

Bifurcation Analysis of a Food Chain in a Chemostat with Distinct Removal Rates

Sarker Md. Sohel Rana*

Department of Mathematics, University of Dhaka, Dhaka-1000, Bangladesh

Abstract: In this paper, we consider a classical food chain model describing predator-prey interaction in a chemostat. The Michaelis-Menten kinetics is used as the uptake for both predator and prey. We observe the dynamical behavior of the model around each of the equilibria and points out the exchange of stability. We use Lyapunov function in the study of the global stability of predator-free equilibrium. Using removal rate of prey as the bifurcation parameter, we prove that the model undergoes a Hopf bifurcation around interior equilibrium. It has been found that the dynamical behavior of the model is very sensitive to the parameter values. With the aid of numerical simulations we analyze the model equations and illustrate the key points of analytical findings, and determine the effects of operating parameters of the chemostat on the dynamics of the system.

Keywords: Chemostat; food chain; global stability; Hopf bifurcation; dissipative; Dulac criteria.

1. Introduction

The chemostat is a laboratory apparatus used to study general properties of population growth and interaction among micro-organisms under nutrient limitation in a controlled environment. The continuous culture model with Monod kinetics for nutrient uptake has received a great deal of attention since it was first introduced and a complete mathematical theory of this model has been developed. There are many articles devoted to the study of the chemostat both from the experimental and the modeling point of view. A detailed exposition of the mathematical theory of the chemostat is given in [1]. Moreover, the chemostat model is the starting point for many variations (food chain, food web etc.) that yield more realistic biological and mathematical problems [2-8]. The dynamics of predator, prey and substrate interaction has become a ubiquitous tool for studying a number of industrial fields such as waste treatment bioreactors [9-10]. Predation is a direct interaction which occurs when individuals from one population derive their nourishment by capturing and ingesting individuals from another population [11-14]. A simple food chain in a chemostat had been studied in [15-19] and related experiments are described in [20-23]. The dynamics of a tri-trophic food chain models that incorporate either Michaelis-Menten or general monotone response functions for all trophic levels and removal rates for the prey and predator populations are either equal to the washout rate of the chemostat or distinct had been examined by many researchers [5, 8, 16-19, 24]. It has been shown that these simple food chain with one predator and one prey exhibit that the predator feeds exclusively on either the prey or the prey and the nutrient, and the prey consumes the nutrient in the chemostat.

* Corresponding author; e-mail: srana.mthdu@gamil.com

Received 29 December 2013

Revised 7 May 2015

©2015 Chaoyang University of Technology, ISSN 1727-2394

Accepted 29 July 2015

In [3], the authors restricted their attentions to the case in which the prey is of logistic growth and predators have Holling's type II functional responses and established the global stability for the case of extinction of top-predator. Several studies used bifurcation analysis to find out if coexistence of all trophic levels is possible [5, 13, 16, 25]. In [16], the authors carried out the analysis of their model numerically, by finding both local and global bifurcations of equilibria and of limit cycles with respect to chemostat control parameters. Li and Kuang [6] considered a simple food chain and studied global stability of equilibria, and presented its dynamics numerically, while in [4] the authors studied analytically the global stability of equilibria of the model which is the extension of this simple food chain. Sarah [8] examined the dynamical behavior of tri-trophic food chain model with global stability of equilibrium points and Hopf bifurcation of solutions. In this paper, we are going to examine the dynamics of a food chain where the predator feeds exclusively on the prey and on the nutrient, and the prey consumes the nutrient in the chemostat. The Michaelis-Menten functional response is used for both predator and prey. In addition, we confine our interest to find criteria under which the model predicts that the populations will be able to persist at a steady state in the culture vessel for an indefinitely long period of time. This study also focus on global stability of equilibrium points, bifurcation analysis around interior equilibrium and sensitivity profiles of state variables with respect model parameters. Our results in this paper are extension to those in [4, 6, 8, 16]. This paper is organized as follows. In Section 2, the food chain model with Michaelis-Menten functional response is described. In section3, some elementary properties such as boundedness, invariance of non-negativity, dissipativity and the equilibria and their stabilities are investigated. Section 4 is devoted to discuss global stability analysis of equilibria. In Section 5, we discuss Hopf bifurcation of solutions. Section 6 deals with sensitivity analysis and numerical simulation. Finally a short discussion is given in Section 7.

2. The model

The food chain we analyze in this paper consists of substrate, prey and predator. Let $s(t)$ denotes the nutrient concentration, $x(t)$ the concentration of the prey population and $y(t)$ the concentration of the predator population at time t . Our model is described by the following ordinary differential equations:

$$\begin{aligned} s' &= (s^0 - s)D - \frac{m_1 s}{\gamma_1(a_1 + s)}x - \frac{m_2 s}{\gamma_2(a_2 + s)}y \\ x' &= \left(\frac{m_1 s}{a_1 + s} - D_1 \right)x - \frac{m_3 x}{\gamma_3(a_3 + x)}y \\ y' &= \left(\frac{m_2 s}{a_2 + s} + \frac{m_3 x}{a_3 + x} - D_2 \right)y \end{aligned} \quad (1)$$

with $s(0) = s_0 \geq 0$, $x(0) = x_0 \geq 0$, $y(0) = y_0 \geq 0$, $' = \frac{d}{dt}$.

In the system (1), s^0 denotes the input concentration of the nutrient, m_i are the maximal uptakes, a_i are the half saturation constants, γ_i are the growth yield constants and D the input rate from the feed pump and the washout rate of the chemostat chamber. D_1 and D_2 are the removal rates of prey and predator populations respectively. All parameters have positive values.

It is convenient to introduce dimensionless variables. In particular, we define

$$\bar{s} = \frac{s}{s^0}, \bar{x} = \frac{x}{\gamma_1 s^0}, \bar{y} = \frac{y}{\gamma_2 s^0}, \quad \bar{a}_1 = \frac{a_1}{s^0}, \bar{a}_2 = \frac{a_2}{s^0}, \bar{a}_3 = \frac{a_3}{\gamma_1 s^0},$$

$$\bar{m}_i = \frac{m_i}{D}, \quad \bar{t} = tD, \quad \gamma_2 = \gamma_1 \gamma_3, \quad \bar{D}_i = \frac{D_i}{D}.$$

Then, omitting the bars to simplify the notation, the system (1) becomes

$$\begin{aligned} s' &= 1 - s - \frac{m_1 s}{a_1 + s} x - \frac{m_2 s}{a_2 + s} y \\ x' &= \left(\frac{m_1 s}{a_1 + s} - D_1 \right) x - \frac{m_3 x}{a_3 + x} y \\ y' &= \left(\frac{m_2 s}{a_2 + s} + \frac{m_3 x}{a_3 + x} - D_2 \right) y \end{aligned} \tag{2}$$

with $s_0 \geq 0, x_0 \geq 0, y_0 \geq 0$.

Without loss of generality, we can consider the system (2) instead of (1) and we can always reinterpret our findings in terms of original variables.

3. Elementary properties, existence of equilibria and their stabilities

3.1. Boundedness and non-negativity of solutions

In this section, we shall show that the system is dissipative by proving that solutions of system (2) are non-negative and bounded.

Theorem 1.

All solutions of the system (2) with initial values in \mathbb{R}_+^3 are non-negative and bounded, and for large t , $s(t) < 1$.

