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Simple Food Chain in Chemostat When the Predator Produces Unaffected Toxin

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In this paper, Simple food chain in chemostat when the predator produces unaffected toxin is considered. This inhibitor is not lethal to neither prey nor nutrient and 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 considered. Local and global stability of other steady states, persistence analysis, as well as numerical simulations are also presented.

Key wards: food chain - toxin – chemostat – prey – predator – Lyapunov function.

1- Introduction

The chemostat is a laboratory apparatus used for the continuous culture of microorganisms. It can be used to study competition between different populations of microorganism or between preys and predators, and has the advantage that the parameters are readily measurable. The monograph of Smith and Waltman (8) has various mathematical methods for analyzing chemostat models. Recently, the inhibitor has been introduced in the models for two competitors in a chemostat, and many authors have studied those models (see (1, 2, 3, 4, 5, 6 and 7)).

In this paper, we consider a model of simple food chain in chemostat when the predator produces unaffected inhibitor. This inhibitor is not lethal to neither prey nor nutrient and results in the 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. 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.

2- The model

The interest equations are

$$\begin{aligned} s'(t) &= (\, s^0 - s(t)\,)\, D - \frac{1}{\gamma_1}\, f_1(s(t))\, x(t), \\ x'(t) &= x(t)\, (\, f_1(s(t)) - D\,) - \frac{1}{\gamma_2}\, f_2(x(t))\, y(t), \qquad (2.1) \\ y'(t) &= y(t)\, (\, (1-k)\, f_2(x(t)) - D\,), \\ p'(t) &= k\, y(t)\, f_2(x(t)) - D\, p, \end{aligned}$$

$$0 < s(0), \qquad 0 < x(o), \qquad 0 < y(0), \qquad 0 < p(0).$$

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. $f_1(s(t)) = \dfrac{m_1\, s(t)}{a_1 + s(t)}$ and $f_2(x(t)) = \dfrac{m_2\, x(t)}{a_2 + x(t)}$ where m_i, $i = 1, 2$, the maximal growth rates, a_i, $i = 1, 2$, the Michaelis- Menten constants and γ_i, $i = 1, 2$, the Yield constants. The constant fraction $k \in (0, 1)$ is the potential growth due to inhibitor growth (see (3) for description the physical meaning of k).

For scaling, let

$$\bar{s} = \frac{s}{s^0}, \qquad \bar{x} = \frac{x}{\gamma_1\, s^0}, \qquad \bar{y} = \frac{y}{\gamma_1\, \gamma_2\, s^0}, \qquad \bar{t} = D\, t,$$

$$\bar{p} = \frac{p}{\gamma_1\, \gamma_2\, s^0}, \qquad \bar{m}_i = \frac{m_i}{D}, \; i = 1, 2, \qquad \bar{a}_1 = \frac{a_1}{s^0}, \; \bar{a}_2 = \frac{a_2}{\gamma_1 s^0}.$$

Substitute into (2.1) and then drop the bars, the model becomes

$$\begin{aligned} s' &= 1 - s - f_1(s)\, x, \\ x' &= x\,(\, f_1(s) - 1\,) - f_2(x)\, y, \qquad (2.2) \\ y' &= y\,(\,(1-k)\; f_2(x) - 1\,), \\ p' &= k\; y\; f_2(x) - p. \end{aligned}$$

3- Existence and local stability

Let $T = s + x + y + p$, then $T' = 1 - T$, or $\limsup_{t\to\infty} T(t) = 1$.

Since each component is non-negative, the system (2.2) is dissipative and thus, has a compact, global attractor. To simplify (2.2), let $z = p - \dfrac{k\, y}{1-k}$, we find that the system (2.2) is taken the form,

$$\begin{aligned} s' &= 1 - s - f_1(s)\, x, \\ x' &= x\,(\, f_1(s) - 1\,) - f_2(x)\, y, \qquad (3.1) \\ y' &= y\,(\,(1-k)\; f_2(x) - 1\,), \\ z' &= -\, z. \end{aligned}$$

