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INTRATROPHIC PREDATION IN A SIMPLE FOOD CHAIN WITH FLUCTUATING NUTRIENT

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Abstract. A model of interaction between nutrient, prey, and predator with intratrophic predation of the predator and a limiting periodic nutrient input is proposed and studied. Dynamics of the system are shown to depend on two thresholds. These thresholds are expressed in terms of certain periodic solutions of the system. Intratrophic predation can have impact on the model only if both thresholds are greater than zero. In this case positive periodic solutions exist. Numerical techniques are then used to explore the effect of intratrophic predation by examining the mean value and stability of these positive periodic solutions. It is demonstrated numerically that intratrophic predation can increase the stability region of the positive periodic solutions. It can also elevate the mean values of prey population and decrease the mean values of nutrient concentration for stable positive periodic solutions. Moreover, intratrophic predation can eliminate the chaotic behavior of the system when the degree of intratrophic predation is large enough.

1. **Introduction.** Mathematical models derived from biological considerations have been studied to help answer some important biological questions. See Brauer [2], Hosono [10], and Tang and Zou [20] for mathematical analyses and biological interpretations of population models. In particular, classical predator-prey models have been used to study nutrient-plankton interaction. The intensive investigation of this simple food chain in various complexity has helped researchers in understanding and interpreting nutrient-plankton phenomenon. In most of these studies, each plankton population is modeled explicitly. Therefore, either the systems are very simple to allow for mathematical analysis, or else numerical simulations are

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used as a tool to study the large systems. Since ecosystems may involve hundreds of species, it is almost impossible to model the interaction within an ecosystem explicitly. Therefore, intratrophic predations arise when a large number of species are lumped together and considered as a single population. In this case it is very likely that some of the species of the population might prey on other species of the same population. Unlike the classical predator-prey models, intratrophic predation on the contrary has received only little attention. Its discussion stems from a survey paper on evolution and intraspecific predation by Polis [16], who demonstrated that cannibalism is an interesting and important mechanism in population dynamics.

By using continuous-time, age-structured population models, Bosch, Roos and Gabriel [22], and Cushing [3] studied cannibalism and have contributed to the understanding of this biological phenomenon. Aside from cannibalism, however, intratrophic predation may include broader biological mechanisms as mentioned above. Kohlmeier and Ebenhoh [13] incorporated intratrophic predation in a simple Lotka-Volterra predator-prey model by assuming that the food resource that is available to the predator is a weighted sum of prey and predator densities. Their numerical simulations indicated a strong increase of both prey and predator as the intensity of intratrophic predation increases. Pitchford and Brindley [15] analyzed the model proposed by Kohlmeier and Ebenhoh [13] and concluded that the numerical findings in [13] may not always be true. However, they showed that intratrophic predation always increases the coexisting equilibrium value of the prey and its stability when such a mechanism is very small.

Unlike the two trophic levels studied by the previous authors [13, 15], Jang and Baglama [12] considered intratrophic predation in a nutrient-prey-predator model with a limiting constant nutrient input. That is, the food resource of prey was modeled explicitly. The incorporation of nutrient concentration as a state variable was motivated by the benthic ecosystem in which different zooplankton species may be regarded as a single predator population and some of the species may prey on the others. Under the same modeling methology as Kohlmeier and Ebenhoh [13], and Pitchford and Bradley [15], they showed that the mechanism of intratrophic predation can influence the dynamics of the model only if basic reproductive numbers of both prey and predator are greater than 1. In this case, the mechanism always decreases the nutrient concentration and increases the prey population for any interior equilibrium. However, unlike the assumption made in Pitchford and Bradley [15] for which the intensity of intratrophic predation is assumed to be very small, the findings presented in [12] are valid for any degree of intratrophic predation.

There are numerous observations supporting the evidence that the input limiting nutrient may vary with time [4, 14]. To incorporate day/night or seasonal cycles, one may model the limiting nutrient input periodically. Our main objective in this study is to investigate the effect of intratrophic predation on the dynamics of such a system. The incorporation of periodic input nutrient has been studied previously for chemostat systems by several researchers which includes Hsu [11], Smith [18], Hale and Somolinos [7], Yang and Freedman[23], and more recently by Ruan [21] for nutrient-plankton system. Our model presented here differs from those classical chemostat systems and nutrient-plankton systems as the food resource that is available to the predator is a linear combination of both prey and predator populations instead of only prey population.

It is proved that the dynamics of the model depend on two thresholds. We show that intratrophic predation can have impact on the dynamics of the model only if

these two thresholds are positive. Numerical techniques are then exploited to study the effect of the mechanism. The simulations clearly indicate that intratrophic predation can increase the mean value of prey population and decrease the mean value of nutrient concentration for stable positive periodic solutions. Moreover, intratrophic predation can also increase the stability of the positive periodic solutions and eliminate the phenomenon of sensitive dependence on initial conditions when the degree of intratrophic predation is sufficiently large. As a result, the mechanism has the effect of stabilizing the nutrient-plankton interaction in a variable nutrient input environment.

In the following section, a mathematical model is presented and its dynamical consequences are discussed. Numerical simulations complementing these analytical results will be given in Section 3. The final section provides a brief summary and 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 chemostat law. To incorporate seasonal or day/night cycles, we assume that the input nutrient concentration varies periodically about a mean value. Consequently, the nutrient concentration in the absence of prey is governed by the periodic equation $\dot{x} = k(x^0 + ae(t) - x)$, where k is the constant input rate, or the washout rate, x^0 is the constant input nutrient concentration, a, where $0 < a < x^0$, is the amplitude of the oscillation, and $e(t)$ is τ-periodic with mean value 0 and $|e(t)| \leq 1$.

Let $y(t)$ be the prey population at time t. The uptake of prey is modeled by the Michaelis-Menten kinetics $\dfrac{m_1 x}{a_1 + x}$, where a_1 is the half-saturation constant and m_1 is 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 [12, 13, 15], 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, and let β be the net prey conversion rate. Putting all these assumptions together, our model is given by the following system of ordinary differential equations.

$$\begin{aligned} \dot{x} &= k(x^0 + ae(t) - x) - \frac{m_1 xy}{a_1 + x} \\ \dot{y} &= \frac{\alpha m_1 xy}{a_1 + x} - \frac{m_2 yz}{a_2 + y + bz} - \gamma y \\ \dot{z} &= \frac{\beta m_2 (y + bz) z}{a_2 + y + bz} - \frac{m_2 b z^2}{a_2 + y + bz} - \delta z \\ & x(0), y(0), z(0) \geq 0, \end{aligned} \tag{1}$$

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

Let us now study system (1). Consider the τ-periodic differential equation

$$\dot{x} = k(x^0 + ae(t) - x). \tag{2}$$

It's easy to see that (2) has a unique τ-periodic solution $x^*(t)$, where

$$x^*(t) = \frac{ke^{-kt}}{e^{k\tau}-1}\int_t^{t+\tau} e^{kr}(x^0+ae(r))dr \tag{3}$$

and every solution $x(t)$ of (2) can be written as $x(t) = x^*(t) + (x(0)-x^*(0))e^{-kt}$ and thus $x(t)-x^*(t)\to 0$ as $t\to\infty$.

