

Analysis of Prey-Predator Model in Chemostat When the Predator Produces Inhibitor

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Abstract

In this work, a prey-predator model in chemostat is considered when the predator produces inhibitor. This inhibitor is lethal to the prey by results in decrease of growth rate of the predator at some cost to its reproductive abilities. A Lyapunov function in the study of the global stability of a predator-free steady state is analysed. Local and global stability of other steady states, persistence analysis, as well as numerical simulations are also presented.

Keywords: Persistence; Inhibitor; Chemostat; Prey; Predator; Lyapunov function

Introduction

The chemostat is one of the standard models of an open system in ecology [1-5]. The monograph of Hsu and Waltman has various mathematical methods for analyzing chemostat models [4]. So, it is quite natural that it should be used as a model for studying detoxification problems. Many authors have studied those models [6-12]. Recently, the inhibitor has been introduced in the models for prey - predator in chemostat when the prey produces unaffected inhibitor which is lethal to neither predator nor nutrient [1]. Moniem [2] has considered a model of simple food chain in chemostat when the predator produces unaffected inhibitor which is lethal to neither prey nor nutrient.

In this paper, we consider a prey-predator model in chemo stat when the predator produces inhibitor. This inhibitor is lethal to the prey by results in decrease of growth rate of the predator at some cost to its reproductive abilities.

This paper is organized as follows: In the next section, the model is presented and some simplifications are achieved. Section 3 deals with the existence and local stability of steady states. In section 4, we shall provide global analysis, including global stability of the boundary steady states and persistence analysis. Discussion, comments and numerical simulation are found in final section.

The Model

The interested equations are

$$\begin{aligned} s'(t) &= (s^0 - s(t))D - \frac{1}{\gamma_1} f_1(s(t))x(t), \\ x'(t) &= x(t) \left(f_1(s(t)) - D - \gamma p \right) - \frac{1}{\gamma_2} f_2(x(t))y(t), \\ y'(t) &= y(t) \left((1-k) f_2(x(t)) - D \right), \\ p'(t) &= k y(t) f_2(x(t)) - D p, \\ 0 &< s(0), \quad 0 < x(0), \quad 0 < y(0), \quad 0 < p(0). \end{aligned} \quad (1.1)$$

Where $s(t)$, $x(t)$, $y(t)$ and $p(t)$ are the concentration of the nutrient, prey, predator and inhibitor at time t respectively. s^0 denotes the input concentration of the nutrient, D denotes the washout rate, and the parameter γ represents the coefficient of the interaction between the inhibitor and the prey. γ_i , $i=1,2$ are the Yield constants. The constant $k \in (0,1)$ represents the fraction of potential growth devoted to producing the inhibitor [3].

Also we have $f_1(s(t)) = \frac{m_1 s(t)}{a_1 + s(t)}$ and $f_2(x(t)) = \frac{m_2 x(t)}{a_2 + x(t)}$, where

m_i , $i=1,2$ are the maximal growth rates, and a_i , $i=1,2$ are the Michaelis-Menten constants.

Now to perform the usual scaling for the chemostat, let

$$\begin{aligned} \bar{s} &= \frac{s}{s^0}, \quad \bar{x} = \frac{x}{\gamma_1 s^0}, \quad \bar{y} = \frac{y}{\gamma_1 \gamma_2 s^0}, \quad \bar{t} = D t, \\ \bar{p} &= \frac{p}{\gamma_1 \gamma_2 s^0}, \quad \bar{m}_i = \frac{m_i}{D}, \quad i=1, 2, \quad \bar{a}_1 = \frac{a_1}{s^0}, \quad \bar{a}_2 = \frac{a_2}{\gamma_1 s^0}. \end{aligned}$$

Substituting in eqn. 1.1 and dropping the bars, the mathematical model will be reduced to the form

$$\begin{aligned} s' &= 1 - s - f_1(s) x, \\ x' &= x (f_1(s) - 1 - \gamma p) - f_2(x) y, \\ y' &= y ((1-k) f_2(x) - 1), \\ p' &= k y f_2(x) - p. \end{aligned} \quad (1.2)$$

