



A nutrient-prey-predator model with intratrophic predation

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Abstract

A simple food chain which consists of nutrient, prey and predator with intratrophic predation of the predator is proposed and analyzed. The dynamics of the model depend on the basic reproductive numbers of the prey and predator. Intratrophic predation can have impact on the system only if the basic reproductive number of the predator is greater than 1. In this case, the system may have multiple coexisting equilibria. However, intratrophic predation can stabilize the system when such an equilibrium is unique. Moreover, it can elevate the magnitude of the prey population and diminish the level of nutrient concentration of any coexisting equilibrium. © 2002 Elsevier Science Inc. All rights reserved.

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1. Introduction

The mechanism of intratrophic predation has been introduced into population models and its dynamical consequences have been examined by several researchers. These studies originate from a survey paper on evolution and intraspecific predation by Polis [7], who demonstrated that cannibalism is an interesting and important mechanism in population dynamics. Aside from the

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cannibalistic point of view, intratrophic predation can occur in models for which a population consists of several species of organism and one or more species may prey on others.

Articles addressing the effect of cannibalism include for example, Bosch et al. [10] and Cushing [2] and have contributed to the understanding of this biological phenomenon. In these papers, age structured models were constructed and used to study cannibalism. In contrast to the method of structured models, Kohlmeier and Ebenhoh [5] considered a Lotka–Volterra predator–prey model with cannibalistic mechanism. Specifically, the food resource that is available to the predator is modeled as a weighted sum of prey and predator densities. Their numerical results indicated a strong increase of the standing stock of both prey and predator.

More recently, Pitchford and Brindley [6] introduced a general predator–prey model with intratrophic predation. They showed that the addition of intratrophic predation has no effect on the existence and local stability of equilibria with the absence of predator. Moreover, using an asymptotic method by assuming that intratrophic predation is sufficiently small, they demonstrated for the model given by Kohlmeier and Ebenhoh [5] that intratrophic predation always increases the coexisting equilibrium value of the prey and its stability. Therefore, their study confirmed an earlier observation made by Kohlmeier and Ebenhoh [5] that cannibalism has a stabilizing effect.

In this paper we propose a nutrient–prey–predator model to study the effect of intratrophic predation and consequently the impact of cannibalism, as cannibalism is a special case of intratrophic predation. Unlike the two trophic levels considered by previous authors [5,6], we model the food resource of prey explicitly. Therefore, our model consists of three trophic levels. The incorporation of nutrient concentration as a state variable is motivated by the benthic ecosystem in which different zooplankton species may be regarded as a single predator population.

Our primary goal in this study is to investigate the effect of intratrophic predation on the dynamics of the system. In particular, global stability of equilibrium with the absence of predator is fully analyzed. It is demonstrated that intratrophic predation has no effect on the dynamics of the system when the basic reproductive number of the predator is less than 1. However, it can stabilize the coexisting equilibrium and has the effect of elevating magnitude of the prey density of coexisting equilibrium if the basic reproductive number of the predator is greater than 1. Consequently, intratrophic predation diminishes the available nutrient concentration as there is a larger prey population present. On the other hand, our system can be regarded as a chemostat predator–prey model with different death rate when the mechanism of intratrophic predation is absent. As a consequence, our results can also apply to this particular chemostat system.

In Section 2, a mathematical model is presented and its dynamical consequences are discussed. Numerical simulations will also be given in Section 3. Section 4 provides a brief discussion.

2. The model

Let $x(t)$ be the nutrient concentration or the food resource of prey at time t . We assume in the absence of prey, the nutrient is governed by the simple chemostat law, $\dot{x} = k(x^0 - x)$, where k is the input, or the washout rate, and x^0 is the constant input nutrient concentration. Thus in the absence of prey population, the nutrient concentration always stabilizes at the input nutrient concentration level x^0 . This chemostat law is commonly used by researchers to model the dynamics of nutrient concentration in lakes or oceans [3,8].

Let $y(t)$ be the prey population at time t . The uptake of prey is modeled by the Michaelis–Menten kinetic $m_1x/(a_1 + x)$, where a_1 is the half-saturation constant and m_1 the maximal nutrient uptake rate of prey. We let α denote the net nutrient conversion rate and γ the death rate of prey. The predator population at time t is denoted by $z(t)$. Similar to the models given in [5,6], the food resource that is available to the predator is modeled by $y + bz$, where b , $0 \leq b \leq 1$, is the measure of intensity of intratrophic predation. If $b = 0$, there is no intratrophic predation and consequently the prey is the only food resource for the predator. If $b = 1$, the predator regards prey and predator alike and thus preys on both populations indiscriminately.

We use a Holling-II functional response to model the predator's uptake rate, with half-saturation constant a_2 . Let m_2 and δ be the maximal uptake rate and the death rate of predator, respectively, with β the net prey conversion rate. Putting all these assumptions together, our model is given by the following system of ordinary differential equations:

$$\begin{aligned} \dot{x} &= k(x^0 - x) - \frac{m_1xy}{a_1 + x}, \\ \dot{y} &= \frac{\alpha m_1xy}{a_1 + x} - \frac{m_2yz}{a_2 + y + bz} - \gamma y, \\ \dot{z} &= \frac{\beta m_2(y + bz)z}{a_2 + y + bz} - \frac{m_2bz^2}{a_2 + y + bz} - \delta z, \\ x(0), y(0), z(0) &\geq 0, \end{aligned} \tag{2.1}$$

where $k, x^0, m_1, a_1, m_2, a_2, \gamma, \delta > 0, 0 < \alpha, \beta \leq 1$ and $0 \leq b \leq 1$.

The first step in understanding system (2.1) is to show that solutions of the system remain nonnegative and are bounded, so that system (2.1) is biologically meaningful.

Lemma 2.1. *Solutions of (2.1) are nonnegative and bounded.*

Proof. Since $\dot{x}|_{x=0} > 0$, $\dot{y}|_{y=0} = 0$ and $\dot{z}|_{z=0} > 0$, solutions of (2.1) remain non-negative for $t \geq 0$. Furthermore, $\dot{x} + \dot{y} + \dot{z} \leq k(x^0 - x) - \gamma y - \delta z \leq kx^0 - \hat{k}(x + y + z)$, where $\hat{k} = \min\{k, \gamma, \delta\}$. Thus $\limsup_{t \rightarrow \infty} x(t) + y(t) + z(t) \leq kx^0/\hat{k}$, i.e., solutions of (2.1) are bounded. In particular, since $\dot{x}|_{x=x^0} \leq 0$, we see that $x(t) \leq x^0$ for t large. \square

Our next step is to find equilibria of (2.1). It is easy to see that a trivial equilibrium $E_0 = (x^0, 0, 0)$ always exists for (2.1), which is moreover independent of b . A straightforward calculation yields another equilibrium $E_1 = (x_1, y_1, 0)$, where

$$x_1 = a_1\gamma/(\alpha m_1 - \gamma) > 0 \quad \text{and} \quad y_1 = \frac{k(a_1 + x_1)(x^0 - x_1)}{m_1 x_1} > 0$$

provided $\alpha m_1 > \gamma$ and $x_1 < x^0$. Notice that this equilibrium E_1 also does not depend on the parameter b and there exists no steady state on the x - z plane.

