

Qualitative behavior of a variable-yield simple food chain with an inhibiting nutrient

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Abstract

A simple food chain which consists of nutrient, prey and predator in which nutrient is growth limiting at low concentrations but growth inhibiting at high concentrations is investigated in this study. It is assumed that the nutrient concentration is separated into internal and external nutrient concentration and only the internal nutrient level is capable of catalyzing cell growth. It is shown that the dynamics of the system depend on thresholds R_0 and R_1 . With inhibition, there exist initial conditions for which the predator becomes extinct but not the prey when $R_0 < 1$. If $R_0, R_1 > 1$, the system is uniformly persistent even in the inhibited environment.

Keywords: cell-quota; inhibition; threshold; uniform persistence

1 Introduction

Several nutrients such as nitrate, nitrite and ammonia limit growth of microorganisms at low concentrations and are inhibitory or even toxic at high concentrations [1, 2, 3, 4]. This inhibitory mechanism of substrates has a profound impact on the living organism. It is the purpose of this work to investigate the inhibition upon the dynamics of a nutrient-prey-predator model.

In most ecological models, it is assumed that the consumption rate of a resource is a function of resource availability and the yield of the organism is constantly proportional to the amount consumed. Such a model is sometimes referred to as a constant-yield model. However, it has been observed in both laboratory and field studies that algal populations could survive for several weeks after external reserves of nutrients were depleted. This is a result of luxury consumption of nutrients, first described by Ketchum [5]. The ability

of algae to store nutrient in excess of their requirements indicates that the growth rate of algae may not respond at once to a change in the external concentration of nutrients.

The Droop model, also called the variable-yield model, effectively decouples specific growth rate of the organism from external nutrient concentration by introducing an intracellular store of nutrient, providing a good fit for microorganism growth [6]. However, unlike the classical constant-yield models, the global dynamics of the variable-yield models were not well understood until recently. Lange and Oyarzum [7, 8] provided a global analysis for a variable-yield chemostat model with a single species of microorganism. Smith and Waltman [9, 10] studied two species of microorganism competing for a single limiting nutrient in a chemostat, where they showed that the competitive exclusion principle remains valid. Smith [11] also studied a periodically forced Droop model with a single species of organism in a chemostat. Jang [12] examined several variable-yield nutrient-phytoplankton-zooplankton models.

Certain nutrients are growth limiting at low concentrations but growth inhibiting or even toxic at high concentrations; nitrate is one example. Kumar et al. [3] include an additional factor $\exp(-cNO_3)$ in the uptake rate to denote this inhibition by nitrate. Other substrates such as nitrite and ammonia are also known to be inhibitory to some bacteria at high concentrations [2]. In addition, industrial waste products such as phenols and thiocyanates are often inhibitory to the bacteria metabolizing them [1, 13]. Several researchers use a nonmonotone uptake rate to model this inhibition.

Chemostat systems with nonmonotone uptake rates consisting of two trophic levels, a substrate and n competing species, have been studied by Butler and Wolkowicz [14] and Wolkowicz and Lui [15]. Jang and Allen [16] examined a simple food chain of three trophic levels with nonmonotone uptake rate for the prey. Other studies include Aris and Humphrey [17], Boon and Laudelout [18] and Bush and Cook [13]. In these studies, they assumed that the yield of the microorganism is constantly proportional to the external nutrient consumed, i.e., they considered constant-yield models.

Our simple food chain studied here consists of a nutrient, prey and predator, where prey feeds on the nutrient and predator feeds on the prey. Moreover, we separate nutrient concentrations into external and internal nutrient level and only the internal nutrient can catalyze cell growth. That is, we use the Droop equation for prey to study the interplay between nutrient, prey and predator. In this model, both prey and predator are modelled in terms of

their nutrient content and it is assumed that there is no net nutrient loss due to death or due to nutrient conversion. Under these assumptions, the total nutrient content is constant for all time and so the system is closed. Furthermore, it is also assumed that the nutrient limits growth at low concentrations but inhibits growth at high concentrations. We use a nonmonotone uptake rate for the prey to model this inhibition.

It has been shown in [12] that if there is no inhibition, the dynamics of the model are very similar to that of classical epidemic models [19]. Particularly, there exist two thresholds R_0 and R_1 such that the system is uniformly persistent if R_0 and $R_1 > 1$. Our focus in this study will be on the inhibitory mechanism. In particular, it is shown that if $R_0 < 1$, there exists a threshold initial prey density for the nutrient-prey model for which the prey can survive in a steady state fashion if the initial population density is above the threshold. On the other hand, if the initial prey population is too small, the population becomes extinct. Thus the inhibition of nutrient has an inverse density dependence effect on the prey population. It requires the prey population to detoxify its environment by consuming enough nutrient so as to lower nutrient concentration. Therefore, if its initial population is not sufficiently large, the prey has no ability to detoxify its habitat and consequently the population becomes extinct. The same conclusion is also valid for the nutrient-prey-predator model. If $R_0 > 1$, we can define one more threshold R_1 . If $R_1 > 1$, then the variable-yield nutrient-prey-predator system is uniformly persistent even in the inhibited environment.

In the following section, a variable-yield nutrient-prey model is derived and analyzed. Section 3 studies a variable-yield simple food chain. Specifically, we use a Lotka-Volterra functional response as the predator's uptake rate. Section 4 provides a numerical example and computer simulations. The conclusion is given in the final section.

2 A nutrient-prey model

In this section, we adopt internal nutrient storage by prey to study the dynamics of a nutrient-prey model with inhibition. We use a nonmonotone uptake function to model nutrient inhibition. The model derivation here is parallel to that of monotone uptake in [12].

Unlike the classical constant-yield model, the specific growth rate of the prey depends on a quantity, $Q(t)$, called the “cell quota”, introduced by

Droop [20, 21], which can be viewed as the average amount of stored nutrient in each cell of the prey at time t . The uptake rate of prey is assumed to depend on both the external and the internal nutrient concentrations.

Let $N(t)$ be the free nutrient at time t and $P(t)$, the concentration (or number of cells) of prey at time t . Then $P(t)Q(t)$ is the total amount of stored nutrient at time t . Let $u(Q)$ and $\rho(N, Q)$ be the per-capita growth rate and the per-capita uptake rate of prey respectively. Motivated by the examples of functions u and ρ in the literature [9, 10, 20, 21, 22, 23, 24, 25, 26, 27] and taking into account of inhibition, we make the following assumptions:

(H1) there exists $Q_0 > 0$ such that $u(Q_0) = 0$, $u'(Q) > 0$ and u' 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 $Q \geq Q_0$; $\rho(N, Q) \geq 0$ and $\frac{\partial \rho}{\partial Q} \leq 0$ for $N \geq 0$, $Q \geq Q_0$. There exists $N_0 > 0$ such that $\frac{\partial \rho}{\partial N} > 0$ for $0 \leq N < N_0$, $Q \geq Q_0$ and $\frac{\partial \rho}{\partial N} < 0$ for $N > N_0$, $Q \geq Q_0$.

