

## DYNAMICS OF A PREDATOR-PREY INTERACTION IN CHEMOSTAT WITH VARIABLE YIELD

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**Abstract:** A simple food chain in chemostat with variable yield for prey population and constant yield for predator population is proposed in this paper. The stability of equilibrium points, the existence of limit cycles, the Hopf bifurcation and the positive invariant set for the system are discussed by qualitative analysis of differential equations. Finally, numerical simulations are carried out in support of the theoretical results.

Keywords: Chemostat, food Chain, variable yield, limit cycles, Hopf bifurcation.

### Introduction

The chemostat is a laboratory apparatus used to study the competition between different populations of microorganisms and has the advantage that the mathematics is tractable and the parameters are readily measurable. Its place in theoretical ecology is well documented in the surveys of Waltman *et al.* (1980) and Wolkowicz & Lu (1992). Moreover, the chemostat model is the threshold for many variations (food chain, food web etc.) that yield more realistic biological and mathematical problems (Smith, 1982; Li, 1998; Li & Kuang, 2000; Grivet, 2001; El-Owaidy & Moniem, 2003; Sarah, 2008; Mada *et al.*, 2012; Suwicha & Kornkanok, 2012; Mada *et al.*, 2013).

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. Over the years, researchers have come to appreciate that the study of predation could apply to studies of many natural ecosystems (Jost *et al.*, 1973; May, 1972; Tsuchiya *et al.*, 1972). In the microbial ecology field, the dynamics of predator-prey interaction have also received a great deal of attention since they are the building elements of food chains and food webs. Early formulation of many simple two species models had been thoroughly explored (Smith & Waltman, 1995). After that, the discoveries expanded to include higher trophic levels (El-Owaidy & Moniem, 2003; Li & Kuang, 2000; Zhu *et al.*, 2002; Nasrin & Rana, 2011).

Most of the models in chemostat assume that the yield coefficient is a constant. The stability of simple food web model consisting of one predator and two preys with a growth limiting substrate had been theoretically investigated by Butler & Wolkowicz (1983). Li & Kuang (2000) considered a simple food chain in a chemostat with one predator and one prey, where predator feeds exclusively on the prey and the prey consumes the nutrient. El-Owaidy & Moniem (2003) also discussed a simple food chain with the extension that the predator feeds exclusively on the prey and the nutrient, and the prey consumes the nutrient in the chemostat. These studies (Butler & Wolkowicz, 1983; El-Owaidy & Moniem, 2003; Li & Kuang, 2000) had limited to the case with constant yield coefficients. But the accumulation of the experimental data suggests that a constant yield fails to explain the observed oscillatory behavior in the chemostat. Crooke & Tanner (1982) suggested a linear function instead of the constant for the yield coefficient and declared a limit cycle may exists in his model. Pilyugin & Waltman (2003) constructed a chemostat with variable yield and studied the multiple limit cycles in the model. In the model the functional response functions were in the Monod type, and the yield coefficients were assumed linear functions of the concentration of nutrient. The stability of the solutions was obtained. Huang & Zhu (2003) generalized the yield function from linear to quadratic, cubic etc. and study the stability of the solutions, existence of the limit

cycles, the Hopf bifurcation and the positive invariant set for their system. Taking these ideas into account we are going to analyze the dynamics of a predator prey interaction with variable yield for prey population and constant yield for predator population. This model is an approximation to the realistic behavior of food chain in continuous culture where each organism is considered to be indifferent trophic levels such as primary producers, primary consumers, secondary consumers, and experimentally in lab by considering bacteria as prey, a protozoan as predator and glucose as the limiting nutrient.

**The Model**

We shall consider the following model in the chemostat by a system of differential equations

$$\begin{aligned} s'(t) &= (s^0 - s(t))D - \frac{1}{\gamma_1} \left( \frac{m_1 s(t)}{k_1 + s(t)} \right) x(t) \\ x'(t) &= x(t) \left( \frac{m_1 s(t)}{k_1 + s(t)} - D \right) - \frac{1}{\gamma_2} \left( \frac{m_2 x(t)}{k_2 + x(t)} \right) y(t) \\ y'(t) &= y(t) \left( \frac{m_2 x(t)}{k_2 + x(t)} - D \right) \end{aligned} \tag{1}$$

with  $s(0) = s_0 > 0, x(0) = x_0 > 0, y(0) = y_0 > 0$ .