To discuss local stability of these equilibria, we turn to the Jacobian matrix of (2.1). The Jacobian matrix J of (2.1) is given by

$$\begin{pmatrix} -k - \frac{m_1 a_1 y}{(a_1 + x)^2} & \frac{-m_1 x}{a_1 + x} & 0 \\ \frac{\alpha m_1 a_1 y}{(a_1 + x)^2} & \frac{\alpha m_1 x}{(a_1 + x)} - \gamma - \frac{m_2 z(a_2 + bz)}{(a_2 + y + bz)^2} & \frac{-m_2 y(a_2 + y)}{(a_2 + y + bz)^2} \\ 0 & \frac{\beta m_2 a_2 z + m_2 b z^2}{(a_2 + y + bz)^2} & d \end{pmatrix},$$

where

$$d = \beta m_2 \frac{(y + 2bz)(a_2 + y + bz) - bz(y + bz)}{(a_2 + y + bz)^2} - \frac{2m_2 bz(a_2 + y + bz) - m_2 b^2 z^2}{(a_2 + y + bz)^2} - \delta.$$

In particular, the Jacobian matrix at E_0 is

$$J(E_0) = \begin{pmatrix} -k & \frac{-m_1 x^0}{a_1 + x^0} & 0 \\ 0 & \frac{\alpha m_1 x^0}{a_1 + x^0} - \gamma & 0 \\ 0 & 0 & -\delta \end{pmatrix},$$

and at E_1 is given by

$$J(E_1) = \begin{pmatrix} -k - \frac{m_1 a_1 y_1}{(a_1 + x_1)^2} & \frac{-m_1 x_1}{a_1 + x_1} & 0 \\ \frac{\alpha m_1 a_1 y_1}{(a_1 + x_1)^2} & 0 & \frac{-m_2 y_1}{a_2 + y_1} \\ 0 & 0 & \frac{\beta m_2 y_1}{a_2 + y_1} - \delta \end{pmatrix}.$$

From these two matrices, we see that E_0 is locally asymptotically stable if $\alpha m_1 x^0 / (a_1 + x^0) < \gamma$ and E_1 is locally asymptotically stable if $m_2 y_1 / (a_2 + y_1) < \delta / \beta$. Clearly, these inequalities do not involve the parameter b . We immediately conclude that intratrophic predation has no effect on the existence and local stability of equilibria for which the predator is absent. This conclusion is consistent with the result obtained by Pitchford and Brindley [6].

We now define two thresholds $R_0 = \alpha m_1 x^0 / (\gamma(a_1 + x^0))$, and $R_1 = \beta m_2 y_1 / (\delta(a_2 + y_1))$ if y_1 exists. In the following, we show that solutions of (2.1) approach equilibrium E_0 independent of b as time gets large if $R_0 < 1$.

Theorem 2.2. *If $R_0 < 1$, then E_0 is the only equilibrium and solutions of (2.1) converge to E_0 for any $0 \leq b \leq 1$.*

Proof. We first show that there exists no steady state other than E_0 . Indeed, if $E_1 = (x_1, y_1, 0)$ exists, then $x_1 < x^0$. This inequality is equivalent to $R_0 > 1$ and we obtain an immediate contradiction. Similarly, if (2.1) has a positive steady state $(\bar{x}, \bar{y}, \bar{z})$, then it follows from the second equation in (2.1) that $\alpha m_1 \bar{x} / (a_1 + \bar{x}) > \gamma$. Then $\bar{x} > x^0$, which is also impossible. We conclude that our assumption of $R_0 < 1$ implies that (2.1) has no steady state other than E_0 .

We now show that E_0 is globally asymptotically stable for (2.1). Observe that $x(t) \leq x^0$ for t large, and thus

$$\dot{y}(t) \leq \left(\frac{\alpha m_1 x^0}{a_1 + x^0} - \gamma \right) y(t)$$

for t large. Since $R_0 < 1$, then $\dot{y}(t) \leq 0$ for t large. Hence $\lim_{t \rightarrow \infty} y(t) = y^* \geq 0$ exists and $\lim_{t \rightarrow \infty} \dot{y}(t) = 0$. If $y^* > 0$, then

$$\lim_{t \rightarrow \infty} \dot{y}(t) \leq \left(\frac{\alpha m_1 x^0}{a_1 + x^0} - \gamma \right) y^* < 0.$$

We obtain a contradiction and conclude that $\lim_{t \rightarrow \infty} y(t) = 0$. Consequently, $\lim_{t \rightarrow \infty} z(t) = 0$ and $\lim_{t \rightarrow \infty} x(t) = x^0$ and the theorem is shown. \square

Threshold R_0 can be regarded as the basic reproductive number of the prey. When $R_0 < 1$, the prey population cannot survive, and consequently the predator also becomes extinct. Therefore, intratrophic predation of the top

predator has no effect on the dynamics of the system if $R_0 < 1$. This is due to the extinction of the prey.

When $R_0 > 1$, $m_1x/(a_1 + x) = \gamma/\alpha$ has a solution $x_1 < x^0$ and thus y_1 exists. Consequently, equilibrium $E_1 = (x_1, y_1, 0)$ exists and an equilibrium of this form is unique. Recall that when $R_0 > 1$ and $R_1 < 1$, E_0 is unstable and E_1 is locally asymptotically stable. In the following we show that E_1 is globally asymptotically stable. Our method is taken from a recent result obtained by Chiu and Hsu [1], where a logistic equation is used to model the growth of the lowest tropic level population. However, their technique can be easily carried over to our system in which a chemostat law is used.

Theorem 2.3. *If $R_0 > 1$ and $R_1 < 1$, then E_0 and E_1 are the only equilibria for (2.1) and solutions $(x(t), y(t), z(t))$ of (2.1) with $y(0) > 0$ satisfy $\lim_{t \rightarrow \infty} (x(t), y(t), z(t)) = E_1$ for $0 \leq b \leq 1$.*

Proof. We first show that (2.1) has no positive steady state. Indeed, if (2.1) has a positive equilibrium $(\bar{x}, \bar{y}, \bar{z})$, then it follows from the second equation of (2.1) that $\bar{x} > x_1$ and thus

$$\bar{y} = \frac{k(a_1 + \bar{x})(x^0 - \bar{x})}{m_1\bar{x}} < \frac{k(a_1 + x_1)(x^0 - x_1)}{m_1x_1} = y_1.$$

On the other hand, y_1 also satisfies

$$\frac{\beta m_2(\bar{y} + b\bar{z})}{a_2 + \bar{y} + b\bar{z}} - \frac{m_2 b\bar{z}}{a_2 + \bar{y} + b\bar{z}} = \delta$$

and thus

$$\frac{\beta m_2 \bar{y}}{a_2 + \bar{y}} > \frac{\beta m_2(\bar{y} + b(1 - 1/\beta)\bar{z})}{a_2 + \bar{y} + b\bar{z}} = \delta.$$

We see that $\bar{y} > y_1$ by the assumption that $R_1 < 1$ and thus obtain a contradiction. We conclude that (2.1) has only equilibria E_0 and E_1 .

Clearly, the positive x - z plane is positively invariant. Since $R_0 > 1$, E_0 is only stable in x - y plane. We apply the Dulac criterion to show that E_1 is globally asymptotically stable on the x - y plane. Indeed, let $B(x, y) = 1/y$ for $x \geq 0, y > 0$. Then

$$\frac{\partial(B\dot{x})}{\partial x} + \frac{\partial(B\dot{y})}{\partial y} = -k/y - \frac{m_1 a_1}{(a_1 + x)^2} < 0 \quad \text{for } x \geq 0, y > 0.$$

Hence there is no periodic solution on the x - y plane and E_1 is asymptotically stable on the x - y plane.