We shall refer to the nutrient concentration N_0 defined in (H2) as the toxic level. It is the level at which the nutrient becomes growth inhibiting.

Let δ be the death rate of prey. Since the prey is modeled in terms of nutrient level and we assume that there is no nutrient loss to the system due to death, the interplay between nutrient and prey is described by the following ordinary differential equations:

$$\begin{aligned}\dot{N} &= -P\rho(N, Q) + \delta PQ \\ \dot{P} &= P[u(Q) - \delta].\end{aligned}\tag{2.1}$$

Let $\sum(t)$ be the total amount of free and stored nutrient at time t , i.e., $\sum(t) = N(t) + P(t)Q(t)$. Since it is assumed that the system is closed, the total nutrient is thus constant, i.e., $\dot{\sum}(t) = 0$ for $t \geq 0$. This implies that $P\dot{Q} = P[\rho(N, Q) - u(Q)Q]$ and consequently $\dot{Q} = \rho(N, Q) - u(Q)Q$ if $P(t) \neq 0$ for all $t \geq 0$. Therefore, we have derived a variable-yield nutrient-prey model

$$\begin{aligned}\dot{N} &= -P\rho(N, Q) + \delta PQ \\ \dot{P} &= P[u(Q) - \delta] \\ \dot{Q} &= \rho(N, Q) - u(Q)Q.\end{aligned}\tag{2.2}$$

As the total nutrient is constant, i.e., $\sum(t) = N_T$ for all $t \geq 0$, system (2.2) is equivalent to the following two-dimensional system

$$\begin{aligned}\dot{P} &= P[u(Q) - \delta] \\ \dot{Q} &= \rho(N_T - PQ, Q) - u(Q)Q.\end{aligned}\tag{2.3}$$

Equation for \dot{P} in (2.1) implies that $P(t) = P(0) \exp(\int_0^t [u(Q(\tau)) - \delta] d\tau)$ and thus $P(t) > 0$ for all $t \geq 0$ if $P(0) > 0$. Note that when $P = 0$, there is no biologically meaningful equation for Q . However, the equation for Q makes mathematical sense even if $P = 0$ as $P = 0$ and $Q = \hat{Q}$ where \hat{Q} satisfies $\rho(N_T, Q) = u(Q)Q$, resulting in a biological equilibrium.

Let $F = \{(P, Q) \in R_+^2 : PQ \leq N_T, Q \geq Q_0\}$. It is straightforward to show that F is positively invariant for (2.3) and that system (2.3) is dissipative. Moreover, steady state $E_0 = (0, \hat{Q})$ always exists with \hat{Q} defined as above. Suppose $u(Q) = \delta$ has a solution Q_1 and consider

$$\rho(N_T - PQ_1, Q_1) = \delta Q_1.\tag{2.4}$$

If $N_T \leq N_0$, then the left hand side of (2.4) is strictly decreasing and thus (2.3) has a positive steady state $E_{11} = (P_1, Q_1)$ if and only if $\rho(N_T, Q_1) > \delta Q_1$. In which case, the positive steady state is unique. If $N_T > N_0$, observe that the left hand side of (2.4) is strictly decreasing if $P > \frac{N_T - N_0}{Q_1}$ and is strictly increasing if $0 \leq P < \frac{N_T - N_0}{Q_1}$. Thus if $\delta Q_1 < \rho(N_T, Q_1)$, then (2.3) has a unique positive steady state $E_{11} = (P_1, Q_1)$, where $N_T - P_1 Q_1 < N_0$. However, if $\rho(N_T, Q_1) < \delta Q_1 < \rho(N_0, Q_1)$, then system (2.3) has two positive steady states $E_{11} = (P_1, Q_1)$ and $E_{12} = (P_2, Q_1)$, where $N_T - P_2 Q_1 > N_0$. On the other hand, if $\delta Q_1 > \rho(N_0, Q_1)$, then system (2.3) has no positive steady state.

In order to discuss the global dynamics of (2.3), the following observation is useful.

Proposition 2.1 *There exists $Q_1 > Q_0$ such that $u(Q_1) = \delta$ and $\rho(N_T, Q_1) > \delta Q_1$ if and only if $u(\hat{Q}) > \delta$.*

Proof. To show necessity, suppose $u(\hat{Q}) \leq \delta$. Then $\hat{Q} \leq Q_1$ and thus $\rho(N_T, \hat{Q}) \geq \rho(N_T, Q_1) > \delta Q_1 \geq u(\hat{Q})\hat{Q}$, a contradiction. Hence $u(\hat{Q}) > \delta$. Conversely, if $u(\hat{Q}) > \delta$, then $u(Q) = \delta$ has a solution Q_1 . Furthermore, $\rho(N_T, Q_1) \geq \rho(N_T, \hat{Q}) = u(\hat{Q})\hat{Q} > \delta\hat{Q} > \delta Q_1$. ■

A simple calculation shows that the Jacobian matrix of (2.3) is given by

$$\begin{pmatrix} u(Q) - \delta & Pu'(Q) \\ -Q\partial\rho/\partial N & -P\partial\rho/\partial N + \partial\rho/\partial Q - u(Q) - u'(Q)Q \end{pmatrix},$$

where $\partial\rho/\partial N$ and $\partial\rho/\partial Q$ are evaluated at $(N_T - PQ, Q)$.

Let Q^* satisfy $\rho(N_0, Q) = u(Q)Q$. Note that Q^* is always well-defined. If $u(\hat{Q}) < \delta$, then it follows from Proposition 2.1 that $\rho(N_T, Q_1) < \delta Q_1$ if Q_1 exists. Therefore if $u(\hat{Q}) < \delta$ and Q_1 exists, we have either $\rho(N_T, Q_1) < \rho(N_0, Q_1) < \delta Q_1$ or $\rho(N_T, Q_1) < \delta Q_1 < \rho(N_0, Q_1)$. The global dynamics of (2.3) is given in the following theorem.

Theorem 2.2 *The dynamics of (2.3) can be summarized as the following.*

- (1) *Let $N_T \leq N_0$. In addition if*
 - (a) *$u(\hat{Q}) < \delta$, then E_0 is the only steady state and every solution of (2.3) converges to E_0 .*
 - (b) *$u(\hat{Q}) > \delta$, then E_0, E_{11} both exist and every solution of (2.3) with $P(0) > 0$ converges to E_{11} .*
- (2) *Let $N_T > N_0$ and $u(\hat{Q}) > \delta$. Then steady states E_0, E_{11} both exist and every solution of (2.3) with $P(0) > 0$ converges to E_{11} .*
- (3) *Let $N_T > N_0$ and $u(\hat{Q}) < \delta$.*
 - (a) *If Q_1 does not exist, then E_0 is the only steady state and every solution converges to E_0 .*
 - (b) *If Q_1 exists and $\rho(N_T, Q_1) < \rho(N_0, Q_1) < \delta Q_1$, then E_0 is the only steady state and every solution converges to E_0 .*
 - (c) *If Q_1 exists and $\rho(N_T, Q_1) < \delta Q_1 < \rho(N_0, Q_1)$, then there are two positive steady states $E_{1i} = (P_i, Q_1)$, $1 \leq i \leq 2$. The stable manifold of E_{12} separates F into two disjoint subsets F_1 and F_2 such that E_0 is a global attractor in F_1 and E_{11} is a global attractor in F_2 .*