Proof.

First let $(s(t), x(t), y(t))$ is a solution of (2). Suppose that $s(t) > 0$ for all $t > 0$ is not true. Let $t_1 = \min\{t : t > 0 \text{ \& } s(t) = 0\}$. Then $s(t) > 0, \forall t \in [0, t_1)$. But from the first equation of (2), we have $s'(t_1) = 1 > 0$. This implies there exists $\varepsilon > 0$ such that $s(t)$ is increasing on $(t_1 - \varepsilon, t_1 + \varepsilon)$. Therefore we have $0 < s(t_1 - \varepsilon/2) < s(t_1)$, a contradiction. Thus $s(t) > 0$ for all $t \geq 0$.

Let now $t_1 = \min\{t : t > 0, x(t)y(t) = 0\}$. We first assume that $x(t_1) = 0$. Then $y(t) \geq 0$ for $t \in [0, t_1]$. Let $A = \min_{0 \leq t \leq t_1} \left\{ \frac{m_1 s}{a_1 + s} - D_1 - \frac{m_3}{a_3 + x} y \right\}$. Then, for $t \in [0, t_1]$, $x'(t) > Ax(t)$, which implies that $x(t_1) > x_0 \exp[At_1] > 0$, a contradiction. Therefore, $x(t) > 0$ for all $t \geq 0$. A similar argument shows that $y(t_1) = 0$ is absurd. Thus, the system (2) with positive initial conditions at $t = 0$ produces a positive solution for $t \geq 0$.

Furthermore, if $\Psi = s + x + y$, then $\Psi' = s' + x' + y' = 1 - (s + D_1 x + D_2 y)$. Let

$D_{\min} = \min\{1, D_1, D_2\}$, then $\Psi' < 1 - D_{\min}\Psi$. If $u(t)$ is a solution of $u' = 1 - D_{\min}u$ with $u(0) = \Psi(0)$, then $u(t) = \frac{1}{D_{\min}} \left[(D_{\min}u(0) - 1)e^{-D_{\min}t} + 1 \right]$ and $\lim_{t \rightarrow \infty} u(t) = \frac{1}{D_{\min}}$. But $\Psi(t) \leq u(t)$

which mean that $s(t) + x(t) + y(t) \leq u(t)$, so we may conclude that $\lim_{t \rightarrow \infty} [s(t) + x(t) + y(t)] \leq \frac{1}{D_{\min}}$.

Therefore, solutions of (2) are bounded and the system (2) is dissipative. Finally, $s' < 1 - s$ for $t \geq 0$, so we have $s(t) < 1 + (s_0 - 1)e^{-t}$ and thus $s(t) < 1$, for large t . This completes the proof.

3.2. The equilibria: existence and local stability

We will find the following possible equilibria of system (2) in the form $E(s, x, y)$. Extinction of all populations: $E_0(1,0,0)$. Survival of population x only: $E_1(s_1, x_1, 0)$, where $s_1 = \frac{a_1 D_1}{m_1 - D_1}$,

$x_1 = \frac{(1 - s_1)(a_1 + s_1)}{m_1 s_1} = \frac{m_1 - D_1(a_1 + 1)}{D_1(m_1 - D_1)}$. Survival of population y only: $E_2(s_2, 0, y_2)$, where

$s_2 = \frac{a_2 D_2}{m_2 - D_2}$, $y_2 = \frac{m_2 - D_2(a_2 + 1)}{D_2(m_2 - D_2)}$. Survival of populations x and y : $E_3(s_3, x_3, y_3)$, where

s_3 and x_3 are defined as the unique solutions of $\frac{m_2 s}{a_2 + s} + \frac{m_3 x}{a_3 + x} = D_2$ and they satisfy the

equation $1 - s_3 - \frac{m_1 s_3}{a_1 + s_3} x_3 - \frac{m_2 s_3}{a_2 + s_3} y_3 = 0$ with $s_3 \in (0,1)$ and $y_3 = \frac{a_3 + x_3}{m_3} \left(\frac{m_1 s_3}{a_1 + s_3} - D_1 \right)$. The

value s_1 and s_2 represent the break-even concentration of nutrient. It is easy to see that if $m_i < D_i, i = 1, 2$ then the corresponding populations tend to zero. Thus, in order to avoid the population vanishing, we shall assume that $m_i > D_i, i = 1, 2$. To discuss the existence of equilibria, we say that equilibrium points will not exist if any one of its components is negative. The washout equilibrium point $E_0(1,0,0)$ always exists. The existence condition for E_1 is

$\frac{m_1}{a_1 + 1} > D_1$ and similarly $\frac{m_2}{a_2 + 1} > D_2$ for E_2 . Finally, the feasibility conditions for the mixed

culture (interior) equilibrium point E_3 , $\frac{m_1 s_3}{a_1 + s_3} - D_1$ must be positive or $s_3 > s_1$. Note that

$Q(s) = 1 - s - \frac{m_1 s}{a_1 + s} x_3 - \frac{m_2 s}{a_2 + s} y_3$ is decreasing in s with $Q(0) = 1, Q(s_3) = 0$ and

$Q(s_1) = 1 - s_1 - D_1 x_3$. So $s_3 > s_1$ if and only if $x_1 > x_3$ or equivalently $\frac{m_2 s_3}{a_2 + s_3} + \frac{m_3 x_1}{a_3 + x_1} > D_2$.

In the next step, we will investigate the local stability of these equilibrium points by finding the eigenvalues of the associated Jacobian matrices. The Jacobian matrix due to the linearization of (2) about an arbitrary equilibrium $E(s, x, y) \in \mathbb{R}_+^3$ is given by

$$J(E) = \begin{bmatrix} -1 - \frac{m_1 a_1}{(a_1 + s)^2} x - \frac{m_2 a_2}{(a_2 + s)^2} y & -\frac{m_1 s}{a_1 + s} & -\frac{m_2 s}{a_2 + s} \\ \frac{m_1 a_1}{(a_1 + s)^2} x & \frac{m_1 s}{a_1 + s} - D_1 - \frac{m_3 a_3}{(a_3 + x)^2} y & -\frac{m_3 x}{a_3 + x} \\ \frac{m_2 a_2}{(a_2 + s)^2} y & \frac{m_3 a_3}{(a_3 + x)^2} y & \frac{m_2 s}{a_2 + s} + \frac{m_3 x}{a_3 + x} - D_2 \end{bmatrix}$$

Define the numbers

$$R_0 = \frac{m_1}{D_1(a_1 + 1)}, \quad R_1 = \frac{m_2}{D_2(a_2 + 1)}, \quad R_2 = \frac{1}{D_2} \left(\frac{m_2 s_3}{a_2 + s_3} + \frac{m_3 x_1}{a_3 + x_1} \right) \quad \text{and} \quad R_3 = \frac{m_3 y_2}{a_3(D_2 - D_1)}.$$

It is easy to show that the eigenvalues of $J(E_0)$ will be negative if $R_0 < 1$ and $R_1 < 1$ or equivalently, $R_0 < 1$ and $s_3 > 1, x_3 > 0$.

