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A Food Chain with Lethal Prey

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A Food Chain with Lethal Prey

James P. Braselton ^α & Martha L. Abell ^σ

Abstract- We form a model of a food chain in the chemostat where the prey species can defend itself against the predator by producing a toxin lethal to the predator. Numerically, we illustrate that if the toxin production by the prey is constant, toxin levels will not vary considerably. On the other hand, if the prey is able to adjust its toxin production based on the density of the predator, toxin levels can vary considerably and periodically. In the context of the biological example we reference, the results indicate that toxic algae blooms might be a regular and periodic occurrence in nature.

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I. INTRODUCTION

We consider a basic, resource-based food chain between two organisms of which the chemostat is the standard example. Such models have applications in ecology to model a simple lake and in biotechnology to model the commercial bioreactor. Experimental verification of the match between theory and experiment in the chemostat can be found in Hansen and Hubble, [6]. For a general discussion of competition see Frederickson and Stephanopoulos, [4], and Smith, [27], while a detailed mathematical description of competition in the chemostat may be found in Smith and Waltman, [26].

Inhibitors (including those added to the environment as well as those produced by the competing organisms) in the chemostat have been studied extensively in [3] as well as in [15, 8, 9, 17, 10, 14]. In ecology, inhibitors are often modeling pollutants and studied in the context of detoxification, [14] but in bio-reactors they play the role of controls. Production of, or resistance to, an inhibitor is often accomplished by a genetic modification through a plasmid. Both the production of allelopathic agents (which we will call anti-competitor toxins or toxins) and the resistance to various agents also occur in nature. Several articles of plasmid models in the chemostat include [7, 12, 13, 16, 18, 25, 28].

In nature, there is an interesting relationship between the zooplankton *Karenia brevis* and various zooplankton that feed on it. *Karenia brevis* is responsible for many of the “red tides” or “toxic algae blooms” that occur off the coast of Florida. Initially, these blooms were limited to the Gulf coast of Florida. Now, *Karenia brevis* is found in the Atlantic as well. “Toxic algae blooms” have become more prevalent off the Florida coast causing the extended closure of many beaches to humans and causing harm to marine life because of the toxin produced by *K. brevis*. *K. brevis* produces a type of neurotoxin called a **bevetoxin**, which causes numerous health issues in other marine animals and humans that include but are not limited to gastrointestinal and neurological problems that may be lethal.

Consequently, studying the causes of toxic algae blooms, understanding their underlying causes, and then learning to control or eliminate harmful algae blooms provides significant health and financial benefits to those affected by them. In the case of *Karenia brevis*, some studies provide evidence suggesting that the algae producing the toxin are producing the toxin as a defense against competitors. For example, Sunda et al, [29], conclude that there is biological evidence that shows that *K. brevis*'s brevetoxin production inhibits nearby zooplankton, which promotes the survival of *K. brevis*. Their study further concludes the following.

Competition experiments reveal that *K. brevis* produces allelopathic compounds, which inhibit the growth of competing phytoplankton and thereby help enable the slow growing species to dominate.

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Braselton and Abell, [1], do a comprehensive numerical study as to when one competitor produces a toxin to defend itself against competitors. Other biological studies indicate that the toxin production is a natural byproduct of *K. brevis*'s metabolism and, consequently, depends on the nutrients that are available to *K. brevis*. Redshaw et al, [21], suggest that introducing a competitor of *K. brevis* such as organisms similar to *Skeletonema grethae*, *Artemia salina*, or *Aiptasia pallida* could be used as a method of biocontrol of *K. brevis* and, consequently, the bevoxin produced by *K. brevis* that affects numerous organisms. Roth et al, [23, 24], study the effects of introducing algicidal bacteria such as *Cytophaga/Flavobacterium/Bacteroidetes* lethal to *K. brevis* to help control *K. brevis*. Mayali et al, [19], reach similar conclusions as Roth but further conclude that bacterial interactions are "crucial factors that must be taken into consideration in future studies." As temperatures increase, the nutrients available increase and, consequently, the increase in toxin production that has been having severe negative effects on many Florida beaches occur, as has been observed. Refer to Pierce and Henry, [20], for further explanation on this theory. Although the complete understanding of the problem is not a chemostat problem, studying the relationships between different organisms and the cause and effects that they have on others that can be studied in the laboratory is a chemostat problem because relationships between species and nutrient levels can be measured and then plans for addressing the problems caused by the species can be devised based on the science learned in the laboratory. Studies suggested such as these have already been completed in the laboratory. For example, refer to Han et al, [5]. Thus, we believe that following the standards established by these prior studies are appropriate scientific approaches to help us understand and try to solve the problem caused by organisms such as *K. brevis* that cause harmful algae blooms.

II. BACKGROUND

Following Smith and Waltman, [26], the scaled equations (dimensionless variables) for a basic food chain in the chemostat are

$$\begin{aligned}\frac{dS}{dt} &= 1 - S - \frac{m_1 S}{a_1 + S} x \\ \frac{dx}{dt} &= x \left[\frac{m_1 S}{a_1 + S} - 1 - \frac{m_2}{a_2 + x} y \right] \\ \frac{dy}{dt} &= y \left[\frac{m_2 x}{a_2 + x} - 1 \right]\end{aligned}\tag{1}$$

$$S(0) = S_0 \geq 0, x(0) = x_0 \geq 0, y(0) = y_0 \geq 0.$$

In system (1), the interpretation is that $S = S(t)$ is the density of the nutrient, the species with density $x = x(t)$ lives on the contents of the nutrient available in the chemostat and the species with density $y = y(t)$ feeds on the the organism with density $x = x(t)$. Further, m_i represents the *maximal growth rate* and the a_i are the *Michaelis-Menton* constants.