Proof. (1) This case has been previously studied in [9, 10]. Since (2.3) is a dissipative planar system, the proof is straightforward. Note that E_{11} exists if and only if $u(\hat{Q}) > \delta$ by Proposition 2.1 and as $\partial\dot{P}/\partial P + \partial\dot{Q}/\partial Q =$

$-\delta - P\partial\rho/\partial N + \partial\rho/\partial Q - u'(Q)Q < 0$ for $(P, Q) \in F$, it follows from the Dulac criterion that there is no periodic solution in F if $u(\hat{Q}) > \delta$. This completes the proof of (1)

(2) If $N_T > N_0$ and $u(\hat{Q}) > \delta$, then $\rho(N_T, Q_1) > \delta Q_1$ by Proposition 2.1 and thus there exists a unique positive steady state $E_{11} = (P_1, Q_1)$. Define a subset Γ of F by $\Gamma = \{(P, Q) \in F : Q < Q^*, N_T - PQ < N_0\}$. Observe that $Q_1 < \hat{Q} < Q^*$ and $E_{11} \in \Gamma$.

Furthermore, as $\dot{Q}|_{Q=Q^*} = \rho(N_T - PQ^*, Q^*) - u(Q^*)Q^* \leq \rho(N_0, Q^*) - u(Q^*)Q^* = 0$ for all $P \geq 0$ and $(\dot{P}Q)|_{PQ=N_T-N_0, Q<Q^*} = P[-\delta Q + \rho(N_T - PQ, Q)]|_{PQ=N_T-N_0, Q<Q^*} = P[\rho(N_0, Q) - \delta Q]|_{PQ=N_T-N_0, Q<Q^*} > P[\rho(N_0, Q^*) - \delta Q^*]|_{PQ=N_T-N_0, Q<Q^*} = P[u(Q^*)Q^* - \delta Q^*]|_{PQ=N_T-N_0, Q<Q^*} > 0$, solutions of (2.3) with $P(0) > 0$ enter Γ in finite time and remain there for all future time. Consequently, as $\partial\dot{P}/\partial P + \partial\dot{Q}/\partial Q < 0$ for $(P, Q) \in \Gamma$, the Dulac criterion implies that there is no periodic solution in Γ . We conclude that E_{11} is a global attractor in $F \setminus Q$ -axis.

(3) (a) If Q_1 does not exist, then E_0 is the only steady state. Since (2.3) is dissipative, it follows from the Poincaré-Bendixson Theorem that E_0 is a global attractor.

(b) In this case $\rho(N_T - PQ_1, Q_1) \leq \rho(N_0, Q_1) < \delta Q_1$ for all $P \geq 0$, there is no positive steady state and thus E_0 is a global attractor for (2.3).

(c) Notice that both positive steady states $E_{11} = (P_1, Q_1)$ and $E_{12} = (P_2, Q_1)$ exist. Also E_0 and E_{11} are local attractors and E_{12} is a saddle point. The stable manifold of E_{12} separates F into two disjoint subsets F_1 and F_2 such that $E_0 \in F_1$ and $E_{11} \in F_2$. Since there is no positive steady state in F_1 , E_0 is a global attractor in F_1 . In the following we show that E_{11} is a global attractor in F_2 .

Let Q^* be defined as above. Clearly, $Q^* > \hat{Q}$. If $Q^* \leq Q_1$, then $\rho(N_T - P_1Q_1, Q_1) = u(Q_1)Q_1 \geq u(Q^*)Q^* = \rho(N_0, Q^*) \geq \rho(N_0, Q_1) > \rho(N_T - P_1Q_1, Q_1)$, a contradiction. Thus $\hat{Q} < Q_1 < Q^*$. Let $\Gamma_1 = \{(P, Q) \in F_2 : Q < Q^*, PQ > N_T - N_0\}$. Then $E_{11} \in \Gamma_1$. Observe that $\dot{Q}|_{Q=Q^*} = \rho(N_T - PQ^*, Q^*) - u(Q^*)Q^* \leq 0$ for all $P \geq 0$ and $(\dot{P}Q)|_{PQ=N_T-N_0, Q<Q^*} = P[\rho(N_0, Q) - \delta Q]|_{PQ=N_T-N_0, Q<Q^*} > P[\rho(N_0, Q^*) - \delta Q^*]|_{PQ=N_T-N_0, Q<Q^*} > 0$. Any solution of (2.3) with initial condition in F_2 enters Γ_1 in finite time and remains there for all future time. Furthermore, the Dulac criterion can be applied to show that there is no periodic solution in Γ_1 . Therefore, any solution of (2.3) with initial condition in F_2 converges to E_{11} . \blacksquare

We now define a threshold $R_0 = \frac{u(\hat{Q})}{\delta}$. If $R_0 > 1$, then with or without inhibition, the prey population can survive. If $R_0 < 1$ and without inhibition, the prey population becomes extinct. However, with inhibition and $R_0 < 1$, it was shown in (3)(c) of Theorem 2.2 that there exist initial populations for which the prey can stabilize in a positive equilibrium fashion.

The result of Theorem 2.2 (3)(c) is very interesting. In addition to the stable boundary equilibrium $E_0 = (0, \hat{Q})$, there are two interior equilibria $E_{1i} = (P_i, Q_1)$, $i = 1, 2$. Equilibrium E_{11} is always locally asymptotically stable with $N_T - P_1Q_1 < N_0$ and $\frac{\partial \rho}{\partial N}(N_T - P_1Q_1, Q_1) > 0$. Therefore, the nutrient stimulates uptake at E_{11} . On the other hand, equilibrium E_{12} is always unstable with $N_T - P_2Q_1 > N_0$ and $\frac{\partial \rho}{\partial N}(N_T - P_2Q_1, Q_1) < 0$. Thus the nutrient inhibits uptake at E_{12} . The stable manifold of E_{12} (as is illustrated in Figure 2) becomes the threshold initial density for population persistence. The prey can survive in a steady state fashion if the initial population density is above the threshold. Otherwise, the prey population is too small to detoxify its environment and consequently becomes extinct. The inhibition of nutrient thus has an inverse density dependent effect on the prey population and the persistence threshold is no longer a single number. This complicated threshold behavior is due to the physiological adjustments of cell quota and uptake rate which are made in the variable-yield model.