We now rescale our system (2.1) by letting $\hat{x} = x/x^0$, $\hat{y} = y/\alpha x^0$, $\hat{z} = z/\alpha\beta x^0$, $\hat{m}_1 = \alpha m_1$, $\hat{m}_2 = \beta m_2$, $\hat{a}_1 = a_1/x^0$ and $\hat{a}_2 = a_2/\alpha x^0$.

After incorporating these new state variables and parameters, and ignoring all the hats, system (2.1) takes the form

$$\begin{aligned}\dot{x} &= k(1-x) - \frac{m_1xy}{a_1+x}, \\ \dot{y} &= \frac{m_1xy}{a_1+x} - \frac{m_2yz}{a_2+y+b\beta z} - \gamma y, \\ \dot{z} &= \frac{m_2(y+b\beta z)z}{a_2+y+b\beta z} - \frac{m_2bz^2}{a_2+y+b\beta z} - \delta z, \\ x(0), y(0), z(0) &\geq 0.\end{aligned}\tag{2.2}$$

It is sufficient to show that E_1 is globally asymptotically stable for system (2.2).

Let $H(x) = (k(1-x)(a_1+x))/m_1x$. It is easy to see that $\lim_{x \rightarrow 0^+} H(x) = \infty$, $\lim_{x \rightarrow \infty} H(x) = -\infty$, $H(1) = 0$ and

$$H'(x) = \frac{-km_1x^2 - km_1a_1}{m_1^2x^2} < 0 \quad \text{for } x > 0$$

with $H(x_1) = y_1$.

Let

$$G(x) = \int_{x_1}^x \left\{ \frac{m_1s}{a_1+s} - \gamma \right\} / \left\{ \frac{m_1s}{a_1+s} \right\} ds = \frac{m_1 - \gamma}{m_1} (x - x_1 - x_1 \ln(x/x_1)).$$

We see that $\lim_{x \rightarrow 0^+} G(x) = \infty$, $G(x_1) = 0$ and $G(x) > 0$ for $x > 0$, $x \neq x_1$.

Let $F(x) = (y_1 - H(x))/G(x)$. Then $F(x) < 0$ for $0 < x < x_1$ and $F(x) > 0$ for $x_1 < x < 1$. Moreover, $\lim_{x \rightarrow 0^+} F(x) = 0$, $\lim_{x \rightarrow x_1^-} F(x) = -\infty$ and $\lim_{x \rightarrow x_1^+} F(x) = \infty$. Let $\theta > 0$ satisfy $\theta < \min_{x_1 < x < 1} F(x)$. Then $\theta > F(x)$ for $x \in (0, x_1)$ and $\theta < F(x)$ for $x \in (x_1, 1)$.

We now use a Lyapunov function constructed in [1] on $\Omega = \{(x, y, z) \in R_+^3 : y > 0, 0 \leq x \leq 1\}$,

$$\begin{aligned}V(x, y, z) &= \frac{1}{\theta + 1} (y^{\theta+1} - y_1^{\theta+1}) - \frac{y_1}{\theta} (y^\theta - y_1^\theta) \\ &\quad + y^\theta \int_{x_1}^x \left\{ \frac{m_1s}{a_1+s} - \gamma \right\} / \left\{ \frac{m_1s}{a_1+s} \right\} ds + cz,\end{aligned}$$

where $c > 0$ will be defined later. Observe that $V \geq 0$ on $\bar{\Omega}$ and $V = 0$ if and only if $x = x_1$, $y = y_1$ and $z = 0$.

The time derivative of V along trajectories of (2.2) is then

$$\dot{V} = y^\theta G'(x) \dot{x} + y^{\theta-1} [y - y_1 + \theta G(x)] \dot{y} + c \dot{z},$$

where

$$G'(x)\dot{x} = \left(\frac{m_1x}{a_1+x} - \gamma \right) \frac{\dot{x}}{\frac{m_1x}{a_1+x}} = \left(\frac{m_1x}{a_1+x} - \gamma \right) [H(x) - y].$$

Thus,

$$\begin{aligned} \dot{V} = & y^\theta \left(\frac{m_1x}{a_1+x} - \gamma \right) [H(x) - y_1 + \theta G(x)] + \left[c \left(\frac{m_2y_1}{a_2+y_1} - \delta \right) z \right. \\ & \left. - \theta y^{\theta-1} G(x) \frac{m_2yz}{a_2+y+b\beta z} \right] + \left[c \left(\frac{m_2(y+b\beta z)}{a_2+y+b\beta z} - \frac{m_2y_1}{a_2+y_1} \right) \right. \\ & \left. - \frac{cm_2bz}{a_2+y+b\beta z} - y^{\theta-1}(y-y_1) \frac{m_2y}{a_2+y+b\beta z} \right] z = \text{I} + \text{II} + \text{III}. \end{aligned}$$

Note that

$$\text{I} = y^\theta \left(\frac{m_1x}{a_1+x} - \gamma \right) [H(x) - y_1 + \theta G(x)] < 0 \quad \text{for } x \neq x_1$$

by the definition of θ . Also, $\text{I} = 0$ if and only if $x = x_1$.

The second part,

$$\text{II} = c \left(\frac{m_2y_1}{a_2+y_1} - \delta \right) z - \theta y^{\theta-1} G(x) \frac{m_2yz}{a_2+y+b\beta z} \leq 0 \quad \text{as } \frac{m_2y_1}{a_2+y_1} < \delta,$$

and $\text{II} = 0$ if and only if $z = 0$.

Finally

$$\begin{aligned} \text{III} = & \left\{ c \left[\frac{m_2(y+b\beta z)}{a_2+y+b\beta z} - \frac{m_2y_1}{a_2+y_1} - \frac{m_2bz}{a_2+y+b\beta z} \right] \right. \\ & \left. - y^{\theta-1}(y-y_1) \frac{m_2y}{a_2+y+b\beta z} \right\} z, \end{aligned}$$

where the first-term

$$c \left[\frac{m_2(y+b\beta z)}{a_2+y+b\beta z} - \frac{m_2y_1}{a_2+y_1} - \frac{m_2bz}{a_2+y+b\beta z} \right] \leq \frac{m_2a_2c}{(a_2+y_1)(a_2+y+b\beta z)} (y-y_1).$$

Thus,

$$\begin{aligned} \text{III} & \leq \left[\frac{m_2a_2c(y-y_1)}{(a_2+y_1)(a_2+y+b\beta z)} - y^{\theta-1}(y-y_1) \frac{m_2y}{a_2+y+b\beta z} \right] z \\ & = \frac{m_2(y-y_1)}{(a_2+y+b\beta z)} \left(\frac{a_2c}{a_2+y_1} - y^\theta \right) z. \end{aligned}$$

Let $c = ((a_2 + y_1)/a_2)y_1^\theta$. Then

$$\text{III} \leq \frac{m_2(y - y_1)}{a_2 + y + b\beta z} (y_1^\theta - y^\theta)z$$

and, consequently, $\text{III} \leq 0$ and $\text{III} = 0$ if and only if $z = 0$. We conclude that $\dot{V} \leq 0$ on $\bar{\Omega}$ and $\dot{V} = 0$ if and only if $x = x_1$ and $z = 0$. Since E_1 is the maximal invariant set on the x - y plane, E_1 is a global attractor for system (2.2) and thus for system (2.1). \square

Observe that R_1 can be viewed as the basic reproductive number of the predator when the prey is stabilized at y_1 . If $R_1 < 1$, then the prey population cannot support the predator and the predator becomes extinct even under the circumstance that the predator can feed itself through its own population. On the other hand, intratrophic predation of the top predator has no effect on the dynamics of the system as the predator cannot persist and thus it has no influence on the lower trophic level.