The analysis of system (1) begins with letting $\Sigma = 1 - S - x - y$. Then, $\Sigma' + \Sigma = 0$ so $\Sigma = Ce^{-t}$ and, consequently, $\lim_{t \rightarrow \infty} \Sigma(t) = 0$. This substitution allows system (1) to be reduced to

$$\begin{aligned}\frac{dx}{dt} &= x \left[\frac{m_1(1 - x - y)}{1 + a_1 - x - y} - 1 - \frac{m_2}{a_2 + x} y \right] \\ \frac{dy}{dt} &= y \left[\frac{m_2 x}{a_2 + x} - 1 \right]\end{aligned}\tag{2}$$

$$x \geq 0, y \geq 0, x + y \leq 1.$$

Following Smith and Waltman, [26], define $\lambda_i = \frac{a_i}{m_i - 1}$. Let $E_1 = (0, 0)$ and $E_2 = (1 - \lambda_1, 0)$ be the two boundary rest points of system (2). A fundamental result for system (2) is that if $\lambda_1 + \lambda_2 > 1$, then there is no positive solution of (2) which means that under these conditions, E_2 is globally asymptotically stable. On the other hand, if $\lambda_1 + \lambda_2 < 1$, there is a unique interior rest point and E_2 is unstable. In this situation, let $E_c = (x_c, y_c)$ denote the interior rest point. E_c is stable if

$$\frac{y_c}{m_2 \lambda_2^2} < \frac{m_1 a_1}{(1 + a_1 - \lambda_2 - y_c)^2}. \tag{3}$$

E_c is unstable if the inequality is reversed so one typically concludes that there are one or more limit cycles for system (2) in this situation. Although the possibility of multiple limit cycles is not eliminated, the examples that follow indicate that they may be rare or do not exist.

III. FORMULATION OF THE MODEL

We consider two species in the chemostat with densities $x = x(t)$ and $y = y(t)$, respectively. We assume that the species with density x feeds on the nutrient S in the chemostat while the species with density y feeds on the species with density x : y is the predator and x is the prey. The equations are scaled so that the variables are dimensionless.

The model we introduce gives the prey species a mechanism to produce a lethal toxin to the prey that is represented by the $k \frac{m_1 S}{a_1 + S} x$ in the P -equation in system (4). We interpret k to be the “effort” that the prey devotes to defending itself against the predator. In this paper we will discuss the cases when k is constant and when k is not but rather depends on the density of the predator with density y .

Taking into consideration the above, the scaled equations for the predator-prey model in the chemostat in which the prey produces a lethal toxins against its predator take the form

$$\begin{aligned} \frac{dS}{dt} &= 1 - S - \frac{m_1 S}{a_1 + S} x \\ \frac{dx}{dt} &= x \left[\frac{(1 - k)m_1 S}{a_1 + S} - 1 - \frac{m_2}{a_2 + x} y \right] \\ \frac{dy}{dt} &= y \left[\frac{m_2}{a_2 + x} x - 1 - \gamma P \right] \\ \frac{dP}{dt} &= k \frac{m_1 S}{a_1 + S} x - P \end{aligned} \tag{4}$$

$$S(0) = S_0 \geq 0, x(0) = x_0 \geq 0, y(0) = y_0 \geq 0.$$

The following analysis considers two situations. For simplicity, we first assume that k is constant. Then, we consider the more likely possibility that the prey’s defense against the predator depends on the density of the predator.

Hsu and Waltman, [10] or [11], study the case when x and y are competitors. Remarkably, the analysis of system (4) can be carried out in a similar manner as to the systems that arise when the species with density $x = x(t)$ and the species with density $y = y(t)$ are competitors. To see the similarities, first let $\Sigma = S + x + y + P$. Then, $\Sigma' + \Sigma = 1 - \gamma y P \leq 1$ which means $\limsup_{t \rightarrow \infty} \Sigma(t) \leq 1$. Each component of system (4) is non-negative so system (4) is dissipative and consequently has a compact, global attractor.

IV. K CONSTANT

If k is constant, to simplify system (4), let $z = S + \frac{1}{k} P$. Then, $z' + z = 1$ and the change of variables results in the system

$$\begin{aligned} \frac{dz}{dt} &= 1 - z \\ \frac{dS}{dt} &= 1 - S - \frac{m_1 S}{a_1 + S} x \\ \frac{dx}{dt} &= x \left[\frac{(1-k)m_1 S}{a_1 + S} - 1 - \frac{m_2}{a_2 + x} y \right] \\ \frac{dy}{dt} &= y \left[\frac{m_2}{a_2 + x} x - 1 - \gamma k(z - S) \right]. \end{aligned} \tag{5}$$

Solving for $z(t)$, we find $z(t) = 1 + Ce^{-t}$ so that $\lim_{t \rightarrow \infty} z(t) = 1$ and as $t \rightarrow \infty$, $P = k(1 - S)$. Thus, (5) can be viewed as an asymptotic system with limiting system

$$\begin{aligned} \frac{dS}{dt} &= 1 - S - \frac{m_1 S}{a_1 + S} x \\ \frac{dx}{dt} &= x \left[\frac{(1-k)m_1 S}{a_1 + S} - 1 - \frac{m_2}{a_2 + x} y \right] \\ \frac{dy}{dt} &= y \left[\frac{m_2}{a_2 + x} x - 1 - \gamma k(1 - S) \right]. \end{aligned} \tag{6}$$

As before, the system is dissipative, the positive cone is positively invariant, and $x = 0$ and $y = 0$ are invariant sets. Once we analyze system (6), because of the works of Thieme, [31] and [30], the results obtained for system (6) will apply to system (5) and subsequently system (4). Observe that if $m_1 < \frac{1}{1-k}$, $\lim_{t \rightarrow \infty} x(t) = 0$. Similarly, if $m_2 < 1$, $\lim_{t \rightarrow \infty} y(t) = 0$. Thus, we assume that $m_1 > \frac{1}{1-k}$ and that $m_2 > 1$.