The Jacobian matrix at E_1 is given by

$$J(E_1) = \begin{bmatrix} -1 - \frac{m_1 a_1}{(a_1 + s_1)^2} x_1 & -\frac{m_1 s_1}{a_1 + s_1} & -\frac{m_2 s_1}{a_2 + s_1} \\ \frac{m_1 a_1}{(a_1 + s_1)^2} x_1 & 0 & -\frac{m_3 x_1}{a_3 + x_1} \\ 0 & 0 & \frac{m_2 s_1}{a_2 + s_1} + \frac{m_3 x_1}{a_3 + x_1} - D_2 \end{bmatrix}$$

Henceforth we let M_{22} define the matrix (upper left hand 2×2 matrix)

$$M_{22} = \begin{bmatrix} -1 - \frac{m_1 a_1}{(a_1 + s_1)^2} x_1 & -\frac{m_1 s_1}{a_1 + s_1} \\ \frac{m_1 a_1}{(a_1 + s_1)^2} x_1 & 0 \end{bmatrix}$$

Since $\text{trace}(M_{22}) < 0$ and $\det(M_{22}) > 0$, by Routh-Hurwitz criterion the eigenvalues of M_{22} have negative real parts. The third eigenvalues of $J(E_1)$ is $\frac{m_2 s_1}{a_2 + s_1} + \frac{m_3 x_1}{a_3 + x_1} - D_2$.

Therefore, E_1 is locally asymptotically stable (LAS) if and only if $\frac{m_2 s_1}{a_2 + s_1} + \frac{m_3 x_1}{a_3 + x_1} < D_2$ or, equivalently, $s_1 < s_3$ and $x_1 < x_3$, that is $R_2 < 1$. Similar calculations show that E_2 is LAS if and only if $R_3 > 1$.

When E_3 exists, the Jacobian matrix due to linearization of (2) about E_3 is given by the expression

$$J(E_3) = [J_{ij}]_{3 \times 3} = \begin{bmatrix} -1 - \frac{m_1 a_1}{(a_1 + s_3)^2} x_3 - \frac{m_2 a_2}{(a_2 + s_3)^2} y_3 & -\frac{m_1 s_3}{a_1 + s_3} & -\frac{m_2 s_3}{a_2 + s_3} \\ \frac{m_1 a_1}{(a_1 + s_3)^2} x_3 & \frac{m_1 s_3}{a_1 + s_3} - D_1 - \frac{m_3 a_3}{(a_3 + x_3)^2} y_3 & -\frac{m_3 x_3}{a_3 + x_3} \\ \frac{m_2 a_2}{(a_2 + s_3)^2} y_3 & \frac{m_3 a_3}{(a_3 + x_3)^2} y_3 & 0 \end{bmatrix}$$

The eigenvalues of $J(E_3)$ satisfy the equation

$$\mu^3 + \alpha_1 \mu^2 + \alpha_2 \mu + \alpha_3 = 0 \tag{3}$$

where

$$\begin{aligned} \alpha_1 &= -\text{trace}(J(E_3)) = -(J_{11} + J_{22}) \\ \alpha_2 &= J_{11}J_{22} - J_{23}J_{32} - J_{13}J_{31} - J_{12}J_{21} \\ \alpha_3 &= -\det(J(E_3)) = J_{11}J_{23}J_{32} - J_{12}J_{23}J_{31} - J_{13}J_{21}J_{32} + J_{13}J_{22}J_{31} \end{aligned} \tag{4}$$

The Routh-Hurwitz criterion says that E_3 will be LAS if and only if $\alpha_1 > 0, \alpha_3 > 0$ and $\alpha_1 \alpha_2 > \alpha_3$. We can summarize the above results in the following theorem.

Theorem 2.

If $R_0 < 1$ and $R_1 < 1$, then only E_0 exists and it is LAS. If $R_0 > 1$ and $R_2 < 1$, then E_0 and E_1 exist, E_0 is unstable and E_1 is LAS. If $R_1 > 1$ and $R_3 > 1$, then E_0 and E_2 exist, E_0 is unstable and E_2 is LAS. If $R_0 > 1$ and $R_2 > 1$, then E_0, E_1 and E_3 exist, and E_0 and E_1 are unstable, E_3 is LAS if $\alpha_1 > 0, \alpha_3 > 0$ and $\alpha_1 \alpha_2 > \alpha_3$ and, therefore, the system will be uniformly persistent.

4. Global analysis

In the previous section, we showed the existence and local stability analysis of all equilibria. In this section, we shall present the global stability of the equilibria of system (2). The proof for E_0 is very straightforward. Most importantly we shall show that if only E_0 and E_1 exist, under a reasonable assumption E_1 is globally asymptotically stable. The proof involves the construction of a Lyapunov function and the application of the Lyapunov-LaSalle theorem. We shall use method similar to [3].

Theorem 3.

If $R_0 < 1$ and $R_1 < 1$, then E_0 is the only equilibrium point and all solutions of (2) converges to E_0 .

Proof.

It is clear that if $R_0 < 1$ and $R_1 < 1$, then by Theorem 2, E_0 is the only equilibrium point and LAS. Now to prove that E_0 is globally asymptotically stable, assume that $(s(t), x(t), y(t))$ is a

solution of (2). Since $s(t) < 1$ for large t and $\frac{m_1}{a_1 + 1} - D_1 < 0$ or $R_0 < 1$, there is a $\nu > 0$ such that $x'(t) < -\nu x(t)$ for t sufficiently large and $\nu = \min_{0 \leq t} \left\{ D_1 - \frac{m_1 s}{a_1 + s} + \frac{m_3}{a_3 + x} y \right\}$. Since $x(t)$ is non-negative, this shows that $\lim_{t \rightarrow \infty} x(t) = 0$. It follows from the third equation of (2) that $y'(t) < -\mathcal{G} y(t)$ where $0 < \mathcal{G} = \min_{0 \leq t} \left\{ D_2 - \frac{m_2 s}{a_2 + s} \right\}$ which implies that $\lim_{t \rightarrow \infty} y(t) = 0$. Then the first equation of (2) yields that $\lim_{t \rightarrow \infty} s(t) = 1$. Hence E_0 is globally asymptotically stable and the theorem is proved.

If $R_0 > 1$ and $R_2 < 1$, then E_1 is locally asymptotically stable. We will apply the Dulac criterion [26] to show that E_1 is globally asymptotically stable in the $s-x$ plane. Let $B(s, x) = \frac{1}{x}, s \geq 0, x > 0$. Then in the solution plane of $y=0$, we have $\frac{\partial}{\partial s}(Bs') + \frac{\partial}{\partial x}(Bx') = -\frac{1}{x} - \frac{m_1 a_1}{(a_1 + s_1)^2} < 0$ (i.e., does not change sign and is not identically zero) for $s \geq 0, x > 0$. Hence there are no periodic solutions on the $s-x$ plane, and E_1 will be globally asymptotically stable in the $s-x$ plane. The following theorem shows that E_1 is global attractor if it exists.

Theorem 4.

If $R_0 > 1$ and $R_2 < 1$, then all solutions of (2) satisfy $\lim_{t \rightarrow +\infty} (s(t), x(t), y(t)) = (s_1, x_1, 0)$.

Proof.