Clearly $z(t) \to 0$ as $t \to \infty$, so the system (3.1) may be viewed as an asymptotically autonomous system with limiting system

$$\begin{aligned} s' &= 1 - s - f_1(s)\, x, \\ x' &= x\,(\, f_1(s) - 1\,) - f_2(x)\, y, \qquad (3.2) \\ y' &= y\,(\,(1-k)\; f_2(x) - 1\,). \end{aligned}$$

It is easy to show that (3.2) in positive cone. As a consequence, the global attractor of (3.1) lies in the set $z = 0$, where (3.2) is satisfied. When the analysis of (3.2) is completed, the work of Thieme (10), relates the corresponding dynamics of (3.1) and (3.2), and hence of (2.2). We will show that all solutions of (3.2) tend to rest points and hence, using Thieme (9), so do those of (2.2).

The equilibrium point $E_0 = (1,0,0)$, always exists. If $1 < f_1(1)$, then there is an equilibrium of (3.2) 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

$E_2 = (s^*, \lambda_x, \lambda_x(1-k)(f_1(s^*)-1))$, where s^*, is the unique value of s, such that $1 - s - \lambda_x\ f_1(s) = 0$, and λ_x, is the unique solution of $(1-k)\ f_2(x) - 1 = 0$.

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 be investigated the local stability of these steady state by finding the eigenvalues of the associated Jacobian matrices.

Theorem 3.1

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, and E_0, E_1, are unstable. E_2, is locally asymptotically stable if $0 < a_1$ and $a_3 < a_1\ a_2$ (a_i, $i = 1, 2, 3$ will be defined in proof)

Proof

The variation matrix of (3.2) is taken the form

$$\begin{bmatrix} -1 - x\ f_1'(s) & -\ f_1(s) & 0 \\ x\ f_1'(s) & f_1(s) - 1 - y\ f_2'(x) & -\ f_2(x) \\ 0 & (1-k)\ y\ f_2'(x) & (1-k)\ f_2(x) - 1 \end{bmatrix}.$$

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

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

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

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

The determinant of the upper left- hand 2×2 matrix is positive and its trace is negative, so its eigevalues have negative real parts. The third eigenvalue is $(1-k)\, f_2(1-\lambda_s)-1.$ Therefore the predator – free steady state is asymptotically stable if and only if $(1-k)\, f_2(1-\lambda_s)-1<0$, or $1<\lambda_s+\lambda_x$.
The variation matrix at E_2, takes the form

$$\begin{bmatrix} -1-\lambda_x\, f_1'(s^*) & -f_1(s^*) & 0 \\ \lambda_x\, f_1'(s^*) & (f_1(s^*)-1)(1-\lambda_x\,(1-k) f_2'(\lambda_x)) & -\dfrac{1}{1-k} \\ 0 & \lambda_x\,(1-k)\,(f_1(s^*)-1)\, f_2'(\lambda_x) & 0 \end{bmatrix}.$$

The eigenvalues of E_2, satisfy $\alpha^3+a_1\,\alpha^2+a_2\,\alpha+a_3=0$, where

$$\begin{aligned} a_1 &= 1+\lambda_x\, f_1'(s^*)+((1-k)\,\lambda_x\, f_2'(\lambda_x)-1)\,(f_1(s^*)-1), \\ a_2 &= \lambda_x\, f_1(s^*)\, f_1'(s^*)+(1-k)\,\lambda_x\, f_2'(\lambda_x)\,(f_1(s^*)-1) \\ &\quad +(1+\lambda_x\, f_1'(s^*))\,((1-k)\,\lambda_x\, f_2'(\lambda_x)-1)\,(f_1(s^*)-1), \\ a_3 &= (1-k)\,\lambda_x\, f_2'(\lambda_x)\,(1+\lambda_x\, f_1'(s^*))\,(f_1(s^*)-1). \end{aligned}$$

Clearly $0<a_3$, so from the Routh-Hurwitz criterion, E_2 is locally asymptotically stable if and only if $0<a_1$ and $a_3<a_1\,a_2$.

4- Global analysis

Theorem 4.1

For $1<\lambda_s$ and for large t, all solutions of (3.2) 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 of (3.2) gives $x(t)<e^{-(1-f_1(1))\,t}$, which imply to $\lim_{t\to\infty} x(t)=0$. The third equation of

(3.2) becomes $y = e^{-t}$, which leads to $\lim_{t\to\infty} y(t) = 0$. The first equation of (3.2) has a solution $s = 1 + (constant)\, e^{-t} \to 1$ as $t \to \infty$.