The first step in understanding system (1) is to show that solutions of the system remain nonnegative and are bounded, so that system (1) is biologically meaningful.

Lemma 2.1 *Solutions of (1) are nonnegative and (1) is dissipative.*

Proof. Since $\dot{x}|_{x=0} = k(x^0+ae(t)) > 0$, $\dot{y}|_{y=0} = 0$ and $\dot{z}|_{z=0} = 0$, solutions of (1) remain nonnegative for $t\geq 0$. Let $S = x+y+z$. Then

$$\begin{aligned}\dot{S} &\leq k(x^0+ae(t)-x)-\gamma y-\delta z\\ &\leq k(x^0+a-x)-\gamma y-\delta z\\ &\leq k(x^0+a)-k_0(x+y+z)\end{aligned}$$

where $k_0 = \min\{k,\gamma,\delta\}$. It follows that

$$\limsup_{t\to\infty}(x(t)+y(t)+z(t)) \leq \frac{k(x^0+a)}{k_0}.$$

Moreover, since $\dot{S}|_{S=\frac{k(x^0+a)}{k_0}} \leq 0$, we have $x(t)+y(t)+z(t) \leq \frac{k(x^0+a)}{k_0}$ for all t large. This shows that system (1) is dissipative. □

Clearly, (1) always has a trivial τ-periodic solution $(x^*(t),0,0)$. We let

$$\sigma_0 = \frac{1}{\tau}\int_0^\tau \left[\frac{\alpha m_1 x^*(t)}{a_1+x^*(t)}-\gamma\right]dt.$$

Theorem 2.2 *If $\sigma_0 < 0$, then solutions $(x(t),y(t),z(t))$ of (1) satisfy $\lim_{t\to\infty} y(t) = \lim_{t\to\infty} z(t) = \lim_{t\to\infty}(x(t)-x^*(t)) = 0$ for all $0\leq b\leq 1$.*

Proof. Since $\dot{x}\leq k(x^0+ae(t)-x)$, it follows from (2) that $x(t)\leq x^*(t)+(x(0)-x^*(0))e^{-kt}$ for $t\geq 0$. Thus for any $\epsilon>0$, there exists $t_0\geq 0$ such that $x(t)\leq x^*(t)+\epsilon$ for $t\geq t_0$. We choose $\epsilon>0$ so that

$$\int_0^\tau \left[\frac{\alpha m_1(x^*(t)+\epsilon)}{a_1+x^*(t)+\epsilon}-\gamma\right]dt < 0.$$

As $\dot{y}\leq y\left(\frac{\alpha m_1 x}{a_1+x}-\gamma\right)$, we have

$$\begin{aligned}y(t) &\leq y(0)e^{\int_0^{t_0}\left[\frac{\alpha m_1 x(r)}{a_1+x(r)}-\gamma\right]dr}e^{\int_{t_0}^{t_0+n\tau}\left[\frac{\alpha m_1(x^*(r)+\epsilon)}{a_1+x^*(r)+\epsilon}-\gamma\right]dr}\\ &= y(0)e^{\int_0^{t_0}\left[\frac{\alpha m_1 x(r)}{a_1+x(r)}-\gamma\right]dr}e^{\int_0^{n\tau}\left[\frac{\alpha m_1(x^*(r)+\epsilon)}{a_1+x^*(r)+\epsilon}-\gamma\right]dr}\end{aligned}$$

for some $n=n(t)>0$. Thus $\lim_{t\to\infty} y(t) = 0$, and as a result $\lim_{t\to\infty} z(t) = 0$.

We are now in a position to show $\lim_{t\to\infty}(x(t)-x^*(t))=0$. Observe that $\frac{d}{dt}(xe^{kt}) = ke^{kt}(x^0+ae(t)) - \frac{m_1xye^{kt}}{a_1+x}$. Thus,

$$x(t) = x(0)e^{-kt} + ke^{-kt}\int_0^t e^{kr}(x^0+ae(r))dr - m_1e^{-kt}\int_0^t \frac{x(r)y(r)e^{kr}}{a_1+x(r)}dr.$$

Notice as $\lim_{t\to\infty} y(t)=0$ and $x(t)$ is bounded, we have

$$\lim_{t\to\infty} e^{-kt}\int_0^t \frac{x(r)y(r)e^{kr}}{a_1+x(r)}dr = 0.$$

On the other hand, $x(0)e^{-kt} + ke^{-kt}\int_0^t e^{kr}(x^0+ae(r))dr$ is the solution of (2) with initial condition $x(0)$. Consequently, $x(t)-x^*(t)\to 0$ as $t\to\infty$ and the proof is complete. □

We conclude that intratrophic predation has no effect on the dynamics of the system if $\sigma_0<0$. This is because the input nutrient concentration is not sufficient to support the prey population and consequently the predator also becomes extinct. Therefore the mechanism of intratrophic predation has no effect to the interaction. Suppose now $\sigma_0>0$. It is straightforward to show that the trivial τ-periodic solution $(x^*(t),0,0)$ of (1) is unstable. Indeed, the linearization of system (1) about the τ-periodic solution yields the following linear periodic system

$$\dot{Z} = \begin{pmatrix} -k & \frac{-m_1x^*(t)}{a_1+x^*(t)} & 0 \\ 0 & \frac{\alpha m_1x^*(t)}{a_1+x^*(t)} - \gamma & 0 \\ 0 & 0 & -\delta \end{pmatrix} Z,$$

where Z is a row vector of functions in one variable. The Floquet multipliers of $(x^*(t),0,0)$ are the eigenvalues of $\Phi(\tau)$, where $\Phi(t)$ is the fundamental matrix solution of the above linear periodic system satisfying $\Phi(0)=I$. A simple calculation yields

$$\Phi(t) = \begin{pmatrix} e^{-kt} & e^{-kt}\int_0^t \frac{-m_1e^{kr}x^*(r)z_2(r)}{a_1+x^*(r)}dr & 0 \\ 0 & e^{\int_0^t [\frac{\alpha m_1x^*(r)}{a_1+x^*(r)}-\gamma]dr} & 0 \\ 0 & 0 & e^{-\delta t} \end{pmatrix},$$

where $z_2(r) = e^{\int_0^r \left[\frac{\alpha m_1x^*(s)}{a_1+x^*(s)}-\gamma\right]ds}$. Thus the eigenvalues of $\Phi(\tau)$ are $e^{-k\tau}, e^{-\delta\tau}$ and $e^{\int_0^\tau \left[\frac{\alpha m_1x^*(t)}{a_1+x^*(t)}-\gamma\right]dt} > 1$. This illustrates that $(x^*(t),0,0)$ is unstable if $\sigma_0>0$.