Existence and Local Stability

Let $T=s+x+y+p$ then we have $T' \leq 1 - T$, or $\limsup_{t \rightarrow \infty} T(t) \leq 1$. Since each component is non-negative, the system in eqn. 1.2 is dissipative and thus, has a compact, global attractor. To simplify in eqn. 1.2, let $z = p - \frac{k y}{1-k}$, we find that the system in eqn. 1.2 will take the form

$$\begin{aligned} s' &= 1 - s - f_1(s) x, \\ x' &= x \left(f_1(s) - 1 - \frac{\gamma k y}{(1-k)} \right) - f_2(x) y, \\ y' &= y ((1-k) f_2(x) - 1). \end{aligned} \quad (2.1)$$

Clearly $z(t) \rightarrow 0$ as $t \rightarrow \infty$ so the system in eqn. (2.1) may be viewed

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as an asymptotically autonomous system with the following equations

$$\begin{aligned} s' &= 1 - s - f_1(s) x, \\ x' &= x \left(f_1(s) - 1 - \frac{\gamma k y}{(1-k)} \right) - f_2(x) y, \\ y' &= y \left((1-k) f_2(x) - 1 \right). \end{aligned} \quad (2.2)$$

The equilibrium point $E_0=(1,0,0)$ always exists. If $1 < f_1(1)$ then there is an equilibrium of in eqn. (2.2) of the form $E_1=(\lambda_s, 1-\lambda_s, 0)$ where λ_s is the unique solution of $f_1(\lambda_s)-1=0$. Similarly, if $\frac{1}{1-k} < f_2(1)$, there is an equilibrium of the form $E_2=(s^*, \lambda_x, y^*)$ where s^* is the unique value of s such that $1 - s - \lambda_x f_1(s)=0$ λ_x is the unique solution of $(1-k) f_2(x)-1=0$ and $y^* = \frac{\lambda_x(1-k)(f_1(s^*)-1)}{(1+k\lambda_x\gamma)}$.

Since the limit plane in (eqn. 2.2) is $\Sigma: s+y+z=1$, then by dropping S equation, the system of equations eqn. (2.2) will be reduced to the form

$$\begin{aligned} x' &= x \left(f_1(1-x-y) - 1 - \frac{\gamma k y}{(1-k)} \right) - f_2(x) y, \\ y' &= y \left((1-k) f_2(x) - 1 \right). \end{aligned} \quad (2.3)$$

It is easy to show that in eqn. 2.3 in positive plane. As a consequence, the global attractor in eqn. (2.1) lies in the set $z=0$ and Σ plane where in eqn. (2.3) is satisfied. When the analysis of in eqn. (2.3) is completed in this paper, the work of Thieme (11), relates the corresponding dynamics in eqns. (2.1) and (2.3), and hence in eqn. (1.2). We will show that all solutions in eqn. (2.3) tend to rest points and hence, using Thieme (10), we can find the rest points of the system in eqn. (1.2).

We now discuss the existence of steady state. The washout steady state E_0 always exists. A predator-free steady state E_1 exists when $\lambda_s < 1$. For the interior steady state E_2 exists when $\lambda_s < 1$ and $\lambda_s + \lambda_x < 1$. Note that $H(s)=1-s-\lambda_x f_1(s)$ is decreasing function in s with $0 < H(0)=1$, $H(s^*)=0$ and $H(\lambda_s)=1-\lambda_s-\lambda_x$ So $\lambda_s < s^*$. If and only if $\lambda_s + \lambda_x < 1$.

Next theorem will discuss the local stability of this steady state by finding the eigenvalues of the associated variation matrices.

Theorem 1

If $1 < \lambda_s$ then only E_0 exists and E_0 is locally asymptotically stable. If $\lambda_s < 1$ and $1 < \lambda_s + \lambda_x$ then only E_0 and E_1 exist, E_0 is unstable, and E_1 is locally asymptotically stable. If $\lambda_s < 1$ and $\lambda_s + \lambda_x < 1$ then E_0, E_1, E_2 exist, E_0, E_1 are unstable and E_2 is locally asymptotically stable if

$$\lambda_x f_1'(s^*) > [1 - \frac{\lambda_x(f_1(s^*)-1)}{1+k\lambda_x\gamma} (k\gamma + (1-k)f_2'(\lambda_x))] [f_1(s^*) - 1]$$

and consequently by an application of the Poincare-Bendixson theorem there is a periodic solution in Σ .