In the following, we illustrate this particular mechanism. Figure 1 provides the graphs of $\rho(N, Q)$ as a function of N for different values of Q when $Q = Q_0$, $Q = \hat{Q}$, $Q = Q_1$ and $Q = Q^*$. The vertical lines $N = N_0$, $N = N_T$ and the horizontal line $y = \delta Q_1$ are also drawn to identify three possible equilibria E_0 , E_{11} and E_{12} . At E_{12} , the physiological adjustment for equilibrium occurs in an inhibited inverse density dependent population, so that E_{12} is unstable. At E_{11} , the physiological adjustment takes place in a density dependent population, which makes E_{11} stable. Therefore, if the initial population is too small to detoxify its habitat, the population approaches E_{12} , but is unable to complete its adjustment and is thus tends toward $E_0 = (0, \hat{Q})$. As $u(\hat{Q}) < \delta$, the prey population is doomed to extinction.

3 A nutrient-prey-predator model

In this section we study the dynamics of a variable-yield nutrient-prey-predator model with inhibition. We assume that the predator's uptake rate is modelled by a Lotka-Volterra functional response. Let b be the maximal predator ingestion rate, d the predator net nutrient conversion rate and ϵ the predator death rate. Clearly, $d \leq b$. The model derivation here is parallel to that of the monotone case in [12]. We assume that the ecosystem is closed. In particular, the prey which is removed through predator's predation becomes either a part of the available external nutrient or predator's biomass. The interplay between external nutrient, prey and predator can be described by the following ordinary differential equations

$$\begin{aligned}\dot{N} &= -P\rho(N, Q) + \delta PQ + \epsilon Z + (b - d)PQZ \\ \dot{P} &= P[u(Q) - \delta] - bPZ \\ \dot{Z} &= Z(dPQ - \epsilon).\end{aligned}\tag{3.1}$$

As the system is closed, i.e., $P(t)Q(t) + Z(t) + N(t) = N_T$ for all $t \geq 0$, we can derive an equation for the cell quota $\hat{Q} = \rho(N, Q) - u(Q)Q$ as we did in section 2. Consequently, the four dimensional system is equivalent to the following three dimensional system

$$\begin{aligned}\dot{P} &= P[u(Q) - \delta - bZ] \\ \dot{\hat{Q}} &= \rho(N_T - PQ - Z, Q) - u(Q)Q \\ \dot{Z} &= Z(dPQ - \epsilon).\end{aligned}\tag{3.2}$$

In addition to (H2), we make the following technical assumption:

$$(H3) \quad \rho(N_T - \epsilon/d, Q_0) < \delta Q_0 \text{ if } N_T > \epsilon/d.$$

Let $\Omega = \{(P, Q, Z) \in R_+^3 : Q \geq Q_0, PQ + Z \leq N_T\}$ and Q^* satisfy $\rho(N_0, Q) = u(Q)Q$. Then Ω is positively invariant for (3.2) and in fact $\hat{\Omega} = \{(P, Q, Z) \in \Omega : P \leq \frac{N_T}{Q_0}, Z \leq N_T, Q \leq Q^*\}$ is a compact global attractor for system (3.2) if $N_T \geq N_0$ and $K = \{(P, Q, Z) \in \Omega : P \leq \frac{N_T}{Q_0}, Z \leq N_T, Q \leq \hat{Q}\}$ is a compact global attractor for (3.2) if $N_T < N_0$.

As predator has no effect on the boundary steady states, the existence conditions for steady states $E_0 = (0, \hat{Q}, 0)$, $E_{11} = (P_1, Q_1, 0)$ and $E_{12} =$

$(P_2, Q_1, 0)$ are the same as previous section. For the existence of a positive steady state $(\bar{P}, \bar{Q}, \bar{Z})$, it is necessary that $N_T > \epsilon/d$, where \bar{Q} must satisfy

$$\rho(N_T - \epsilon/d - \frac{u(Q) - \delta}{b}, Q) = u(Q)Q. \quad (3.3)$$

Note that (3.3) is always solvable for Q . But since $\rho(N, Q)$ is not monotone in N , \bar{Q} may not be unique. Moreover, a positive steady state $E_2 = (\bar{P}, \bar{Q}, \bar{Z})$ exists if and only if $u(\bar{Q}) > \delta$. In which case $\bar{P} = \frac{\epsilon}{d\bar{Q}}$ and $\bar{Z} = \frac{u(\bar{Q}) - \delta}{b}$.

The Jacobian matrix of (3.2) has the following form

$$\begin{pmatrix} u(Q) - \delta - bZ & Pu'(Q) & -bP \\ -Q\partial\rho/\partial N & -P\partial\rho/\partial N + \partial\rho/\partial Q - u(Q) - u'(Q)Q & -\partial\rho/\partial N \\ dQZ & dPZ & dPQ - \epsilon \end{pmatrix},$$

where $\partial\rho/\partial N$ and $\partial\rho/\partial Q$ are evaluated at $(N_T - PQ - Z, Q)$. In particular, the Jacobian matrix at E_0 is given by

$$\begin{pmatrix} u(\hat{Q}) - \delta & 0 & 0 \\ -\hat{Q}\partial\rho/\partial N & \partial\rho/\partial Q - u(\hat{Q}) - u'(\hat{Q})\hat{Q} & -\partial\rho/\partial N \\ 0 & 0 & -\epsilon \end{pmatrix},$$

where $\partial\rho/\partial N$ and $\partial\rho/\partial Q$ are evaluated at (N_T, \hat{Q}) and the Jacobian matrix at E_{1i} is given by

$$\begin{pmatrix} 0 & P_i u'(Q_1) & -bP_i \\ -Q_1 \partial\rho/\partial N & -P_i \partial\rho/\partial N + \partial\rho/\partial Q - u(Q_1) - u'(Q_1)Q_1 & -\partial\rho/\partial N \\ 0 & 0 & dP_i Q_1 - \epsilon \end{pmatrix},$$

where $\partial\rho/\partial N$ and $\partial\rho/\partial Q$ are evaluated at $(N_T - P_i Q_1, Q_1)$ for $1 \leq i \leq 2$. Consequently, it is easy to see that E_0 is a local attractor if $u(\hat{Q}) < \delta$. If $u(\hat{Q}) > \delta$, then E_0 is a saddle point with stable manifold lying in the Q - Z -plane. E_{11} is a local attractor if $P_1 Q_1 < \epsilon/d$. If $P_1 Q_1 > \epsilon/d$, then E_{11} is a saddle point which is unstable in the positive direction orthogonal to the P - Q -plane. Moreover, E_{12} is always a saddle point. The stable manifold of E_{12} is two dimensional if $P_2 Q_1 < \epsilon/d$ and is one dimensional if $P_2 Q_1 > \epsilon/d$.

System (3.2) is said to be *persistent* if $\liminf_{t \rightarrow \infty} P(t) > 0$, $\liminf_{t \rightarrow \infty} Q(t) > Q_0$ and $\liminf_{t \rightarrow \infty} Z(t) > 0$ for any solution $(P(t), Q(t), Z(t))$ of (3.2) with $P(0) > 0$, $Q(0) > Q_0$ and $Z(0) > 0$. (3.2) is said to be *uniformly persistent* if

there exists $\hat{a} > 0$ such that for any solution of (3.2) with $P(0) > 0$, $Q(0) > Q_0$ and $Z(0) > 0$ we have $\liminf_{t \rightarrow \infty} P(t) \geq \hat{a}$, $\liminf_{t \rightarrow \infty} Q(t) \geq \hat{a}$ and $\liminf_{t \rightarrow \infty} Z(t) \geq \hat{a}$.

