutrient input

As usual we let $N(t)$, $P(t)$ and $Z(t)$ denote the nutrient concentration, the concentrations (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. As a result there is a new state variable, $Q(t)$, the cell quota, which is the average amount of stored nutrient per algal cell at time t. Notice that $Q(t)$ is dimensionless. In this type of models, the growth rate of the phytoplankton depends on the cell quota, while the uptake rate depends on the ambient nutrient, and possibly also on the cell quota. We let $u(Q)$ and $\rho(N, Q)$ be the per-capita growth rate and per-capita uptake rate of phytoplankton, respectively. Motivated by the explicit examples of functions u and ρ in the literature [3, 4, 6, 7, 14], we make the following assumptions as in [8, 11, 15, 18, 19, 20].

(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 for any cell division. Parameters $\delta > 0$ and $\epsilon > 0$ are the death rates of phytoplankton and zooplankton respectively. The zooplankton's grazing rate is modeled by a simple linear functional response. Such a simple linear functional response was also used in the study of a closed Droop nutrient-plankton model when the nutrient is inhibiting [9].

Similar to [10, 12, 13, 16], we assume the food resource that is available to the zooplankton is $P + bZ$, where $0 \leq b \leq 1$ is the intensity of intratrophic predation. If $b = 0$, then phytoplankton is the only food resource for zooplankton. If $b = 1$, then zooplankton consumes both phytoplankton and its own population indiscriminatly. Since we model nutrient-plankton interaction in an open ecological system, it is assumed in this section that there is a constant input nutrient concentration N^0 continuously pouring into the system with a constant input rate D. Both populations and the nutrient concentration are also flowing out of the system continuously. For simplicity, it is assumed that the washout rate is a constant and equals to D. Since the two plankton populations are modeled in terms of their nutrient content and there is no nutrient loss due to death or due to nutrient conversion, the model takes the following form

$$\begin{aligned}
\dot{N} &= D(N^0 - N) - P\rho(N,Q) + \delta PQ + \epsilon Z + m(1-\alpha)PQZ + (1-\alpha)bZ^2 \\
\dot{P} &= P[u(Q) - \delta - D - mZ] \\
\dot{Q} &= \rho(N,Q) - u(Q)Q \\
\dot{Z} &= [\alpha(mPQ + bZ) - bZ - \epsilon - D]Z \\
& \quad P(0) \geq 0, Q(0) \geq Q_0, Z(0) \geq 0, N(0) \geq 0,
\end{aligned} \tag{2.1}$$

where m is the maximal zooplankton grazing rate, and α is the zooplankton conversion rate, $0 < \alpha \leq 1$.

Clearly solutions of system (2.1) exist for all positive time. Also as $\dot{Q}|_{Q=Q_0} \geq 0$, we see that solutions of (2.1) remain nonnegative with $Q(t) \geq Q_0$ for $t > 0$. Letting $S = N + PQ + Z$. Then $\dot{S} = D(N^0 - S)$, and we conclude

that (2.1) has the following limiting system

$$\begin{aligned} \dot{P} &= P[u(Q) - \delta - D - mZ] \\ \dot{Q} &= \rho(N^0 - PQ - Z, Q) - u(Q)Q \\ \dot{Z} &= [\alpha(mPQ + bZ) - bZ - \epsilon - D]Z \\ & P(0) \geq 0, Q(0) \geq Q_0, Z(0) \geq 0, P(0)Q(0) + Z(0) \leq N^0. \end{aligned} \tag{2.2}$$

We shall analyze system (2.2) and discuss its dynamical consequence with respect to the parameter b, the intensity of intratrophic predation.

Let

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

Then Δ is positively invariant for (2.2). We first derive the existence conditions for steady states. Clearly $E_0 = (0, \hat{Q}, 0)$ always exists, where $\hat{Q}$ satisfies

$$\rho(N^0, Q) = u(Q)Q.$$

Steady states of the form $(P, Q, 0)$ on the interior of nonnegative PQ- plane satisfy $u(Q) = \delta + D$ and $\rho(N^0 - PQ, Q) = (\delta + D)Q$. Thus steady state $E_1 = (P_1, Q_1, 0)$ exists if and only if $u(\infty) > \delta + D$ and $\rho(N^0, Q_1) > (\delta + D)Q_1$, where Q_1 solves $u(Q) = \delta + D$. Note that in this case $Q_1 < \hat{Q}$ and steady state E_1 is unique if it exists. It can be easily seen that there is no steady state on the interior of nonnegative PZ or QZ- plane and steady states E_0 and E_1 do not depend on b. Therefore intratrophic predation has no effect on the existence and magnitude of the boundary steady states. We shall see that this conclusion in general is not true for the interior steady states.

Indeed, we first consider $b = 0$ when there is no intratrophic predation. Notice $\bar{Q}_0$ of steady state $E_2^0 = (\bar{P}_0, \bar{Q}_0, \bar{Z}_0)$ must satisfy

$$\rho(N^0 - \frac{\epsilon + D}{\alpha m} - \frac{u(Q) - \delta - D}{m}, Q) = u(Q)Q. \tag{2.3}$$

Let the left hand side of (2.3) be denoted by $f(Q)$. Then $f'(Q) < 0$ for $Q \geq Q_0$ and thus $\bar{Q}_0 > 0$ exists if and only if

$$N^0 > \frac{\epsilon + D}{\alpha m} - \frac{\delta + D}{m}. \tag{2.4}$$

Hence $E_2^0 = (\bar{P}_0, \bar{Q}_0, \bar{Z}_0)$ exists if and only if (2.4) holds and $u(\bar{Q}_0) > \delta + D$. In this case $\bar{Z}_0 = \dfrac{u(\bar{Q}_0) - \delta - D}{m}$, $\bar{P}_0 = \dfrac{\epsilon + D}{\alpha m \bar{Q}_0}$, $\bar{Q}_0 > Q_1$ and the positive steady state is unique.

When $0 < b \leq 1$, $\bar{Q}_b$ of a positive steady state $E_2^b = (\bar{P}_b, \bar{Q}_b, \bar{Z}_b)$ must satisfy

$$\rho(N^0 - \frac{\epsilon + D + b(1-\alpha)\dfrac{u(Q) - \delta - D}{m}}{\alpha m} - \frac{u(Q) - \delta - D}{m}, Q) \;\; = \;\; u(Q)Q.$$

Similar to the case for $b = 0$, the derivative of the left hand side of the above equation, denoted by $g(Q)$, with respect to Q, is negative for $Q \geq Q_0$. Hence E_2^b exists if and only if

$$N^0 > \frac{\epsilon + D}{\alpha m} - \frac{b(1-\alpha)(\delta + D)}{\alpha m^2} - \frac{\delta + D}{m}, \tag{2.5}$$

and $u(\bar{Q}_b) > \delta + D$. Also E_2^b is unique if it exists, and $\bar{Q}_b > Q_1$.

We proceed to compare the effect of b on the existence and magnitude of the positive steady state. Clearly $f(Q_1) = g(Q_1)$ and the graph of $y = g(Q)$ lies above the graph of $y = f(Q)$ when $Q_0 \leq Q < Q_1$ and below the graph of $y = f(Q)$ when $Q > Q_1$. Since $\bar{Q}_b, \bar{Q}_0 > Q_1$, we see that $\bar{Q}_b < \bar{Q}_0$ for $0 < b \leq 1$. On the other hand it is more likely for (2.5) to occur when $b > 0$ than that of (2.4). Since $\bar{Q}_b < \bar{Q}_0$, it is more likely that $u(\bar{Q}_0) > \delta + D$ than $u(\bar{Q}_b) > \delta + D$. Therefore intratrophic predation may or may not promote the existence of the coexisting steady state. However, if the input nutrient concentration N^0 is sufficiently large so that (2.4) holds, then intratrophic predation can diminish the existence of coexisting steady state as $\bar{Q}_b < \bar{Q}_0$ and $u(\bar{Q}_b) > \delta + D$ is less likely than $u(\bar{Q}_0) > \delta + D$. Furthermore, since $\bar{Q}_b < \bar{Q}_0$, we have $\bar{Z}_b < \bar{Z}_0$ and

$$\bar{P}_b = \frac{\epsilon + D + b(1-\alpha)\dfrac{u(\bar{Q}_b) - \delta - D}{m}}{\alpha m \bar{Q}_b} > \frac{\epsilon + D}{\alpha m \bar{Q}_b} > \frac{\epsilon + D}{\alpha m \bar{Q}_0} = \bar{P}_0.$$

Thus intratrophic predation can increase phytoplankton population and decrease zooplankton population of the coexisting steady state (cf. [10]).

Once the mechanism of intratrophic predation is investigated for the existence and magnitude of the steady states of (2.2), we turn to examine its effect on the stability of these simple solutions. Since $\limsup_{t\to\infty} N(t) \leq N^0$ and $\dot{Q} \leq \rho(N^0, Q) - u(Q)Q$, it follows that $\limsup_{t\to\infty} Q(t) \leq \hat{Q}$. Therefore $\hat{Q}$ may be viewed as the maximum cell quota that a phytoplankton cell can obtain.