Proof: The Jacobian matrix in eqn. (2.3) is taken the form

$$\begin{bmatrix} -1 - y f_2'(x) + f_1(s) - x f_1'(s) - \frac{k\gamma y}{(1-k)} & -x f_1'(s) - f_2(x) - \frac{k\gamma y}{(1-k)} \\ y(1-k)f_2'(x) & (1-k)f_2(x) - 1 \end{bmatrix}$$

At $(1,0,0)$ this is

$$\begin{bmatrix} -1 + f_1(1) & 0 \\ 0 & -1 \end{bmatrix}$$

The eigenvalues are on the diagonal and the washout steady state will be locally asymptotically stable if and only if $f_1(1) < 0$ or $1 < \lambda_s$.

At $(\lambda_s, (1-\lambda_s), 0)$ the Jacobian matrix becomes

$$\begin{bmatrix} -(1-\lambda_s)f_1'(\lambda_s) & -(1-\lambda_s)f_1(\lambda_s) - f_2((1-\lambda_s)) - \frac{(1-\lambda_s)k\gamma}{(1-k)} \\ 0 & (1-k)f_2((1-\lambda_s)) - 1 \end{bmatrix}$$

The two eigenvalues are $-(1-\lambda_s)f_1'(\lambda_s)$ and $(1-k)(f_2((1-\lambda_s))-1)$. Therefore the predator-free steady state is asymptotically stable if and only if $(1-k)f_2((1-\lambda_s))-1 < 0$ or $1 < \lambda_s + \lambda_x$.

At E_2 the Jacobian matrix takes the form

$$\begin{bmatrix} -\lambda_x f_1'(s^*) + f_1(s^*) - 1 - y^* f_2'(\lambda_x) - \frac{k\gamma y^*}{(1-k)} & -\lambda_x [f_1'(s^*) + \frac{k\gamma}{(1-k)}] - f_2(\lambda_x) \\ y^*(1-k)f_2'(\lambda_x) & 0 \end{bmatrix}$$

Then E_2 is locally asymptotically stable if the determinant of this matrix is positive and its trace is negative, it means that

$$[1 - \frac{(f_1(s^*) - 1)}{\lambda_x \gamma} (k\gamma + (1-k)f_2'(\lambda_x))] [f_1(s^*) - 1] < \lambda_x f_1'(s^*).$$

Global Analysis

Theorem 2

For $1 < \lambda_s$ and for large t all solutions in eqn. 2.2 tends to E_0 .

Proof: For $1 < \lambda_s$ and for large t we get $s(t) < 1$ and $f_1(1) < 1$. Therefore, the second equation 2.2 gives $x(t) < e^{-(1-f_1(1))t}$, which imply $\lim_{t \rightarrow \infty} x(t) = 0$. The third eqn. (2.2) becomes $y = e^{-t}$, which leads to $\lim_{t \rightarrow \infty} y(t) = 0$. The first equation (2.2) has a solution $s=1+(\text{constant})e^{-t} \rightarrow 1$ as $t \rightarrow \infty$.

Theorem 3

If $\lambda_s < 1, 1 < \lambda_s + \lambda_x$ and for large t then all solutions in eqn. 2.2 tend to E_1 .

Proof

Let

$$\eta = 1 + \frac{(1-k)f_2(x) + kx\gamma}{(1-k)x} \frac{(1-\lambda_s - x)}{(1-(1-k)f_2(x))}, \quad \text{for } 0 < x \leq 1 - \lambda_s, \quad (3.1)$$

and

$$\beta = \frac{\eta(1-k)}{[(1-k)f_2(x) + k\gamma]} [(1-k)f_2(x) - 1] \quad \text{for } \lambda_x \leq x. \quad (3.2)$$