If $N_T \leq N_0$, then since $\partial\rho/\partial N > 0$ for $0 \leq N < N_T$, $Q \geq Q_0$, there is no inhibition effect. The dynamics of (3.2) is given by the following theorem which is cited from [12, Theorem 2.3, 2.4 and 2.5].

Theorem 3.1 *If $N_T \leq N_0$, then the dynamics of (3.2) can be summarized as the following.*

- (1) *If $u(\hat{Q}) < \delta$, then $E_0 = (0, \hat{Q}, 0)$ is the only steady state and it is a global attractor for (3.2).*
- (2) *If $u(\hat{Q}) > \delta$, then $E_0 = (0, \hat{Q}, 0)$ and $E_{11} = (P_1, Q_1, 0)$ both exist. If in addition $P_1 Q_1 < \epsilon/d$, then there is no positive steady state and every solution of (3.2) with $P(0) > 0$ converges to E_{11} . If $P_1 Q_1 > \epsilon/d$, then there exists a unique positive steady state which is a local attractor. Moreover, system (3.2) is uniformly persistent.*

If $N_T > N_0$, we separate our discussion into $u(\hat{Q}) > \delta$ and $u(\hat{Q}) < \delta$. We first discuss the case when $u(\hat{Q}) > \delta$.

Theorem 3.2 *If $N_T > N_0$ and $u(\hat{Q}) > \delta$, then $E_0 = (0, \hat{Q}, 0)$ and $E_{11} = (P_1, Q_1, 0)$ both exist.*

- (1) *If $P_1 Q_1 < \epsilon/d$, then there is no positive steady state and every solution of (3.2) with $P(0) > 0$ converges to E_{11} .*
- (2) *If $P_1 Q_1 > \epsilon/d$, then system (3.2) is uniformly persistent.*

Proof. It follows from Proposition 2.1 that Q_1 exists and $\rho(N_T, Q_1) > \delta Q_1$. Thus $E_{11} = (P_1, Q_1, 0)$ is the only steady state on the positive P - Q plane, where $N_T - P_1 Q_1 < N_0$. Moreover, since $u(\hat{Q}) > \delta$, E_0 is a saddle point with stable manifold lying in the positive Q - Z plane.

(1) If $P_1 Q_1 < \epsilon/d$, then E_{11} is a local attractor. We first show that there is no positive steady state. Clearly if $N_T \leq \epsilon/d$, then there is no positive steady state. We assume $N_T > \epsilon/d$ and let \bar{Q} satisfy (3.3). If $\bar{Q} > Q_1$, then since $N_T - P_1 Q_1 < N_0$ and $P_1 Q_1 < \epsilon/d$, $N_T - \epsilon/d < N_0$. Consequently, $u(\bar{Q})\bar{Q} = \rho(N_T - \epsilon/d - \frac{u(\bar{Q}) - \delta}{b}, \bar{Q}) \leq \rho(N_T - P_1 Q_1, \bar{Q}) \leq$

$\rho(N_T - P_1Q_1, Q_1) = u(Q_1)Q_1$, a contradiction. We conclude that there is no positive steady state. On the other hand, since the positive P - Q plane is positively invariant, by using an argument as in the proof of Theorem 2.2, it can be shown that E_{11} is a global attractor in the positive P - Q plane. It remains to show that solutions of (3.2) with $P(0) > 0$ converge to E_{11} .

Observe that if $N_T \leq \epsilon/d$, then $\dot{Z}(t) \leq 0$ for $t \geq 0$ and thus $\lim_{t \rightarrow \infty} Z(t) = z^* \geq 0$. If $z^* > 0$, then since $\lim_{t \rightarrow \infty} \dot{Z}(t) = 0$, $\lim_{t \rightarrow \infty} P(t)Q(t) = \epsilon/d$, an immediate contradiction. Thus $\lim_{t \rightarrow \infty} Z(t) = 0$ and (1) is shown. Otherwise, let $\tilde{\Omega} = \{(P, Q, Z) \in \Omega : P > 0\}$ and partition $\tilde{\Omega}$ into three pairwise disjoint subsets: $\tilde{\Omega}_1 = \{(P, Q, Z) \in \tilde{\Omega} : PQ < \epsilon/d\}$, $\tilde{\Omega}_2 = \{(P, Q, Z) \in \tilde{\Omega} : PQ = \epsilon/d\}$ and $\tilde{\Omega}_3 = \{(P, Q, Z) \in \tilde{\Omega} : PQ > \epsilon/d\}$. If there exists a trajectory which remains in $\tilde{\Omega}_3$ for all large time, then $\dot{Z}(t) \geq 0$ for all t large and thus $\lim_{t \rightarrow \infty} Z(t) = z^* \geq 0$. Since $\dot{Z}(t)$ is bounded above, $\lim_{t \rightarrow \infty} \dot{Z}(t) = 0$. Thus if $z^* > 0$, then $\lim_{t \rightarrow \infty} P(t)Q(t) = \epsilon/d$, i.e., the ω -limit set of such a trajectory lies in the set $C = \{(P, Q, z^*) \in \tilde{\Omega} : PQ = \epsilon/d\}$. We need to show that the only nonempty invariant, connected subset in C is a point.

Indeed, let \tilde{C} be an arbitrary invariant, connected subset of C such that (\hat{p}, \hat{q}, z^*) and $(\tilde{p}, \tilde{q}, z^*) \in \tilde{C}$. We may assume $\hat{p} < \tilde{p}$ and thus $\hat{q} > \tilde{q}$. Hence any p, q with $\hat{p} < p < \tilde{p}$, $\hat{q} > q > \tilde{q}$ and $pq = \epsilon/d$, (p, q, z^*) is also in \tilde{C} by connectedness. However, $0 = (\dot{P}Q)|_{PQ=\epsilon/d, Z=z^*} = P[-\delta Q - bQZ + \rho(N_T - PQ - Z, Q)]|_{PQ=\epsilon/d, Z=z^*}$ if and only if $\rho(N_T - \epsilon/d - z^*, Q) = \delta Q + bQz^*$. This latter equation has at most one solution. We conclude that \tilde{C} consists of at most one point. Since the ω -limit set is nonempty and there is no positive steady state, $z^* = 0$. But then such a trajectory would converge to E_{11} . We thus obtain a contradiction and conclude that no trajectory remains in $\tilde{\Omega}_3$ for all large time.