When $R_0, R_1 > 1$, the prey population is able to sustain the predator. This is the only situation in which the predator can survive. We now review some basic concepts of persistence [4,9]. A population $p(t)$ is said to be *strongly persistent* if $p(0) > 0$ and $\liminf_{t \rightarrow \infty} p(t) > 0$. $p(t)$ is said to be *uniformly persistent* if there exists $\epsilon > 0$ such that if $p(0) > 0$ then $\liminf_{t \rightarrow \infty} p(t) \geq \epsilon$. A system is said to be *strongly persistent (uniformly persistent)* if each component population is strongly persistent (uniformly persistent).

Notice that when $R_0, R_1 > 1$, then E_0 and E_1 are both unstable. It can be easily shown that E_1 is asymptotically stable on the x - y plane by using the Dulac criterion. Moreover, E_1 is unstable in the positive direction orthogonal to the x - y plane. On the other hand, if $y(0) = 0$, then the solution has ω -limit set $\{E_0\}$. Therefore, system (2.1) is strongly persistent by [4, Theorem 2.1]. Furthermore, since every solution of (2.1) satisfies $\limsup_{t \rightarrow \infty} x(t) + y(t) + z(t) \leq kx^0/\hat{k}$, system (2.1) is indeed uniformly persistent by [9, Theorem 4.5].

We summarize our discussion into the following theorem.

Theorem 2.4. *Let $R_0, R_1 > 1$. System (2.1) is uniformly persistent for any b , $0 \leq b \leq 1$.*

Although Theorem 2.4 tells us that both populations persist in the face of intratrophic predation if the basic reproductive numbers of prey and predator are both greater than 1, it does not provide us any detailed information on the existence or magnitude of the positive steady states. We next examine the effect of intratrophic predation on the existence, magnitude and local stability of the positive equilibrium when $R_0, R_1 > 1$.

For the case when $b = 0$, system (2.1) becomes

$$\begin{aligned} \dot{x} &= k(x^0 - x) - \frac{m_1xy}{a_1 + x}, \\ \dot{y} &= \frac{\alpha m_1xy}{a_1 + x} - \frac{m_2yz}{a_2 + y} - \gamma y, \\ \dot{z} &= \frac{\beta m_2yz}{a_2 + y} - \delta z, \\ x(0), y(0), z(0) &\geq 0. \end{aligned} \tag{2.3}$$

This is a chemostat predator–prey model with different death rate and thus the chemostat conservation principal does not apply to this particular model. However, a simple calculation shows that $\bar{y} = a_2\delta/(\beta m_2 - \delta) > 0$ is feasible as $R_1 > 1$ and \bar{x} always exists where \bar{x} satisfies $k(x^0 - x) = m_1x/(a_1 + x)\bar{y}$. Consequently,

$$\bar{z} = \frac{a_2 + \bar{y}}{m_2} \left(\frac{\alpha m_1 \bar{x}}{a_1 + \bar{x}} - \gamma \right) > 0 \quad \text{if } \bar{x} > x_1.$$

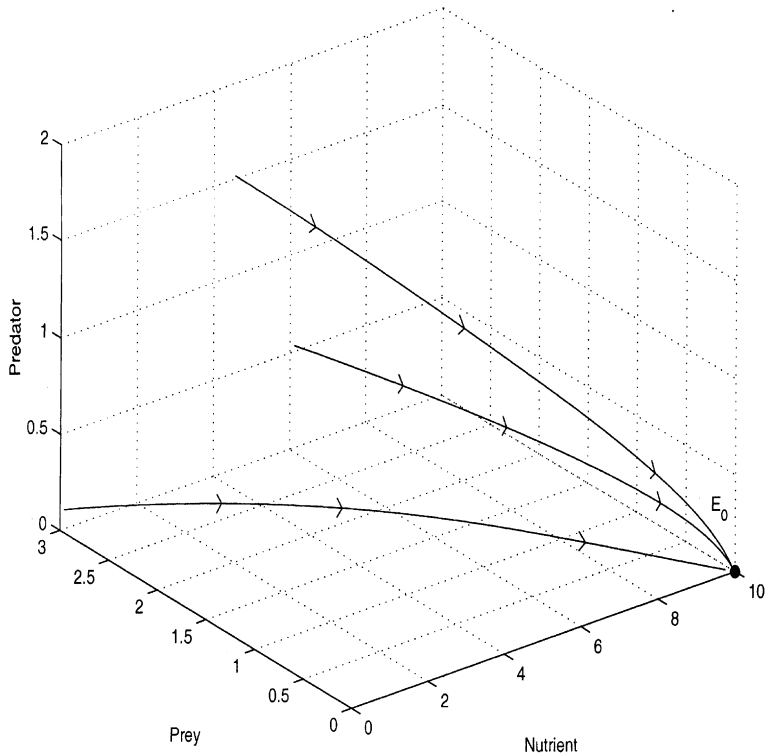


Fig. 1. Plot of trajectories of system (2.1) using $\alpha = 0.1, \beta = 0.1, \gamma = 0.2$ and $b = 0$. Solutions converge to $E_0 = (10, 0, 0)$.

The inequality $\bar{x} > x_1$ follows from an observation that $\bar{y} < y_1$ as $R_1 > 1$. Therefore, we conclude that when $R_0, R_1 > 1$, a positive steady state $E_2 = (\bar{x}, \bar{y}, \bar{z})$ always exists for system (2.1) when $b = 0$ and in this case the positive steady state is unique with $\bar{y} < y_1$.

When $0 < b \leq 1$, the x -isocline

$$y = \frac{k(x^0 - x)(a_1 + x)}{m_1 x} := h(x)$$

satisfies $\lim_{x \rightarrow 0^+} h(x) = \infty$, $h(x^0) = 0$, $\lim_{x \rightarrow \infty} h(x) = -\infty$ and $h'(x) < 0$ for $x \geq 0$. By using this equality, the nontrivial z -isocline can be expressed as

$$z = \frac{(\beta m_2 - \delta)h(x) - \delta a_2}{b(m_2 - \beta m_2 + \delta)} := g(x),$$