As a result, both populations go to extinction if the maximal growth rate of phytoplankton, $u(\hat{Q})$, is less than its total removal rate, $\delta + D$, as stated in the next theorem.

Theorem 2.1 *If $u(\hat{Q}) < \delta + D$, then system (2.2) has only the trivial steady state $E_0 = (0, \hat{Q}, 0)$ and every solution of (2.2) converges to E_0 for $0 \le b \le 1$.*

Proof. We first show that E_0 is the only steady state for system (2.2). If $u(Q) = \delta + D$ has a solution Q_1, then $Q_1 > \hat{Q}$. Thus $\rho(N^0, Q_1) \le \rho(N^0, \hat{Q}) = u(\hat{Q})\hat{Q} < u(Q_1)Q_1$, which implies that E_1 does not exist. Similarly if $E_2^b = (\bar{P}_b, \bar{Q}_b, \bar{Z}_b)$ exists for some $0 \le b \le 1$, then $\bar{Q}_b > \hat{Q}$. But then $\rho(N^0 - \bar{P}_b\bar{Q}_b - \bar{Z}_b, \bar{Q}_b) < \rho(N^0, \bar{Q}_b) \le \rho(N^0, \hat{Q}) = u(\hat{Q})\hat{Q} < u(\bar{Q}_b)\bar{Q}_b$ and we obtain a contradiction. Hence E_2^b does not exist and E_0 is the only steady state for the system.

It remains to show that E_0 is globally asymptotically stable for $0 \le b \le 1$. If $u(Q) < \delta + D$ for $Q \ge Q_0$, then $\dot{P}(t) \le 0$ for $t \ge 0$ and thus $\lim_{t\to\infty} P(t) = P^* \ge 0$ exists. Since $\lim_{t\to\infty} \dot{P}(t) = 0$, we must have $P^* = 0$ and hence $\lim_{t\to\infty} P(t)Q(t) = 0$ as solutions of (2.2) are bounded. Thus for any $\eta > 0$ there exists $t_0 \ge 0$ such that $P(t)Q(t) < \eta$ for $t \ge t_0$. We choose $\eta > 0$ such that $\alpha m\eta < \epsilon$. Then $\dot{Z}(t) \le (\alpha m\eta - \epsilon)Z$ for $t \ge t_0$ implies $\lim_{t\to\infty} Z(t) = 0$. Therefore for any $\eta > 0$ there exists $t_1 > 0$ such that $P(t)Q(t) + Z(t) < \eta$ for $t \ge t_1$. We choose $\eta > 0$ such that $\eta < N^0$. Since $\dot{Q}(t) \ge \rho(N^0 - \eta, Q) - u(Q)Q$ for $t \ge t_1$, a simple comparison argument yields $\liminf_{t\to\infty} Q(t) \ge \hat{Q}$. Combining this with $\limsup_{t\to\infty} Q(t) \le \hat{Q}$, we have $\lim_{t\to\infty} Q(t) = \hat{Q}$, and solutions of (2.2) converge to E_0.

Suppose now $u(Q) = \delta + D$ has a solution Q_1. We show that $Q(t) < Q_1$ for all t large and this will complete our proof. Suppose on the contrary that $Q(t) \ge Q_1$ for $t \ge 0$. Then $\dot{Q} \le \rho(N^0, Q) - u(Q)Q \le \rho(N^0, Q_1) - u(Q_1)Q_1 < 0$ as E_1 does not exist, which implies $\lim_{t\to\infty} Q(t) = Q^* \ge Q_1$ exists. But then this contradicts $\lim_{t\to\infty} \dot{Q}(t) = 0$. Therefore there must exist $t_0 \ge 0$ such that $Q(t_0) = Q_1$. Consequently $Q(t) < Q_1$ for $t > t_0$ as $\dot{Q}(t_0) < 0$. ■

It follows from the above theorem that intratrophic predation has no impact on the global dynamics of the system if $u(\hat{Q}) < \delta + D$. The inequality $u(\hat{Q}) < \delta + D$ implies that the maximal growth rate of phytoplankton is less than its total removal rate, i.e., phytoplankton's net growth rate is negative.

Therefore phytoplankton population becomes extinct due to insufficient nutrient concentration available to the population. Consequently, zooplankton population also becomes extinct and intratrophic predation has no effect on the dynamics of the system.

Suppose now $u(\hat{Q}) > \delta + D$. Then $u(Q) = \delta + D$ has a solution Q_1 and $\rho(N^0, Q_1) \geq \rho(N^0, \hat{Q}) = u(\hat{Q})\hat{Q} > (\delta + D)Q_1$, which implies steady state $E_1 = (P_1, Q_1, 0)$ exists and E_0 is a saddle point with stable manifold lying on the QZ-plane. Dynamics of system (2.2) when $u(\hat{Q}) > \delta + D$ and $P_1Q_1 < \dfrac{\epsilon + D}{\alpha m}$ can be summarized below.

Theorem 2.2 *Let $u(\hat{Q}) > \delta + D$ and $P_1Q_1 < \dfrac{\epsilon + D}{\alpha m}$. Then $E_0 = (0, \hat{Q}, 0)$ and $E_1 = (P_1, Q_1, 0)$ are the only steady states for system (2.2). In addition $\rho(N^0 - \dfrac{\epsilon + D}{\alpha m}, Q_0) < (\delta + D)Q_0$ if $N^0 > \dfrac{\epsilon + D}{\alpha m}$, then solutions of (2.2) with $P(0) > 0$ converge to E_1 for $0 \leq b \leq 1$.*

Proof. If $E_2^b = (\bar{P}_b, \bar{Q}_b, \bar{Z}_b)$ exists for some $0 \leq b \leq 1$, then it follows from the second equation of (2.2) that $\bar{P}_b\bar{Q}_b < P_1Q_1$. But since

$$\bar{P}_b\bar{Q}_b = \frac{\epsilon + D + b\bar{Z}_b - \alpha b\bar{Z}_b}{\alpha m} > \frac{\epsilon + D}{\alpha m} > P_1Q_1,$$

we obtain a contradiction. Thus E_2^b does not exist for any b, $0 \leq b \leq 1$. Since the positive PQ- plane is positively invariant and $\dfrac{\partial \dot{P}}{\partial P} + \dfrac{\partial \dot{Q}}{\partial Q} = -\delta - D - P\dfrac{\partial \rho}{\partial N} + \dfrac{\partial \rho}{\partial Q} - u'(Q)Q < 0$ for $P > 0, Q \geq Q_0$, it follows from the Dulac criterion that E_1 is globally asymptotically stable on the positive PQ- plane.

We show that $\lim\limits_{t\to\infty} Z(t) = 0$ for any solution $(P(t), Q(t), Z(t))$ of (2.2) with $P(0) > 0$. This is trivially true if $Z(0) = 0$. Let $Z(0) > 0$. Then $Z(t) > 0$ for $t \geq 0$. If $N^0 \leq \dfrac{\epsilon + D}{\alpha m}$, then $\dot{Z} \leq (\alpha m N^0 - \epsilon - D)Z \leq 0$ implies $\lim\limits_{t\to\infty} Z(t) = 0$. Suppose now $N^0 > \dfrac{\epsilon + D}{\alpha m}$. If $P(t)Q(t) > \dfrac{\epsilon + D}{\alpha m}$ for $t \geq 0$,

then by our assumption

$$\begin{aligned}(\dot{PQ})(t) &= -(\delta+D)PQ - mPQZ + P\rho(N^0 - PQ - Z, Q) \\ &\leq P[\rho(N^0 - PQ, Q) - (\delta+D)Q] \\ &< P[\rho(N^0 - \frac{\epsilon+D}{\alpha m}, Q_0) - (\delta+D)Q_0] \\ &< 0\end{aligned}$$

implies $\lim_{t\to\infty} P(t)Q(t) = A$ exists where $0 < A < \infty$. But since $A \geq \frac{\epsilon+D}{\alpha m}$ and $\rho(N^0 - \frac{\epsilon+D}{\alpha m}, Q_0) < (\delta+D)Q_0$, it contradicts to $\lim_{t\to\infty}(\dot{PQ}) = 0$. Therefore there must exist $t_0 \geq 0$ such that $(PQ)(t_0) = \frac{\epsilon+D}{\alpha m}$. But then $(\dot{PQ})(t_0) < 0$ and thus $(PQ)(t) < \frac{\epsilon+D}{\alpha m}$ for all t large. Consequently $\dot{Z}(t) \leq 0$ for all t large and $\lim_{t\to\infty} Z(t) = z_* \geq 0$ exists. Using the fact that $\lim_{t\to\infty} \dot{Z}(t) = 0$, we have $z_* = 0$. As a result, the ω-limit set lies on the positive PQ-plane and E_1 is globally asymptotically stable on the indicated region. ■

We conclude from Theorem 2.2 that intratrophic predation has no effect on the asymptotic dynamics of the system if $u(\hat{Q}) > (\delta + D)$ and $P_1Q_1 < \frac{\epsilon+D}{\alpha m}$. Note that $\alpha m P_1 Q_1$ is the maximal growth rate of zooplankton when phytoplankton population is stabilized at the steady state E_1. Consequently, $\alpha m P_1 Q_1 - (\epsilon + D)$ is the net growth rate of zooplankton. Intratrophic predation has no influence on the system if zooplankton's net growth rate is negative when phytoplankton's net growth rate is positive. The case when both populations' net growth rate is positive is summarized below.