Suppose a trajectory crosses $\tilde{\Omega}_2$ at time t_0 . Since $N_T - \epsilon/d < N_T - P_1Q_1 < N_0$, $(PQ)(t_0) = [P\rho(N_T - PQ - Z, Q) - \delta PQ - bPQZ](t_0) \leq P[\rho(N_T - PQ - Z, Q) - \delta Q](t_0) = P[\rho(N_T - \epsilon/d - Z, Q) - \delta Q](t_0) \leq P[\rho(N_T - \epsilon/d, Q) - \delta Q](t_0) < 0$ for all $Q \geq Q_0$ by (H3), such a trajectory enters $\tilde{\Omega}_1$ and remains there for all future time. Consequently, $\dot{Z}(t) \leq 0$ for all t large and $\lim_{t \rightarrow \infty} Z(t) = z^* \geq 0$. Similar argument as in the previous paragraph can be applied to show that $z^* = 0$ and hence E_{11} is a global attractor in $\tilde{\Omega}$.

(2) To show uniform persistence of system (3.2), we apply criterion derived by Thieme [28]. Let $X_1 = \{(P, Q, Z) \in \Omega : P > 0, Q > Q_0, Z > 0\}$ and $X_2 = \Omega \setminus X_1$. Then X_1 is open and positively invariant for (3.2). By using the Jacobian matrix at E_{11} and the fact that $P_1Q_1 > \epsilon/d$, E_{11} is unstable

in the positive direction orthogonal to the P - Q plane. A result of Freedman and Waltman [29] shows that system (3.2) is persistent, i.e., X_2 is a strong repeller for X_1 and hence a weak repeller for X_1 . Since (3.2) has a compact global attractor $\hat{\Omega}$, applying Theorem 4.4 of Thieme [28] and conclude that X_2 is a uniform weak repeller for X_1 . Proposition 1.2 of Thieme [28] can then be used to show that X_2 is a uniform strong repeller for X_1 . Therefore, we conclude that system (3.2) is uniformly persistent. \blacksquare

We next consider the case when $N_T > N_0$ and $u(\hat{Q}) < \delta$. Proposition 2.1 implies that $\rho(N_T, Q_1) < \delta Q_1$ if Q_1 exists. Therefore if Q_1 exists, then either $\rho(N_T, Q_1) < \rho(N_0, Q_1) < \delta Q_1$ or $\rho(N_T, Q_1) < \delta Q_1 < \rho(N_0, Q_1)$ can occur.

Theorem 3.3 *If $N_T > N_0$ and $u(\hat{Q}) < \delta$. The dynamics of (3.2) can be summarized as the following.*

- (1) *If Q_1 does not exist, then E_0 is the only steady state and it is a global attractor.*
- (2) *If Q_1 exists and such that $\rho(N_T, Q_1) < \rho(N_0, Q_1) < \delta Q_1$, then E_0 is the only steady state and it is a global attractor.*
- (3) *If Q_1 exists and such that $\rho(N_T, Q_1) < \delta Q_1 < \rho(N_0, Q_1)$, then $E_{11} = (P_1, Q_1, 0)$ and $E_{12} = (P_2, Q_1, 0)$ both exist. If in addition $P_1 Q_1 < \epsilon/d$, then except a set of initial conditions of Lebesgue measure 0, solutions of (3.2) either converge to E_0 or to E_{11} .*

Proof. Since $u(\hat{Q}) < \delta$, E_0 is a local attractor.

(1) In this case $u(Q) < \delta$ for all $Q \geq Q_0$ and thus $\dot{P}(t) \leq 0$ for all $t \geq 0$. Hence $\lim_{t \rightarrow \infty} P(t) = p^* \geq 0$ exists. Since $\dot{P}(t)$ is bounded below, $\lim_{t \rightarrow \infty} \dot{P}(t) = 0$. Hence if $p^* > 0$, then it follows from system (3.2) and the assumption of (1) that $\lim_{t \rightarrow \infty} Q(t) = \infty$. We arrive at a contradiction. Thus $\lim_{t \rightarrow \infty} P(t) = 0$ and hence $\lim_{t \rightarrow \infty} Z(t) = 0$, i.e., E_0 is a global attractor for (3.2).

(2) If $\rho(N_T, Q_1) < \rho(N_0, Q_1) < \delta Q_1$, then $\rho(N_T - PQ_1, Q_1) \leq \rho(N_0, Q_1) < \delta Q_1$ and there is no steady state of the form $(P, Q, 0)$. Let Q^* satisfy $\rho(N_0, Q) = u(Q)Q$. If $Q^* \geq Q_1$, then $\rho(N_0, Q^*) = u(Q^*)Q^* \geq u(Q_1)Q_1 = \delta Q_1 > \rho(N_0, Q_1) \geq \rho(N_0, Q^*)$, a contradiction. Hence if $N_T > \epsilon/d$ and \bar{Q} satisfies (3.3), then since $\rho(N_T - \epsilon/d - \frac{u(Q) - \delta}{b}, Q) \leq \rho(N_0, Q)$ for all $Q \geq Q_0$,

$\bar{Q} \leq Q^* < Q_1$, i.e., $u(\bar{Q}) < \delta$. We conclude that (3.2) has no positive steady state.

To show that E_0 is a global attractor for (3.2), we partition Ω into three pairwise disjoint subsets: $\Omega_1 = \{(P, Q, Z) \in \Omega : Q < Q_1\}$, $\Omega_2 = \{(P, Q, Z) \in \Omega : Q = Q_1\}$ and $\Omega_3 = \{(P, Q, Z) \in \Omega : Q > Q_1\}$. If there exists a trajectory which remains in Ω_3 for all large time, then $\dot{Q} = \rho(N_T - PQ - Z, Q) - u(Q)Q < \rho(N_T - PQ - Z, Q_1) - u(Q_1)Q_1 \leq \rho(N_0, Q_1) - \delta Q_1 < 0$ for all large time. Hence $\lim_{t \rightarrow \infty} Q(t) = q^* \geq Q_1$ exists. Since $\ddot{Q}(t)$ is bounded below, $\lim_{t \rightarrow \infty} \dot{Q}(t) = 0$. But as $\dot{Q}(t) < \rho(N_0, Q_1) - \delta Q_1 < 0$ we obtain a contradiction. Therefore, no trajectory remains in Ω_3 for all large time. Suppose there exists $t_0 \geq 0$ such that $Q(t_0) = Q_1$. Then $\dot{Q}(t_0) < \rho(N_0, Q_1) - \delta Q_1 < 0$. Such a trajectory enters Ω_1 and remains there for all future time. A similar argument as in (1) can then be applied to show that E_0 is a global attractor.

(3) There are two steady states of the form $E_{11} = (P_1, Q_1, 0)$ and $E_{12} = (P_2, Q_1, 0)$. If $P_1 Q_1 < \epsilon/d$, then E_{11} is a local attractor and E_{12} is a saddle point with two dimensional stable manifold. Similar analysis as in the proof of Theorem 3.2 can be used to show that there is no positive steady state. To show our desired result, it is enough to show that $\lim_{t \rightarrow \infty} Z(t) = 0$ for all solution of (3.2). The idea of the proof is similar to that (1) of Theorem 3.2.