Theorem 4.2

If $\lambda_s < 1$, $1 < \lambda_s + \lambda_x$ and for large t, then all solutions of (3.2) tend to E_1.

Proof

Let

$$\eta = 1 + \frac{(1 - \lambda_s - x)\ f_2(x)}{(1 - (1-k)\ f_2(x))\ x}, \qquad for \quad 0 < x \le 1 - \lambda_s, \qquad (4.1)$$

and

$$\beta = \frac{\eta}{f_2(x)}\left((1-k)\, f_2(x) - 1\right) \qquad for \quad \lambda_x \le x. \qquad (4.2)$$

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

$$C'(u) = \begin{cases} 0 & if \quad u \le 1 - \lambda_s, \\ \beta \dfrac{(u + \lambda_s - 1)}{(\lambda_s + \lambda_x - 1)} & if \quad 1 - \lambda_s < u < \lambda_x, \\ \beta & if \quad \lambda_x \le u. \end{cases} \qquad (4.3)$$

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

$$V(s,x,y) = \int_{\lambda_s}^{s} \frac{(1-\lambda_s)\,(f_1(\xi)-1)}{(1-\xi)}\, d\xi + x - \overset{*}{x} \ln(x) + \eta\, y + C(x). \qquad (4.4)$$

on the set $\Psi = \{(s,x,y): 0 < s + x + y < 1\}$, where $\overset{*}{x} = 1 - \lambda_s$.
Differentiate (4.4) with respect to time t, we obtain

$$\dot{V} = x\,(f_1(s)-1)\,[1 + C'(x) - \frac{(1-\lambda_s)\ f_1(s)}{(1-s)}]$$
$$+\ y\,[\frac{f_2(x)}{x}(1 - \lambda_s - x) + \eta\,[(1-k)\ f_2(x) - 1] - f_2(x)\, C'(x)]. \qquad (4.5)$$

First the term $x\,(f_1(s)-1)\,[1 - \frac{(1-\lambda_s)\ f_1(s)}{(1-s)}]$ is nonpositive 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 $\lambda_s \le s$ and $C'(u) \ge 0$ for $u \ge 0$, then the term $x\,(f_1(s)-1)\, C'(x)$ is nonpositive for $s \in [0,1)$.

Define

$$h(s,x,y) = [\frac{f_2(x)}{x}(1-\lambda_s - x) + \eta\,[(1-k)\; f_2(x) - 1] - f_2(x)\, C'(x)]. \qquad (4.6)$$

If $0 < x \le 1-\lambda_s$,
Then

$$[(1-k)\; f_2(x) - 1] \le 0, \quad 0 \le [\frac{f_2(x)}{x}(1-\lambda_s - x)$$

And

$$0 \le f_2(x)\, C'(x).$$

Use the definition of η, we find that $h(s,x,y) \le 0$.
If $1-\lambda_s < x < \lambda_x$, then all terms of $h(s,x,y)$ are nonpositive.
If $\lambda_x \le x$, then $C'(x) = \beta$ and use definition of β and η, we find that $h(s,x,y)$ will be nonpositive and the second term of $\dot{V}$ equal zero at $y = 0$. therefore $\dot{V}$ is nonpositive on Ψ.

A largest invariant subset M of $\phi = \{(s,x,y) \in \Psi : \dot{V} = 0\}$ such that $\dot{V} = 0$ at $s = \lambda_s$ *or* $x = 0$ and $y = 0$. More further, V is bounded above, any point of the form $(s,0,0)$ can not be in the $\omega -$ limit set Ω 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 of (3.2), we get $x = 1-\lambda_s$. Therefore $M = \{E_1\}$. This complete the proof.

Theorem 4.3

If $\lambda_s < 1$ and $\lambda_s + \lambda_x < 1$, then the system (3.2) is uniformly persistence.

Proof

Let $Y_1 = \{(s,x,y) : s \in [0,1],\;\; x, y \in (0,1]\}$,
Y_2 represents $sx-plane$: $0 \le s, x \le 1$,
Y_3 represents $sy-plane$: $0 \le s, y \le 1$,
and $Y = Y_2 \cup Y_3$.