Let $H(s) = \frac{(1-s)(a_1 + s)}{m_1 s}$. Then $\lim_{s \rightarrow 0^+} H(s) = +\infty$, $\lim_{s \rightarrow \infty} H(s) = -\infty$, $H(1) = 0$,

$$H(s_1) = \frac{(1-s_1)(a_1 + s_1)}{m_1 s_1} = x_1 \text{ and } H'(s) = -\frac{(a_1 + s^2)}{m_1 s^2} < 0 \forall s.$$

$$\text{Let } G(s) = \int_{s_1}^s \left[\frac{\left(\frac{m_1 \xi}{a_1 + \xi} - D_1 \right)}{\left(\frac{m_1 \xi}{a_1 + \xi} \right)} \right] d\xi = \frac{m_1 - D_1}{m_1} \left[s - s_1 - s_1 \ln \left(\frac{s}{s_1} \right) \right]. \text{ Then } G(s_1) = 0,$$

$\lim_{s \rightarrow 0^+} G(s) = +\infty$ and $G(s) > 0$ for $s > 0, s \neq s_1$.

$$\text{Let } F(s) = \frac{x_1 - H(s)}{G(s)}. \text{ Since } H'(s) < 0 \text{ and } H(s_1) = x_1, F(s) \text{ satisfies}$$

$$F(s) < 0 \text{ for } 0 < s < s_1, \lim_{s \rightarrow 0^+} F(s) = -\infty, \lim_{s \rightarrow s_1} F(s) = -\infty \text{ and}$$

$$F(s) > 0 \text{ for } s_1 < s < 1, \lim_{s \rightarrow s_1^+} F(s) = +\infty.$$

Define a Lyapunov function as in [3] on the region $\Omega = \{(s, x, y) \in \mathbb{R}_+^3 \mid s \in (0,1), x > 0, y > 0\}$,

$$\begin{aligned}
 V(s, x, y) &= \int_{x_1}^x \xi^{\theta-1} (\xi - x_1) d\xi + x^\theta \int_{s_1}^s \left[\left(\frac{m_1 \xi}{a_1 + \xi} - D_1 \right) / \left(\frac{m_1 \xi}{a_1 + \xi} \right) \right] d\xi + cy \\
 &= \frac{1}{\theta+1} [x^{\theta+1} - x_1^{\theta+1}] - \frac{x_1}{\theta} [x^\theta - x_1^\theta] + x^\theta G(s) + cy
 \end{aligned}$$

where $c > 0$ will be defined later. Then $V \geq 0$ on Ω and $V = 0$ iff $s = s_1, x = x_1$ and $y = 0$. The time derivative of V along trajectories of (2) is given by

$$\begin{aligned}
 V' &= x^\theta G'(s)s' + x^{\theta-1} [x - x_1 + \theta G(s)]x' + cy' \\
 &= x^\theta \left[\frac{m_1 s}{a_1 + s} - D_1 \right] \left[H(s) - x_1 + \theta G(s) - \frac{m_2(a_1 + s)}{m_1(a_2 + s)} y \right] - x^{\theta-1} (x - x_1) \frac{m_3 x}{a_3 + x} y \\
 &\quad - \theta x^{\theta-1} G(s) \frac{m_3 x}{a_3 + x} y + c \left[\frac{m_2 s}{a_2 + s} + \frac{m_3 x}{a_3 + x} - D_2 \right] y \\
 &= x^\theta G(s) \left[\frac{m_1 s}{a_1 + s} - D_1 \right] \left[\theta - F(s) - \frac{m_2(a_1 + s)}{m_1(a_2 + s)G(s)} y \right] \\
 &\quad + c \left[\frac{m_2 s_3}{a_2 + s_3} + \frac{m_3 x_1}{a_3 + x_1} - D_2 \right] y - \theta x^{\theta-1} G(s) \frac{m_3 x}{a_3 + x} y + c \left[\frac{m_2 s}{a_2 + s} - \frac{m_2 s_3}{a_2 + s_3} \right] y \\
 &\quad + \left[c \left(\frac{m_3 x}{a_3 + x} - \frac{m_3 x_1}{a_3 + x_1} \right) - x^{\theta-1} (x - x_1) \frac{m_3 x}{a_3 + x} \right] y \\
 &= V_1 + V_2 + V_3 + V_4
 \end{aligned}$$

To discuss the sign of V' , we will investigate each term of V' . Let $\theta > 0$ satisfies

$$\max_{0 < s < s_1} F(s) < \theta - \frac{m_2(a_1 + s)}{m_1(a_2 + s)G(s)} y < \theta < \min_{s_1 < s < 1} F(s)$$

For $V_1 = x^\theta G(s) \left[\frac{m_1 s}{a_1 + s} - D_1 \right] \left[\theta - F(s) - \frac{m_2(a_1 + s)}{m_1(a_2 + s)G(s)} y \right]$, since $\frac{m_1 s}{a_1 + s} - D_1 < 0$ for

$0 < s < s_1$ and $\frac{m_1 s}{a_1 + s} - D_1 > 0$ for $s_1 < s < 1$, by definition of θ , $V_1 < 0$ for $s \neq s_1$ and

$V_1 = 0$ iff $s = s_1$. For V_2 , since $R_2 < 1$ we have $V_2 < 0$ for any choice of c and $V_2 = 0$ iff $y = 0$. For V_3 , if $s < s_3$ then $V_3 < 0$ for any choice of c and $V_3 = 0$ iff $y = 0$. Finally, for V_4 , we have

$$\begin{aligned}
 V_4 &= \left[c \left(\frac{m_3 x}{a_3 + x} - \frac{m_3 x_1}{a_3 + x_1} \right) - x^{\theta-1} (x - x_1) \frac{m_3 x}{a_3 + x} \right] y \\
 &= \left[c \frac{m_3 a_3 (x - x_1)}{(a_3 + x)(a_3 + x_1)} - x^{\theta-1} (x - x_1) \frac{m_3 x}{a_3 + x} \right] y = \frac{m_3 (x - x_1)}{a_3 + x} \left[c \frac{a_3}{a_3 + x_1} - x^\theta \right] y
 \end{aligned}$$

Let $c = \frac{a_3 + x_1}{a_3} x_1^\theta$, then $V_4 = \frac{m_3(x - x_1)}{a_3 + x} [x_1^\theta - x^\theta] y < 0$ and $V_4 = 0$ iff $y = 0$. Therefore, each term of V' is non-positive. Hence E_1 is global attractor by Lasalle's invariance principle [1, 27]. This completes the proof.

5. Hopf bifurcation analysis

In this section, we shall discuss that our model undergoes a Hopf bifurcation by using D_1 as a bifurcation real parameter. Clearly (by theorem 2) there is no Hopf bifurcation at E_0 , E_1 and E_2 . So we are going to vary D_1 in order to obtain the desired Hopf bifurcation for $D_1 = D_1^*$ around E_3 . First we recall that the eigenvalues of $J(E_3)$ satisfy the equation (3) and its components are defined as in (4).