Theorem 2.3 *Let* $u(\hat{Q}) > (\delta + D)$ *and* $P_1Q_1 > \frac{\epsilon+D}{\alpha m}$. *Then* $E_2^b = (\bar{P}_b, \bar{Q}_b, \bar{Z}_b)$ *exists for* $0 \leq b \leq 1$. *Moreover,*

(a) System (2.2) is uniformly persistent for $0 \leq b \leq 1$.

(b) $\bar{P}_b > \bar{P}_0$ *and* $\bar{Z}_b < \bar{Z}_0$ *for any* b, $0 < b \leq 1$.

Proof. Since $P_1Q_1 > \dfrac{\epsilon+D}{\alpha m}$, $N^0 \geq P_1Q_1 > \dfrac{\epsilon+D}{\alpha m} > \dfrac{\epsilon+D}{\alpha m} - \dfrac{\delta+D}{m}$. Thus if E_2^0 does not exist we must have $u(\bar{Q}_0) \leq (\delta+D)$, where $\bar{Q}_0$ satisfies (2.3). Hence

$$\begin{aligned}\rho(N^0 - \frac{\epsilon+D}{\alpha m}, \bar{Q}_0) &\leq \rho(N^0 - \frac{\epsilon+D}{\alpha m} - \frac{u(\bar{Q}_0)-\delta-D}{m}, \bar{Q}_0) \\ &= u(\bar{Q}_0)\bar{Q}_0 \leq u(Q_1)Q_1 = \rho(N^0 - P_1Q_1, Q_1)\end{aligned}$$

and thus

$$\rho(N^0 - \frac{\epsilon+D}{\alpha m}, Q_1) \leq \rho(N^0 - \frac{\epsilon+D}{\alpha m}, \bar{Q}_0) \leq \rho(N^0 - P_1Q_1, Q_1),$$

which yields $P_1Q_1 \leq \dfrac{\epsilon+D}{\alpha m}$ and contradicts our assumption. This shows that E_2^0 exists. Similar arguments imply that E_2^b exists for $0 < b \leq 1$. The proof of (b) follows from an earlier analysis. To show (a), observe that the system is weakly persistent by the Jacobian matrix evaluated at E_0 and E_1 [5], and thus uniformly persistent by [21] as the system is dissipative. ■

The above analysis was carried out on the limiting system (2.2). As in [10] we can make the same conclusion for the original system (2.1) by applying the asymptotic autonomous arguments derived by Thieme [21].

3 A model with periodic nutrient input

In this section we shall relax the assumption made in the previous section that the input nutrient concentration is a constant. To incorporate day/night or seasonal 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 $a, 0 < a < N^0$, 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 denote by $\langle h(t)\rangle = \dfrac{1}{\tau}\displaystyle\int_0^\tau h(t)dt$ the mean value of a τ-periodic function h.

Model (2.1) with a fluctuating nutrient input takes the following form.

$$\begin{aligned}
\dot{N} &= D(N^0 + ae(t) - N) - P\rho(N,Q) + \delta PQ + m(1-\alpha)PQZ + \epsilon Z \\
&\quad +(1-\alpha)bZ^2 \\
\dot{P} &= P[u(Q) - \delta - D - mZ] \\
\dot{Q} &= \rho(N,Q) - u(Q)Q \\
\dot{Z} &= [\alpha(mPQ + bZ) - bZ - \epsilon - D]Z \\
&\quad N(0) \geq 0, P(0) \geq 0, Q(0) \geq Q_0, Z(0) \geq 0.
\end{aligned} \tag{3.1}$$

The parameters appeared in (3.1) are defined as in section 2. Similar to [8], we begin by considering the τ-periodic equation

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

Notice that (3.2) has a unique positive τ-periodic solution $N^*(t)$ and every solution $N(t)$ of (3.2) satisfies $\lim_{t\to\infty}(N(t) - N^*(t)) = 0$, where $N^0 - a \leq N^*(t) \leq N^0 + a$ for $t \geq 0$.

We let $S = N^*(t) - N - PQ - Z$ and notice that $\dot{S} = -DS$. As a result $\lim_{t\to\infty}(N(t) + P(t)Q(t) + Z(t) - N^*(t)) = 0$, and system (3.1) has the following limiting system

$$\begin{aligned}
\dot{P} &= P[u(Q) - \delta - D - mZ] \\
\dot{Q} &= \rho(N^*(t) - PQ - Z, Q) - u(Q)Q \\
\dot{Z} &= [\alpha(mPQ + bZ) - bZ - \epsilon - D]Z \\
&\quad P(0) \geq 0, Q(0) \geq Q_0, P(0)Q(0) + Z(0) \leq N^*(0).
\end{aligned} \tag{3.3}$$

It can be easily verified that solutions of (3.3) satisfy $P(t) \geq 0, Q(t) \geq Q_0, Z(t) \geq 0$, $P(t)Q(t) + Z(t) \leq N^*(t)$ for $t \geq 0$, and system (3.3) is dissipative. Several variable-yield models with periodic nutrient input were studied in [11, 20]. Our analysis presented here is similar to that of [11].

Let

$$\Gamma = \{(P,Q,Z) \in R^3_+ : Q \geq Q_0, PQ + Z \leq N^*(0)\}.$$

Since (3.3) is τ-periodic, we shall consider the Poincaré map $\mathcal{P}$ induced by (3.3), where $\mathcal{P} : \Gamma \to \Gamma$ is defined by $\mathcal{P}(P(0), Q(0), Z(0)) = (P(\tau), Q(\tau), Z(\tau))$, and $(P(t), Q(t), Z(t))$ is the solution of (3.3) with initial condition $(P(0), Q(0), Z(0))$. Since (3.3) is dissipative, $\mathcal{P}$ has a global attractor K, i.e., K is the maximal compact invariant set such that $\lim_{n\to\infty} \mathcal{P}^n x \in K$ for any $x \in \Gamma$.

Consider the following trivial τ-periodic equation

$$\begin{aligned} \dot{q} &= \rho(N^*(t), q) - u(q)q, \\ & q(0) \geq Q_0. \end{aligned} \tag{3.4}$$

Notice that (3.4) has a unique τ-periodic solution $Q^*(t)$ which is moreover globally asymptotically attracting for (3.4) by [20]. Consequently, (3.3) always has a trivial τ-periodic solution $(0, Q^*(t), 0)$, although $Q^*(t)$ is biologically irrelevant as there is no phytoplankton present.

Theorem 3.1 *If* $\langle u(Q^*(t))\rangle < \delta + D$, *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 (3.3) and* $0 \leq b \leq 1$.

Proof. Since $\dot{Q} \leq \rho(N^*(t), Q) - u(Q)Q$, we have $Q(t) \leq q(t)$ for $t \geq 0$, where $q(t)$ is the solution of (3.4) with $q(0) = Q(0)$. Furthermore, $q(t) - Q^*(t) \to 0$ as $t \to \infty$, we have for all t sufficiently large that

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

Thus $\lim_{t\to\infty} P(t) = 0$ by our assumption, and $\lim_{t\to\infty} P(t)Q(t) = 0$ as solutions of (3.3) are bounded. Therefore it can be proved that $\lim_{t\to\infty} Z(t) = 0$.

It remains to show $\lim_{t\to\infty}(Q(t) - Q^*(t)) = 0$. Notice that the global attractor K of the Poincaré map $\mathcal{P}$ lies on the Q-axis as $\lim_{t\to\infty} P(t) = \lim_{t\to\infty} Z(t) = 0$. Restricted to the Q-axis, $\mathcal{P}^n(0, Q(0), 0) = (0, \mathcal{P}_1^n(Q(0)), 0)$, where $\mathcal{P}_1$ is the Poincaré map induced by (3.4). Since $Q^*(0)$ is the unique fixed point of $\mathcal{P}_1$ which is moreover globally asymptotically stable for $\mathcal{P}_1$, it follows that $\mathcal{P}$ has a unique fixed point $(0, Q^*(0), 0)$ which is globally asymptotically stable for $\mathcal{P}$. Therefore the trivial τ-periodic solution $(0, Q^*(t), 0)$ is globally attracting for (3.3) and this completes the proof. ■

Since $N^*(t)$ is the maximum external nutrient concentration available to the system at any time t, $< u(Q^*(t)) >$ can be viewed as the average maximal growth rate of phytoplankton. Both populations go to extinction if the net growth rate of phytoplankton is negative, i.e., if $< u(Q^*(t)) >< \delta + D$. Consequently, intratrophic predation has no effect on the global dynamics of the limiting system if phytoplankton has a negative net growth rate.