We proceed to show that (1) has a nontrivial τ-periodic solution of the form $(\bar{x}(t),\bar{y}(t),0)$, where $\bar{x}(t),\bar{y}(t)>0$, when $\sigma_0>0$. Let

$$\Gamma = \left\{(x,y,z)\in R^3_+ : x+y+z \le \frac{k(x^0+a)}{k_0}\right\}$$

and $\Lambda^+(e)$ denote the ω-limit set of $e \in R^3_+$. Since (1) is dissipative, $\Lambda^+(e) \neq \emptyset, \Lambda^+(e)$ is compact and invariant, and $\Lambda^+(e) \subset \Gamma$ for any $e \in R^3_+$. Let B be a subset of Γ. The stable set $W^+(B)$ of B is defined to be $\{e \in R^3_+ : \Lambda^+(e) \subset B\}$. The weak stable set $W^+_w(B)$ is defined as $W^+_w(B) = \{e \in R^3_+ : \Lambda^+(e) \cap B \neq \emptyset\}$. Let $M_0 = \{(x^*(t), 0, 0) : t \in [0, \tau]\}$ and $A = \{(x, y, z) \in R^3_+ : y = 0\}$. Similar to Ruan [21], and Yang and Freedman [23], we need the following two lemmas to show the existence of a τ-periodic solution of the form $(\bar{x}(t), \bar{y}(t), 0)$.

Lemma 2.3 *For system (1), $A \subset W^+(M_0)$, and if $e(0) \in A \backslash M_0$ then $\lim_{t\to-\infty} \|e(t)\| = \infty$.*

Proof. $A \subset W^+(M_0)$ is trivial. Let $e(0) = (x(0), 0, 0) \in A \setminus M_0$. Since $y(t) = z(t) = 0$ for all t and $x(t) = x^*(t) + (x(0) - x^*(0))e^{-kt}$, $\lim_{t\to-\infty} x(t) = \pm\infty$. Thus $\lim_{t\to-\infty} \|e(t)\| = \infty$. Let $\hat{e}(0) = (\hat{x}(0), 0, \hat{z}(0)) \in A \setminus M_0$. Then $\lim_{t\to-\infty} \|\hat{e}(t)\| = \lim_{t\to-\infty} \|e(t)\| = \infty$, where $e(0) = (\hat{x}(0), 0, 0)$, and the assertion is shown. □

Lemma 2.4 *If $\sigma_0 > 0$, then $\liminf_{t\to\infty} y(t) > 0$ for any solution $(x(t), y(t), z(t))$ of (1) with $y(0) > 0$.*

Proof. Let $e = (x(0), y(0), z(0)) \in R^3_+$ with $y(0) > 0$ be given. If $\liminf_{t\to\infty} y(t) = 0$, then $\Lambda^+(e) \cap A \neq \emptyset$ and $M_0 \subset \Lambda^+(e)$, and thus $e \in W^+_w(M_0)$. On the other hand if $\bar{e} \in W^+_w(M_0)$, then $\liminf_{t\to\infty} y_{\bar{e}}(t) = 0$. Thus $W^+_w(M_0) = \{\hat{e} \in R^3_+ : \liminf_{t\to\infty} y_{\hat{e}(t)=0}\}$. We wish to show that $A = W^+(M_0)$. It is necessary to show $W^+(M_0) \subset A$. Let $\hat{e} \in R^3_+ \setminus A$. If $\hat{e} \in W^+(M_0)$, then $\Lambda^+(\hat{e}) \subset M_0$. Thus $\lim_{t\to\infty} y_{\hat{e}}(t) = \lim_{t\to\infty} z_{\hat{e}}(t) = 0$, and there exists $\hat{\alpha} > 0$ such that $x_{\hat{e}}(t) - x^*(t + \hat{\alpha}) \to 0$ as $t \to \infty$.

We choose $\epsilon > 0$ and $t_0 > 0$ so that $z_{\hat{e}}(t) < \epsilon, x_{\hat{e}}(t) > x^*(t + \hat{\alpha}) - \epsilon$ for $t \geq t_0$ and $\int_0^\tau \left[\frac{\alpha m_1(x^*(t+\hat{\alpha})-\epsilon)}{a_1 + x^*(t+\hat{\alpha}) - \epsilon} - \frac{m_2\epsilon}{a_2 + b\epsilon} - \gamma\right] dt > 0$. Consequently,

$$\begin{aligned} \dot{y}(t) &\geq \left[\frac{\alpha m_1 x(t)}{a_1 + x(t)} - \frac{m_2 z(t)}{a_2 + bz(t)} - \gamma\right] y(t) \\ &\geq \left[\frac{\alpha m_1(x^*(t+\hat{\alpha})-\epsilon)}{a_1 + x^*(t+\hat{\alpha}) - \epsilon} - \frac{m_2\epsilon}{a_2 + b\epsilon} - \gamma\right] y(t) \end{aligned}$$

for all $t \geq t_0$, and thus $\lim_{t\to\infty} y(t) = \infty$. We obtain a contradiction and conclude that $W^+(M_0) \subset A$.

We next show that M_0 is isolated for F, the flow generated by system (1), i.e., we need to find a neighborhood N of M_0 such that M_0 is the maximal invariant set in N. Let

$$c = \max_{y \in [0, \frac{k(x^0+a)}{k_0}]} f'(y)$$

where $f(y) = \dfrac{m_2 y}{a_2 + y}$. We choose $\Delta_0 > 0$ such that

$$\frac{1}{\tau}\int_0^\tau \left[\frac{\alpha m_1(x^*(r) - \frac{\Delta_0}{c})}{a_1 + x^*(r) - \frac{\Delta_0}{c}} - (\gamma + \Delta_0)\right] dr = \sigma_0/2 > 0.$$

Let $\Delta = \Delta_0/c$. It can be shown that $N = \{e \in R^3_+ : d(e, M_0) < \Delta_0/c\}$ is an isolated neighborhood of M_0, where d is the usual Euclidean metric in R^3. For if

this were not true, then there exists an invariant set V such that $M_0 \subset V \subset N$ and $V \setminus M_0 \neq \emptyset$. Since V is invariant, it follows from Lemma 2.3 that $(V \setminus M_0) \cap A = \emptyset$. Therefore if $\hat{e} \in V \setminus M_0$, then $y_{\hat{e}}(0) > 0$. Consequently, since $V \subset N$, we have

$$y_{\hat{e}}(t) > y_{\hat{e}}(0) e^{\int_0^t \left[\frac{\alpha m_1 (x^*(r) - \Delta)}{a_1 + x^*(r) - \Delta} - (\gamma + \Delta_0) \right] dr}$$

for all t large and thus $\lim_{t\to\infty} y_e(t) = \infty$. We obtain a contradiction and conclude that M_0 is isolated for F.