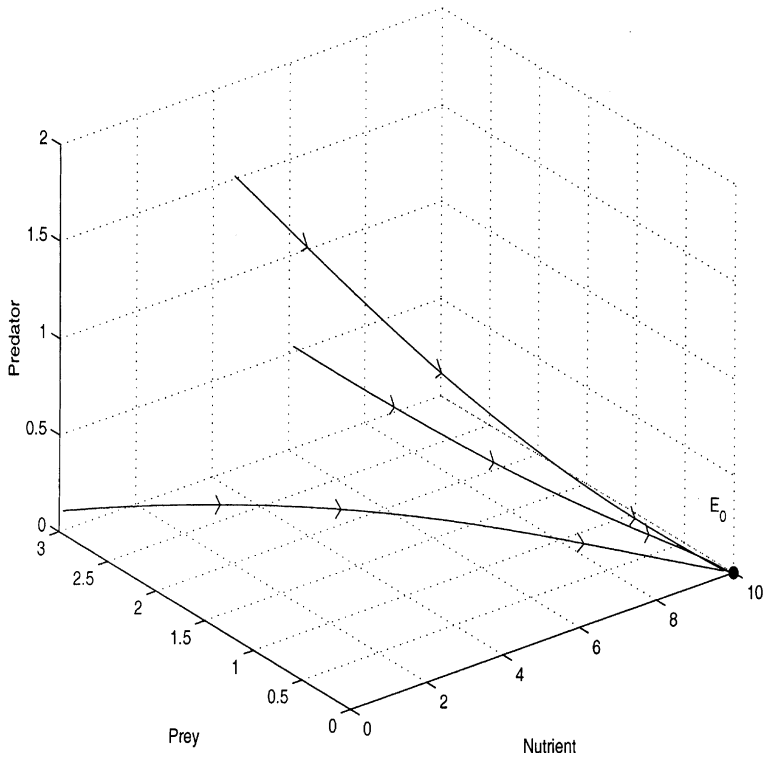


Fig. 2. Plot of trajectories of system (2.1) using $\alpha = 0.1, \beta = 0.1, \gamma = 0.2$ and $b = 0.5$. Solutions converge to $E_0 = (10, 0, 0)$.

where $m_2 - \beta m_2 + \delta > 0$. Thus $g'(x) < 0$ for $x \geq 0$ and $\lim_{x \rightarrow 0^+} g(x) = \infty$. Note that since $R_1 > 1$, then $h(\bar{x}) = \bar{y} > 0$, where $E_2 = (\bar{x}, \bar{y}, \bar{z})$ is the positive steady state of (2.1) when $b = 0$. Therefore $g(\bar{x}) = 0$ where $\bar{x} > x_1$.

Similarly, the nontrivial y -isocline satisfies

$$z = \left\{ \left(\frac{\alpha m_1 x}{a_1 + x} - \gamma \right) (a_2 + h(x)) \right\} / \left\{ m_2 + b\gamma - \frac{b\alpha m_1 x}{a_1 + x} \right\} := f(x),$$

where $\lim_{x \rightarrow 0^+} f(x) = -\infty$ and $f(x_1) = 0$. Clearly, $f(x) < 0$ for $0 < x < x_1$. Let x^* denote the solution of $m_2 + b\gamma = b\alpha m_1 x / (a_1 + x)$. If $x^* > x^0$, then $f(x) > 0$ for $x_1 < x < x^0$ and there exists at least one $\bar{x}_b > 0$ satisfying $f(x) = g(x)$. Consequently, $\bar{y}_b > 0, \bar{z}_b > 0$ exist. Therefore a positive steady state $E_2^b = (\bar{x}_b, \bar{y}_b, \bar{z}_b)$ exists with $\bar{x}_b < \bar{x}$. However, a positive steady state may not be unique. A similar argument can be applied to the case when $x^* < x^0$. We conclude that when $R_0, R_1 > 1$, a positive steady state $E_2^b = (\bar{x}_b, \bar{y}_b, \bar{z}_b)$ exists for system (2.1) for $0 < b \leq 1$. Unlike the case when $b = 0$, there are several positive steady states

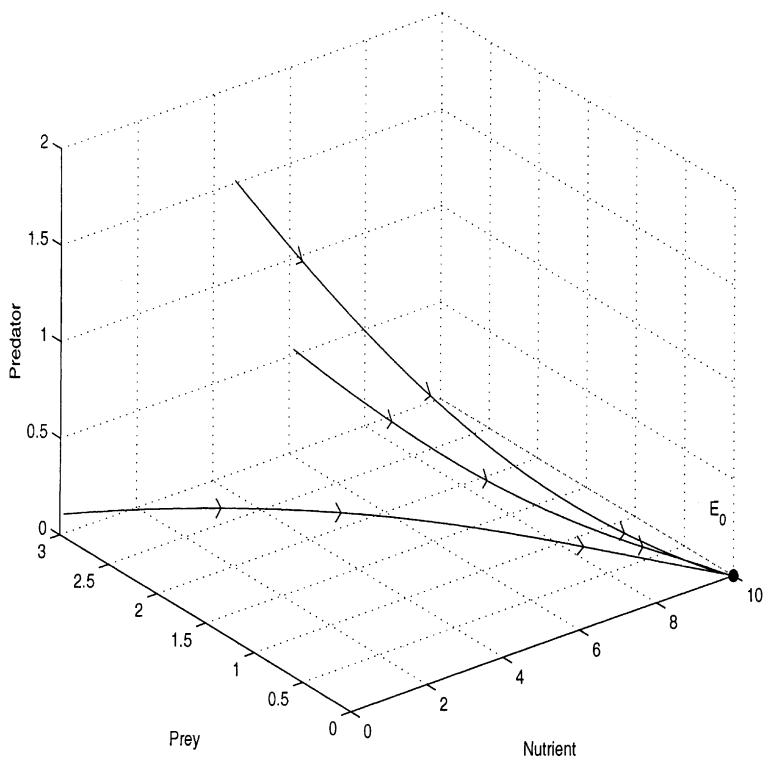


Fig. 3. Plot the trajectories of system (2.1) using $\alpha = 0.1, \beta = 0.1, \gamma = 0.2$ and $b = 1$. Solutions converge to $E_0 = (10, 0, 0)$.

possible when $0 < b \leq 1$. However, it is straightforward to see that $\bar{x}_b < \bar{x}$ and $\bar{y}_b > \bar{y}$. The preceding discussion can be summarized into the following.

Theorem 2.5. *Let $R_0, R_1 > 1$. The following are true.*

1. A unique positive steady state $E_2 = (\bar{x}, \bar{y}, \bar{z})$ exists for system (2.1) when $b = 0$.
2. At least one positive steady state $E_2^b = (\bar{x}_b, \bar{y}_b, \bar{z}_b)$ exists for system (2.1) when $0 < b \leq 1$.
3. E_2 and E_2^b satisfy $\bar{x}_b < \bar{x}$ and $\bar{y}_b > \bar{y}$.