Clearly if $N_T \leq \epsilon/d$, then $\lim_{t \rightarrow \infty} Z(t) = 0$. We now assume $N_T > \epsilon/d$. We partition Ω into three pairwise disjoint subsets: $\Delta_1 = \{(P, Q, Z) \in \Omega : PQ < \epsilon/d\}$, $\Delta_2 = \{(P, Q, Z) \in \Omega : PQ = \epsilon/d\}$ and $\Delta_3 = \{(P, Q, Z) \in \Omega : PQ > \epsilon/d\}$. If there exists a trajectory which remains in Δ_3 for all large time, then $\dot{Z}(t) \geq 0$ for all large time and thus $\lim_{t \rightarrow \infty} Z(t) = z^* \geq 0$ exists. If $z^* > 0$, then $\lim_{t \rightarrow \infty} P(t)Q(t) = \epsilon/d$, i.e., the ω -limit set of this trajectory lies in $C = \{(P, Q, z^*) \in \Omega : PQ = \epsilon/d\}$. We can show that the only nonempty invariant, connected subset in C is a point. Since there is no positive steady state, $z^* = 0$. But then we obtain a contradiction. Similarly, if there exists $t_0 > 0$ such that $P(t_0)Q(t_0) = \epsilon/d$, then it can be shown that $(\dot{P}Q)(t_0) < 0$. We conclude that every trajectory of (3.2) will enter Δ_1 and remain there for all large time. Hence, $\lim_{t \rightarrow \infty} Z(t) = 0$ is shown. Note that restricted on the boundary where $Z = 0$, (3.2) becomes (2.3). Therefore, except a set of initial conditions of Lebesgue measure 0, every trajectory of (3.4) either converges to E_0 or to E_{11} by Theorem 2.2 (3)(c). ■

Note that Theorem 3.3 does not discuss the cases for which $P_2 Q_1 < \epsilon/d < P_1 Q_1$ or $\epsilon/d < P_2 Q_1$. As $u(\hat{Q}) < \delta$, E_0 is a local attractor. We can immediately conclude that system (3.2) is not persistent. Numerical example

in the next section reveals that the system is indeed not persistent for either of these cases.

As in section 2, we let $R_0 = \frac{u(\hat{Q})}{\delta}$. If $N_T \leq N_0$ and $R_0 < 1$, the prey population becomes extinct as was shown in Theorem 3.1. For $N_T > N_0$ and $R_0 < 1$, if either $u(Q) < \delta$ for $Q \geq Q_0$ or Q_1 exists and $\rho(N_0, Q_1) < \delta Q_1$, then the prey population become extinct and so does the predator. Otherwise, there are two steady states $E_{11} = (P_1, Q_1, 0)$ and $E_{12} = (P_2, Q_1, 0)$ and we can define two more thresholds $R_{1i} = \frac{dP_i Q_1}{\epsilon}$, $1 \leq i \leq 2$. It is known that $R_{12} < R_{11}$. If $R_{11} < 1$, then predator can not survive and there are initial conditions for which the prey population can stabilize in an equilibrium fashion. That is, the inhibition allows the prey to survive at a concentration level which is too low for predator survival. In the next section, numerical simulations will demonstrate that if either $R_{12} < 1 < R_{11}$ or $R_{12} > 1$, the system is not persistent.

If $R_0 > 1$, since there is only one steady state of the form $(P, Q, 0)$, we define threshold $R_1 = \frac{dP_1 Q_1}{\epsilon}$. If $R_1 < 1$, then only the prey population can survive. However, if $R_1 > 1$, both prey and predator can exist in coexistence with each other in either the inhibited or the uninhibited environment.

4 Numerical Simulations

A very preliminary numerical study of model (3.2) is given in [30]. In this section we provide a more detailed numerical simulation. In fact, we use numerical examples to illustrate analytical results of Theorem 2.2, Theorem 3.2 and Theorem 3.3.

We adopt growth rate u and uptake rate ρ taken from Grover [26, 27] and incorporated with inhibition

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

$$\rho(N, Q) = \rho_{\max}(Q) \frac{N}{N^2 + N + 4}, \quad (4.2)$$

where $\rho_{\max}(Q) = \rho_{\max}^{\text{high}} - (\rho_{\max}^{\text{high}} - \rho_{\max}^{\text{low}}) \frac{(Q - Q_{\min})_+}{Q_{\max} - Q_{\min}}$ and $(Q - Q_{\min})_+$ denotes the positive part of $Q - Q_{\min}$, i.e., $(Q - Q_{\min})_+ = Q - Q_{\min}$ if $Q \geq Q_{\min}$ and $(Q - Q_{\min})_+ = 0$ if $Q < Q_{\min}$. Specific parameter values are $\rho_{\max}^{\text{high}} = 15$, $\rho_{\max}^{\text{low}} = 0.9$, $k = 2$, $Q_{\min} = 3$, $Q_{\max} = 30$ and $u_{\max} = 2.16$. From (4.2), it is known that the toxic level N_0 is 2. The nutrient-prey model is then given by

$$\begin{aligned}\dot{P} &= P[2.16 \frac{(Q-3)_+}{2+(Q-3)_+} - \delta] \\ \dot{Q} &= [15 - 0.522(Q-3)_+] \frac{N_T - PQ}{(N_T - PQ)^2 + (N_T - PQ) + 4} - 2.16 \frac{(Q-3)_+ Q}{2+(Q-3)_+}.\end{aligned}\tag{4.3}$$

We use parameter values $\delta = 0.35$ and $N_T = 15$. Then $\hat{Q} = 3.294274$ and $u(\hat{Q}) = 0.2771 < \delta = 0.35$. Moreover, $Q_1 = 3.3867$ exists with $\rho(N_T, Q_1) = 0.9097 < \delta Q_1 = 1.1854 < \rho(N_0, Q_1) = 2.9596$. Thus $E_0 = (0, \hat{Q})$, $E_{11} = (P_1, Q_1)$ and $E_{12} = (P_2, Q_1)$ all exist with $P_1 = 4.3229$ and $P_2 = 1.1443$. Fig.2 shows that the stable manifold of E_{12} separates $\tilde{F} = \{(P, Q) \in R_+^2 : PQ \leq 15\}$ into disjoint subsets \tilde{F}_1 and \tilde{F}_2 such that solutions with initial conditions in \tilde{F}_1 converge to E_0 and solutions with initial conditions in \tilde{F}_2 converge to E_{11} . Therefore the separatrix shown in Figure 2 becomes the threshold for population persistence.