Since $e \in W_w^+(M_0) \setminus W^+(M_0)$ and M_0 is isolated for F, Theorem 4.1 of Butler and Waltman [1] implies that there exists $\bar{e} \in \Lambda^+(e) \cap (W^+(M_0) \setminus M_0) = \Lambda^+(e) \cap (A \setminus M_0)$. But then $\Lambda^+(e)$ is unbounded by Lemma 2.3. We obtain a contradiction and therefore $\liminf_{t\to\infty} y(t) > 0$ is shown. □

Theorem 2.5 *If $\sigma_0 > 0$, then system (1) has a τ-periodic solution of the form $(\bar{x}(t), \bar{y}(t), 0)$, where $\bar{x}(t), \bar{y}(t) > 0$ for $0 \leq b \leq 1$.*

Proof. Since the positive xy-plane is positively invariant, it is enough to show that the xy-subsystem of (1) has a τ-periodic solution $(\bar{x}(t), \bar{y}(t))$ with $\bar{x}(t), \bar{y}(t) > 0$. We consider the Poincaré map T induced by the xy subsystem of (1), $T : R_+^2 \to R_+^2$ by $T(x_0, y_0) = (x(\tau), y(\tau))$, where $(x(t), y(t), z(t))$ is the solution of (1) with initial condition $(x_0, y_0, 0)$. Since (1) is dissipative, $\{T^n(x_0, y_0)\}_{n=0}^{\infty}$ has a convergent subsequence for each (x_0, y_0) with the subsequential limit in the interior of R_2^+ by Lemma 2.4. Also T is orientation preserving and a diffeomorphism, Massera's fixed point theorem [17] implies that T has a fixed point $(\bar{x}, \bar{y})$ in the interior of R_+^2. Consequently, (1) has a τ-periodic solution $(\bar{x}(t), \bar{y}(t), 0)$ with $\bar{x}(t), \bar{y}(t) > 0$. □

Theorem 2.5 asserts the existence of a τ-periodic solution of the form $(\bar{x}(t), \bar{y}(t), 0)$ with $\bar{x}(t), \bar{y}(t) > 0$ when $\sigma_0 > 0$. In the following we show that such a τ-periodic solution is unique when $k = \gamma$.

Suppose $k = \gamma$. We rescale system (1) by letting $\hat{x} = x/x^0, \hat{y} = y/\alpha x^0, \hat{z} = z/\alpha x^0, \hat{m}_1 = \alpha m_1, \hat{a} = a/x^0, \hat{a}_1 = a_1/x^0$ and $\hat{a}_2 = a_2/\alpha x^0$. After incorporating these new state variables and parameters, and ignoring all the hats, system (1) takes the form

$$\begin{aligned} \dot{x} &= k(1 + ae(t) - x) - \frac{m_1 xy}{a_1 + x} \\ \dot{y} &= \frac{m_1 xy}{a_1 + x} - \frac{m_2 yz}{a_2 + y + bz} - ky \\ \dot{z} &= \frac{\beta m_2 (y + bz) z}{a_2 + y + bz} - \frac{m_2 b z^2}{a_2 + y + bz} - \delta z \\ & \quad x(0), y(0), z(0) \geq 0. \end{aligned} \tag{4}$$

We will use system (4) to study (1).

Theorem 2.6 *If $\sigma_0 > 0$ and $k = \gamma$, then system (1) has a unique τ-periodic solution $(\bar{x}(t), \bar{y}(t), 0)$ with $\bar{x}(t), \bar{y}(t) > 0$. Moreover, solutions $(x(t), y(t), z(t))$ of (1) with $z(0) = 0$ and $y(0) > 0$ satisfy $\lim_{t\to\infty} |x(t) - \bar{x}(t)| = \lim_{t\to\infty} |y(t) - \bar{y}(t)| = \lim_{t\to\infty} z(t) = 0$ for $0 \leq b \leq 1$, i.e., $(\bar{x}(t), \bar{y}(t), 0)$ is globally attracting in the interior of the positive xy-plane.*

Proof. It is enough to show that system (4) has the desired property. Since $z(t) = 0$ for $t \geq 0$ as $z(0) = 0$, we consider the xy-subsystem of (4)

$$\begin{aligned} \dot{x} &= k(1 + ae(t) - x) - \frac{m_1 xy}{a_1 + x} \\ \dot{y} &= \frac{m_1 xy}{a_1 + x} - ky \\ & \quad x(0), y(0) \geq 0. \end{aligned} \tag{5}$$

We let $N = \hat{x}^*(t) - x - y$, where $\hat{x}^*(t)$ is the unique τ-periodic solution of $\dot{x} = k(1 + ae(t) - x)$. Then $\dot{N} = -kN$, and system (5) can be rewritten as

$$\begin{aligned} \dot{N} &= -kN \\ \dot{y} &= \left[\frac{m_1(\hat{x}^*(t) - N - y)}{a_1 + \hat{x}^*(t) - N - y} - \gamma\right] y. \end{aligned} \tag{6}$$

Since $\lim_{t\to\infty} N(t) = 0$, the ω-limit set of (6) lies on the set $N = 0$. Restricted to the set $N = 0$, we have

$$\begin{aligned} \dot{y} &= \left[\frac{m_1(\hat{x}^*(t) - y)}{a_1 + \hat{x}^*(t) - y} - k\right] y \\ & \quad 0 \leq y(0) \leq \hat{x}^*(0). \end{aligned} \tag{7}$$

It is easy to see that $y(t) \leq x^*(t)$ for $t \geq 0$ for any solution of (7).

We consider the Poincaré map S induced by (7), $S : [0, \hat{x}^*(0)] \to [0, \hat{x}^*(0)]$ by $Sy_0 = y(\tau, y_0)$, where $y(t, y_0)$ is the solution of (7) with $y(0, y_0) = y_0$. Note that $S0 = 0, S\hat{x}^*(0) < \hat{x}^*(0)$ and $\dot{S}y_0 = \dfrac{\partial y(\tau, y_0)}{\partial y_0} = v(\tau)$, where $v(t)$ satisfies

$$\begin{aligned} \dot{v} &= \left[\frac{m_1 a_1 y}{(a_1 + \hat{x}^*(t) - y)^2} + \frac{m_1(\hat{x}^*(t) - y)}{a_1 + \hat{x}^*(t) - y} - k\right] v \\ v(0) &= 1. \end{aligned}$$

Since $v(t) > 0$ for $t > 0$, we see that S is strictly increasing on $[0, x^*(0)]$. In particular, $\dot{S}0 > 1$ by our assumption. Thus S has at least one positive fixed point. If S has two fixed points, or equivalently if (7) has two positive τ-periodic solution $\bar{y}_i(t) > 0$, $i = 1, 2$, it follows from (7) that $\bar{y}_1(t_0) = \bar{y}_2(t_0)$ for some $t_0 \in (0, \tau)$. Consequently, $y_1(t) = y_2(t)$ for all t and (7) has a unique positive τ-periodic solution $\bar{y}(t)$, $0 < \bar{y}(t) < \hat{x}^*(t)$.