In the system (1),  $s(t)$  denotes the nutrient concentration,  $x(t)$  the concentration of the prey population and  $y(t)$  the concentration of the predator population.  $s^0$  denotes the input concentration of nutrient,  $D$  is the washout rate,  $m_i$  the maximal growth rates,  $k_i$  the Michaelis-Menton constants and  $\gamma_i, i = 1,2$ , the yield coefficients. This is usually called the Monod model or the model with Michaelis-Menton dynamics. The system (1) with the constant yield coefficients was studied by (Li & Kuang, 2000). Here we will investigate (1) with  $\gamma_i = A + Bs$  ( $A, B$  are positive constants) and which implies that the production of the microbial biomasses is sensitive to the concentration of the nutrient in the vessel.

Performing the standard scaling to the

$$\bar{s} = \frac{s}{s^0}, \bar{x} = \frac{x}{s^0}, \bar{y} = \frac{y}{s^0 \gamma_2}, \tau = Dt, \bar{m}_i = \frac{m_i}{D}, \bar{k}_i = \frac{k_i}{s^0} \tag{2}$$

and then drop the bars and replacing  $\tau$  by  $t$ , the system (1) becomes

$$\begin{aligned} s'(t) &= 1 - s - \frac{x}{A + Bs s^0} \left( \frac{m_1 s}{k_1 + s} \right) \\ x'(t) &= x \left( \frac{m_1 s}{k_1 + s} - 1 \right) - \left( \frac{m_2 x}{k_2 + x} \right) y \\ y'(t) &= y \left( \frac{m_2 x}{k_2 + x} - 1 \right) \end{aligned} \tag{3}$$

The parameters have been scaled by the operating environment of the food chain, which are determined by  $s^0$  and  $D$ . The variables are non-dimensional and the discussion is in  $R_+^3 = \{(s,x,y): 0 \leq s < 1, x \geq 0, y \geq 0\}$ .

**Theoretical Results**

*Equilibrium Points and their Stability*

The equilibrium points (in the form  $\equiv E(s,x,y)$ ) of the system (3) will be denoted  $E_1 = (1,0,0), E_2 = (\lambda_s, (A + Bs^0 \lambda_s)(1 - \lambda_s), 0), E_C = (\hat{s}, \lambda_x, \left( \frac{m_1 \hat{s}}{k_1 + \hat{s}} - 1 \right) \lambda_x)$ ,

where  $\lambda_s$  and  $\lambda_x$  are respectively unique solutions of  $\frac{m_1 s}{k_1 + s} - 1 = 0$  and  $\frac{m_2 x}{k_2 + x} - 1 = 0$  and  $\hat{s}$  is defined as the unique solution of

$$1 - s - \frac{\lambda_x}{A + Bs^0 s} \left( \frac{m_1 s}{k_1 + s} \right) = 0 \text{ with } \hat{s} \in (0,1).$$

The values of  $\lambda_s$  and  $\lambda_x$  represent the breakeven concentration of nutrient and prey respectively. Note that, prey free with predator steady state does not exist. The points  $E_1, E_2$  and  $E_C$  will be considered as the equilibrium points if all of their components are nonnegative.

We will now discuss the existence of the steady states. The washout steady state  $E_1 = (1,0,0)$ , always exists.  $E_2$  is a equilibrium point provided  $0 < \lambda_s < 1$  and

$$\frac{m_1 s}{k_1 + s} = 1 \Leftrightarrow m_1 > k_1 + 1.$$

Finally for  $E_C$  to exists,  $\left( \frac{m_1 \hat{s}}{k_1 + \hat{s}} - 1 \right)$  must be positive or  $\hat{s} > \lambda_s$ .

Note that  $F(s) = 1 - s - \frac{\lambda_x}{A + Bs^0 s} \left( \frac{m_1 s}{k_1 + s} \right)$  is decreasing in  $s \in [0,1]$  with  $F(0) = 1 > 0$  and  $F(1) = -\frac{\lambda_x}{A + Bs^0} \left( \frac{m_1}{k_1 + 1} \right) < 0$ . Since  $F(\hat{s}) = 0$ , so  $\hat{s} > \lambda_s$  if and only if

$$\lambda_x < (A + Bs^0 \lambda_s)(1 - \lambda_s).$$

In this case where  $\frac{m_2 x}{k_2 + x} < 1$  for all  $x > 0$ , we regard  $\lambda_x = +\infty$ . Therefore  $E_2$  exists if and only if  $\lambda_s < 1$ ,

and  $E_C$  exists if and only if  $\lambda_s < 1$  and  $\lambda_x < (A + Bs^0\lambda_s)(1 - \lambda_s)$ .