Since the nonnegative PQ-plane is positively invariant, we consider the

PQ-subsystem of (3.4)

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

By introducing a new state variable, (3.5) was transformed into a competitive system for which the dynamics were easily understood. Indeed, if $\langle u(Q^*(t))\rangle > \delta + D$, then system (3.5) 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 (3.5) with $P(0) > 0$ all converge to $(\bar{P}(t), \bar{Q}(t))$ [20]. It follows that system (3.3) has a unique τ-periodic solution of the form $(\bar{P}(t), \bar{Q}(t), 0)$ if $\langle u(Q^*(t))\rangle > \delta + D$, where $\bar{P}(t) > 0$ and $\bar{Q}(t) > Q_0$. Since $\langle N^*(t)\rangle$ is the maximum average nutrient concentration available in the system, we have the following immediate consequence.

Theorem 3.2 *If $\langle u(Q^*(t))\rangle > \delta + D$ and $\alpha m \langle N^*(t)\rangle < \epsilon + D$, then solution $(P(t), Q(t), Z(t))$ of (3.3) with $P(0) > 0$ converges to $(\bar{P}(t), \bar{Q}(t), 0)$ as $t \to \infty$ for $0 \leq b \leq 1$.*

Proof. As in [11] we consider the Poincaré map $\mathcal{P} : \Gamma \to \Gamma$ induced by system (3.3). By the assumption $\alpha m \langle N^*(t)\rangle < \epsilon + D$, we have $\lim_{t\to\infty} Z(t) = 0$ and the global attractor K of $\mathcal{P}$ lies on the PQ-plane. Restricted to this set, $\mathcal{P}^n(P(0), Q(0), 0) = (\mathcal{S}^n(P(0), Q(0)), 0)$, where $\mathcal{S}$ is the Poincaré map associated with system (3.5). It follows that $\mathcal{P}$ has two fixed points $(0, Q^*(0), 0)$ and $(\bar{P}(0), \bar{Q}(0), 0)$. We shall show that $\lim_{n\to\infty} \mathcal{P}^n(P(0), Q(0), Z(0)) = (\bar{P}(0), \bar{Q}(0), 0)$ if $P(0) > 0$. To this end, let $A = \{(P, Q, Z) \in \Gamma : P = 0\}$ be 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 PQ-plane. The Jacobian derivative $D(\mathcal{P})$ of $\mathcal{P}$ at $(0, Q^*(0), 0)$ is given by $\Phi(\tau)$, where $\Phi(t)$ is the fundamental matrix solution of $\dot{X} = B(t)X$ with

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

It follows from $B(t)$ that the stable set $W^s(M)$ of M, $\{x \in \Gamma : \lim_{n\to\infty} \mathcal{P}^n x \in M\}$, lies on A. Therefore, $\mathcal{P}$ is uniformly persistent with respect to A by [25], i.e., there exists $\eta > 0$ such that $\liminf_{n\to\infty} d(\mathcal{P}^n(P(0), Q(0), Z(0)), A) > \eta$

for any $(P(0), Q(0), Z(0)) \in \Gamma$ with $P(0) > 0$. Consequently, the ω-limit set of $\mathcal{P}$ has the form $(P, Q, 0)$ with $P > \eta$. Therefore, $\mathcal{P}^n(P(0), Q(0), Z(0)) \to (\bar{P}(0), \bar{Q}(0), 0)$ as $n \to \infty$ if $P(0) > 0$ and the assertion follows. ■

We conclude from Theorem 3.2 that intratrophic predation has no effect on the global asymptotic dynamics of the limiting system if phytoplankton's net growth rate is positive but zooplankton has a negative net growth rate. By using periodic solutions $(0, Q^*(t), 0)$ and $(\bar{P}(t), \bar{Q}(t), 0)$ and their associated Floquet multipliers, we obtain a sufficient condition for the persistence of both populations on the ω-limit set of system (3.1) as given below.

Theorem 3.3 *If $\langle u(Q^*(t))\rangle > \delta + D$ and $\alpha m \langle \bar{P}(t)\bar{Q}(t)\rangle > \epsilon + D$, then system (3.3) is uniformly persistent and has a positive τ-periodic solution $(P_b^0(t), Q_b^0(t), Z_b^0(t))$, where $P_b^0(t), Z_b^0(t) > 0$ and $Q_b^0(t) > Q_0$ for $0 \le b \le 1$.*

Proof. As $\langle u(Q^*(t))\rangle > \delta + D$, the τ-periodic solution $(\bar{P}(t), \bar{Q}(t), 0)$ exists. Similar to [11], we apply Theorem 3.1 of Butler and Waltman [**?**] to show uniform persistence of (3.3). Let $\mathcal{F}$ be the continuous semiflow generated by (3.3) and $\partial\mathcal{F}$ be $\mathcal{F}$ restricted to the boundary $\partial\Gamma$. It is easy to verify that $\partial\mathcal{F}$ is isolated and acyclic. Indeed, let $M_0 = \{(0, Q^*(t), 0) | 0 \le t \le \tau\}$, $M_1 = \{(\bar{P}(t), \bar{Q}(t), 0) | 0 \le t \le \tau\}$, and let $\omega(x)$ denote the ω-limit set of x. Then the invariant set of $\partial\mathcal{F}$, $\Omega(\partial\mathcal{F}) = \cup_{x\in\partial\Gamma}\omega(x)$, is $\{M_0, M_1\}$. Clearly $\partial\mathcal{F}$ is acyclic as M_0 and M_1 are globally attracting on the positive Q-axis, and the positive PQ-plane, respectively so that no subset of $\{M_0, M_1\}$ forms a cycle. It remains to show that each M_i is isolated for $\partial\mathcal{F}$ and for $\mathcal{F}$ respectively, for $i = 0, 1$. We only prove that M_0 is isolated for $\mathcal{F}$ as the remaining assertion can be shown similarly.

Since $\langle u(Q^*(t))\rangle > \delta + D$, we can choose $\rho > 0$ such that

$$1/\tau \int_0^\tau [u(Q^*(t) - \rho) - (\delta + D + m\rho)]dt > 0. \tag{3.6}$$

Let $\mathcal{N} = \{(P, Q, Z) \in \Gamma : d((P, Q, Z), M_0) < \rho\}$, where d denotes the 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 is globally attracting in the positive PQ-plane, there exists $x(0) = (P(0), Q(0), Z(0)) \in V \setminus M_0$ such that $P(0), Z(0) > 0$ and $x(t) \in V$ for all t.

But $V \subset \mathcal{N}$ implies

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

and thus $\lim_{t\to\infty} P(t) = \infty$ by (3.6). We obtain a contradiction and conclude that M_0 is isolated for $\mathcal{F}$. Let $\overset{\circ}{\Gamma}$ denote the interior of Γ. It follows from the Floquet multipliers of the τ-periodic solutions $(0, Q^*(t), 0)$ and $(\bar{P}(t), \bar{Q}(t), 0)$ that $W^s(M_i) \cap \overset{\circ}{\Gamma} = \emptyset$ for $i = 0, 1$, where $W^s(M_i)$ denotes the stable set of M_i. Therefore, we can conclude that (3.3) is uniformly persistent by Theorem 3.1 of [**?**]. Furthermore, since the system is dissipative and uniformly persistent, the interior of Γ has a τ-periodic solution by Theorem 4.11 of [26]. Thus (3.4) has a positive τ-periodic solution for $0 \leq b \leq 1$ and this completes the proof. ■

Once the dynamics of system (3.3) are well understood, we can apply the same technique used in [12] to conclude that systems (3.1) and (3.3) have the same asymptotic dynamics. Therefore, intratrophic predation may have impact on the model only if the maximum average net growth rates of both plankton populations are positive. However, unlike the autonomous system for which comparison of magnitude between interior steady states can be easily made, it is not clear for the interior periodic solutions presented here. We will rely mainly on numerical simulations given in the next section to make such further comparison.

4 Numerical simulations

It was shown analytically in the previous sections that intratrophic predation has no impact on the dynamics of the systems if population's net growth rate is negative. In this section we will use numerical examples to study the mechanism when both population's net growth rate is positive. We use the growth rate u and uptake rate ρ proposed by Grover in his experimental study [6, 7] to simulate our models (cf. [11]). Specifically,

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

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

where $\rho_{max}(Q) = \rho_{max}^{high} - (\rho_{max}^{high} - \rho_{max}^{low})\dfrac{(Q-Q_{min})_+}{Q_{max}-Q_{min}}$ 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 $k = 2$. From $Q_{min} = 3$, we see that $Q_0 = 3$. These parameter values are within the wide range studied by Grover [6, p. 817].