It is then straightforward to show $\lim_{n\to\infty} S^n y_0 = \bar{y}(0)$ for $0 < y_0 \leq \hat{x}^*(0)$. Indeed, $Sy_0 > y_0$ if $0 < y_0 < \bar{y}(0)$ and $\{S^n y_0\}$ is an increasing sequence which is bounded above. Thus $\lim_{n\to\infty} S^n y = \bar{y}$, where $\bar{y} > 0$ is a fixed point of S by the continuity of S. But then $\lim_{n\to\infty} S^n y_0 = \bar{y}(0)$. Similarly, $\lim_{n\to\infty} S^n y_0 = \bar{y}$ if $\bar{y}(0) < y_0 \leq x^*(0)$. Thus (7) has a unique positive τ-periodic solution $\bar{y}(t)$ which is globally asymptotically stable for (7). We apply Lemma A.4 of Hale and Somolinos [7] and conclude that (6) has a globally attracting τ-periodic solution $(0, \bar{y}(t))$. As a result, (5) has a τ-periodic solution $(\bar{x}(t), \bar{y}(t))$ where $\bar{x}(t) = \hat{x}^*(t) - \bar{y}(t) > 0$ and is globally attracting in the interior of positive xy-plane for system (5). Therefore, (1) has a unique τ-periodic solution $(\bar{x}(t), \bar{y}(t), 0)$, which is globally attracting for system (1) on the interior of the positive xy-plane. □

We now assume $\sigma_0 > 0$ and $k = \gamma$ so that system (1) has a unique τ-periodic solution $(\bar{x}(t), \bar{y}(t), 0)$ where $\bar{x}(t), \bar{y}(t) > 0$. We let

$$\sigma_1 = \frac{1}{\tau}\int_0^\tau \left[\frac{\beta m_2 \bar{y}(t)}{a_2 + \bar{y}(t)} - \delta\right] dt.$$

Theorem 2.7 *Let $\sigma_0 > 0$ and $k = \gamma$. If $\sigma_1 < 0$, then solution $(x(t), y(t), z(t))$ of (1) with $y(0) > 0$ satisfies $\lim_{t\to\infty}(x(t) - \bar{x}(t)) = \lim_{t\to\infty}(y(t) - \bar{y}(t)) = \lim_{t\to\infty} z(t) = 0$ for $0 \le b \le 1$.*

Proof. Similar to the proof of Theorem 2.6 we consider the rescaled system (4). We first claim that $\lim_{t\to\infty} z(t) = 0$. Letting $v(t) = \hat{x}^*(t) - x(t) - y(t)$, then $\dot{v}(t) = -kv + \dfrac{m_2 yz}{a_2 + y + bz}$ and thus

$$v(t) = e^{-kt}\left[v(0) + \int_0^t \frac{e^{kr} m_2 y(r) z(r)}{a_2 + y(r) + bz(r)} dr\right].$$

It follows that either there exists $t_1 > 0$ such that $v(t) \ge 0$ for $t \ge t_1$ or $v(t) \le 0$ for $t \ge 0$. For the latter case, we let $w = z - v$. Then $\dot{w} \le -\delta z + kv \le -\hat{k}(z - v)$, where $\hat{k} = \min\{\delta, k\} > 0$. Thus $\lim_{t\to\infty} w(t) = 0$. Since $z(t), -v(t) \ge 0$, we conclude that $\lim_{t\to\infty} z(t) = 0$. For the former case, since $x(t) + y(t) \le \hat{x}^*(t)$ for $t \ge t_1$ and solutions of system (7) are asymptotically attracted to $\bar{y}(t)$, we have $\liminf_{t\to\infty}(\bar{y}(t) - y(t)) \ge 0$. Thus for every $\epsilon > 0$, there exists $t_2 \ge t_1$ such that $y(t) \le \bar{y}(t) + \epsilon$ for $t \ge t_2$. We choose $\epsilon > 0$ such that $\dfrac{1}{\tau}\displaystyle\int_0^\tau \left[\frac{\beta m_2(\bar{y}(t) + \epsilon)}{a_2 + \bar{y}(t) + \epsilon} - \delta\right] dt = \frac{\sigma_1}{2} < 0$. Then $\dot{z} \le (\dfrac{\beta m_2 y}{a_2 + y} - \delta) z$ implies

$$\begin{aligned} z(t) &\le z(0) e^{\displaystyle\int_0^{t_2}\left[\frac{\beta m_2 y(s)}{a_2 + y(s)} - \delta\right] ds} e^{\displaystyle\int_{t_2}^{n\tau + t_2}\left[\frac{\beta m_2(\bar{y}(s) + \epsilon)}{a_2 + \bar{y}(s) + \epsilon} - \delta\right] ds} \\ &= z(0) e^{\displaystyle\int_0^{t_2}\left[\frac{\beta m_2 y(s)}{a_2 + y(s) + \epsilon} - \delta\right] ds} e^{\displaystyle\frac{1}{2} n\sigma_1\tau} \to 0 \text{ as } t \to \infty. \end{aligned}$$

Thus $\lim_{t\to\infty} z(t) = 0$ is shown.

We now use the Poincaré map induced by system (4) to study global attractibility. Defining $P : R^3_+ \to R^3_+$ by $P(x_0, y_0, z_0) = (x(\tau), y(\tau), z(\tau))$, where $(x(t), y(t), z(t))$ is the solution of system (4) with $x(0) = x_0, y(0) = y_0$ and $z(0) = z_0$ where $y_0 > 0$. Since (4) is dissipative, P is also dissipative. Moreover, P has a global attractor, that is, there is a maximal, compact invariant set X such that $\lim_{n\to\infty} P^n x \in X$ for any $x \in R^3_+$. Since $\lim_{t\to\infty} z(t) = 0$, X lies on the xy-coordinate plane. Restricted to the xy-plane, $P^n(x(0), y(0), 0) = (S^n(x(0), y(0)), 0)$, where S is the Poincaré map induced by system (5). Consequently, P has two fixed points $(\hat{x}^*(0), 0, 0)$ and $(\bar{x}(0), \bar{y}(0), 0)$. We wish to show $\lim_{n\to\infty} P^n(x(0), y(0), 0) = (\bar{x}(0), \bar{y}(0), 0)$.

Recall that $A = \{(x, y, z) \in R^3_+ : y = 0\}$ is a closed subset of R^3_+. Clearly $M = \{(x^*(0), 0, 0)\}$ is the maximal compact invariant set in A and it is isolated in X. The stable set of M is A by the proof of Lemma 2.4 as $\sigma_0 > 0$. Thus it follows from Theorem 4.1 of Hofbauer and So [8] that P is uniformly persistent with respect to A, i.e., there exists $\zeta > 0$ such that $\liminf_{n\to\infty} d(P^n(x, y, z), A) > \zeta$ for

all $(x, y, z) \in R^3_+$ with $y > 0$. Therefore any subsequential limit of P has the form $(x, y, 0)$, where $y > 0$. We conclude that $\lim_{n\to\infty} P^n(x, y, z) = (\bar{x}(0), \bar{y}(0), 0)$ and the proof is now complete. □