By the Routh–Hurwitz criteria, necessary and sufficient conditions for all the roots of (3) to have negative real parts are

$$H_1: \alpha_1 > 0, \alpha_3 > 0 \text{ and } H_2: \alpha_1 \alpha_2 > \alpha_3.$$

Now in order to have Hopf bifurcation, we must violate either H_1 or H_2 . Suppose $\alpha_1 > 0, \alpha_3 > 0$. Clearly (3) will have two pure imaginary roots if and only if

$$\alpha_1 \alpha_2 = \alpha_3 \tag{5}$$

for some values of D_1 , say $D_1 = D_1^*$. Since $\alpha_2 > 0$ at $D_1 = D_1^*$, there is an open interval containing D_1^* , say $(D_1^* - \varepsilon, D_1^* + \varepsilon)$ for some $\varepsilon > 0$ for which $D_1^* - \varepsilon > 0$, such that $\alpha_2 > 0$ for $D_1 \in (D_1^* - \varepsilon, D_1^* + \varepsilon)$. Thus for $D_1 \in (D_1^* - \varepsilon, D_1^* + \varepsilon)$, the characteristic equation (3) cannot have positive real roots. For $D_1 = D_1^*$, we have (see [20, p.80])

$$(\mu^2 + \alpha_2)(\mu + \alpha_1) = 0 \tag{6}$$

which has three roots

$$\mu_1 = i\sqrt{\alpha_2}, \quad \mu_2 = -i\sqrt{\alpha_2}, \quad \mu_3 = -\alpha_1.$$

For $D_1 \in (D_1^* - \varepsilon, D_1^* + \varepsilon)$, the roots are in general of the form

$$\begin{aligned} \mu_1(D_1) &= \alpha(D_1) + i\beta(D_1), \\ \mu_2(D_1) &= \alpha(D_1) - i\beta(D_1), \\ \mu_3(D_1) &= -\alpha_1(D_1). \end{aligned}$$

To apply Hopf's bifurcation theorem to (2) (see [28]) we need to verify the transversality condition

$$\operatorname{Re}[\mu'_i(D_1)]_{D_1=D_1^*} \neq 0, i=1,2 \tag{7}$$

Substituting $\mu_1(D_1) = \alpha(D_1) + i\beta(D_1)$ and $\mu_2(D_1) = \alpha(D_1) - i\beta(D_1)$ into (3), and calculating the derivatives with respect to D_1 , we obtain

$$\begin{aligned} K(D_1)\alpha'(D_1) - L(D_1)\beta'(D_1) + M(D_1) &= 0, \\ L(D_1)\alpha'(D_1) + K(D_1)\beta'(D_1) + N(D_1) &= 0, \end{aligned} \tag{8}$$

where

$$\begin{aligned} K(D_1) &= 3\alpha^2(D_1) + 2b_1(D_1)\alpha(D_1) + b_2(D_1) - 3\beta^2(D_1), \\ L(D_1) &= 6\alpha(D_1)\beta(D_1) + 2b_1(D_1)\beta(D_1), \\ M(D_1) &= b'_1(D_1)(\alpha^2(D_1) - \beta^2(D_1)) + b'_2(D_1)\alpha(D_1) + b'_3(D_1), \\ N(D_1) &= 2b'_1(D_1)\alpha(D_1)\beta(D_1) + b'_2(D_1)\beta(D_1). \end{aligned}$$

Since $K(D_1^*)M(D_1^*) + L(D_1^*)N(D_1^*) \neq 0$, we have

$$\operatorname{Re}[\mu'_i(D_1)]_{D_1=D_1^*} = \alpha'(D_1) \Big|_{D_1=D_1^*} = - \frac{K(D_1)M(D_1) + L(D_1)N(D_1)}{K^2(D_1) + L^2(D_1)} \Big|_{D_1=D_1^*} \neq 0, i = 1, 2$$

and $\mu_3(D_1^*) = -\alpha_1(D_1^*) \neq 0$. Hence there is a Hopf bifurcation at $D_1 = D_1^*$. We can now formulate the following:

Theorem 5.

Suppose H_1 holds. Then system (2) exhibits a Hopf bifurcation leading to a family of periodic solutions that bifurcate from E_3 for suitable values of D_1 in the neighborhood of D_1^* .

6. Sensitivity analysis and Numerical simulation

Many dynamic models of biological processes can be written under the following general form:

$$\frac{dX(\theta, t)}{dt} = f(X(\theta, t), \theta, t), X(0) = X_0; Y(\theta, t) = g(X(\theta, t), \theta, t) \tag{9}$$

where $X = (s, x, y)$ is a vector of state variables, $\theta = (m_1, m_2, m_3, a_1, a_2, a_3, d_1, d_2)$ a vector of parameters, Y a vector of outputs and t the independent variable. Let $Z = \frac{\partial X}{\partial \theta}$ be the sensitivity of state variable X with respect to parameter θ , then the sensitivity matrix equations can be expressed in a compact formula:

$$\frac{dZ}{dt} = \frac{\partial f}{\partial X} Z + \frac{\partial f}{\partial \theta}, Z(0) = 0 \tag{10}$$

Equation (10) is also called first forward sensitivity equation. Simultaneous integration of equations of systems (9) and (10) provides values of sensitivity functions [29] with respect to time. According to (9), the sensitivity of the output Y_i w.r.t. the parameter θ is evaluated as

$$\frac{\partial Y}{\partial \theta} = \frac{\partial g}{\partial X} Z + \frac{\partial g}{\partial \theta}, \frac{\partial Y}{\partial \theta}(0) = 0 \tag{11}$$

However, these absolute sensitivity functions are not normalized and they are not useful for comparing the effects of different input factors for what relative sensitivity functions should be used. Relative sensitivities are ideal for comparing parameters, because they are dimensionless, normalized functions. Hence, L_1 -norm of the relative sensitivity of the function Y_i to variations in the parameter θ_j is given by:

$$sen_{norm} = \sum \left| \frac{\theta_j}{Y_i} \left(\frac{\partial Y_i}{\partial \theta_j} \right) \right| \quad (12)$$

6.1. Numerical simulation

In this section, our aim is to present numerical simulations to illustrate the key results of theoretical findings, especially bifurcation around interior equilibrium and sensitivity of state variables w.r.t. parameters. We left the simulation works for other equilibria as these are simple. The figures have been constructed by proper choice of the kinetic parameters so that all the interesting behaviors of the system are observed. We choose the basic parameters of the model (2) to be $m_1 = 3.6, m_2 = 1.5, m_3 = 2.5, a_1 = 0.8, a_2 = 0.4, a_3 = 0.6, D_1 = 1.4, D_2 = 1.5$. The initial condition $(s_0, x_0, y_0) = (0.6, 0.2, 0.7)$ is used to generate solution curves and trajectories in all figures. Our simulation work (Fig. 1) suggests that E_3 is a global attractor if it is locally asymptotically stable.

As certain parameters increase or decrease further away, E_3 loses its stability and oscillatory solutions appear which is to be the results of Hopf bifurcations. For showing the dynamics of the system (2) change, the parameter set $\{m_1, m_2, m_3, a_1, a_2, a_3, D_2\} = \{2, 0.05, 2, 0.35, 0.5, 0.25, 1\}$ given as a fixed parameters and D_1 as a varied parameters (real bifurcation parameter). Fig. 2 shows a case in which $D_1 = 1$ and system (2) possesses periodic solutions and results a Hopf bifurcation around E_3 . Fig. 3 indicates that perturbing D_1 (while changing $D_1 = 1$ to $D_1 = 1.1$ and keeping other parameters in Fig. 2 fixed) leads to a bifurcation. This seems to destroy the periodic solutions and possibly leads to the global stability of E_3 whereas Fig. 4 (while changing $D_1 = 1$ to $D_1 = 0.9$ and keeping other parameters in Fig. 2 fixed) leads to the instability of E_3 . Therefore varying the values of D_1 and D_2 may affect the dynamics of (2) in a very surprising and significant way. Furthermore, at each stage we have presented the normalized sensitivity profile by Eq. (12) to see the affect of parameters on the dynamics of the model. Highest value indicates the most sensitivity of the parameter. All of the computations and visualizations have been performed in MATLAB R2007a.