Let  $\lambda_s = \frac{k_1}{m_1 - 1}$  &  $\lambda_x = \frac{k_2}{m_2 - 1}$ . It is easy to see that

(i) If  $0 \leq m_i \leq 1, i = 1, 2$ , then  $\frac{dx}{dt} < 0, \frac{dy}{dt} < 0$  and  $\lim_{t \rightarrow +\infty} x(t) = 0$  and  $\lim_{t \rightarrow +\infty} y(t) = 0$ ,

(ii) If  $\lambda_s \geq 1$ , then  $\frac{dx}{dt} < 0$  and  $\lim_{t \rightarrow +\infty} x(t) = 0$ ,

(iii) If  $\lambda_x \geq 1$ , then  $\frac{dy}{dt} < 0$  and  $\lim_{t \rightarrow +\infty} y(t) = 0$ .

Note that, if  $\lambda_s \geq 1$ , the prey microorganism in the chemostat extinct, as so does the predator if  $\lambda_x \geq 1$ . Thus in order to avoid the microorganisms vanishing, we need to make certain arrangement between the growth rates  $m_i$  and the Michaelis-Menton constant  $k_i$  before the experiments or the bio-reactor starts.

$$\text{Let } R_1 = s^0 \frac{(1 - \lambda_s)\{(k_1 + \lambda_s)^2 - k_1 m_1 \lambda_s\} - \lambda_s(k_1 + \lambda_s)^2}{(k_1 + \lambda_s)^2 + (1 - \lambda_s)k_1 m_1}.$$

In the next step we will investigate the local stability of these steady states by finding the eigenvalues of the associated Jacobian matrices. The Jacobian matrix of (3) takes the form  $J(E) =$

$$\begin{bmatrix} -1 - \frac{xm_1k_1}{(A+Bs^0s)(k_1+s)^2} + \frac{xBs^0m_1s}{(A+Bs^0s)^2(k_1+s)} & -\frac{m_1s}{(A+Bs^0s)(k_1+s)} & 0 \\ \frac{xm_1k_1}{(k_1+s)^2} & \frac{m_1s}{(k_1+s)} - 1 - \frac{ym_2k_2}{(k_2+x)^2} & -\frac{m_2x}{(k_2+x)} \\ 0 & \frac{ym_2k_2}{(k_2+x)^2} & \frac{m_2x}{(k_2+x)} - 1 \end{bmatrix}.$$

At  $E_1$ , the eigenvalues of  $J(E_1)$  are all negative if  $\frac{m_1}{(k_1+1)} < 1$  or, equivalently,  $\lambda_s > 1$ .

When  $E_2$  exists, the eigenvalues of  $J(E_2)$  satisfy the equation

$$(r - a_1)(r^2 - b_1r + c_1) = 0, \text{ where}$$

$$\begin{aligned} a_1 &= \frac{m_2(A + Bs^0\lambda_s)(1 - \lambda_s)}{(k_2 + (A + Bs^0\lambda_s)(1 - \lambda_s))} - 1, \\ b_1 &= 1 + (1 - \lambda_s) \left\{ \frac{m_1k_1}{(k_1 + \lambda_s)^2} - \frac{Bs^0}{(A + Bs^0\lambda_s)} \right\}, \\ c_1 &= (1 - \lambda_s) \frac{k_1m_1}{(k_1 + \lambda_1)^2} > 0. \end{aligned}$$

When  $\frac{A}{B} > R_1$ , then  $b_1 > 0$ , and therefore by Routh-Hurwitz criteria, the roots of  $r^2 - b_1r + c_1 = 0$  have negative real parts. The stability of  $E_2$  is determined by the sign of  $a_1$ . Thus  $E_2$  is stable if  $\lambda_x > (A + Bs^0\lambda_s)(1 - \lambda_s)$ .

Finally when the interior steady state,  $E_C$  exists, the eigenvalues of  $J(E_C)$  satisfy  $r^3 + a_1r^2 + a_2r + a_3 = 0$ , where

$$\begin{aligned} a_1 &= 1 + \frac{\lambda_x m_1 k_1}{(A + Bs^0s)(k_1 + s)^2} - \frac{\lambda_x Bs^0 m_1 s}{(A + Bs^0s)^2 (k_1 + s)} \\ &\quad + \left( \frac{\lambda_x m_2 k_2}{(k_2 + \lambda_x)^2} - 1 \right) \left( \frac{m_1 s}{(k_1 + s)} - 1 \right), \\ a_2 &= \frac{\lambda_x m_2 k_2}{(k_2 + \lambda_x)} \left( \frac{m_1 s}{(k_1 + s)} - 1 \right) \\ &\quad + \left( 1 + \frac{\lambda_x m_1 k_1}{(A + Bs^0s)(k_1 + s)^2} - \frac{\lambda_x Bs^0 m_1 s}{(A + Bs^0s)^2 (k_1 + s)} \right) \left( \frac{\lambda_x m_2 k_2}{(k_2 + \lambda_x)^2} - 1 \right) \left( \frac{m_1 s}{(k_1 + s)} - 1 \right) \\ &\quad + \frac{\lambda_x m_1^2 k_1 s}{(A + Bs^0s)(k_1 + s)^3}, \\ \text{and } a_3 &= \frac{\lambda_x m_2 k_2}{(k_2 + \lambda_x)} \left( 1 + \frac{\lambda_x m_1 k_1}{(A + Bs^0s)(k_1 + s)^2} - \frac{\lambda_x Bs^0 m_1 s}{(A + Bs^0s)^2 (k_1 + s)} \right) \left( \frac{m_1 s}{(k_1 + s)} - 1 \right). \end{aligned}$$