It follows from Theorem 2.7 that intratrophic predation has no effect on the dynamics of system (1) if $\sigma_0 > 0, k = \gamma$ and $\sigma_1 < 0$. Let $\sigma_0 > 0, k = \gamma$ and $\sigma_1 > 0$. The linearization of (1) with respect to $(\bar{x}(t), \bar{y}(t), 0)$ gives the linear periodic system $\dot{X} = B(t)X$, where

$$B(t) = \begin{pmatrix} -k - \dfrac{m_1 a_1 \bar{y}(t)}{(a_1 + \bar{x}(t))^2} & \dfrac{-m_1 \bar{x}(t)}{a_1 + \bar{x}(t)} & 0 \\ \dfrac{\alpha m_1 a_1 \bar{y}(t)}{(a_1 + \bar{x}(t))^2} & \dfrac{\alpha m_1 \bar{x}(t)}{a_1 + \bar{x}(t)} - k & \dfrac{-m_2 \bar{y}(t)}{a_2 + \bar{y}(t)} \\ 0 & 0 & \dfrac{\beta m_2 \bar{y}(t)}{a_2 + \bar{y}(t)} - \delta \end{pmatrix}.$$

Notice from Lemma 6.4 of [19] that the Floquet multipliers of $(\bar{x}(t), \bar{y}(t), 0)$ are s_1, s_2 and $e^{\int_0^\tau \left[\frac{\beta m_2 \bar{y}(t)}{a_2 + \bar{y}(t)} - \delta\right] dt}$, where s_1, s_2 are the Floquet multipliers of $(\bar{x}(t), \bar{y}(t))$ for the xy-subsystem of (1). Observe that $|s_1|, |s_2| < 1$ by Theorem 2.6. Since $\sigma_1 > 0$, we have

$$e^{\int_0^\tau \left[\frac{\beta m_2 \bar{y}(t)}{a_2 + \bar{y}(t)} - \delta\right] dt} > 1.$$

Therefore $(\bar{x}(t), \bar{y}(t), 0)$ is unstable with stable set lies on the xy-plane.

Theorem 2.8 *Let $\sigma_0 > 0, k = \gamma$ and $\sigma_1 > 0$. Then system (1) is uniformly persistent and (1) has a positive τ-periodic solution $(\hat{x}(t), \hat{y}(t), \hat{z}(t))$ for $0 \le b \le 1$.*

Proof. We apply Theorem 3.1 of Butler and Waltman [1]. Let ∂F be F restricted to $\partial\Gamma$, the boundary of Γ. Then $\Omega(\partial F) = \{\Lambda^+(e) : e \in \partial\Gamma\} = \{M_0, M_1\}$, where $M_1 = \{(\bar{x}(t), \bar{y}(t), 0) : 0 \le t \le \tau\}$. Clearly ∂F is acyclic as M_0 and M_1 are globally attracting on the positive xz and xy-plane respectively so that no subset of $\{M_0, M_1\}$ forms a cycle. Since $\sigma_0, \sigma_1 > 0$, M_0 and M_1 are isolated for F respectively. Similarly, we can show that M_0 and M_1 are also isolated for ∂F respectively. Therefore ∂F is isolated and acyclic with acyclic covering $\{M_0, M_1\}$. Observe that $W^+(M_i) \cap \overset{\circ}{\Gamma} = \emptyset$ for $i = 0, 1$ as $\sigma_0, \sigma_1 > 0$, where $\overset{\circ}{\Gamma}$ denotes the interior of Γ. Theorem 3.1 of Butler and Waltman [1] implies that (1) is uniformly persistent. Using Horn's results concerning interior fixed points of Poincaré maps [9], Yang and Freedman [23] established explicit existence criteria of interior periodic solutions for certain ecological models. Since system (1) satisfies each of these conditions given in [23], (1) has a τ-periodic solution in $\overset{\circ}{\Gamma}$ and we conclude that (1) has a positive τ-periodic solution. □

3. **Numerical Simulations.** In this section we use numerical examples to study system (1). Although there is evidence suggesting that input nutrient varies periodically, to our knowledge there are no specific periodic functions that model a realistic system in the literature. Therefore, we choose

$$e(t) = \sin\left(\frac{\pi t}{10}\right) \text{ and } a = 5.$$

Then the input nutrient concentration is periodic with amplitude 5 and period 20. The parameter values for the model are $a_1 = a_2 = 1, k = 0.5, x^0 = 10, m_1 = m_2 = 0.8, \gamma = 0.5$ and $\beta = 0.8$ for all simulations. These parameter values are within the range of the parameter values studied in several nutrient-plankton models [5, 6]. The wide range of the parameter values cited in the literature on one hand reflects uncertainties associated with the natural systems. On the other hand, different natural systems have different biological complexity and as a result their parameter values may differ.

Our analysis in the previous section is carried out only when the functional responses of both prey and predator are Michaelis-Menten. This particular functional response was also used in [15] in their study of intratrophic predation. System (1) with these parameter values and functionals then takes the following form.

$$\begin{aligned} \dot{x} &= 0.5(10 + 5\sin(\frac{\pi t}{10}) - x) - \frac{0.8xy}{1+x} \\ \dot{y} &= \frac{0.8\alpha xy}{1+x} - \frac{0.8yz}{1+y+bz} - 0.5y \\ \dot{z} &= \frac{0.64(y+bz)z}{1+y+bz} - \frac{0.8bz^2}{1+y+bz} - \delta z \\ & x(0), y(0), z(0) \geq 0. \end{aligned} \tag{8}$$

The periodic solution $(x^*(t), 0, 0)$ can be obtained analytically. When $\alpha = 1$, $\sigma_0 = \frac{1}{20}\int_0^{20}\left(\frac{0.8x^*(t)}{1+x^*(t)} - 0.5\right)dt = 0.2212 > 0$. Therefore $(x^*(t), 0, 0)$ is unstable. We use $\alpha = 1$ for the remainder of the simulations. Since $k = \gamma = 0.5$, (8) has a unique 20-periodic solution $(\bar{x}(t), \bar{y}(t), 0)$ for which solutions of (8) with $y(0) > 0$ are asymptotic to when

$$\sigma_1 = \frac{1}{20}\int_0^{20}\left[\frac{0.64\bar{y}(t)}{1+\bar{y}(t)} - \delta\right]dt < 0.$$

This is true if $\delta = 0.561$. When $\sigma_1 > 0$, system (8) has a positive 20-periodic solution $(\hat{x}(t), \hat{y}(t), \hat{z}(t))$. The linearlization about the positive periodic solution yields the linear periodic system $\dot{Z} = A(t)Z$, with $A(t)$ given below.