4.1. The Boundary Rest Points. To help us classify the rest points, we first observe that the Jacobian of system (6) is

$$\mathbf{J} = \begin{pmatrix} -\frac{a_1 m_1 x}{(a_1 + S)^2} - 1 & -\frac{m_1 S}{a_1 + S} & 0 \\ -\frac{a_1(k-1)m_1 x}{(a_1 + S)^2} & -\frac{a_1 + (k-1)m_1 S + S}{a_1 + S} - \frac{a_2 m_2 y}{(a_2 + x)^2} & -\frac{m_2 x}{a_2 + x} \\ ky\gamma & \frac{a_2 m_2 y}{(a_2 + x)^2} & \frac{m_2 x}{a_2 + x} + k(S - 1)\gamma - 1 \end{pmatrix}. \tag{7}$$

If $x = 0$ it follows that (6) has boundary rest point $E_0 = (S_0, x_0, y_0) = (1, 0, 0)$. Evaluated at E_0 , the Jacobian is

$$\mathbf{J}(E_0) = \begin{pmatrix} -1 & -\frac{m_1}{a_1 + 1} & 0 \\ 0 & \frac{m_1 - km_1}{a_1 + 1} - 1 & 0 \\ 0 & 0 & -1 \end{pmatrix}$$

with eigenvalues $\lambda_{1,2} = -1$ and $\lambda_3 = \frac{(1-k)m_1}{a_1 + 1} - 1$. For the problem to be meaningful, E_0 must be unstable. Therefore, to guarantee that E_0 is unstable we must further assume that

$$\frac{(1-k)m_1}{a_1 + 1} > 1 \quad \text{or} \quad \frac{m_1}{a_1 + 1} > \frac{1}{1-k}, \tag{8}$$

Observe that this assumption implies that $m_1 > \frac{1}{1-k}$. Thus, with our assumptions, E_0 is always unstable.

If $y = 0$, we obtain the restpoint, $E_y = (S_y, x_y, 0)$, where

$$S_y = \frac{a_1}{(1-k)m_1 - 1} \quad \text{and} \quad x_y = 1 - k - \frac{(1-k)a_1}{(1-k)m_1 - 1}.$$

At E_y , the Jacobian is

$$J(E_y) = \begin{pmatrix} \frac{((k-1)m_1+1)^2+a_1}{a_1(k-1)m_1} & \frac{1}{k-1} & 0 \\ \frac{((k-1)m_1+1)(a_1+(k-1)m_1+1)}{a_1m_1} & 0 & -\frac{(k-1)(a_1+(k-1)m_1+1)m_2}{a_1(k-1)-(a_2-k+1)((k-1)m_1+1)} \\ 0 & 0 & a_1((k-1)m_1+1) \left(\frac{(k-1)m_2}{a_1(k-1)-(a_2-k+1)((k-1)m_1+1)} - \frac{k\gamma}{(k-1)m_1+1} \right) - 1 \end{pmatrix}.$$

Table 1: The stability of the rest points using $m_1 = 2.0$, $a_1 = 0.5$, $m_2 = 1.5$, $a_2 = 0.25$, $k = 0.1$, and $\gamma = 0.5$.

Rest Point	Eigenvalues of Jacobian evaluated at rest point	Classification
$E_0 = (1, 0, 0)$	$-1, -1, 0.2$	Unstable
$E_y = (0.625, 0.3375, 0)$	$-1, -0.7299, -0.157$	Locally stable

The eigenvalues of $J(E_y)$ are $\lambda_1 = -1$,

$$\lambda_2 = -\frac{(1 - (1 - k)m_1)(a_1 + 1 - (1 - k)m_1)}{a_1(1 - k)m_1}$$

and

$$\lambda_3 = \frac{1}{((k-1)m_1+1)(a_1(k-1)-(a_2-k+1)((k-1)m_1+1))} \left[-a_1^2\gamma(1-k)k + a_1((1-k)m_1-1)(-k((a_2+2)\gamma+m_2-1)+2\gamma k^2+m_2-1) + ((k-1)m_1+1)^2(a_2\gamma k+a_2-(k-1)(\gamma k-m_2+1)) \right].$$

Because we are assuming that $m_1 > \frac{m_1}{a_1+1} > \frac{1}{1-k}$ and $m_1(1-k)-a_1-1 > 0$, $\lambda_2 < 0$. Observe that with our assumptions regarding the parameter values, the denominator of λ_3 is always negative. The numerator of λ_3 will be negative so that $\lambda_3 > 0$ and unstable if

$$m_2 > \frac{(a_1(k-1)-(a_2-k+1)((k-1)m_1+1))((a_1+1)\gamma k+(k-1)m_1(\gamma k+1)+1)}{(k-1)((k-1)m_1+1)(a_1+(k-1)m_1+1)}$$

and positive otherwise. Thus, we see that λ_3 will be positive for a wide range of parameter values. Because the focus of our problem is to see if the species with density $y(t)$ can control the density of the species with density $x(t)$, we will choose parameter values so that λ_3 has positive real part so that E_y is unstable.