The zooplankton's grazing rate is modeled by a simple linear function mP, and we choose $m = 5$ for our simulations. A linear functional form was also used in the study of nutrient-plankton interaction with a limiting nutrient inhibiting the growth rate of phytoplankton [8]. Limiting system (2.3) with the above functional forms becomes

$$\begin{aligned}
\dot{P} &= P[2.16\frac{(Q-3)_+}{2+(Q-3)_+} - \delta - D - 0.5Z] \\
\dot{Q} &= [15 - 0.522(Q-3)_+]\frac{N^0 - PQ - Z}{N^0 - PQ - Z + 4} - 2.16\frac{(Q-3)_+ Q}{2+(Q-3)_+} \qquad (4.1)\\
\dot{Z} &= [\alpha(0.5PQ + bZ) - bZ - \epsilon - D]Z \\
&\quad P(0) \geq 0, Q(0) \geq 3, Z(0) \geq 0, P(0)Q(0) + Z(0) \leq N^0.
\end{aligned}$$

We use the same death rates $\delta = 0.7$ and $\epsilon = 0.1$ as in [22, 23] to simulate model (4.1). Since we are more interested in the dynamics of the system when both populations can coexist, we choose $N^0 = 4.85$ and $D = 0.4$ so that conditions in Theorem 2.3 are true. Specifically $u(\hat{Q}) = 1.2629 > \delta + D = 1.1$, $P_1 = 0.4079$, $Q_1 = 5.0755$ and $P_1Q_1 = 2.0703 > \dfrac{\epsilon + D}{\alpha m} = 1$. For the functional forms and parameters chosen, the autonomous system, model (4.1), has no periodic solutions for $0 \leq b \leq 1$. Figure 1 plots components of the interior steady state as a function of b. It demonstrates that intratrophic predation can increase phytoplankton population and decrease zooplankton population levels of the interior steady state (cf. [10]) as shown in section 2.

Put figure 1 here

For periodic nutrient input model we use $N^0 = 4.85$ as given above, and choose $a = 3$ and $e(t) = \sin(\pi/10t)$. This particular functional form

was also used in the study of intratrophic predation for a constant-yield periodic nutrient-plankton system ([12]). In particular, the period is 20 for the example given. We calculate $N^*(t)$ analytically. The limiting system (3.4) now takes the following form.

$$\begin{aligned}
\dot{P} &= P[2.16\frac{(Q-3)_+}{2+(Q-3)_+} - \delta - D - 0.5Z] \\
\dot{Q} &= [15 - 0.522(Q-3)_+]\frac{N^*(t) - PQ - Z}{N^*(t) - PQ - Z + 4} - 2.16\frac{(Q-3)_+ Q}{2+(Q-3)_+} \\
\dot{Z} &= [\alpha(0.5)PQ + bZ) - bZ - \epsilon - D]Z \\
& P(0) \geq 0, Q(0) \geq 3, Z(0) \geq 0, P(0)Q(0) + Z(0) \leq N^*(0).
\end{aligned} \tag{4.2}$$

We use the same parameter values as in the constant nutrient input model. With these parameters, conditions given in Theorem 3.3 are satisfied. Therefore, the corresponding full system is uniformly persistent and has a positive periodic solution. Figure 2 plots trajectories $(N(t), P(t), Z(t))$ with two slight different initial conditions: $(N(0), P(0), Q(0), Z(0)) = (1.25, 0.5, 3.5, 1)$, and $(N(0), P(0), Q(0), Z(0)) = (1.26, 0.51, 3.51, 1.01)$ when $b = 0$. It is clear that both solutions are aperiodic and moreover the system is sensitive to initial conditions. Therefore the interaction between nutrient and plankton populations without intratrophic predation seems chaotic. However, this is not true when $b = 1$ as shown in Figure 3. System (4.2) now has a locally asymptotically attracting positive periodic solution when $b = 1$. A bifurcation diagram using b as the bifurcation parameter is presented in Figure 4. The diagram plots 25 maximum phytoplankton population levels after transient behavior has been eliminated. From these figures we conclude that intratrophic predation can stabilize the system.

Put figures 2, 3 and 4 here

Since the input nutrient concentration may vary randomly in the natural system, we next add an environmental noise to system (4.1) as given below.

$$
\begin{aligned}
\dot{N} &= D(N^0 - N) + c\frac{dW(t)}{dt} - P\rho(N,Q) + \delta PQ + \epsilon Z + m(1-\alpha)PQZ + (1-\alpha)bZ^2 \\
\dot{P} &= P[u(Q) - \delta - D - mZ] \\
\dot{Q} &= \rho(N,Q) - u(Q)Q \\
\dot{Z} &= [\alpha(mPQ + bZ) - bZ - \epsilon - D]Z \\
& P(0) \geq 0, Q(0) \geq Q_0, Z(0) \geq 0, N(0) \geq 0,
\end{aligned} \tag{4.3}
$$

where $\{W(t)\}$, $t \in [0, \infty)$, is a Wiener process denoting the white noise. In particular, $prob\{W(0) = 0\} = 1$, the increment $W(t_1) - W(t_0)$ is normally distributed with mean zero and variance $t_1 - t_0$, and the increment only depends on the length of the time interval but not on any specific time. System (4.3) satisfies the existence and uniqueness conditions given in []. However, we do not study the asymptotic behavior of (4.3) as we did for the deterministic systems. We use a first order Euler approximation to simulate the model.

$$
\begin{aligned}
N_{i+1} &= N_i + D(N^0 - N_i)\Delta t + c\eta_i\sqrt{\Delta t} - P_i\rho(N_i,Q_i)\Delta t + \delta P_iQ_i\Delta t + \epsilon Z_i\Delta t \\
&+ m(1-\alpha)P_iQ_iZ_i\Delta t + (1-\alpha)bZ_i^2\Delta t \\
P_{i+1} &= P_i + P_i[u(Q_i) - \delta - D - mZ_i]\Delta t \\
Q_{i+1} &= Q_i + \rho(N_i,Q_i)\Delta t - u(Q_i)Q_i\Delta t \\
Z_{i+1} &= Z_i + [\alpha(mP_iQ_i + bZ_i) - bZ_i - \epsilon - D]Z_i\Delta t \\
& N_0, P_0, Z_0 \geq 0, Q_0 \geq 3,
\end{aligned} \tag{4.4}
$$

where η_i has a standard normal distribution, i.e., $\eta_i \sim N(0,1)$.

We use step size $\Delta t = 0.01$ for all simulations. Figures 5-7 plots 3 sample paths of the system when $b = 0$ and $c = 0.1$, $c = 0.5$ and $c = 1$, respectively. The initial condition for each sample path is $(1.25, 0.5, 3.5, 1.0)$ for all simulations. Figures 8 and 9 plot 3 sample paths for system (4.4) for $b = 0.1$, and $b = 0.5$ with $c = 0.1$, respectively. From these figures we see that populations may go to extinction even when both populations net growth rates are positive.

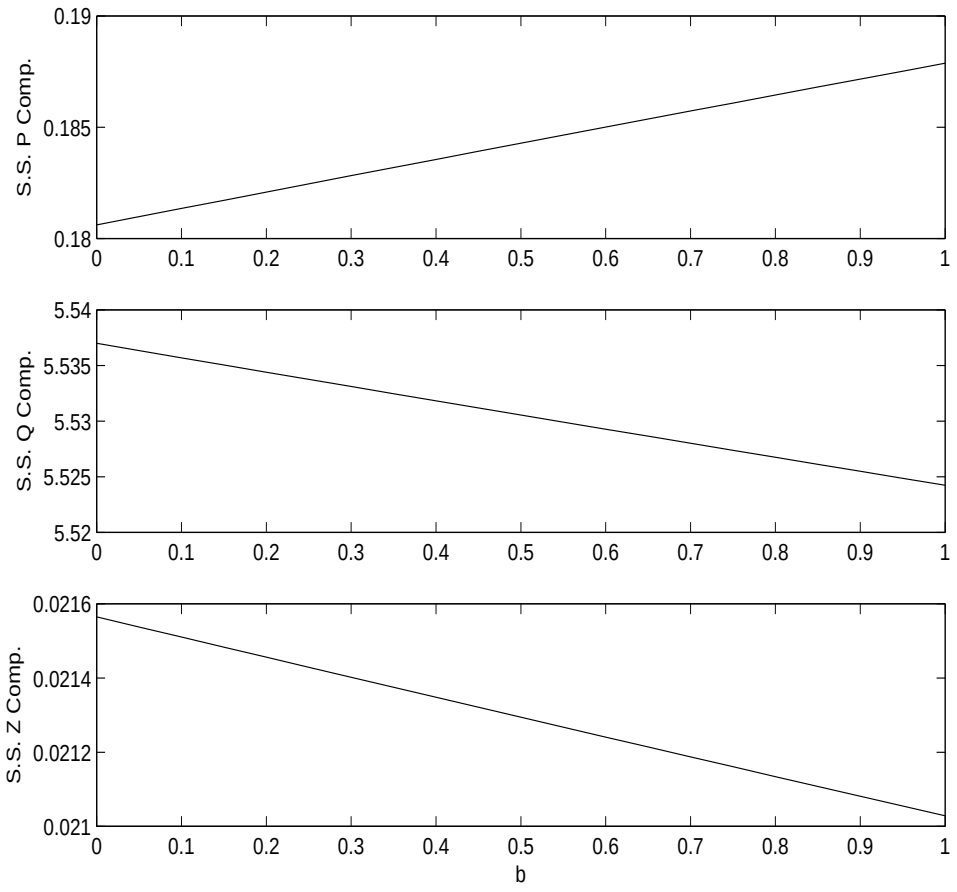

Figure 1: The P-component of the interior steady state increases while the Z-component decreases as b increases.