$$A(t) = \begin{pmatrix} -0.5 - \frac{0.8\hat{y}(t)}{(1+\hat{x}(t))^2} & \frac{-0.8\hat{x}(t)}{1+\hat{x}(t)} & 0 \\ \frac{0.8\hat{y}(t)}{(1+\hat{x}(t))^2} & a_{22} & \frac{-0.8\hat{y}(t)(1+\hat{y}(t))}{(1+\hat{y}(t)+b\hat{z}(t))^2} \\ 0 & \frac{0.64\hat{z}(t)+0.8b\hat{z}(t)^2}{(1+\hat{z}(t)+b\hat{z}(t))^2} & a_{33} \end{pmatrix},$$

where $a_{22} = \frac{0.8\hat{x}(t)}{1+\hat{x}(t)} - 0.5 - \frac{0.8\hat{z}(t)(1+b\hat{z}(t))}{(1+\hat{y}(t)+b\hat{z}(t))^2}$, and

$$a_{33} = 0.64\frac{(y+2bz)(1+y+bz) - bz(y+bz)}{(1+y+bz)^2} - \frac{0.16bz(1+y+bz) - 0.8b^2z^2}{(1+y+bz)^2} - \delta,$$

with $y = \hat{y}(t)$ and $z = \hat{z}(t)$. The fundamental matrix $\Phi(t)$ of the linear system $\dot{Z} = A(t)Z$ is obtained via numerical interpolations. We start from the situation when there is no introtrophic predation $b = 0$, and vary δ so that the eigenvalues of

$\Phi(20)$ has modulus 1. Denote the minimum value of δ by δ_0 for which the positive periodic solution is non-hyperbolic, and determine whether the positive periodic solution is stable when $\delta > \delta_0$ or when $\delta < \delta_0$. We then increase b and look for δ_0. The bifurcation diagram with b as our bifurcation parameter is presented in Fig.1. The figure demonstrates that intratrophic predation can increase the stability of the positive periodic solutions even when such a mechanism is very small. The mean values of the corresponding stable positive periodic solutions are plotted in Fig. 2, 3, and 4. The graphs clearly indicate that intratrophic predation can increase the mean values of the prey population and decrease the mean values of both the nutrient concentration and predator population of the stable positive periodic solutions.

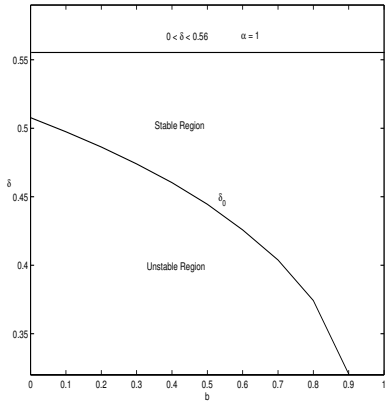

FIGURE 1. We use $\alpha = 1$ and plot the stable and unstable regions of the positive periodic solutions by using the intensity of the intratrophic predation b as our bifurcation parameter.

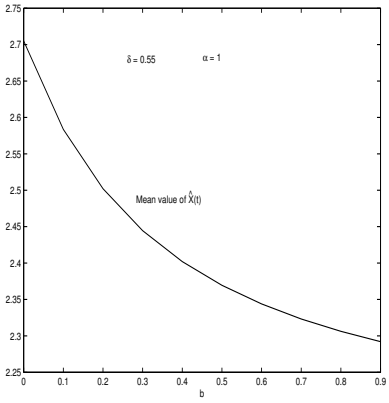

FIGURE 2. The mean values of the nutrient concentration for the stable positive periodic solutions are plotted when $\delta = 0.55$.

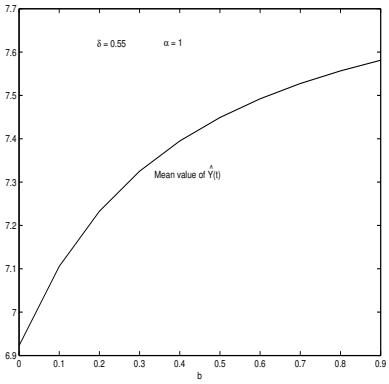

FIGURE 3. The mean values of the prey population for the stable positive periodic solutions are plotted by using b as the independent variable.

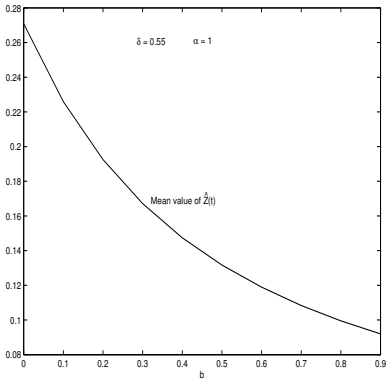

FIGURE 4. The mean values of the predator population for the stable positive periodic solutions are given in the figure. The mean values decrease as the parameter b increases.

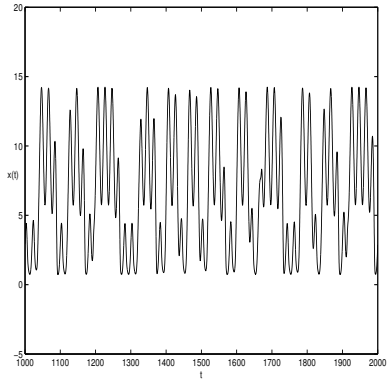

FIGURE 5. The nutrient concentration $x(t)$ is plotted against t when $b = 0$ and $\delta = 0.300016$. The x component of the solution is aperiodic.

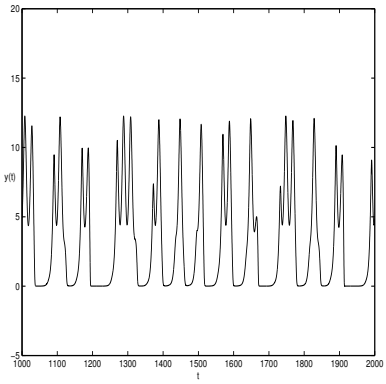

FIGURE 6. The prey population $y(t)$ is plotted against t when $b = 0$ and $\delta = 0.300016$. The plot also reveals that the predator population is aperiodic.

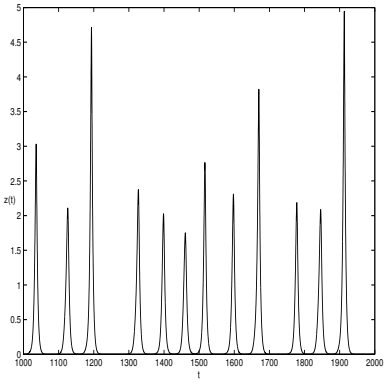

FIGURE 7. This is the predator population for the aperiodic solution with $b = 0$ and $\delta = 0.300016$.

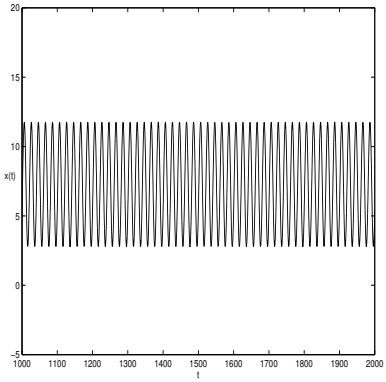

FIGURE 8. As we increase b to $b = 0.92$, system (8) has a locally asymptotically stable positive periodic solution as demonstrated in Figure 1 when $\delta = 0.300016$. The plot provides the nutrient concentration of the stable positive periodic solution.