4.2. The Interior Rest Points. If interior rest points of system (6) exist, they take the form $E_c = (S_c, x_c, y_c)$ where

$$x_c = a_2 \left(\frac{m_2}{\gamma k(S_c - 1) + m_2 - 1} - 1 \right) \quad \text{and} \quad y_c = -\frac{a_2(a_1 + (k-1)m_1S_c + S_c)}{(a_1 + S_c)(\gamma k(S_c - 1) + m_2 - 1)}. \tag{9}$$

S_c satisfies the cubic

$$k\gamma S_c^3 + [\gamma k(a_1 - a_2m_1 - 2) + m_2 - 1]S_c^2 + [a_1(-2\gamma k + m_2 - 1) + a_2m_1(\gamma k + 1) + \gamma k - m_2 + 1]S_c + a_1(\gamma k - m_2 + 1) = 0. \tag{10}$$

As indicated in the examples that follow, the system is sensitive to parameter values. To see so, we fix all but one parameter value, then allow the remaining value to change. The example illustrates sensitivity to constant k . We obtained the same results when studying sensitivity to γ , but chose to illustrate sensitivity to constant k here as we consider nonconstant k in the next section.

Example 1. For our first example, we choose $m_1 = 2.0$, $a_1 = 0.5$, $m_2 = 1.5$, $a_2 = 0.25$, $k = 0.1$, and $\gamma = 0.5$. These parameter values result in the rest points $E_0 = (1, 0, 0)$ and $E_y = (0.625, 0.3375, 0)$. There are no interior rest points. The eigenvalues of the Jacobian evaluated at each rest point and their local stability are illustrated in Table 1.

Parametric plots of x -vs- y are shown in Figure 1. In the figure, observe that the stability of E_x appears to be global rather than local.

Depending on the parameter values, an interior rest point can be stable.

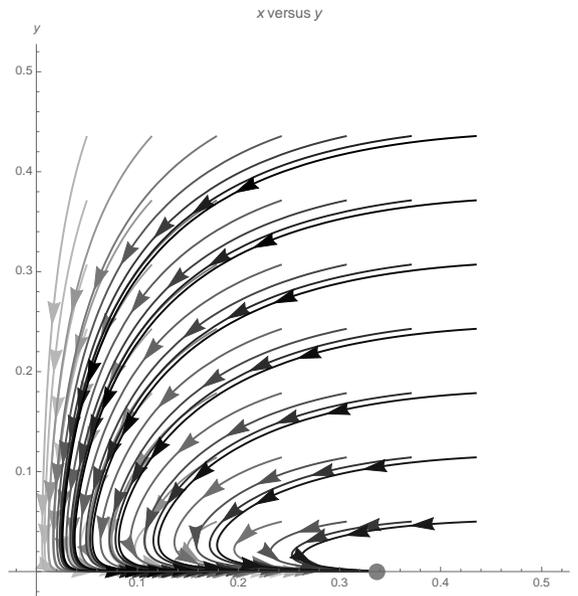


Figure 1: Notice that all nontrivial solutions appear to approach E_y .

Table 2: The stability of the rest points using $m_1 = 1.121$, $a_1 = 0.05$, $m_2 = 1.5$, $a_2 = 0.25$, $k = 0.01$, and $\gamma = 3.25$.

Rest Point	Eigenvalues of Jacobian evaluated at rest point	Classification
$E_0 = (1, 0, 0)$	-1, -1, 0.0569	Unstable
$E_y = (0.455, 0.539, 0)$	-1, -0.11829, 0.007	Unstable
$E_c = (0.466, 0.5269, 0.0013)$	-1.0, -0.1011, -0.008	Locally stable

Example 2. To illustrate a locally stable interior rest point, we choose $m_1 = 1.121$, $a_1 = 0.05$, $m_2 = 1.5$, $a_2 = 0.25$, $k = 0.01$, and $\gamma = 3.25$. These parameter values result in the rest points $E_0 = (1, 0, 0)$, $E_y = (0.455, 0.539, 0)$, and $E_c = (0.466, 0.5269, 0.0013)$. The eigenvalues of the Jacobian evaluated at each rest point and their local stability are illustrated in Table 2.

Parametric plots of x -vs- y are shown in Figure 2. In the figure, observe that the stability of E_c appears to be global rather than local.

Our next example illustrates sensitivity to parameter values. Because we will consider nonconstant k next, we illustrate sensitivity to k here. We obtained similar results with sensitivity to γ or the other parameters.

Example 3. We begin with $m_1 = 2.0$, $a_1 = 0.5$, $m_2 = 5.5$, $a_2 = .25$, $k = 0.15$ and $\gamma = 0.5$. For these parameter values we obtain $E_0 = (1, 0, 0)$, $E_y = (0.714, 0.243, 0)$, and $E_c = (0.927, 0.0559, 0.00581)$. The eigenvalues of the Jacobian evaluated at each rest point and their local stability are illustrated in Table 3. We classify E_c as a stable spiral. In Figure 3 observe that it appears that all nontrivial solutions approach E_c .

Next, we use nearly the same parameter values except for changing k from $k = 0.15$ to $k = 0.1$.