The Routh-Hurwitz criterion says that  $E_C$  will be locally asymptotically stable if and only if  $a_1 > 0, a_2 > 0$  and  $a_1 a_2 > a_3$ .

We can summarize the above results in the following theorems.

**Theorem 1.** If  $\lambda_s > 1$ , then only  $E_1$  exists and  $E_1$  is locally asymptotically stable. If  $\lambda_s < 1, \frac{A}{B} > R_1$  and  $\lambda_x > (A + Bs^0\lambda_s)(1 - \lambda_s)$ , then only  $E_1$  and  $E_2$  exist,  $E_1$  is unstable and  $E_2$  is locally asymptotically stable. If  $\lambda_s < 1$  and  $\lambda_x > (A + Bs^0\lambda_s)(1 - \lambda_s)$ , then  $E_1, E_2$  and  $E_C$  exist, and  $E_1$  and  $E_2$  are unstable.  $E_C$  is locally asymptotically stable if  $a_1 > 0, a_2 > 0$  and  $a_1 a_2 > a_3$ .

**Global Stability and Hopf Bifurcation Analysis**

In the previous section, we showed that if only  $E_1$  exists, then  $E_1$  is asymptotically stable, if  $E_1$  and  $E_2$  exist, then  $E_1$  is unstable and  $E_2$  is locally asymptotically stable. In this section, we will show that  $E_1$  and  $E_2$  are globally asymptotically stable if exist. Hopf bifurcation analysis will be discussed of the system (3) in the solution plane  $y = 0$ .

**Theorem 2.** (i) If  $\lambda_s > 1$ , the equilibrium point  $E_1$  is globally asymptotically stable in  $R_+^3$ ; (ii) If  $\lambda_s < 1, \frac{A}{B} > R_1$ , and  $\lambda_x > (A + Bs^0\lambda_s)(1 - \lambda_s)$  the equilibrium point  $E_2$  is globally asymptotically stable, too.

**Proof.** Let

$$\Theta = \left\{ (s, x, y) : 0 \leq s \leq l - x - y, 0 \leq x \leq (A + Bs^0\lambda_1)(1 - \lambda_1) + \varepsilon_0, 0 \leq y \leq \left( \frac{m_1 s^0}{k_1 + s^0} - 1 \right) \lambda_x + \varepsilon_0 \right\}.$$

We first prove that  $\Theta$  is positively invariant set of (3). Consider the face,  $s = 0$  and by equation (3),  $\frac{ds}{dt}|_{s=0} = 1 > 0$ . Thus any trajectory in  $\{(s, x, y) : s < 0, \bar{x} > 0, y > 0\}$  will go through  $s = 0$  into  $R_+^3$ , but the reverse is not true.

For the face  $M = s + x + y - l = 0, (0 < l < +\infty)$ ,

$$\frac{dM}{dt}|_{M=0} = 1 - l - x \left( \frac{m_1(l-x-y)}{k_1 + (l-x-y)} \right) \left( \frac{1}{A + Bs^0(l-x-y)} - 1 \right).$$

Since both  $x$  and  $y$  are bounded and all the parameters are positive,  $\frac{dM}{dt}|_{M=0} < 0$  if  $l$  is sufficiently larger. That is any trajectory in  $R_+^3$  will cross  $M = s + x + y - l = 0$  into  $\Theta$ . Moreover, because both  $x = 0, y = 0$  are the solutions of equation (3),  $\Theta$  is a positively invariant set of equation (3). In other words, any trajectory initiating in  $R_+^3$  will go to  $\Theta$  when  $t \rightarrow +\infty$ . Therefore, both  $E_1$  and  $E_2$  are globally asymptotically stable.

For  $E_2$ , in the solution plane  $y = 0$ , the system (3) is reduced to

$$\begin{aligned} \frac{ds}{dt} &= 1 - s - \frac{x}{A + Bs s^0} \left( \frac{m_1 s}{k_1 + s} \right) \\ \frac{dx}{dt} &= x \left( \frac{m_1 s}{k_1 + s} - 1 \right) \end{aligned} \tag{4}$$

We would like to point out that (4) is a special case of the following system (Huang, 1990)

$$\begin{aligned} \frac{dx}{dt} &= x(g(y) - 1) \\ \frac{dy}{dt} &= 1 - y - \frac{g(y)}{F(y)} x \end{aligned} \tag{5}$$

with  $y = s, g(y) = \frac{m_1 s}{k_1 + s}, F(y) = A + Bs s_0$ .