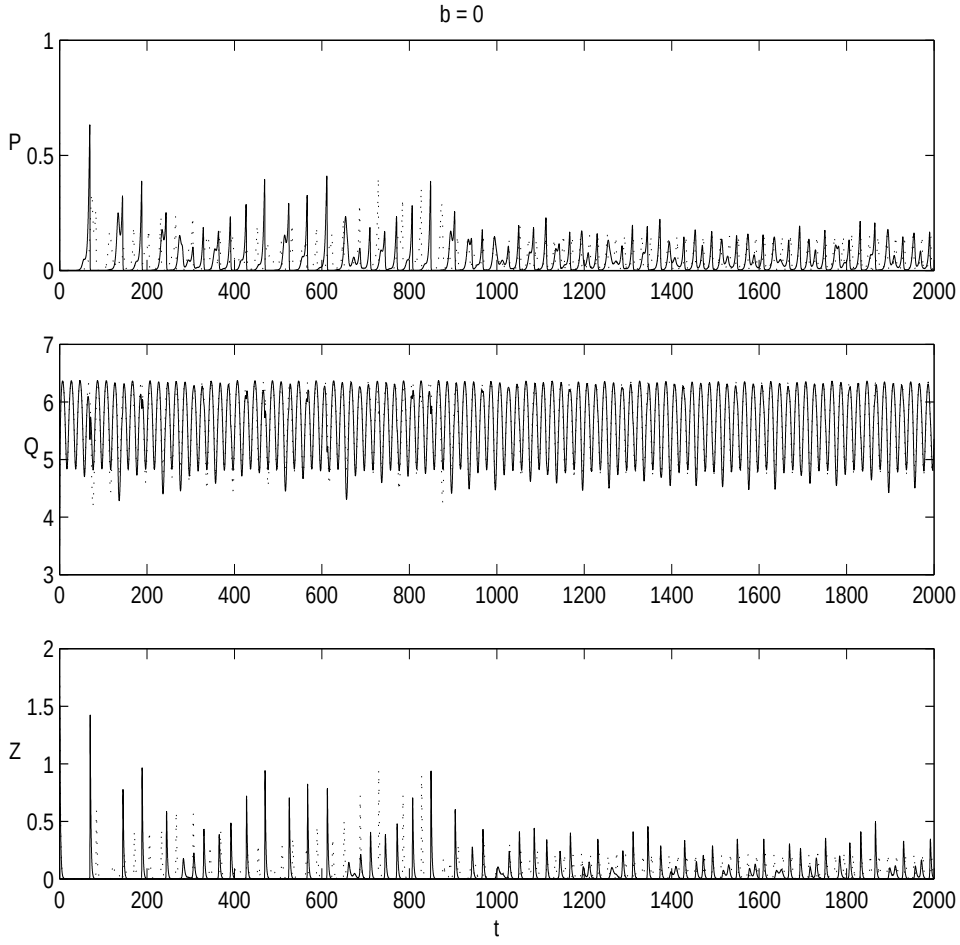

Figure 2: The plot for two solutions of system (4.2) with a slight change of initial conditions by adding 0.01 to each component. The system exhibits aperiodic solutions and is sensitive dependent on initial conditions.

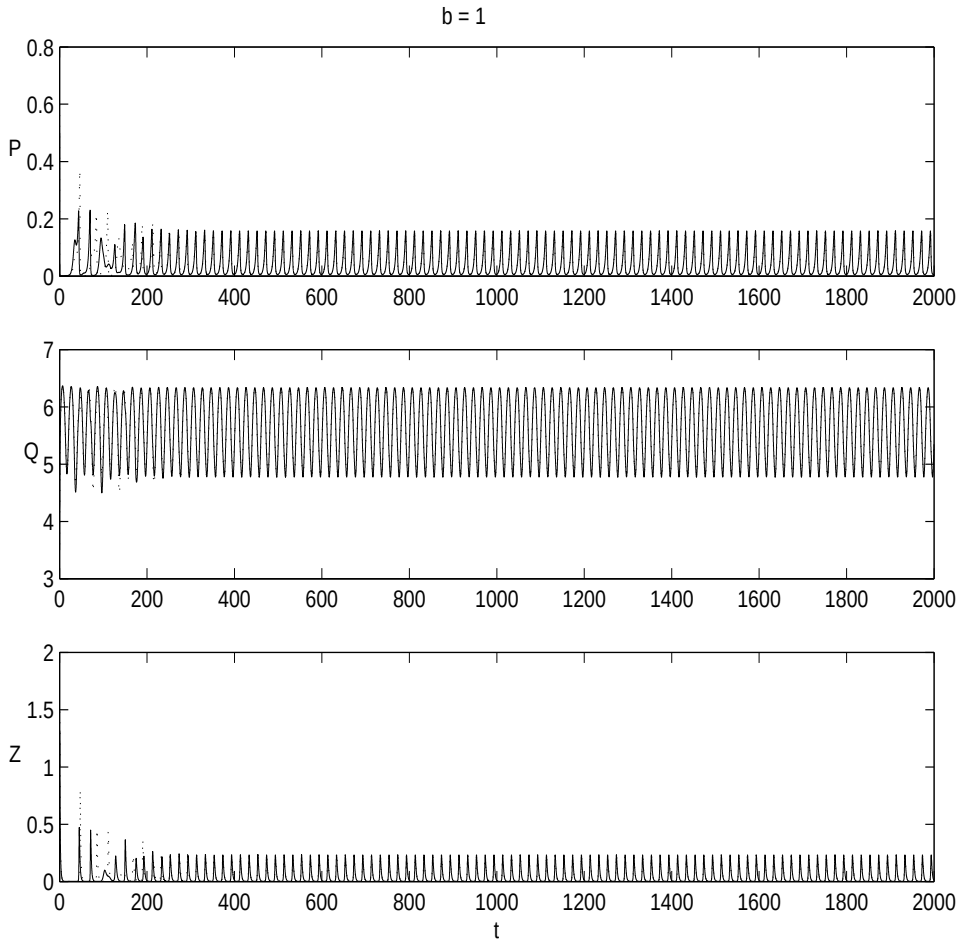

Figure 3: The chaotic behavior found when $b = 0$ disappears when $b = 1$. The positive periodic solution is locally asymptotically stable.

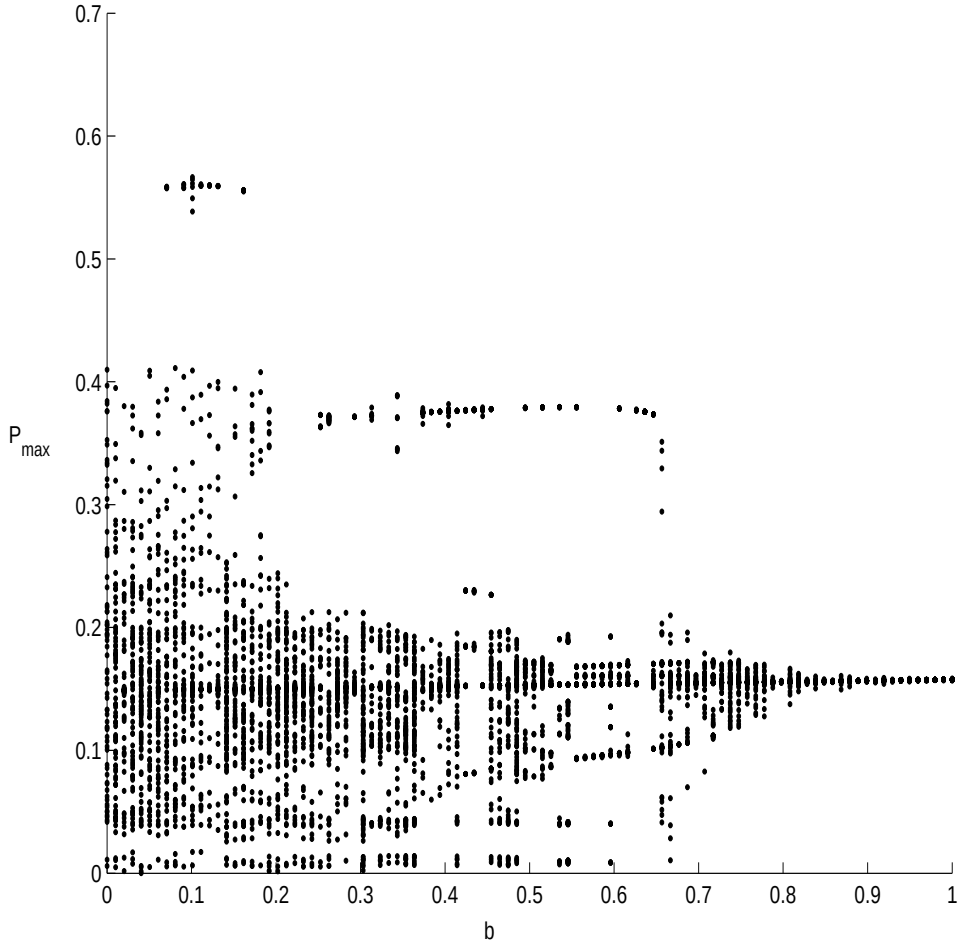

Figure 4: The diagram plots 25 maximum phytoplankton population levels of model (4.2) after the transient behavior has been eliminated.