With these parameter values, E_0 and E_y are unstable, while E_c is classified as an unstable spiral. See Figure 4. In the figure, observe that all nontrivial solutions appear to



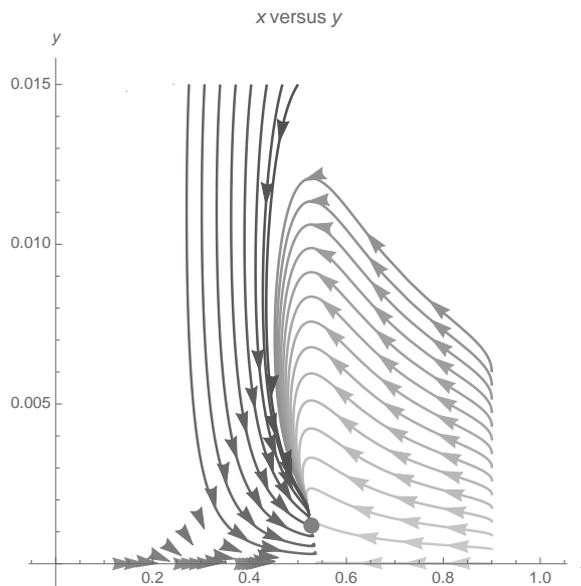


Figure 2: All nontrivial solutions appear to approach E_c .

Table 3: The stability of the rest points using $m_1 = 2.0, a_1 = 0.5, m_2 = 5.5, a_2 = .25, k = 0.15$ and $\gamma = 0.5$.

Rest Point	Eigenvalues of Jacobian evaluated at rest point	Classification
$E_0 = (1, 0, 0)$	-1, -1, 0.133	Unstable
$E_y = (0.714, 0.243, 0)$	-1, -0.1647, 1.68872	Unstable
$E_c = (0.927, 0.00581, 0.0559)$	-1.0, -0.00443 ± 0.296i	Stable spiral

Table 4: The stability of the rest points using $m_1 = 2.0, a_1 = 0.5, m_2 = 5.5, a_2 = .25, k = 0.1$ and $\gamma = 0.5$.

Rest Point	Eigenvalues of Jacobian evaluated at rest point	Classification
$E_0 = (1, 0, 0)$	-1, -1, 0.2	Unstable
$E_y = (0.625, 0.3375, 0)$	-1, -0.2667, 2.14	Unstable
$E_c = (0.927, 0.0559, 0.009425)$	-1.0, 0.00151 ± 0.3773i	Unstable spiral

approach a unique limit cycle. In (a), we illustrate the periodicity of x (in black) and y (in gray) in the limit cycle. On the other hand, (b) illustrates that all nontrivial solutions appear to approach a unique limit cycle while (c) illustrates a possible unique limit cycle. It is important to remember that although the calculations indicate the existence of a limit cycle, they do not establish its uniqueness, which might be an interesting topic in a future study.

The sensitivity to the parameter values is striking. Changing the value of k from $k = 0.1$ to $k = .1127$ and keeping the remaining parameter values the same yields the results show in Table 5. In Table 5, notice that the real part of the eigenvalues for the Jacobian of E_c are “small”—and might be interpreted to be zero.

However, E_c is a stable spiral as illustrated in Figure 5.

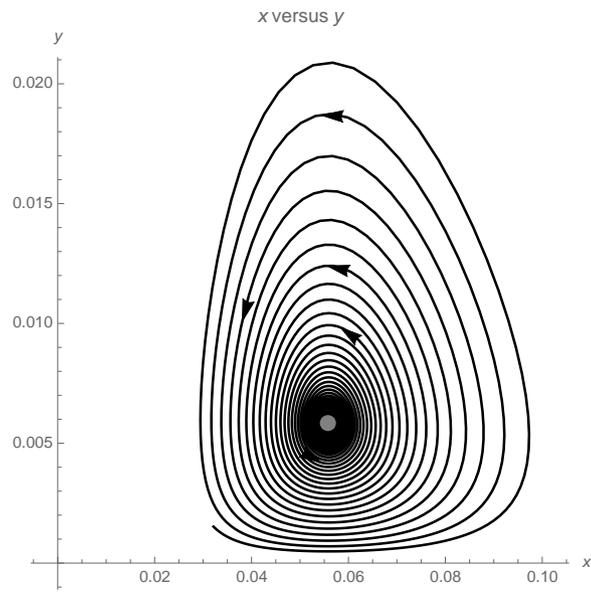


Figure 3: All nontrivial solutions appear to approach E_c .

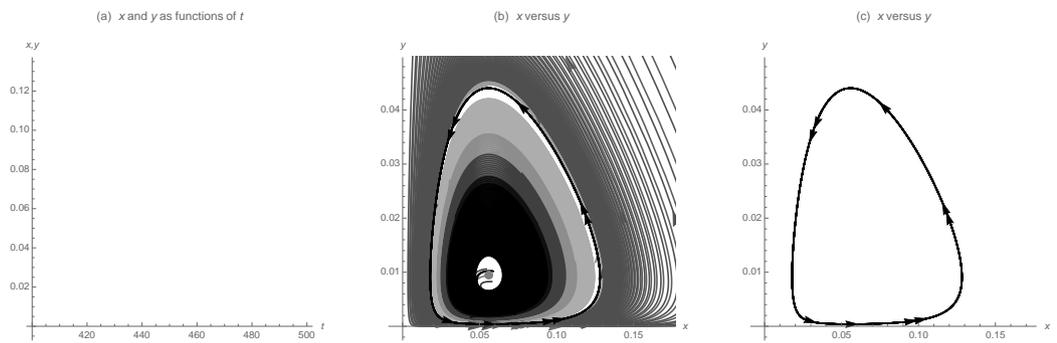


Figure 4: All nontrivial solutions appear to approach a unique limit cycle.

Table 5: The stability of the rest points using $m_1 = 2.0$, $a_1 = 0.5$, $m_2 = 5.5$, $a_2 = .25$, $k = 0.1127$ and $\gamma = 0.5$.