By assuming that intratrophic predation is sufficiently small, i.e., $b \ll 1$, Pitchford and Brindley [6] applied an asymptotic method and showed that intratrophic predation always increases the prey's density for the coexisting equilibrium. Our result of Theorem 2.5 also gives the same conclusion. In particular, we showed that in this three trophic levels system, intratrophic

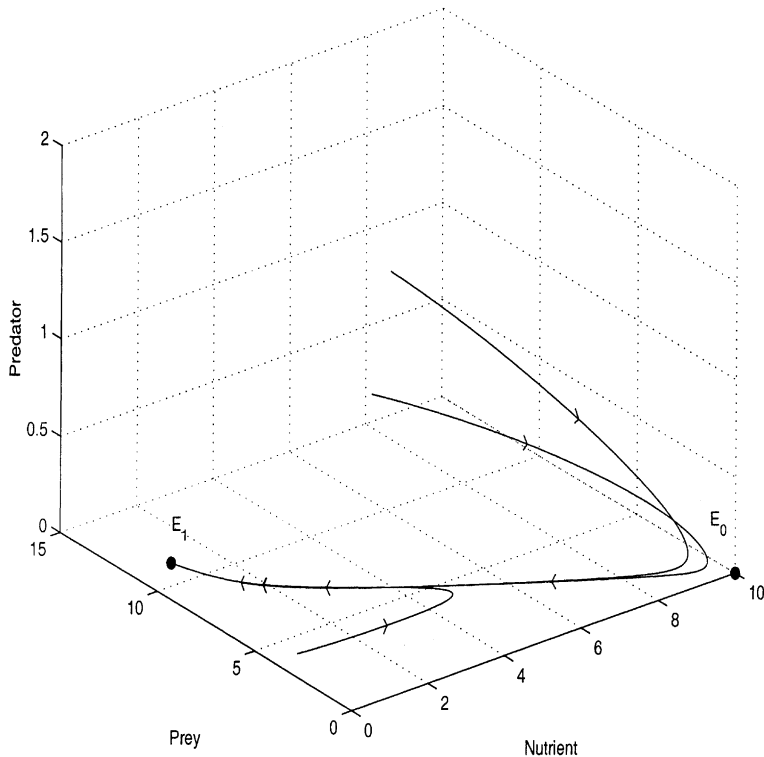


Fig. 4. Plot of trajectories of system (2.1) using $\alpha = 0.5, \beta = 0.1, \gamma = 0.2$ and $b = 0$. Solutions converge to $E_1 = (1, 11.25, 0)$.

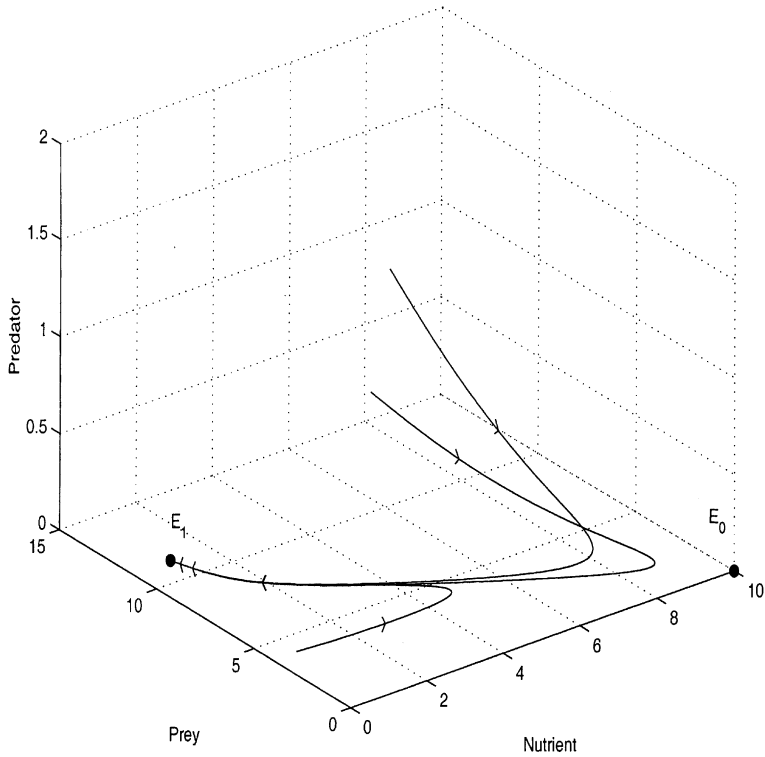


Fig. 5. Plot of trajectories of system (2.1) with $\alpha = 0.5, \beta = 0.1, \gamma = 0.2$ and $b = 0.5$. Solutions converge to $E_1 = (1, 11.25, 0)$.

predation always increases the magnitude of the prey population of coexisting equilibrium. As a result, intratrophic predation also lowers the nutrient concentration for the coexisting equilibrium as there is a larger prey population present. However, the assumption of $b \ll 1$ in [6] is not necessary for this particular system.

Numerical simulation in the next section illustrates that when E_2 is unstable, E_2^b is locally asymptotically stable if b is large. Therefore, intratrophic predation does change the local stability of coexisting equilibrium and consequently has the effect of stabilizing the system. This result agrees with the finding obtained in [6].

3. Numerical simulations

In this section, we use numerical tools to study system (2.1). In particular, Theorems 2.2–2.4 and 2.5 will be illustrated numerically. We use parameters

$a_1 = 1$, $a_2 = 1$, $\delta = 0.35$, $k = 0.5$, $m_1 = 0.8$, $m_2 = 0.8$ and $x^0 = 10$ for all simulations.

If $\alpha = 0.1$, $\beta = 0.1$ and $\gamma = 0.2$, then $R_0 = \alpha m_1 x^0 / \gamma (a_1 + x^0) = 0.36 < 1$. Thus, according to Theorem 2.2, solutions of system (2.1) converge to steady state $E_0 = (10, 0, 0)$ independent of b . Figs. 1–3 illustrate this result for $b = 0$, $b = 0.5$ and $b = 1$, respectively.

If $\alpha = 0.5$, $\beta = 0.1$ and $\gamma = 0.2$, then $R_0 = 1.8 > 1$. Thus steady state $E_1 = (x_1, y_1, 0) = (1, 11.25, 0)$ exists and $R_1 = \beta m_2 y_1 / \delta (a_2 + y_1) = 0.21 < 1$. It follows from Theorem 2.3 that solutions of system (2.1) converge to $E_1 = (1, 11.25, 0)$ independent of b . Figs. 4–6 demonstrate this result for $b = 0$, $b = 0.5$ and $b = 1$, respectively.

If $\alpha = 0.5$, $\beta = 0.5$ and $\gamma = 0.1$, then $R_0 = 3.6 > 1$ and $E_1 = (0.3333, 24.1667, 0)$ exists. Moreover, $R_1 = 1.097 > 1$ and a unique positive steady state $E_2 = (2.2481, 7, 1.7685)$ exists when $b = 0$. Fig. 7 reveals a periodic solution for these parameter values.

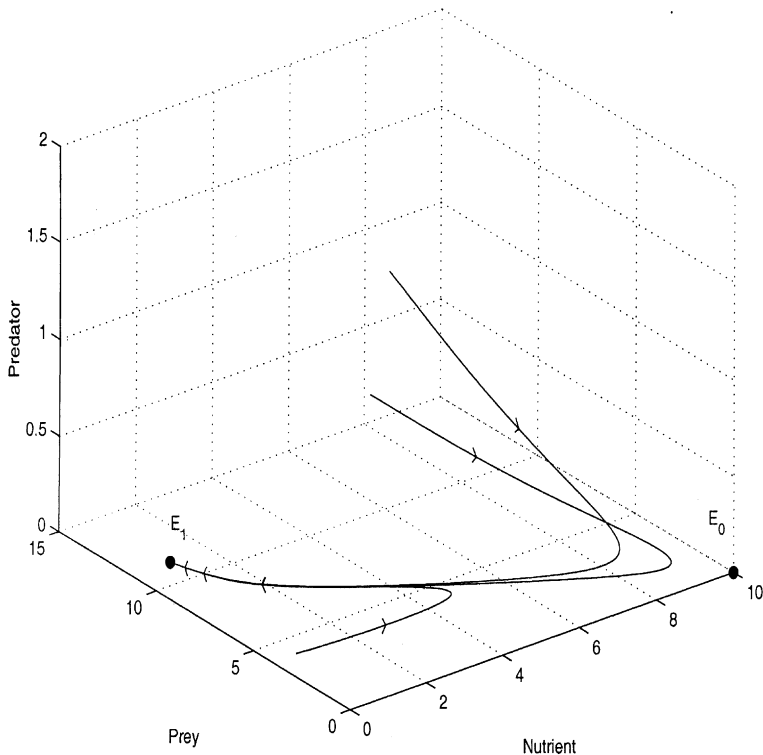


Fig. 6. Plot of trajectories of system (2.1) using $\alpha = 0.5$, $\beta = 0.1$, $\gamma = 0.2$ and $b = 1$. Solutions converge to $E_1 = (1, 11.25, 0)$.