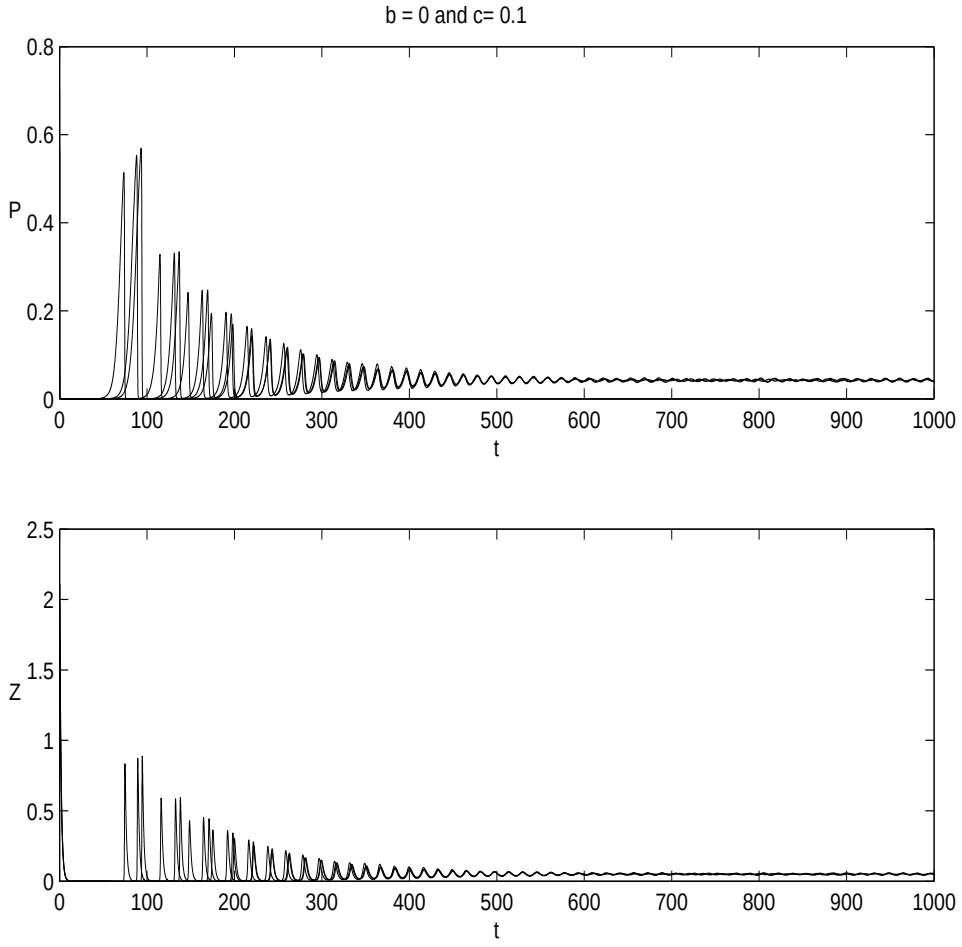

Figure 5: The figure plots three sample paths for both plankton populations when $b = 0$ and $c = 0.1$ with the same initial condition. One sample path of zooplankton population goes extinct.

5 Discussion

Several nutrient-phytoplankton-zooplankton models are proposed to investigate intratrophic predation. The predator population is consisted of several different species of zooplankton and some of the species may consume its own population. Our analytical results for the deterministic models obtained in this study are similar to those found in [10, 12]. Specifically, intratrophic predation has no impact on the global asymptotic dynamics of both the constant and periodic input nutrient models when the population's net growth rate is negative. When net growth rates of both populations are positive, it was shown that intratrophic predation can increase the phytoplankton population level and decrease zooplankton population level for the coexisting steady state when the input nutrient is modeled constantly. No such a conclusion can be achieved for the periodic input nutrient model. However, simulations performed in this study suggests that intratrophic predation can eliminate the chaotic behavior of the system even when the degree of intratrophic predation is very small.

A simple stochastic model simulates a randomly varying nutrient input was also proposed in this study. Although the system possesses a unique solution, we do not study its asymptotic dynamics as we did for the deterministic systems. A first Euler method was used to approximate the solutions. It is found numerically that both populations may go to extinction even when the population's net growth rates are positive. Therefore, the interaction between the plankton populations with intratrophic predation may be much more complicated and unpredictable.

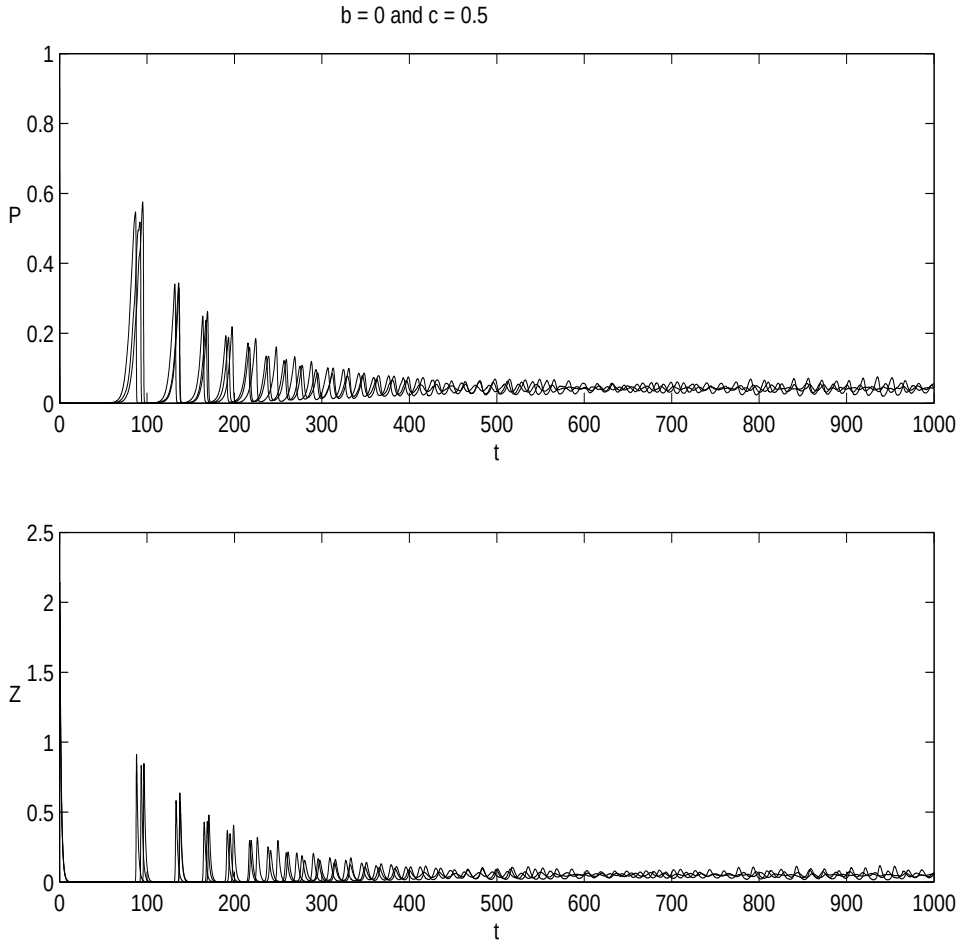

Figure 6: The figure plots three sample paths for both populations with the same initial conditions as given in Figure 5 when $b = 0$ and $c = 0.5$.