Rest Point	Eigenvalues of Jacobian evaluated at rest point	Classification
$E_0 = (1, 0, 0)$	$-1, -1, 0.183$	Unstable
$E_y = (0.645, 0.3146, 0)$	$-1, -0.2379, 2.04$	Unstable
$E_c = (0.927, 0.0559, 0.00851)$	$-1.0, -5.6512 \times 10^{-6} \pm 0.3584i$	Stable spiral

Alternatively, changing the k -value to $k = 0.1126$ and keeping the remaining parameter values the same yields quite different results than using $k = 0.1127$. See Table 6

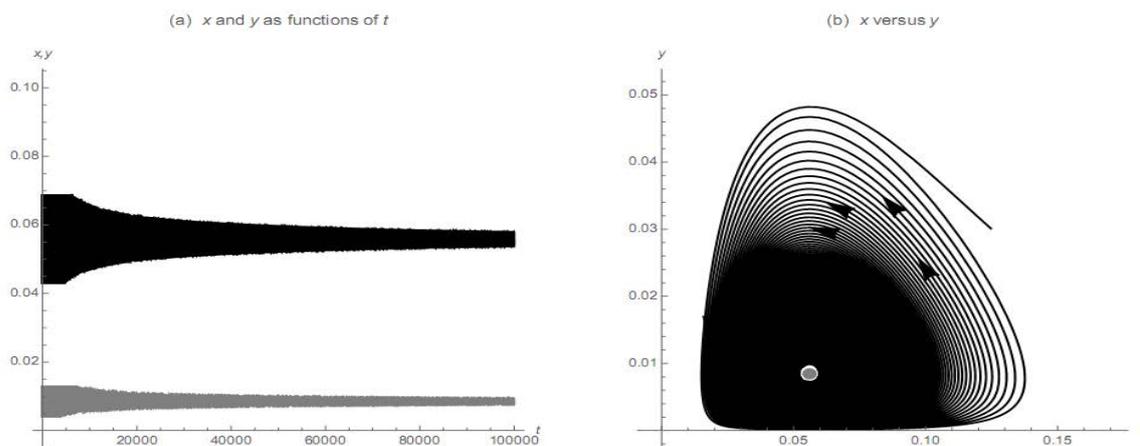


Figure 5: All nontrivial solutions appear to approach E_c .

Table 6: The stability of the rest points using $m_1 = 2.0$, $a_1 = 0.5$, $m_2 = 5.5$, $a_2 = .25$, $k = 0.1126$ and $\gamma = 0.5$.

Rest Point	Eigenvalues of Jacobian evaluated at rest point	Classification
$E_0 = (1, 0, 0)$	$-1, -1, 0.183$	Unstable
$E_y = (0.645, 0.3147, 0)$	$-1, -0.2399, 2.045$	Unstable
$E_c = (0.927, 0.0558, 0.00851)$	$-1.0, 6.2822 \times 10^{-6} \pm 0.3586i$	Unstable spiral

In Table 6, notice that the real part of the eigenvalues for the Jacobian of E_c are “small”—and might be interpreted to be zero. However, E_c is an unstable spiral as illustrated in Figure 6.

Our numerical results seem to indicate that when the parameter values are chosen so that the eigenvalues of the Jacobian evaluated at E_c are “close” to zero, numerical error and precision are important. When the real part of an eigenvalue of the Jacobian evaluate at E_c is positive, the result appears to be convergence of solutions to a unique limit cycle. However, when the real part is “small” it may take computationally and time intense numerical work to illustrate the limit cycle. The results indicate that the convergence to the limit cycle will take larger t -values. In our cases we carried t to $t = 1000000$ (remember that the system is dimensionless so these t -values do not represent days, minutes, years, and so on). As the real part of the eigenvalue corresponding to E_c becomes smaller but remains positive, the limit cycle about E_c will become smaller and smaller. Once the parameter values are chosen so that the real part of the eigenvalues corresponding to E_c are negative, it appears to take larger (or longer) t -values to observe the convergence of the solutions to E_c .

We were not able to find multiple limit cycles nor prove that they do not exist.

V. NONCONSTANT K

We believe that studying the case when k is nonconstant is important because studies such as those done by Roth et al, [23, 24] indicate that dinoflagellates such as *K. brevis* may be able to detect (and probably even develop defenses) against organisms threatening it. Mayali and Doucette, [19], conclude that situations such as these indicate that “bacterial



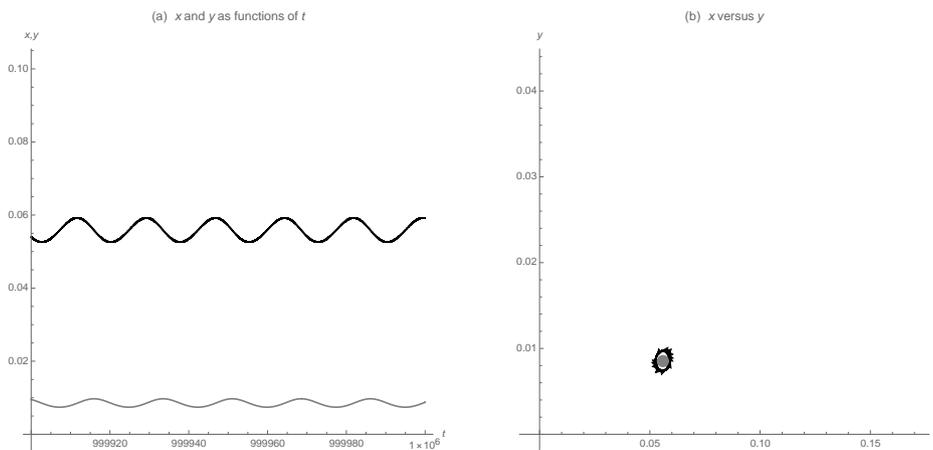


Figure 6: All nontrivial solutions appear to approach a unique limit cycle about E_c .

interactions are crucial factors that must be taken into consideration in future studies.” Situations such as these indicate that the parameter k is not constant.