System (5) has two equilibrium points  $(0,1)$  and  $(\bar{x}, \bar{y})$ , where  $\bar{x} = (1 - \bar{y})F(\bar{y})$  and  $\bar{y} = g^{-1}(1)$  with the condition  $g(1) > 1$ . It is easy to see that  $(0,1)$  is stable if  $g(1) < 1$ .

Denote  $p = 1 + \bar{x} \left( \frac{g}{F} \right) |_{y=\bar{y}}$  (6)

The following theorem is proved in (Huang, 1990).

**Theorem 3:** Assume  $g(1) > 1$ , if  $p > 0$ , then  $(\bar{x}, \bar{y})$  is stable; if  $p < 0$ , it is unstable and there

exists at least one limit cycle in (3) surrounding the equilibrium  $(\bar{x}, \bar{y})$ .

Then, we have,

**Theorem 4:** System (4) has two equilibrium points  $M_1(1,0)$  and  $M_2(\lambda_s, (1 - \lambda_s)(A + Bs^0\lambda_s))$ . In which  $M_1$  always exists and is stable whenever  $m_1 < k_1 + 1$ . Again  $M_2$  is stable if  $\frac{A}{B} > R_1$  and unstable if  $\frac{A}{B} < R_1$ . In the case when  $M_2$  is unstable, there is at least one limit cycle in equation (4) surrounding  $M_2$ .

**Theorem 5:** System (4) undergoes a Hopf bifurcation at  $\frac{A}{B} = R_1$ .

**Proof:** Let  $J(\bar{s}, \bar{x})$  be the Jacobian of (4) at  $M_2$ . The corresponding characteristic equation is  $r^2 + b_1 r + c_1 = 0$  (7)

Let  $\frac{A}{B} = \mu$ . Denote  $b_1$ , the coefficient of  $r$  in the above equation as  $trJ\left(\frac{A}{B}\right)$  or  $trJ(\mu)$  where

$$\begin{aligned} trJ(\mu) &= 1 + (1 - \lambda_s) \left\{ \frac{m_1 k_1}{(k_1 + \lambda_s)^2} - \frac{Bs^0}{(A + Bs^0\lambda_s)} \right\} \\ &= 1 + (1 - \lambda_s) \left\{ \frac{m_1 k_1}{(k_1 + \lambda_s)^2} - \frac{s^0}{(\mu + s^0\lambda_s)} \right\}. \end{aligned}$$

Since,  $\frac{d}{d\mu} trJ(\mu) \Big|_{\mu=R_1} = (1 - \lambda_s) \frac{s^0}{(R_1 + s^0\lambda_s)^2} > 0$ ,

the function  $trJ(\mu)$  is increasing at  $\mu = R_1$ . Notice that

$$trJ(\mu) = \begin{cases} < 0 & \text{if } \mu < R_1 \\ = 0 & \text{if } \mu = R_1 \\ > 0 & \text{if } \mu > R_1. \end{cases}$$

The sign of the real parts of the roots for (7) have been changed from positive to negative. That means the phase structure of  $M_2(\lambda_s, (1 - \lambda_s)(A + Bs^0\lambda_s))$  changes from stable to unstable at  $R_2$  as  $\mu$  increases. Thus, equation (4) undergoes a Hopf bifurcation at  $\frac{A}{B} = R_1$  by the definition (Zhang, 1987).

### Numerical Simulation

The numerical experiments performed on the system (3) using experimental data confirm our theoretical findings. The model we considered exhibits a sequence of different stages of global behavior as various parameters change. The figures were constructed by proper choice of the kinetic parameters so that all the interesting behaviors of the system are observed. At each