For the nutrient-prey-predator model, the system is given below

$$\begin{aligned}\dot{P} &= P[2.16 \frac{(Q-3)_+}{2+(Q-3)_+} - \delta - bZ] \\ \dot{Q} &= [15 - 0.522(Q-3)_+] \frac{N_T - PQ - Z}{(N_T - PQ - Z)^2 + (N_T - PQ - Z) + 4} - 2.16 \frac{(Q-3)_+ Q}{2+(Q-3)_+}, \\ \dot{Z} &= Z(dPQ - \epsilon).\end{aligned}\tag{4.4}$$

We use $N_T = 3.5$, $\delta = 0.2$ and $b = 0.8$. In this case, $Q_1 = 3.2041$, $\hat{Q} = 3.8858$, $u(\hat{Q}) = 0.663078 > \delta = 0.2$ and $P_1 = 1.0358$. If we let $\epsilon = 0.35$ and $d = 0.1$, then $P_1 Q_1 = 3.3188 < \frac{\epsilon}{d} = 3.5$. Fig.3(a) shows that solutions with $P(0) > 0$ converge to $E_{11} = (P_1, Q_1, 0)$. If we choose $\epsilon = 0.35$ and $d = 0.8$, then $P_1 Q_1 > \frac{\epsilon}{d} = 0.4375$. Fig.3(b) shows that solutions with positive initial

conditions are eventually trapped in a compact subset which is a positive distance from the boundary.

We next use $N_T = 10$. If $\delta = 0.8$, then $Q_1 = 4.1765$, $\hat{Q} = 3.4249$ and $u(\hat{Q}) = 0.3785 < \delta = 0.8$. Moreover, $\rho(N_T, Q_1) = 1.3002 < \rho(N_0, Q_1) = 2.8771 < \delta Q_1 = 3.3412$. Fig.4(a) demonstrates that solutions converge to $E_0 = (0, \hat{Q}, 0)$. If we choose $\delta = 0.4$, then $Q_1 = 3.4545$ and $\rho(N_T, Q_1) = 1.2950 < \delta Q_1 = 1.3818 < \rho(N_0, Q_1) = 2.9525$. Thus $E_{11} = (P_1, Q_1, 0)$ and $E_{12} = (P_2, Q_1, 0)$ both exist with $P_1 = 2.7696$ and $P_2 = 0.2167$. If $\epsilon = 0.97$ and $d = 0.1$, then $P_1 Q_1 = 9.5676 < \frac{\epsilon}{d} = 9.7$. Fig.4(b) illustrates that solutions either converge to E_0 or to E_{11} .

Finally, we let $N_T = 10$, $\delta = 0.4$ and $b = 0.1$. If $\epsilon = 0.41$ and $d = 0.05$, then $P_2 Q_1 = 0.7486 < \frac{\epsilon}{d} = 8.2 < P_1 Q_1 = 9.5676$. There exists a unique positive steady state $E_2 = (2.2608, 3.6270, 1.155)$ and there are trajectories which converge to E_2 . However, system (4.4) is not persistent. For example, the solution with $P(0) = 0.6$, $Q(0) = 2.1$ and $Z(0) = 8$ converges to E_0 as is shown in Fig.5(a). Similarly, if we choose $\epsilon = 0.05$ and $d = 0.1$, then $P_1 Q_1 > P_2 Q_1 > \frac{\epsilon}{d} = 0.5$ and system (4.4) is not persistent, as is shown in Fig.5(b). This is in part due to the fact that $u(\hat{Q}) < \delta$ and E_0 is a local attractor.

5 Discussion

A variable-yield simple food chain with a growth inhibiting nutrient is derived and analyzed. The model provides us a better understanding of the impact of inhibition upon the dynamics of a simple nutrient-prey-predator system with internal nutrient storage by prey.

Our analytical results can be interpreted in terms of several thresholds. If $R_0 < 1$, the system in general is not persistent, i.e., there exist solutions with $P(0) > 0$, $Z(0) > 0$ such that either $P(t) \rightarrow 0$ as $t \rightarrow \infty$ and consequently $Z(t) \rightarrow 0$ as $t \rightarrow \infty$ or only $Z(t) \rightarrow 0$ as $t \rightarrow \infty$. In certain cases as was shown in (3) of Theorem 3.3 we can define two more thresholds given by $R_{1i} = \frac{dP_i Q_1}{\epsilon}$. Each R_{1i} can be viewed as the basic reproductive number of predator when prey's population is stabilized at P_i . If $R_{11} < 1$, then there exist initial populations for which the predator becomes extinct but not the prey under the inhibited environment. This inhibition provides prey

an environment to survive at a density level which is too low for predator survival. If either $R_{12} < 1 < R_{11}$ or $1 < R_{12} < R_{11}$, then system (3.2) is not persistent. This is a direct implication of local stability of steady state E_0 . However, computer simulation demonstrates that there do exist initial populations with large prey densities for which both prey and predator become extinct.

If $R_0 > 1$, we can define one more threshold $R_1 = \frac{dP_1Q_1}{\epsilon}$. If $R_1 < 1$, only the prey population can survive. If $R_1 > 1$, the system is uniformly persistent. However, the dynamics are much more complicated than simply converging to a steady state as illustrated in Fig.3(b) of section 4.

Although a simple Lotka-Volterra functional response is used as the predator's uptake rate, our study of a variable-yield simple food chain with non-monotone uptake functions provided here gives us an insight of how inhibition alters the dynamics of a simple food chain without inhibition. The results obtained here can be applied to nutrient-based population models for which inhibition is likely. In particular, they are applicable to toxicology and bioremediation where microbial food chain and consortia are used to detoxify contaminants.

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Footnote

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Figure legends

Figure1: Graphs of functions $\rho(N, Q)$ for $Q = Q_0$, $Q = \hat{Q}$, $Q = Q_1$ and $Q = Q^*$ are plotted against N . Three possible equilibria E_0 , E_{11} and E_{12} are shown as occurs in Theorem 2.2 (3)(c), where E_0 and E_{11} are stable and E_{12} is unstable.

Figure2: Plot of trajectories of system (4.3) using $\delta = 0.35$ and $N_T = 15$. Solutions of (4.3) either converge to $E_0 = (0, 3.294274)$ or to $E_{11} = (4.3229, 3.3867)$ with the exception of the stable manifold of $E_{12} = (1.1443, 3.3867)$.

Figure3: Trajectories of system (4.4) plotted using $N_T = 3.5$, $b = 0.8$ and $\delta = 0.2$. In part (a), $\epsilon = 0.35$ and $d = 0.1$. Solutions of (4.4) with positive initial conditions converge to $E_{11} = (1.0358, 3.2041, 0)$. In part (b), $\epsilon = 0.35$ and $d = 0.8$. Solutions of (4.4) seem to converge to a periodic solution.

Figure4: Plot of trajectories of system (4.4) using $N_T = 10$. In part (a) $\delta = 0.8$ and all solutions converge to $E_0 = (0, 3.4249, 0)$. In part (b), $\delta = 0.4$. Solutions either converge to $E_0 = (0, 3.4249, 0)$ or to $E_{11} = (2.7696, 3.4545, 0)$.

Figure5: Trajectories of system (4.4) plotted using $N_T = 3.5$, $b = 0.8$ and $\delta = 0.2$. In part (a), $\epsilon = 0.35$ and $d = 0.1$. Solutions of (4.4) with positive initial conditions converge to $E_{11} = (1.0358, 3.2041, 0)$. In part (b), $\epsilon = 0.35$ and $d = 0.8$. Solutions of (4.4) seem to converge to a periodic solution.

(a)

(b)

(a)

(b)

(a)

(b)