If we assume that k is not constant but rather a function of x and y (or even t), In the case that k is not constant we consider the functions $k = k(x, y)$ used by Braselton and Waltman, [2],

$$k = k_y(x, y) = \frac{\alpha y}{\beta + x + y} \quad \text{or} \quad k = k_x(x, y) = \frac{\alpha x}{\beta + x + y}. \quad (11)$$

These two choices represent quite different strategies. For k_x , if x is large the species with density $x = x(t)$ devotes more of its resources to producing the toxin, which may not be a sensible assumption in a predator-prey relationship when the species with density $x = x(t)$ is the prey. If the species with density $y = y(t)$ is not present (and β is small), toxin production is essentially constant, which was studied in the previous examples. Thus, we will not further discuss the $k = k_x$ strategy. In a predator-prey relationship, the $k = k_x$ strategy does not seem sensible. If the prey is able to detect its predator, why would it continue to increase its toxin production at the expense of its own growth rate once the predator is eliminated?

On the other hand, if y is large the k_y strategy causes the species with density $x = x(t)$ to increase its toxin production. The form of system (4) remains the same but now k is no longer assumed to be constant. System (12) cannot be reduced from four equations to three as we did when we assumed that k was constant as with system (4).

$$\begin{aligned} \frac{dS}{dt} &= 1 - S - \frac{m_1 S}{a_1 + S} x \\ \frac{dx}{dt} &= x \left[\frac{(1 - k(x, y)) m_1 S}{a_1 + S} - 1 - \frac{m_2}{a_2 + x} y \right] \\ \frac{dy}{dt} &= y \left[\frac{m_2}{a_2 + x} x - 1 - \gamma P \right] \\ \frac{dP}{dt} &= k(x, y) \frac{m_1 S}{a_1 + S} x - P \end{aligned} \quad (12)$$

$$S(0) = S_0 \geq 0, x(0) = x_0 \geq 0, y(0) = y_0 \geq 0.$$

Table 7: The stability of the rest points (S, x, y, P) using $m_1 = 2.0$, $a_1 = 0.5$, $m_2 = 5.5$, $a_2 = .25$, $\gamma = 0.5$, and $k = k_y$ with $\alpha = 1.0$ and $\beta = 0.01$.

Rest Point	Eigenvalues of Jacobian evaluated at rest point	Classification
$E_0 = (1, 0, 0, 0)$	-1, -1, 0.333, 0	Unstable
$E_y = (0.5, 0.5, 0, 0)$	-1, -0.5, 2.67, 0	Unstable
$E_c = (0.927, 0.056, 0.00844, 0.008245)$	-1.0044, 0.0027754, 0.0565 ± 0.4874	Unstable spiral

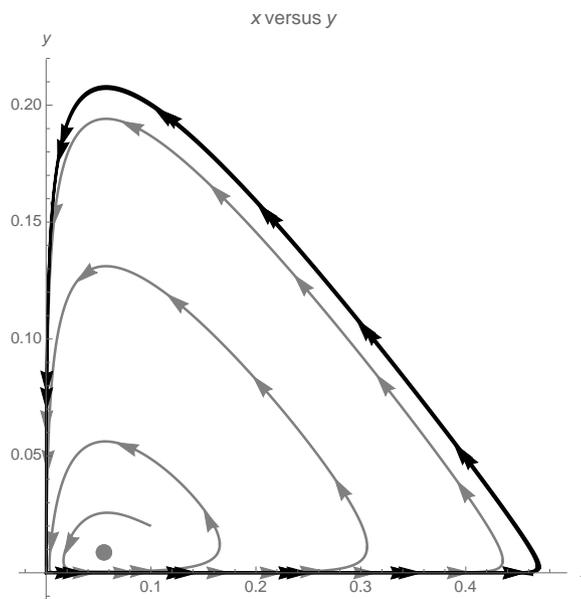


Figure 7: All nontrivial solutions appear to approach a unique limit cycle about E_c .

Example 4.

allocated inhibitor production, with the exception of the k -value we use the same values as those used previously: $m_1 = 2.0$, $a_1 = 0.5$, $m_2 = 5.5$, $a_2 = .25$, and $\gamma = 0.5$. Now allow $k = k_y$ and choose $\alpha = 1.0$ and $\beta = 0.01$.

In Figure 7, we parametrically plot a typical solution of the system for these parameter values as a function of x -vs- y . The long term plot is shown in black. Observe that all non-trivial solutions to the system appear to approach a unique limit cycle about E_c .

On the other hand, in Figure 8, we illustrate the limit cycle with long term plots of x , y , and P as functions of t .

Next in Figure 9 we plot P as a function of t using the k -values used in the previous examples.

Observe the striking difference between Figure 8 (c) and Figure 9. Constant toxin production appears to stabilize the system. On the other hand, when the prey is able to adjust its toxin production based on the density of the predator, "extreme" periodic limit cycles occur.