Next, we see how the parameters D_1 and D_2 affect the dynamics of (2) if s^0 is fixed. Assume that $D_i (i = 1, 2)$ are large enough so that $R_0 < 1$ and $R_1 < 1$, then all populations will be washed out (E_0 is stable) in the chemostat. As D_1 is gradually decreased, eventually there is a bifurcation when $R_0 > 1$ and $R_2 < 1$. In this case, E_0 loses its stability and the new bifurcated steady state E_1 is asymptotically stable. As D_2 is gradually decreased, the next bifurcation occurs when $R_1 > 1$ and $R_3 > 1$ hold. In this case E_1 loses its stability, and a new steady state

E_2 appears.

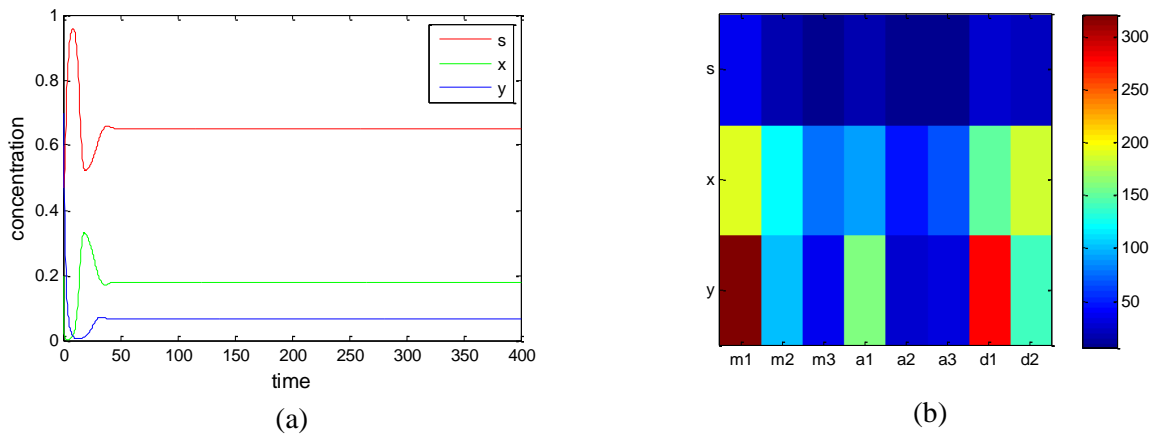


Figure 1: (a) The solution curves approach a positive equilibrium E_3 (b) L_1 - norm of the normalized sensitivity of the state variables w.r.t. parameters.

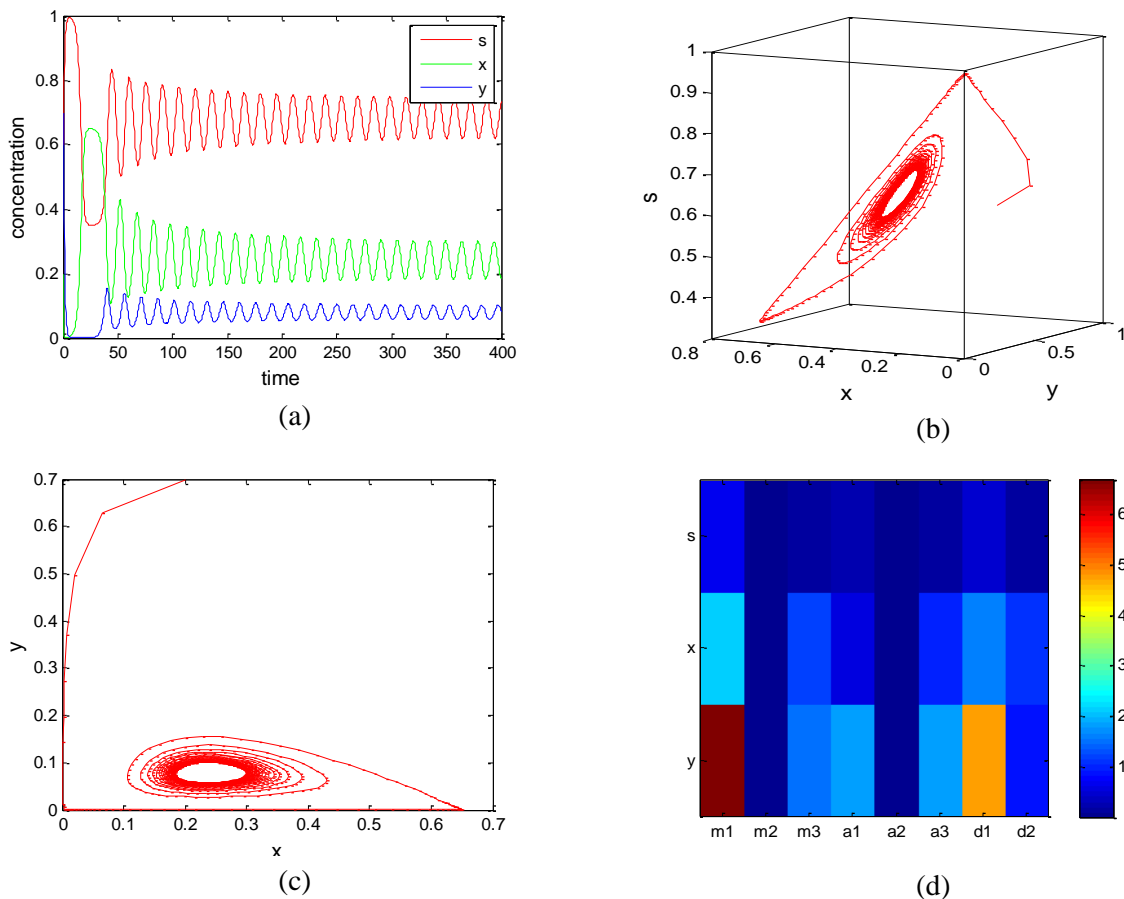


Figure 2: (a) The solution appears to approach a periodic solution and Hopf bifurcation occurs around E_3 (b) A plot of trajectories in three dimensional view (c) Projection of trajectories onto the xy plane (d) L_1 - norm of the normalized sensitivity of the state variables w.r.t. parameters.