Let $C(u)$ be a continuously differentiable function and $C'(u)$ be defined by

$$C'(u) = \begin{cases} 0 & \text{if } u \leq 1 - \lambda_s, \\ \beta \frac{(u + \lambda_s - 1)}{(\lambda_s + \lambda_x - 1)} & \text{if } 1 - \lambda_s < u < \lambda_x, \\ \beta & \text{if } \lambda_x \leq u. \end{cases} \quad (3.3)$$

Note that $C'(u)$ is linear on $[1-\lambda_s, \lambda_x]$. We may construct a Lyapunov function as follows:

$$V(s, x, y) = \int_{\lambda_s}^s \frac{(1-\lambda_s)(f_1(\xi) - 1)}{(1-\xi)} d\xi + x - x \ln(x) + \eta y + C(x). \quad (3.4)$$

on the set $\Psi = \{(s, x, y): 0 < s + x + y < 1\}$ where $x = 1 - \lambda_s$.

Differentiate in eqn. 3.4 with respect to time t , we obtain

$$\begin{aligned} \dot{V} &= x(f_1(s) - 1) [1 + C'(x) - \frac{(1-\lambda_s)f_1'(s)}{(1-s)}] \\ &+ y [(1-k)f_2(x) + kx\gamma] (1-\lambda_s - x) + \eta [(1-k)f_2(x) - 1] - (f_2(x) + \frac{k\gamma}{(1-k)}) C'(x). \end{aligned} \quad (3.5)$$

The term $x(f_1(s) - 1) [1 - \frac{(1-\lambda_s)f_1'(s)}{(1-s)}]$ is non-positive for $0 < s < 1$ and equal zero for $s \in [0, 1]$ if and only if $s = \lambda_s$ or $x = 0$. Since $C'(x) = 0$ for

$\lambda_s \leq s$ and $C'(u) \geq 0$ for $u \geq 0$, then the term $x(f_1(s) - 1)C'(x)$ is non-positive for $s \in [0, 1]$.

Define

$$h(s, x, y) = \left[\left(\frac{f_2(x)}{x} + \frac{k\gamma}{(1-k)} \right) (1 - \lambda_s - x) + \eta [(1-k)f_2(x) - 1] - \left(f_2(x) + \frac{k\gamma}{(1-k)} \right) C'(x) \right]. \quad (3.6)$$

If $0 < x \leq 1 - \lambda_s$, then $[(1-k)f_2(x) - 1] \leq 0$, $0 \leq \left(\frac{f_2(x)}{x} + \frac{k\gamma}{(1-k)} \right) (1 - \lambda_s - x)$

and $0 \leq \left(f_2(x) + \frac{k\gamma}{(1-k)} \right) C'(x)$.

Using the definition of η we find that $h(s, x, y) \leq 0$. If $1 - \lambda_s < x < \lambda_x$ then all terms of $h(s, x, y)$ are non-positive. If $\lambda_x \leq x$, then $C'(x) = \beta$ and making use of definition of β and η we find that $h(s, x, y)$ will be non-positive and the second term of V vanishes at $y=0$ therefore V is non-positive on Ψ .

Let M be the largest invariant subset of $\varphi = \{(s, x, y) \in \Psi : V=0\}$ such that $V=0$ at $S = \lambda_s$ or $x=0$ and $y=0$. More further, V is bounded above, any point of the form $(s, 0, 0)$ cannot be in the limit set of any solution initiating in the interior of R_+^3 . $(\lambda_s, x, 0) \in M$ implies that $S = \lambda_s$ and from the first equation (2.2), we get $x = 1 - \lambda_s$.

Therefore $M = \{E_1\}$. This completes the proof.

Theorem 4

If $\lambda_s < 1$ and $\lambda_s + \lambda_x < 1$ then the system in eqn. (2.2) is uniformly persistence.