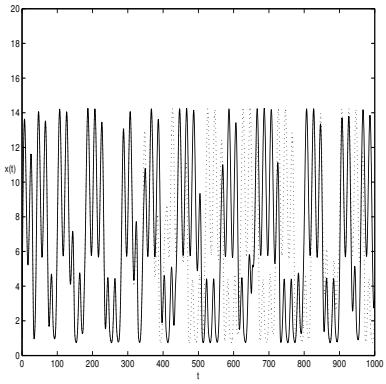

FIGURE 9. We use two very similar initial conditions to test for sensitive dependence on initial condition for model (8) when $b = 0$ and $\delta = 0.300016$. Both prey and predator have the same population level. The dotted line is the nutrient concentration with initial concentration only 0.01 more than the other one. It is clear that two nutrient concentrations behave quite differently even when time t is small.

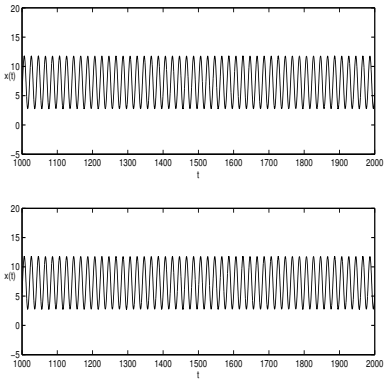

FIGURE 10. This is the figure when $b = 0.92$ by using $\delta = 0.300016$. The plot on the bottom uses initial condition almost exactly same as the top plot except $x(0)$ is increased by 0.01. From the figure it can be seen that the nutrient concentration of the two solutions are asymptotically the same.

Although from Figure 1 we can conclude that intratrophic predation can produce larger stability region for the positive periodic solution, it does not provide any information as to what happens when the periodic solution is unstable. To further illustrate the stabilizing effect of intratrophic predation, we first demonstrate that model (8) has aperiodic solutions when $b = 0$. See Figures 5-7 for nutrient, prey and predator populations of the solution, respectively. In these figures, $\alpha = 1$ and $\delta = 0.300016$ are used. We next fix every other parameters but increase b to $b = 0.92$. Then system (8) has a stable positive periodic solution as was demonstrated in Figure 1. Figure 8 shows the nutrient concentration $x(t)$ of the periodic solution.

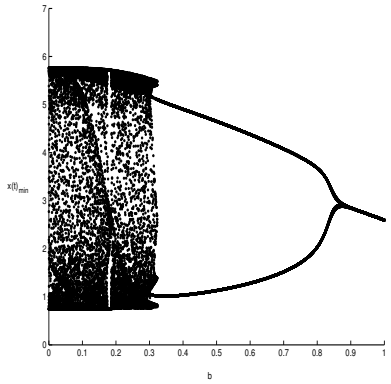

FIGURE 11. This is a bifurcation diagram using b as a bifurcation parameter with $\delta = 0.300016$. The figure plots 25 minimum values of x-component of the solutions of (8) after transitive behavior has been removed.

We next test for sensitive dependence on initial conditions when $b = 0$. We use the same initial condition as in Figure 5 and compare the solution with the initial condition by adding 0.01 to the nutrient concentration, while both prey and predator populations are kept at the same level. The dotted line in Figure 9 is the solution with new initial condition. The figure illustrates the x-component of the two solutions. It is clear from Figure 9 that the model is sensitively dependent on initial conditions when $b = 0$. This is an indication of chaos. When $b = 0.92$, since the positive periodic solution is locally asymptotically stable as given in Figure 1, the two solutions look alike. See Figure 10 for the case when $b = 0.92$.

From our numerical simulations of model (8) so far we know that intratrophic predation can make the system more stable and it can also eliminate the sensitive dependence on initial conditions as was found when there is no intratrophic predation. We now use b, the intensity of intratrophic predation, as our bifurcation parameter and numerically plot the last 25 minimum values of x-component of the solutions of system (8) after ignore the first 20000 iterations. From Figure 11 it is clear that intratrophic predation can eliminate the chaotic behavior of this three species food chain and make the nutrient-plankton interaction more stable.

4. **Discussion.** In this manuscript we study a nutrient-prey-predator model with periodic nutrient input to incorporate day/night or seasonal variations of the natural systems. Moreover, the predator population is assumed to be either cannibalism or may consist of several different species and some of the species may prey on other species of the same population. This consideration in particular models the realistic plankton system, where different species of larger zooplankton may prey on smaller species of zooplankton, and all the zooplankton species are considered as a single population. Our modeling methodology of intratrophic predation is similar to that considered by Kohlmeier and Ebenhoh [13], Pitchford and Brindley [15], and Jang and Baglama[12]. 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 [13], in which North Sea benthic ecosystem was considered.

It was shown that the dynamics of this simple food chain depend on the thresholds σ_0 and σ_1. The threshold σ_0 can be regarded as the average net reproductive number of the prey. If $\sigma_0 < 0$, then the system has only a unique periodic solution $E_0 = (x^*(t), 0, 0)$ and all solutions are asymptotic to E_0. We conclude that intratrophic predation has no effect 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 $\sigma_0 > 0$, then the periodic solution $E_0 = (x^*(t), 0, 0)$ is unstable. System (1) has a periodic solution of the form $E_1 = (\bar{x}(t), \bar{y}(t), 0)$. When $k = \gamma$, then such a periodic solution on the xy-plane is unique and globally attracting on the xy-plane. We can define another threshold σ_1, where σ_1 can be viewed as the net reproductive number of the predator when the prey population is stabilized at $\bar{y}(t)$. If $\sigma_1 < 0$, then the prey population cannot sustain the predator and the predator becomes extinct independent of b. Therefore solutions with positive initial prey population all asymptotic to E_1 and intratrophic predation has no influence on the dynamics of the system.

The more interesting case is when $\sigma_0 > 0$ and $\sigma_1 > 0$. This is the case when both prey and predator populations can persist as shown by Theorem 2.8. We then use b, the intensity of the intratrophic predation, as our bifurcation parameter. The bifurcation given in Figure 1 clearly demonstrates that intratrophic predation has the stabilization effect even when $b > 0$ is very small. Since positive periodic solutions depend on δ, we calculate numerically the critical value δ_0 such that the positive periodic solution is non-hyperbolic when $\delta = \delta_0$. Numerical simulations in this study suggest that intratrophic predation can increase the mean values of the prey populations of the stable positive periodic solutions, decrease the mean values of the nutrient concentration and predator population of the stable positive periodic solution, and it can also eliminate sensitive dependence on initial conditions of the system.

Our study of intratrophic predation in this three trophic level food chain with periodic nutrient input illustrates that intratrophic predation has the effect on the system only if the net reproductive numbers of the prey and predator are greater than zero. Under these circumstances, intratrophic predation can stabilize the system. That is, intratrophic predation can change the stability of the coexisting periodic solutions, and it has the effect of elevating the prey population of the coexisting periodic solutions. Consequently, the mechanism of intratrophic predation also decreases the nutrient concentration of the positive periodic solutions. Moreover, our numerical simulations demonstrated that a moderate degree of intratrophic predation can eliminate the chaotic behavior of the system.

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