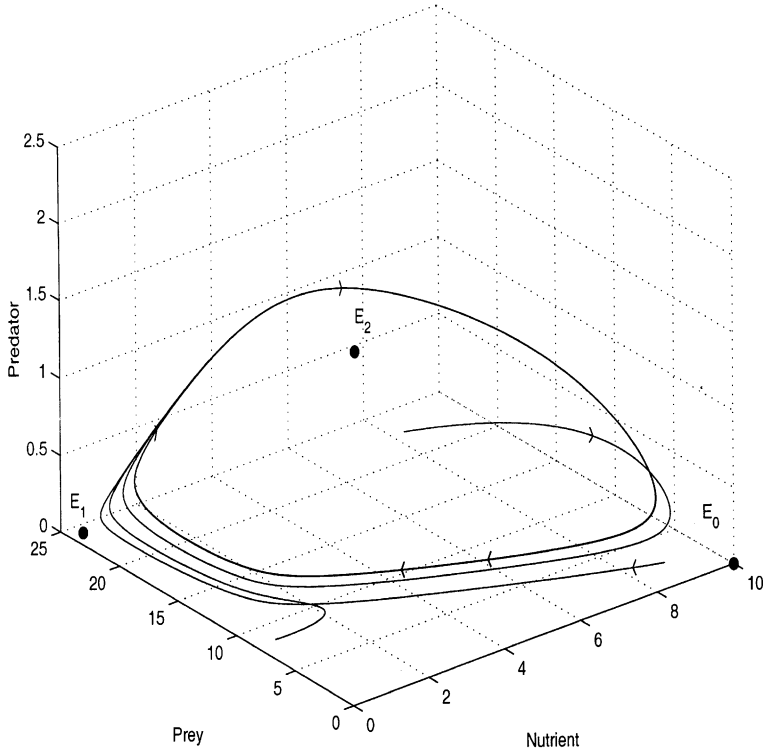


Fig. 7. Plot of trajectories of system (2.1) using $\alpha = 0.5, \beta = 0.5, \gamma = 0.1$ and $b = 0$. There are three equilibria $E_0 = (10, 0, 0)$, $E_1 = (0.3333, 24.1667, 0)$ and $E_2 = (2.2481, 7, 1.7685)$. The plot clearly reveals the existence of a periodic solution.

Using the above parameters with the exception of $b = 0.125$, Fig. 8 plots functions f and g defined in Section 2. The figure demonstrates that there exists a unique positive solution $\bar{x}_b = 1.192$ and consequently there exists a unique positive steady state $E_2^b = (1.192, 10.121, 1.66)$ for system (2.1) Other steady states are $E_0 = (10, 0, 0)$ and $E_1 = (0.333, 24.1667, 0)$. If we use $b = 0.5$, then E_2^b becomes $E_2^b = (0.6175, 15.3598, 1.11465)$ and trajectories in Fig. 9 clearly converge to this positive steady state E_2^b .

We now use γ as our bifurcation parameter. We calculate numerically the critical value γ_0 for which the Jacobian matrix J at E_2^b has eigenvalue of zero real part when $\gamma = \gamma_0$. Moreover, numerical simulation also demonstrates that E_2^b is locally asymptotically stable if $\gamma > \gamma_0$ and is unstable if $\gamma < \gamma_0$. Fig. 10 plots the bifurcation diagram. It is clear from this diagram that intratrophic predation can stabilize the system even when $b > 0$ is very small.

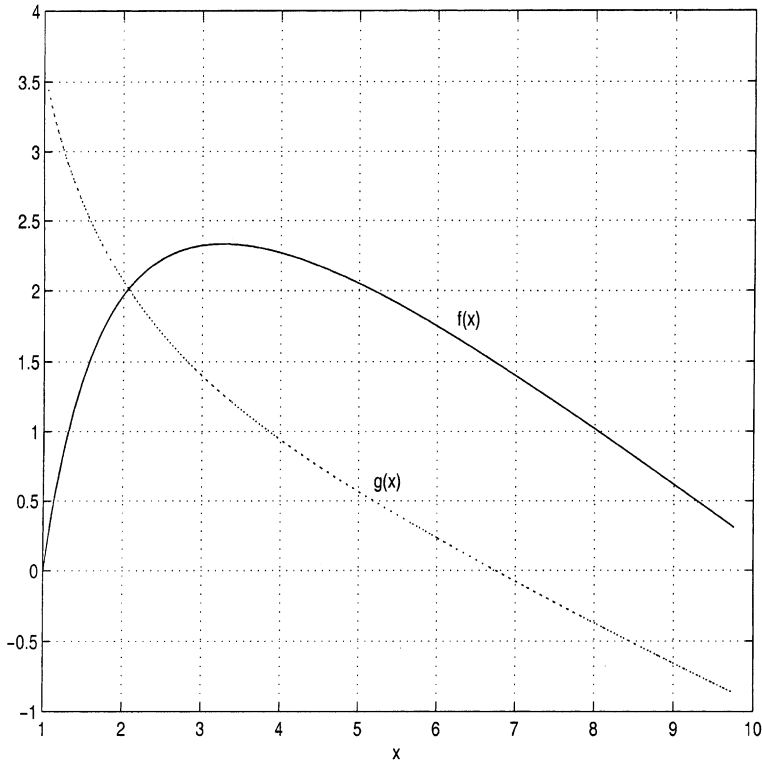


Fig. 8. Graphs of f and g demonstrate that there exists a unique positive solution \bar{x}^b using $\alpha = 0.5$, $\beta = 0.5$, $\gamma = 0.1$ and $b = 0.125$.

4. Discussion

A nutrient–prey–predator model with intratrophic predation of the top predator is introduced in this paper. Our modeling methodology of intratrophic predation is similar to that considered by Kohlmeier and Ebenhoh [5] and by Pitchford and Bridley [6]. We use a parameter b , $0 \leq b \leq 1$ to specify the intensity of intratrophic predation. The motivation for this three trophic level food chain is based on the study given by Kohlmeier and Ebenhoh [5], in which North Sea benthic ecosystem was considered. Our model treated here can be regarded as a nutrient–phytoplankton–zooplankton system for which several zooplankton species are lumped into a single population and some of the zooplankton species may feed on other zooplankton species. Furthermore, system (2.1) can be viewed as a chemostat predator–prey system with different death rate when $b = 0$. Therefore, our results obtained here for $b = 0$ also apply to this particular chemostat model.