In the context of our example of *K. brevis* and its potential toxin production against predators, these numerical results indicate that if the prey is able to adjust its toxin production based on the density of the predator, the density of the toxin will be periodic

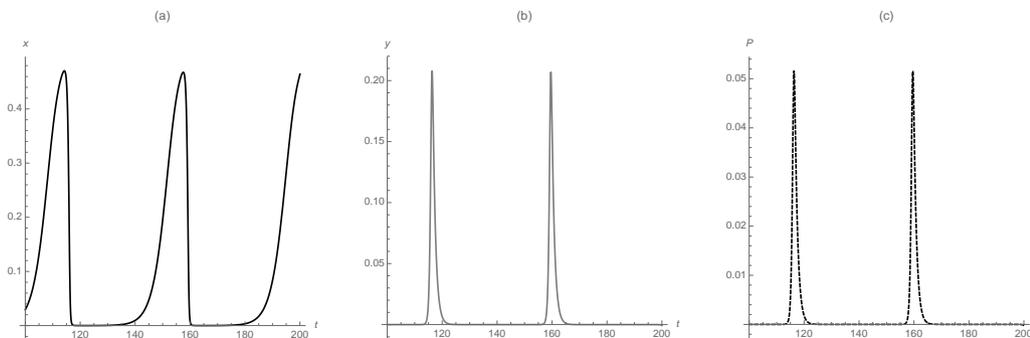


Figure 8: (a) x (prey) as a function of t , (b) y (predator) as a function of t , (c) P (toxin) as a function of t .

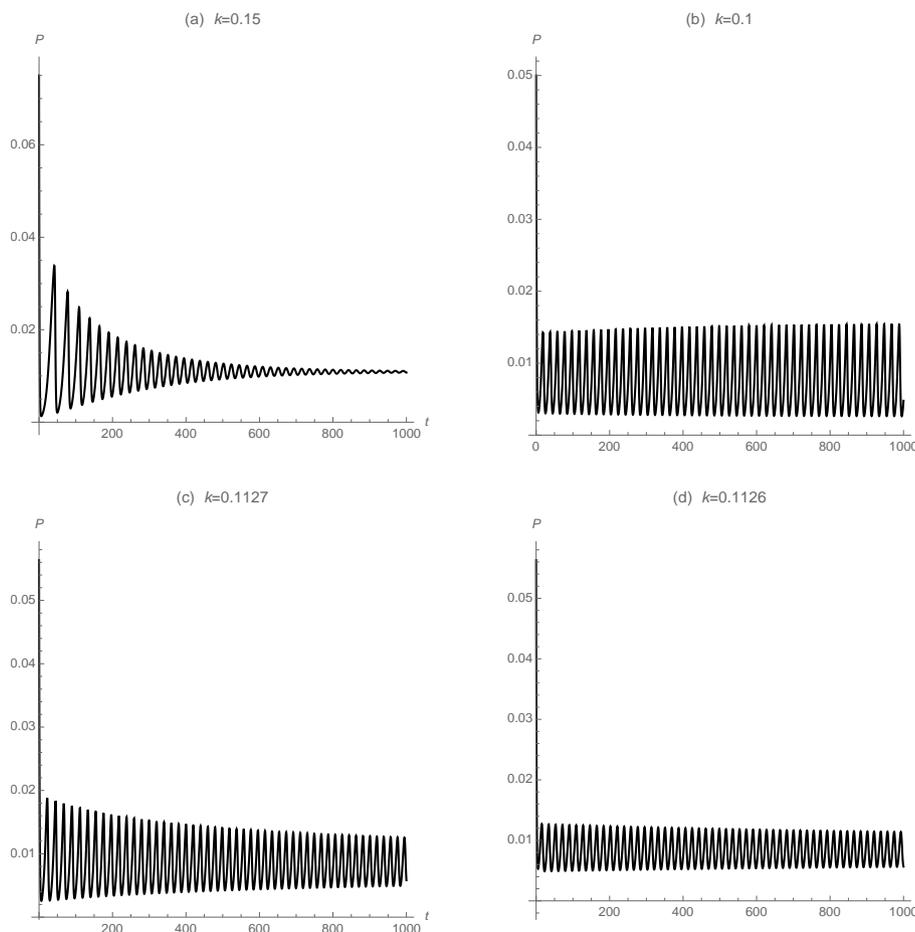


Figure 9: (a) $k = 0.15$, (b) $k = 0.1$, (c) $k = 0.1127$, (d) $k = 0.1126$.

and more extreme than when the prey produces toxin at a constant level. Thus, if this is a model that most accurately describes the *K. brevis* algae blooms, the algae blooms should be expected to occur periodically and be extreme rather than be a persistent menace (Figure 9).

VI. CONCLUSION

We have numerically studied a simple food chain in the chemostat where the prey species is given a defense against the predator by being able to produce a toxin that is lethal to the predator. We have considered the situation when the prey's defense is constant as well as when the prey's defense depends on the density of the predator. The numerical results indicate that constant toxin production lead to predictable, although mildly periodic, toxin levels. On the other hand, when the prey can adjust its toxin production based on its ability to detect the predator, extremes can occur. In the context of the biological example considered here, the results indicate that it is possible that harmful algae blooms should be periodically expected and expected to be extreme.

Species evolve as do predator-prey relationships. Waltman et al, [32], study a predator-prey relationship where the predator and prey evolve. The prey evolves to produce a toxin more lethal against the predator while the predator evolves so that it is immune or less harmed by the toxin produced by the prey species. We have not considered the possibility of evolving predators or prey in this theoretical study but hope to do so in the future.

It is important to observe that Roth et al, [23, 24], provide evidence that *K. brevis* may be able to develop resistance to algicidal bacteria. We have not considered that possibility here but hope to do so in a future study.

COMPUTATIONAL NOTES

The graphics and computations in this paper were carried out with *Mathematica 12.0*, [22]. You can receive a copy of the *Mathematica* notebooks used here by sending a request to jbraselton@georgiasouthern.edu.

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