Proof

Let $Z_1 = \{(s, x, y) : s \in [0, 1], x, y \in (0, 1]\}$,

Z_2 represents sx -plane : $0 \leq s, x \leq 1$,

Z_3 represents sy -plane : $0 \leq s, y \leq 1$, and

$Z = Z_2 \cup Z_3$

We want to show that Z is a uniformly strong repeller for Z_1 . Since E_0 and E_1 are the only steady states in Z . E_0 is saddle in R^3 and its stable manifold is $\{(s, 0, y) : 0 \leq y\}$. Also, E_1 is saddle in R^3 and its stable

manifold is $\{(s, x, 0) : 0 < x\}$. Then, they are weak repellers for Z_1 . The stable manifold structures of E_0 and E_1 imply that they are not cyclically chained to each other on the boundary Z . Therefore Z is a uniform strong repeller for Z_1 (see proposition in eqn.(1.2) of Thieme [12]).

So, there are $\varepsilon_1 > 0$ and $\varepsilon_2 > 0$. such that $\liminf_{t \rightarrow \infty} x(t) > \varepsilon_1$ and $\liminf_{t \rightarrow \infty} y(t) > \varepsilon_2$ where ε_1 and ε_2 are not depending on the initial values in Z_1 . By using (Thieme [12]), the first eqn. (2.2) yields that there is $\varepsilon_3 > 0$ such that $\liminf_{t \rightarrow \infty} s(t) > \varepsilon_3$ where ε_3 is not depending on the initial values in Z_1 . Proof is completed.

Conclusion and Numerical Simulation

In this paper, we consider a prey-predator model in chemostat when the predator produces inhibitor. This inhibitor is lethal to the prey by results in decrease of growth rate of the predator at some cost to its reproductive abilities. We found that the washout steady state is the global attractor, if it is the only steady state and $\lambda_s > 1$. When the washout and the predator free steady states are the only steady states, we found that E_0 is unstable and E_1 is locally asymptotically stable. E_1 is global attractor by constructing a Lyapunov function under condition that $\lambda_s < 1$ and $\lambda_s + \lambda_x > 1$. We also showed that E_2 exists in the sense that the system is uniformly persistent and E_2 is locally asymptotically stable if the determinant of this matrix is positive and its trace is negative, it means that

$$\left[1 - \frac{\lambda_x (f_1(s^*) - 1)}{1 + k \lambda_x \gamma} (k \gamma + (1 - k) f_2'(\lambda_x)) [f_1(s^*) - 1] \right] < \lambda_x f_1'(s^*).$$

We find by numerical simulation that eight iterative examples are presented here to show the influence of increasing the parameter k on the dynamical behaviour. In all examples, parameters values in eqn. (2.2) are as follows [2]:

$$(s(0), x(0), y(0)) = (0.1, 0.7, 0.8), m_1 = 4.0, m_2 = 5.0, a_1 = 0.6, a_2 = 0.5, \gamma = 0.2$$

And we deduce that when $k \in [0, 0.4]$ the solution appears to approach a periodic solution. So, E_0 , E_1 and E_2 lose their stability (Figures 1-3). Those oscillatory solutions appear to be the results of