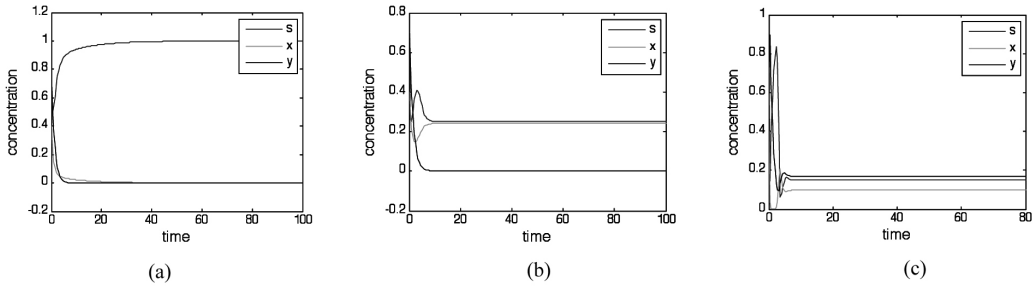


Figure 1: (a)  $m_1 = 1.2, m_2 = 1.1, k_1 = 0.3, k_2 = 0.5, A = 0.3, B = 0.45, s^0 = 0.2$ . The solution curves tend to  $E_1$ , (b)  $m_1 = 2.2$  and other parameter values are as given in (a). The solution curves tend to the predator-free equilibrium point  $E_2$ , (c)  $m_1 = 8.2, m_2 = 6.1$ , and other parameter values are as given in (a). The solution approaches a positive equilibrium point  $E_C$ .

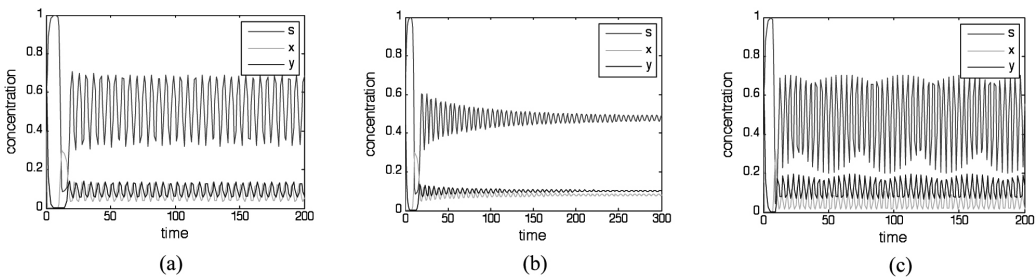


Figure 2: (a)  $m_1 = 3.2, m_2 = 4.5, k_1 = 0.2, k_2 = 0.25, A = 0.3, B = 0.5, s^0 = 0.2$ . The solution appears to approach a periodic solution, (b)  $m_2 = 4.1$  and other parameter values are as given in (a). The solution oscillates but eventually approaches positive equilibrium point, (c)  $m_1 = 5, m_2 = 6$ , and other parameter values are as given in (a). The solution oscillates and seems to approach a periodic solution.

stage, conditions have become sufficiently favorable for a new population to survive. We choose the basic parameters of the model (3) to be  $k_1 = 0.3, k_2 = 0.5, A = 0.3, B = 0.45, s^0 = 0.2$ . The initial condition  $(s_0, x_0, y_0) = (0.6, 0.4, 0.7)$  is used to generate solution curves and trajectories in Figures 1-2. Now we see how the parameters affect the dynamics of (3) if  $s^0$  is fixed. Assume that  $m_i (i = 1, 2)$  are small enough so that  $\lambda_s > 1$ , then all populations will be washed out ( $E_1$  is stable) in the chemostat (Figure 1a). As  $m_i$  is gradually increased, eventually there is a bifurcation when  $\lambda_s < 1, \frac{A}{B} < R_1$  and  $\lambda_x > (A + Bs^0 \lambda_s)(1 - \lambda_s)$  hold. In this case,  $E_1$  loses its stability and the new bifurcated steady state  $E_2$  is asymptotically stable (Figure 1b). This interprets that only the prey population will survive. As  $E_2$  becomes unstable, a locally asymptotically stable interior steady state bifurcates from it. Figure 1c, shows a case in which  $m_1 = 8.2$  and  $m_2 = 6.1$ , and our simulation work suggests that  $E_C$  is a global attractor if it is locally asymptotically stable. As

certain parameters increase or decrease further away,  $E_C$  loses its stability and oscillatory solutions appear. These oscillatory solutions (see Figures 2a and 2c) appear to be the results of Hopf bifurcations. Figure 2a shows a case in which  $m_1 = 3.2, m_2 = 4.5, k_1 = 0.2, k_2 = 0.25, A = 0.3, B = 0.5, s^0 = 0.2$  and the system (3) possesses a periodic solutions. Figure 2b indicates that perturbing  $m_2$  (while changing  $m_2 = 4.5$  to  $m_2 = 4.1$  and keeping other parameters in Figure 2a fixed) leads to a bifurcation. This seems to destroy the periodic solutions and possibly leads to the global stability of  $E_C$ . Therefore, varying the values of maximal growth rates may affect the dynamics of (3) in a very significant way.