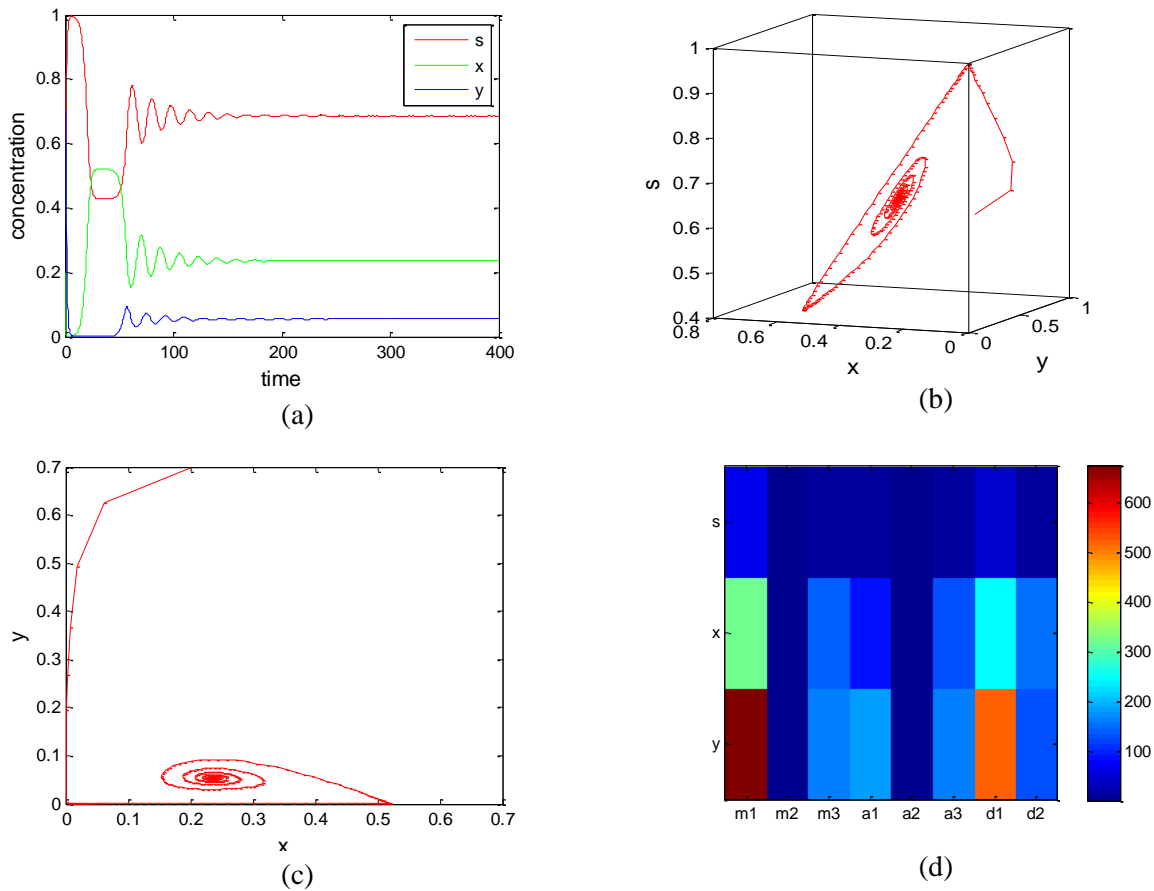


Figure 3: (a) The solution oscillates but eventually approaches a positive equilibrium E_3 (b) A plot of trajectories in three dimensional view (c) Projection of trajectories onto the xy plane (d) L_1 -norm of the normalized sensitivity of the state variables w.r.t. parameters.

7. Discussion and conclusions

In this paper, we considered a food chain with one prey and one predator in the chemostat where the prey consumes the nutrient and the predator consumes the prey and the nutrient. We assumed that the functional response functions are in Michaelis-Menten form and the removal rates are different. We performed a detailed computational analysis of this model. The dynamic behavior of this model depends on the numbers R_0, R_1, R_2 and R_3 . We established that system (2) has solutions which are eventually bounded in the future. We also established sufficient conditions for the existence and local stability of the equilibria by using Routh-Hurwitz criterion for system (2). We found that all the populations cannot persist if the removal rate of the prey is relatively large. This happens when E_0 is a global attractor of system (2). We constructed Lyapunov function on the base of [10], to show that E_1 is globally asymptotically stable. The global asymptotic stability of E_1 implies that nutrient as well as the prey population cannot support the predator and consequently the predator will be washed out in the chemostat regardless of the initial density levels of prey and predator. Next, when E_3 exists, then all the

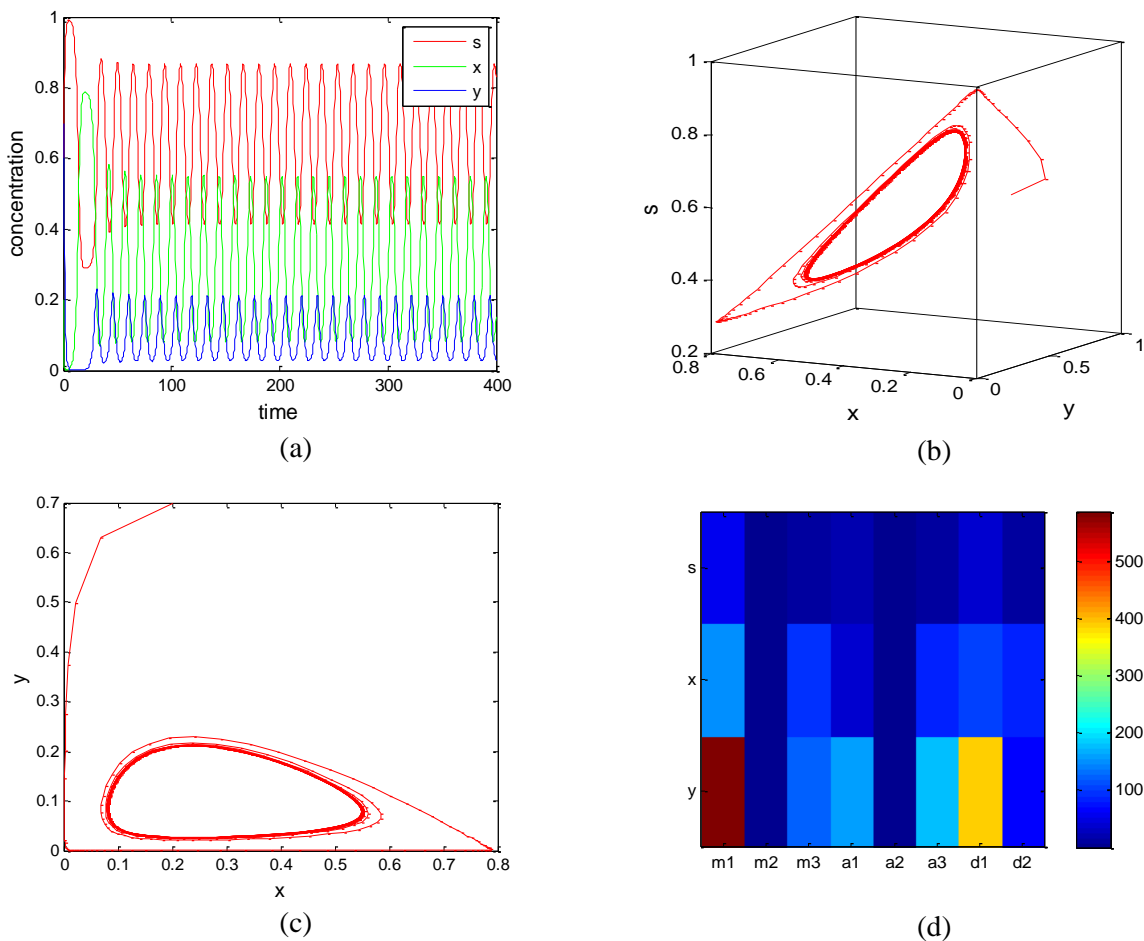


Figure 4: (a) The solution oscillates and seems to approach a periodic solution (b) A plot of trajectories in three dimensional view (c) Projection of trajectories onto the xy plane (d) L_1 - norm of the normalized sensitivity of the state variables w.r.t. parameters.