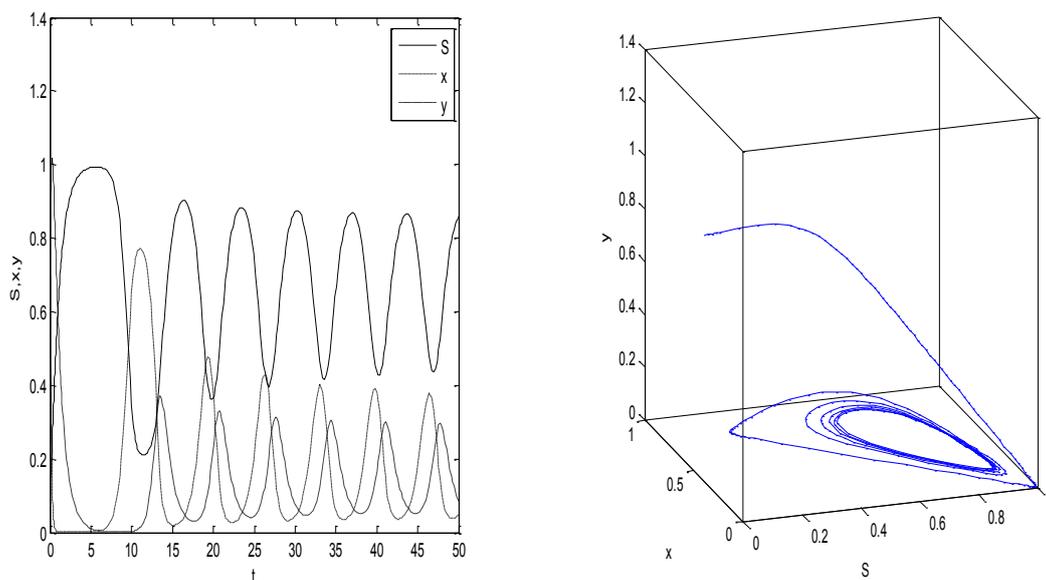


Figure 1: The results of Hopf bifurcations and oscillatory solutions are $k=0.1$.

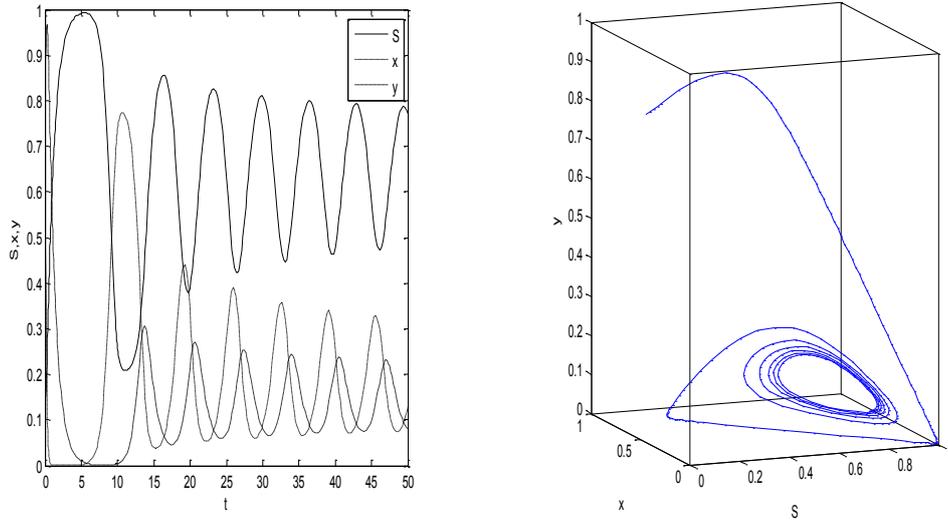


Figure 2: The results of Hopf bifurcations and oscillatory solutions are $k=0.2$

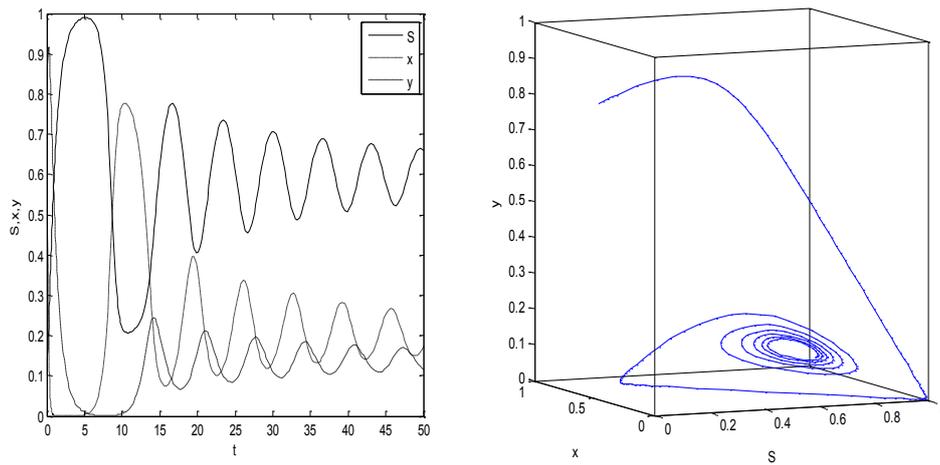


Figure 3: The results of Hopf bifurcations and oscillatory solutions oscillatory solutions are $k=0.3$.