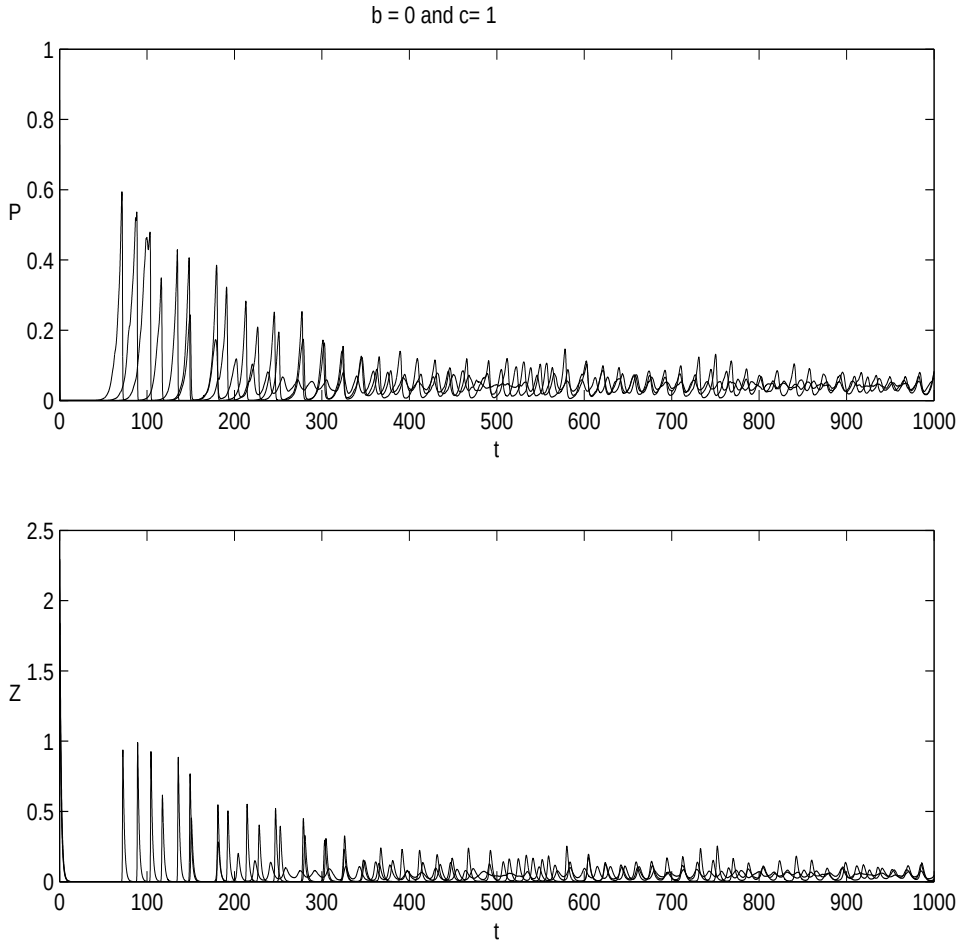

Figure 7: The figure plots three sample paths for both populations with the same initial conditions as given in Figure 5 when $b = 0$ and $c = 1$.

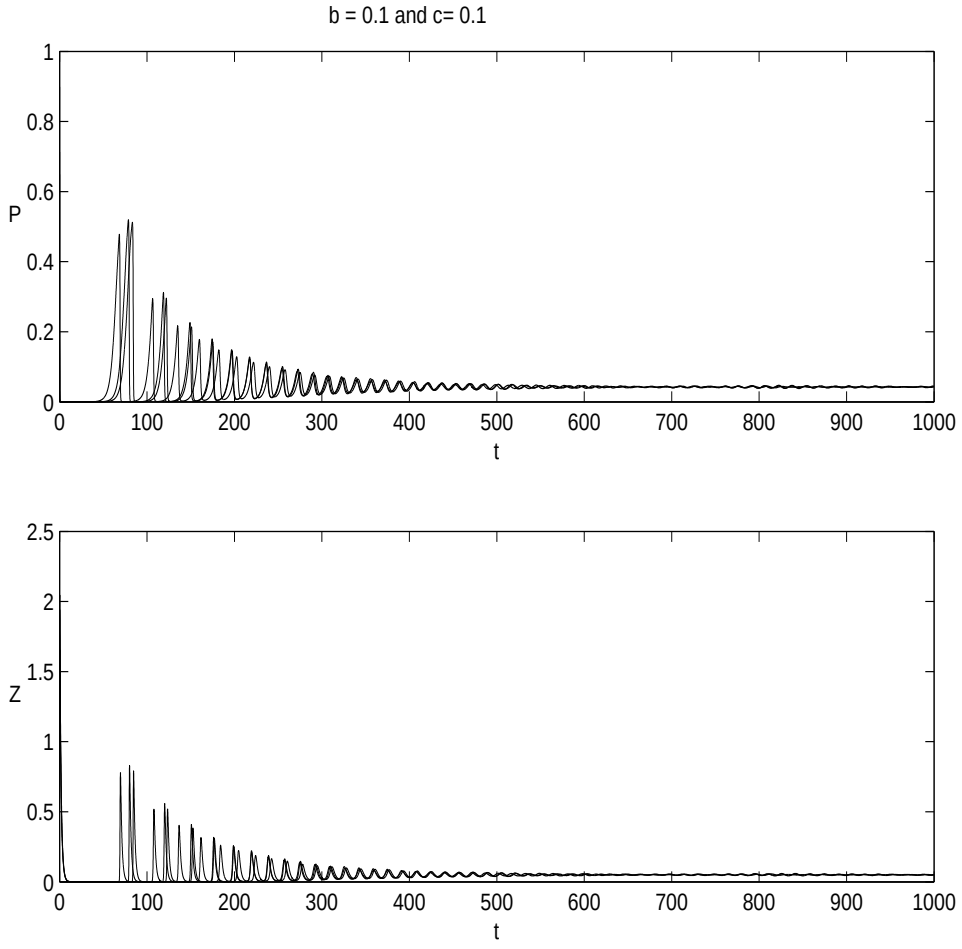

Figure 8: The figure plots three sample paths for both populations with the same initial conditions as given in Figure 5 when $b = 0.1$ and $c = 0.1$.

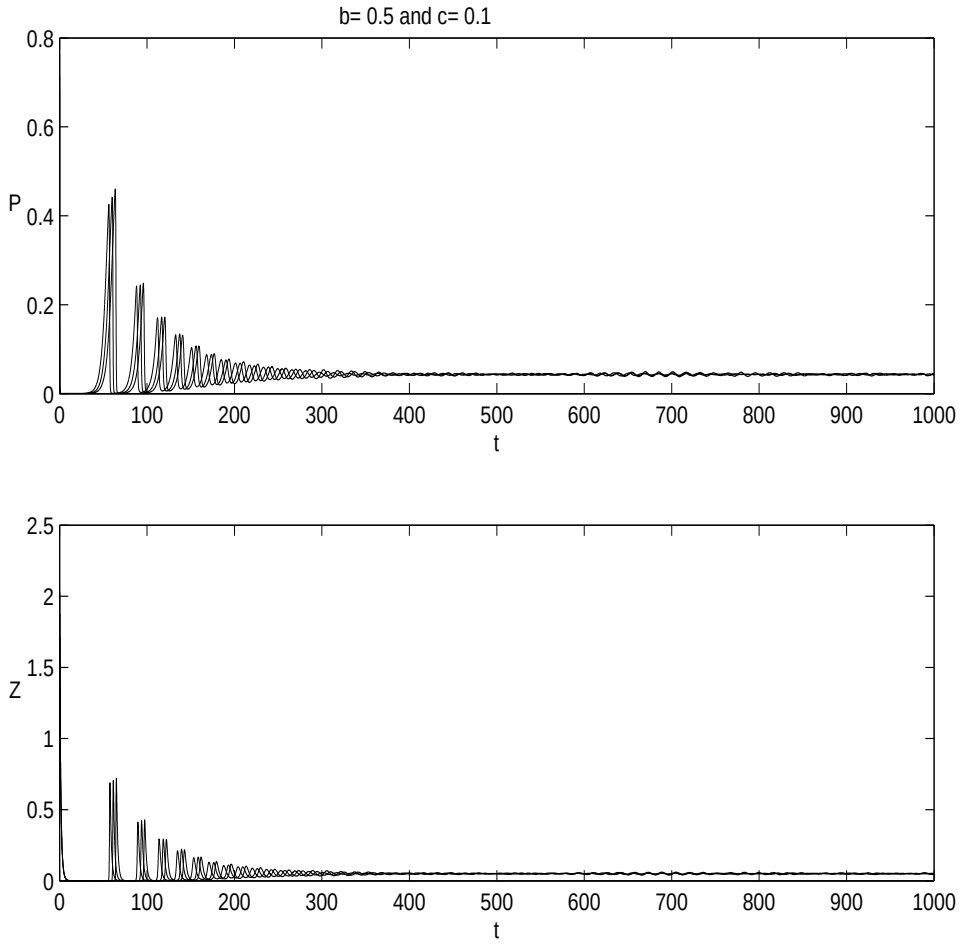

Figure 9: The figure plots three sample paths for both populations with the same initial conditions as given in Figure 5 when $b = 0.5$ and $c = 0.1$.

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