Furthermore, Figure 3 shows the dynamics of the system (4) which is the reduced form of the system (3) in the solution plane  $y = 0$ . For  $m_1 = 3.25, k_1 = 0.2, A = 0.0189179, B = 2, s^0 = 0.4$ , we have  $R_1 = 0.00945896$ . Figures 3a-3b contain the solution curves and phase structure of  $M_2$  of

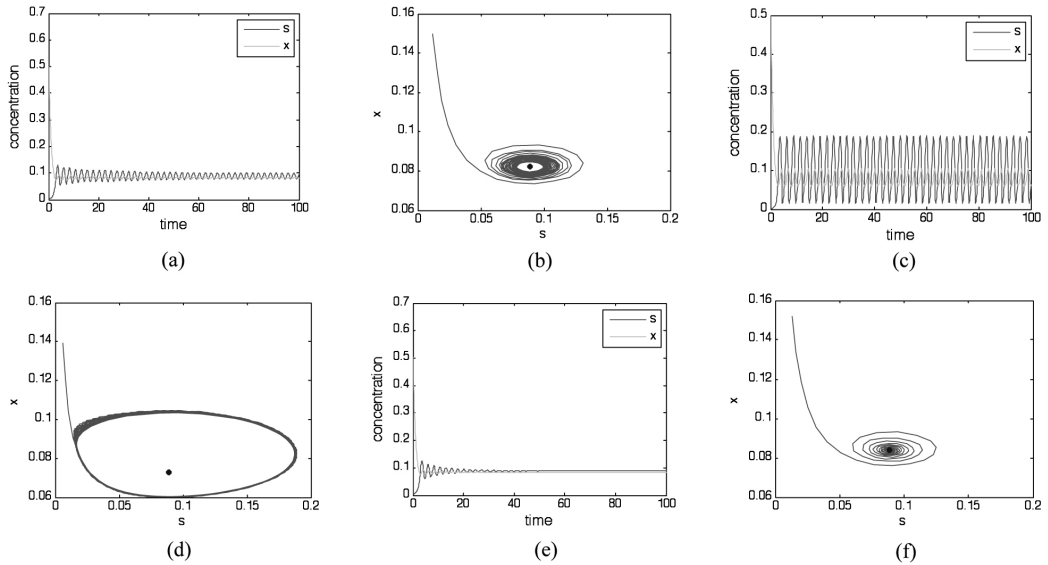


Figure 3: (a)  $m_1 = 3.25, k_1 = 0.2, A = 0.0189179, B = 2, s^0 = 0.4, (s_0, x_0) = (0.4, 0.5)$ . The solution curves of the system (4) when  $\frac{A}{B} = R_1$ , (b) The system (4) undergoes a Hopf bifurcation at  $\frac{A}{B} = R_1$ , (c) The solution curves of system (4) when  $\frac{A}{B} < R_1$ , (d) A plot of trajectories of the system (4) when  $\frac{A}{B} < R_1$ , (e) The solution curves of system (4) when  $\frac{A}{B} > R_1$ , (f) A plot of trajectories of the system (4) when  $\frac{A}{B} > R_1$ .

the system (4), resulting the system undergoes a Hopf bifurcation at  $\frac{A}{B} = R_1$ . The two plots in figures 3c-3d (while changing  $A = 0.0189179$  to  $A = 0.0089179$  and keeping other parameters in Figure 3a fixed) have  $\frac{A}{B} < R_1$  and the system (4) is unstable through limit cycle oscillation. The two plots in figures 3e-3f (while changing  $A = 0.0189179$  to  $A = 0.0209179$  and keeping other parameters in Figure 3a fixed) have  $\frac{A}{B} > R_1$  and all plotted trajectories tend to  $M_2$ , resulting in a stable situation.

**Discussion**

In this paper, we considered a simple food chain in chemostat with variable yield for prey population and constant yield for predator population. In this model, the prey consumes the nutrient and the predator consumes the prey but the predator does not consume the nutrient. We assume that the functional response functions are in Michaelis-Menton type. In this study we established sufficient conditions for the existence and local stability of the equilibria by using Routh-Hurwitz criterion for system (3). We found that the washout equilibrium point

is a global attractor if it is the only steady state (this happens when  $\lambda_s > 1$ ). This confirms the intuition that all the populations cannot persist if the growth rates of the prey and predator are relatively small and close to one. When  $E_1$  and  $E_2$  are the only equilibrium points, we found that  $E_1$  is unstable and  $E_2$  is locally asymptotically stable. The global stability of  $E_2$  implies that the washout of the predator in the chemostat does not depend on the initial density levels of prey and predator. Therefore, the principle of competitive exclusion has been well established and confirmed. That is, when two, and only two, species compete for a limiting substrate, one must be eliminated, as seen in Figure 1b. We also showed that when  $E_C$  exists and is locally asymptotically stable, then the prey and predator coexist in the sense that the system is uniformly persistent and the conservation principle is circumvented. In this case, a switch of the stability of  $E_C$  may occur. Finally, it has been analytically and numerically shown that in certain regions of the parameter space, the model with variable yield leads to oscillatory coexistence of the population in chemostat and

a local Hopf bifurcation is possible. Therefore, this population dynamics permits a limit cycle behavior.