species (prey and predator) coexist in the sense that the system (2) is uniformly persistent and the conservation principle is circumvented. In this case, a switch of the stability of E_3 may occur. We then use the removal rate of prey, as a bifurcation real parameter. We found that Hopf bifurcation occur, under certain conditions, at the interior equilibrium point E_3 leading to a family of periodic solutions bifurcates from E_3 . Finally, both analytically and numerically, simulation shows that in certain regions of the parameter space, the food chain system has rich dynamics including periodic and asymptotic behavior and the model sensitively depends on the parameter values. The results of the considered system (2) in this study are extension to the system of [4, 6, 8, 16] and is useful in the further study of the coexistence of competing populations in the chemostat. Since most of the food chain models in a chemostat incorporate Michaelis-Menten-type (type II) response function with constant yield coefficient, a more detailed analysis for this system with other type response functions or substrate inhibition (with variable yield coefficient) focus on bifurcation analysis, limit cycle and sensitivity profiles of state variables with respect model parameters will be provided in near future.

Acknowledgement

The author would like to thank the referees for their valuable comments.

References

- [1] Smith, H. L. and Waltman, P. 1995. “*The Theory of Chemostat*”. Cambridge University Press, Cambridge (UK).
- [2] Alhumazi, K. and Ajbar, A. 2005. Dynamics of Predator-Prey Interaction in Continuous Culture. *Engineering in Life Science*, 5, 2: 139-147.
- [3] Chiu, C.-H. and Hsu, S.-B. 1998. Extinction of top-predator in a three-level food-chain model, *Journal of Mathematical Biology*, 37, 4: 372-380.
- [4] El-Owaidy, H. M. and Moniem, A. A. 2003. On food chain in a chemostat with distinct removal rates. *Applied Mathematics E-Notes*, 3: 183-191.
- [5] El-Sheikh, M. M. A. and Mahrouf, S. A. A. 2005. Stability and bifurcation of a simple food chain in a chemostat with removal rates, *Chaos, Solitons and Fractals*, 23, 4: 1475-1489.
- [6] Li, B. and Kuang, Y. 2000. Simple food chain in a chemostat with distinct removal rates. *Journal of Mathematical Analysis and Applications*, 242, 1: 75-92.
- [7] Nasrin, F. and Rana, S. M. S. 2011, Three species food web in a chemostat, *International Journal of Applied Science and Engineering*, 9, 4: 301-313.
- [8] Al-Sheikh, S. A. 2008. The Dynamics of a Tri-Trophic Food Chain in the Chemostat, *International Journal of Pure and Applied Mathematics*, 47, 1: 101-111.
- [9] Alqahtani, R. T., and Nelson, M. I., and Worthy, A. L. 2012. Analysis of a chemostat model with variable yield coefficient: Contois kinetics. *ANZIAM Journal (EMAC2011)*. 53: C155-C171.
- [10] Alqahtani, R. T., Nelson, M. I., and Worthy, A. L. 2013. A fundamental analysis of continuous flow bioreactor models governed by Contois kinetics. IV. Recycle around the whole reactor cascade. *Chemical Engineering Journal*, 218: 99–107.
- [11] Ws, M. S., Mohd, I. B., Mamat, M., and Salleh, Z., 2012. Mathematical model of three species food chain interaction with mixed functional response. *International Journal of Modern Physics: Conference Series*. Vol. 9: 334–340.
- [12] Waryano Sunaryo, M. S., Salleh, Z., and Mamat, M., 2013. Mathematical model of three species food chain with Holling Type-III functional response. *International Journal of Pure and Applied Mathematics*, 89, 5: 647-657.
- [13] Boonrangsiman, S. and Bunwong, K. 2012. Hopf bifurcation and dynamical behavior of a stage-structured predator sharing a prey. *International Journal of Mathematical Models and Methods in Applied Sciences*, 8, 6: 893-900.
- [14] Upadhyay, R. K., and Raw, S. N. 2011. Complex dynamics of a three species food-chain model with Holling type IV functional response. *Nonlinear Analysis: Modelling and Control*, 16, 3: 353–374.
- [15] Butler, G. J., Hsu, S. B., and Waltman, P. 1983. Coexistence of competing predators in a chemostat, *Journal of Mathematical Biology*, 17, 2: 133-151.
- [16] Boer, M. P., Kooi, B. W., and Koojiman, S. A. L. M. 1998. Food chain dynamics in the chemostat, *Mathematical Biosciences*, 150, 1: 43-62.
- [17] Freedman, H. I. and Waltman, P. 1977. Mathematical analysis of some three-species food chain models, *Mathematical Biosciences*, 33, 3-4: 257-276.

- [18] Hastings, A. and Powell, T. 1991. Chaos in a three-species food chain, *Ecology*, 72, 3: 896-903.
- [19] Klebanoff, A. and Hastings, A. 1994. Chaos in three species food chain, *Journal of Mathematical Biology*, 32, 5: 427-451.
- [20] Drake, J. F. and Tsuchiya, H. M. 1976. Predation of *Escherichia coli* by *Colpoda stenii*. *Applied and Environmental Microbiology*, 31, 6: 870-874.
- [21] Jost, J. L., Drake, J. F., Tsuchiya, H. M., and Fredrickson, A. G. 1973. Microbial food chains and food webs. *Journal of Theoretical Biology*, 41, 3: 461-484.
- [22] Jost, J. L., Drake, J. F., Fredrickson, A. G., and Tsuchiya, H. M. 1973. Interactions of *Tetrahymena pyriformis*, *Escherichia coli*, *Azotobacter vinelandii*, and glucose in a minimal medium. *Journal of Bacteriology*, 113, 2: 834-840.
- [23] Tsuchiya, H. M., Drake, S. F., Jost J. L., and Fredrickson, A. G. 1972. Predator-prey interaction of *Dictyostelium discoideum* and *Escherichia coli* in continuous culture. *Journal of Bacteriology*, 110, 3: 1147-1153.
- [24] Ali, E., Asif, M., and Ajbbar, A. 2013. Study of chaotic behavior in predator-prey interactions in a chemostat. *Ecological Modelling*, 259: 10– 15.
- [25] Freedman, H. I. and Ruan, S. 1992. Hopf bifurcation in three-species food chain models with group defense, *Mathematical Biosciences*, 111, 1: 73-87.
- [26] Marin, A. M., Rubén, D. O. and Rodríguez, J. A. 2013. A Dulac function for a quadratic system. *Theoretical Mathematics & Applications*, 3, 2: 49-54.
- [27] Wolkowicz, G. S. K. and Lu, Z. 1992. Global dynamics of a mathematical model of competition in the chemostat: General response function and differential death rates. *SIAM Journal of Applied Mathematics*, 52, 1: 222-233.
- [28] Marsden, J. E. and Mckracken, M. 1976. “*The Hopf Bifurcation and its Applications*”. Springer-Verlag, New York.
- [29] Walter, E. and Pronzato, L. 1997. “*Identification of Parametric Models from Experimental Data*”. Springer, London.