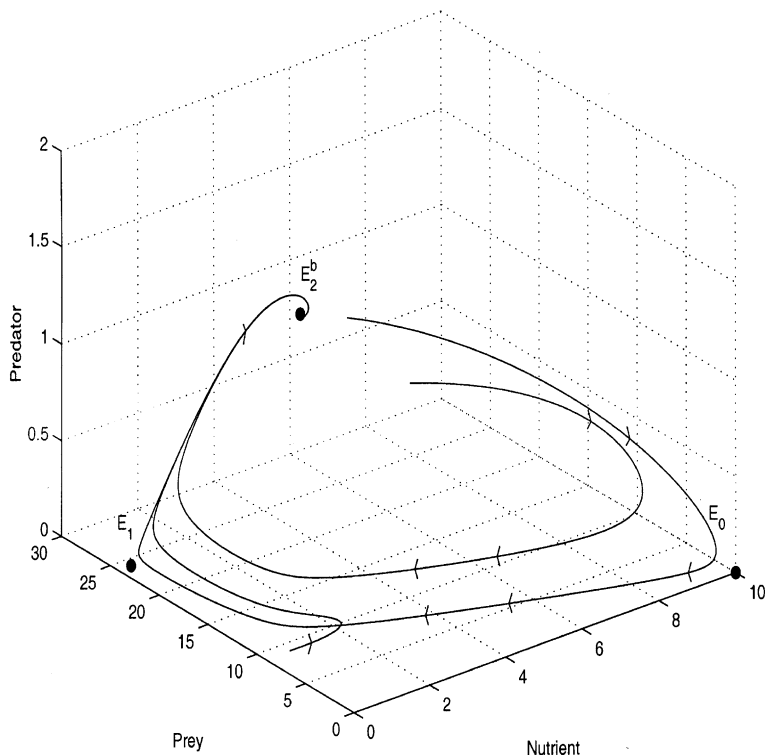


Fig. 9. Plot of trajectories of system (2.1) using $\alpha = 0.5, \beta = 0.5, \gamma = 0.1$ and $b = 0.5$. Solutions converge to $E_2^b = (0.6175, 15.3598, 1.11465)$.

The dynamics of this simple food chain depend on the thresholds R_0 and R_1 . The threshold R_0 can be regarded as the basic reproductive number of the prey. If $R_0 < 1$, there exists a unique steady state $E_0 = (x^0, 0, 0)$ for the system and all solutions converge to E_0 , where x^0 is the constant input nutrient concentration. We immediately conclude that intratrophic predation has no influence on the dynamics of the system. This phenomenon is due to the extinction of the prey. Since the nutrient concentration cannot sustain the prey population, the predator population also becomes extinct and consequently intratrophic predation of the predator has no impact on the system.

If threshold $R_0 > 1$, then the system has two steady states $E_0 = (x^0, 0, 0)$ and $E_1 = (x_1, y_1, 0)$. We can define another threshold R_1 , where R_1 can be viewed as the basic reproductive number of the predator when the prey population is stabilized at y_1 . If $R_1 < 1$, then the prey population cannot sustain the predator and the predator becomes extinct independent of b . Therefore solutions with positive initial prey population all converge to E_1 and intratrophic predation

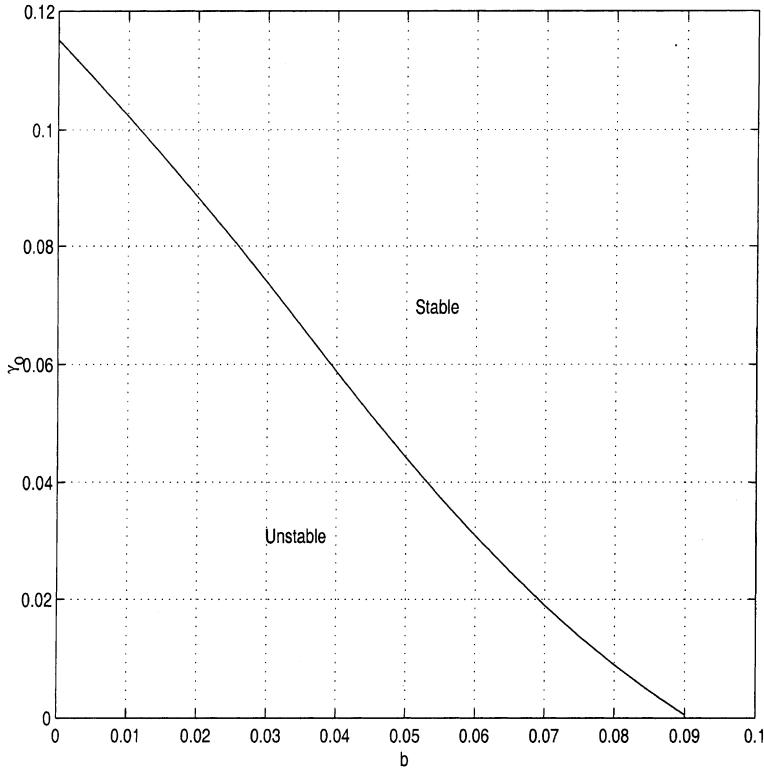


Fig. 10. Bifurcation diagram of critical value γ_0 as a function of intratrophic predation parameter, b , for system (2.1). It is clear from this diagram that the range of local stability of the coexisting equilibrium can be significantly increased as b increases.

has no influence on the dynamics of the system. This is due to the extinction of the predator.

The more interesting case is when $R_0, R_1 > 1$. This is the case when both prey and predator population can persist. It is easily shown that the system has a unique positive steady state $E_2 = (\bar{x}, \bar{y}, \bar{z})$ when $b = 0$ and if $0 < b \leq 1$ it is shown that the system has at least one positive equilibrium $E_2^b = (\bar{x}_b, \bar{y}_b, \bar{z}_b)$ with $\bar{x}_b < \bar{x}$ and $\bar{y}_b > \bar{y}$. Therefore, intratrophic predation yields higher prey density of coexisting equilibrium. Numerical simulation provides a periodic solution for certain parameter values when $b = 0$. For the same parameters with $b = 0.5$, the model has a unique positive steady state $E_2^b = (\bar{x}_b, \bar{y}_b, \bar{z}_b)$ and E_2^b is locally asymptotically stable with $\bar{y}_b > \bar{y}$ and $\bar{x}_b < \bar{x}$. From here we can conclude that intratrophic predation can stabilize the system, yield higher prey population and hence lower the nutrient concentration of coexisting equilibrium.

We then use γ , the per capita mortality rate of the prey, as our bifurcation parameter. We calculate numerically the critical value γ_0 so that the positive steady state E_2^b is nonhyperbolic when $\gamma = \gamma_0$. The bifurcation diagram given in Fig. 10 clearly demonstrates that intratrophic predation has the stabilization effect even when the intensity $b > 0$ is small.

Our study of intratrophic predation in this three trophic level food chain shows that intratrophic predation has the effect on the system only if the basic reproductive number of the top predator is greater than 1. Under these circumstances, intratrophic predation may yield multiple coexisting equilibria and stabilize the system when such an equilibrium is unique. That is, intratrophic predation can change the stability of the coexisting equilibrium, and it has the effect of elevating the prey population of the coexisting equilibria. Consequently, the mechanism of intratrophic predation also decreases the nutrient concentration of the coexisting equilibria.

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