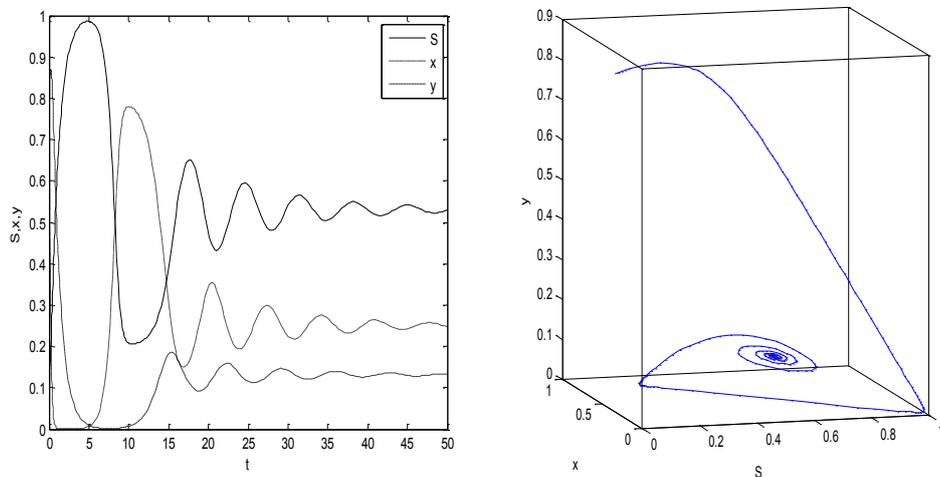


Figure 4: The solution approaches positive steady, unstable, stable states and oscillatory solutions are $k=0.4$.

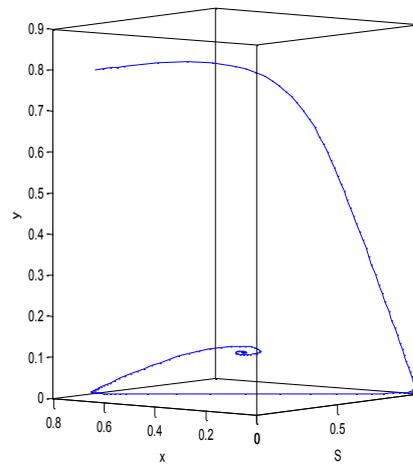
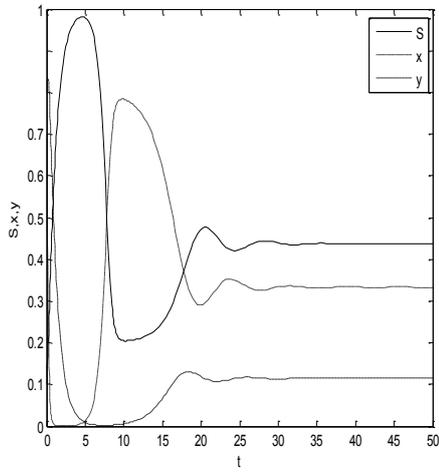


Figure 5: The solution approaches positive steady, unstable, stable states and oscillatory solutions are $k=0.5$.

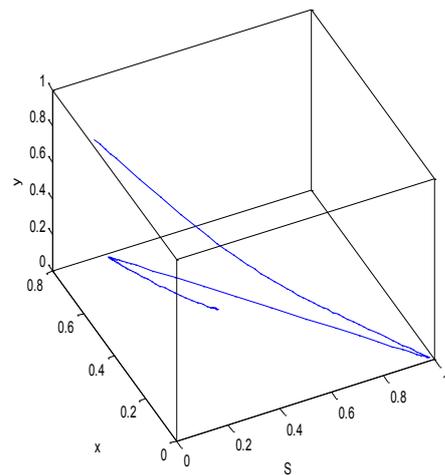
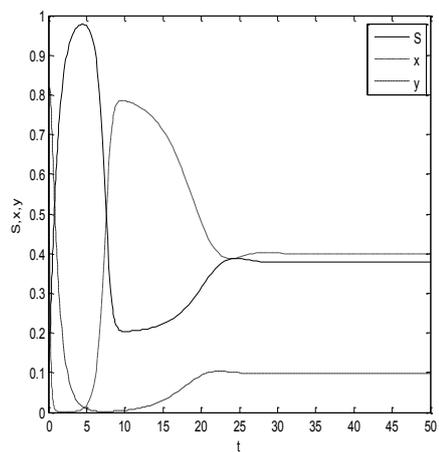