## References

- Alhumazi, K., & Ajar, A. (2005). Dynamics of Predator-prey Interaction in Continuous Culture. *Eng. Life Sci.*, 5-2:139-147.
- Butler, G. J., & Wolkowicz, G. S. K. (1983). A Mathematical Model of the Chemostat with a General Class of Functions Describing Nutrient Uptake. *SIAM J. Appl. Math.*, 43:138-131.
- Crooke, P. S., & Tanner, R. D. (1982). Hopf Bifurcation of a Variable Yield Continuous Fermentation Model. *Int. J. Eng. Sci.*, 20:439-443.
- El-Owaidy, H. M., & Moniem, A. A. (2003). On Food Chain in a Chemostat with Distinct Removal Rates. *Appl. Math. E-Notes*, 3:183-191.
- Grivet, J. P. (2001). Nonlinear Population Dynamics in the Chemostat. *Computing in Science and Engineering*, 3-1: 48-55.
- Huang, X. (1990). Limit Cycle in a Continuous Fermentation Model. *J. Math. Chem.*, 3: 287-296.
- Huang, X., & Zhu, L. (2003). A Three Dimensional Chemostat with Quadratic Yields. *J. Math. Chem.*, 38-4: 575-588.
- Jost, J. L., Drake, J. F., Fredrickson, A. G., & Tsuchiya, H. M. (1973). Interactions of *Tetrahymena pyriformis*, *Escherichia coli*, *Azotobacter vinelandii* and Glucose in a Minimal Medium. *J. Bacteriol.*, 113: 834-840.
- Li, B. (1998). Analysis of Chemostat-related Models with Distinct Removal Rates. Ph. D. thesis, Arizona State University.
- Li, B., & Kuang, Y. (2000). Simple Food Chain in a Chemostat with Distinct Removal Rates. *J. Math. Anal. Appl.*, 242: 75-92.
- May, R. M. (1972). *Stability and Complexity in Model Ecosystems*. NJ (USA): Princeton University Press.
- Mada, S. W. S., Mohd, I., Mamat, M., & Salleh, Z. (2012). Mathematical Model of Three Species Food Chain Interaction with Mixed Functional Response. *International Journal of Modern Physics: Conference Series*. 9: 334-340.
- Mada, S. W. S., Salleh, Z., & 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. doi: <http://dx.doi.org/10.12732/ijpam.v89i5.1>
- Nasrin, F., & Rana, S. M. S. (2011). Three Species Food Web in a Chemostat, *Int. J. Appl. Sci. Eng.*, 9(4): 301-313.
- Pilyugin, S. S., & Waltman, P. (2003). Multiple Limit Cycle in the Chemostat with Variable Yield. *Math. Bio. Sci.*, 182:151-166.
- Sarah, A. Al-Sheikh. (2008). The Dynamics of a Tri-trophic Food Chain in the Chemostat, *Int. J. Pure. Appl. Math.*, 47(1): 101-111.
- Smith, H. L. (1982). The Interaction of Steady State and Hopf Bifurcations in a Two-predator-one-prey Competition Model. *SIAM J. Appl. Math.*, 42: 27-43.
- Smith, H. L., & Waltman, P. (1995). *The Theory of Chemostat*. Cambridge (UK): Cambridge Univ. Press.
- Suwicha, B., & Kornkanok, B. (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.
- Tsuchiya, H. M., Drake, S. F., Jost J. L., & Fredrickson, A. G. (1972). Predator-prey Interaction of *Dictyostelium discoideum* and *Escherichia coli* in Continuous Culture. *J. Bacteriol.*, 110: 1147-1153.
- Waltman, P., Hubbel, S. P., & Hsu, S. B. (1980). Theoretical and Experimental Investigation of Microbial Competition in Continuous Culture. *Modeling and Differential Equations in Biology*, T. Burton (ed.), 107-152.
- Wolkowicz, G. S. K., & Lu, Z. (1992). Global Dynamics of a Mathematical Model of

Competition in the Chemostat; General Response Function and Differential Death Rates. *SIAM J. Appl. Math.*, 52: 222-233.

Zhang, J. (1987). “*The Geometric Theory and Bifurcation Problem of Ordinary Differential Equation*”. Beijing: Perking University Press.

Zhu, H., Campbell, S. A., & Wolkowicz, G. S. K. (2002). Bifurcation Analysis of a Predator-prey System with Nonmonotonic Functional Response. *SIAM J. Appl. Math.*, 63-2: 636-682.