Figure 6: The solution approaches positive steady, unstable, stable states and oscillatory solutions are $k=0.6$

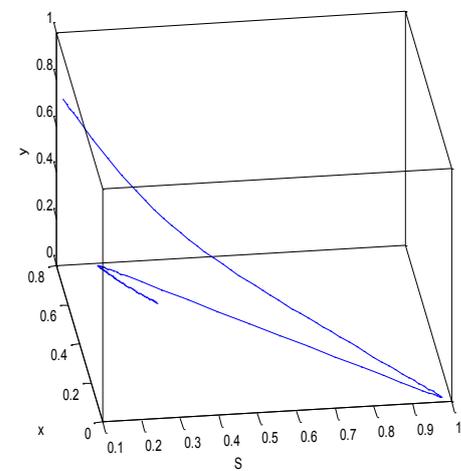
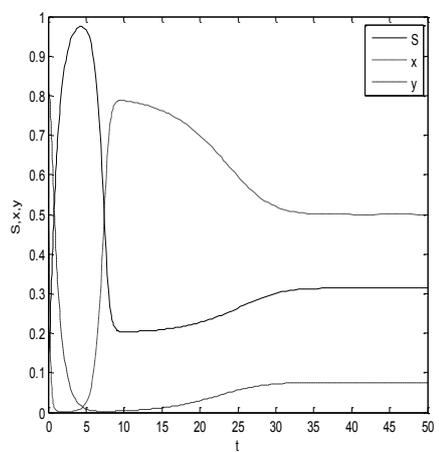


Figure 7: The solution approaches positive steady, unstable, stable states and oscillatory solutions are $k=0.8$

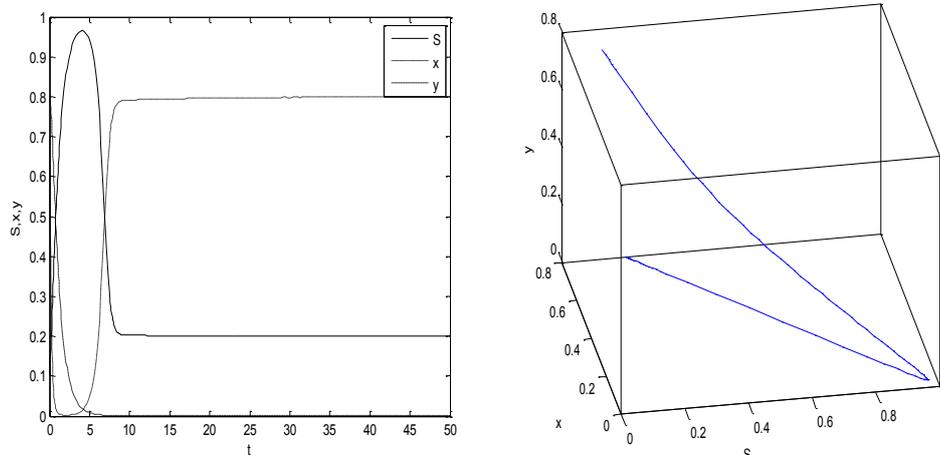


Figure 8: The solution approaches the predator-free steady, unstable, stable states and oscillatory solutions $k=0.7$

Hopf bifurcations. The numerical simulation shows that the system in eqn. (2.2) has an attracting limit cycle.

Also, at $k \in [0.4, 6.5]$ the solution approaches a positive steady state. Both E_0 and E_1 are unstable and E_2 is globally asymptotically stable (Figures 4-7).

For $k \in [6.5, 1]$ the solution approaches the predator-free steady state. E_0 is unstable and E_1 is globally asymptotically stable (Figure 8). All left figures plot in time courses and all right figures plot the trajectory in (s, x, y) space. We also, deduce that no difference between this paper and Moniem [2] as numerical simulation, even γ changes its value on interval $[0, 1]$ for each value of k .

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