We want to show that Y is a uniformly strong repeller for Y_1. Since E_0 and E_1 are the only steady states in Y. E_0 is saddle in R^3 and its stable manifold is $\{(s,0,y) : 0 \le y\}$. Also, E_1 is saddle in R^3 and its stable manifold is $\{(s,x,0) : 0 < x\}$. Then, they are weak reppelers for Y_1. The stable manifold structures of E_0 and E_1 imply that they are not cyclically chained to each other on the boundary Y. Therefore Y is a uniform strong repeller for Y_1 (see proposition (1.2) of Thieme (10)).
So, there are $\varepsilon_1 > 0$ and $\varepsilon_2 > 0$ such that $\liminf_{t\to\infty} x(t) > \varepsilon_1$ and $\liminf_{t\to\infty} y(t) > \varepsilon_2$ with ε_1 and ε_2 are not depending on the initial values in Y_1. By proposition (2.2) of Thieme (10) to the first equation of (3.2) yields that there is $\varepsilon_3 > 0$: $\liminf_{t\to\infty} s(t) > \varepsilon_3$ with ε_3 is not depending on the initial values in Y_1. Proof is completed.

Conclusion and numerical simulation

In this work, we consider a food chain with one prey and one predator in the chemostat, when the predator produces unaffected toxin. This inhibitor is not lethal to neither prey nor nutrient and 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 is locally asymptotically stable if and only if $0 < a_1$ and $a_3 < a_1\, a_2$. E_2 exists in the sense that the system is uniformly persistent.

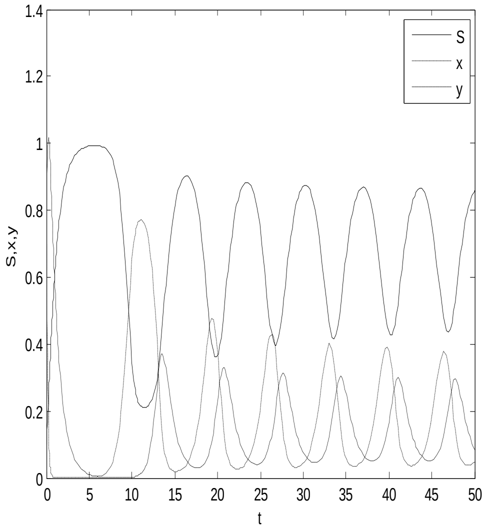
We find by numerical simulation that its dynamical behavior is complex. Eight iterative examples are presented here to show the influence of increasing the parameter k on the dynamical behavior. In all examples, parameters values of (3.2) are as follows:

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

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 (see figs. 1a, 1b, 2a, 2b, 3a and 3b). These oscillatory solutions appear to be the results of Hopf bifurcations. The numerical simulation shows that the system (3.2) has an attracting limit cycle.

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 (see figs. 4a, 4b, 5a, 5b, 6a, 6b, 7a and 7b).

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 (see figs. 8a and 8b). All left figures plot in time courses and all right figurers plot the trajectory in (s, x, y) space.



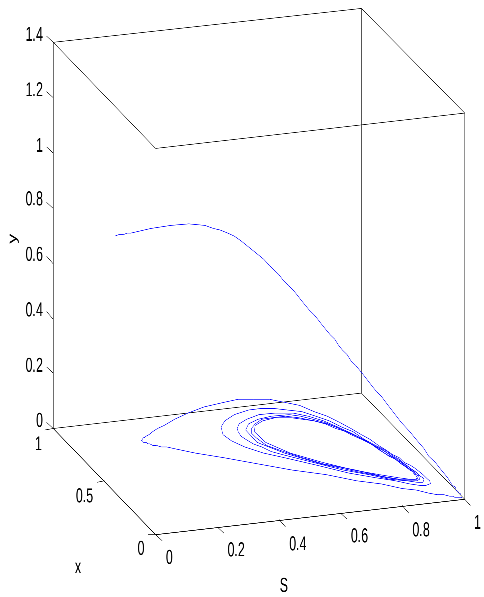
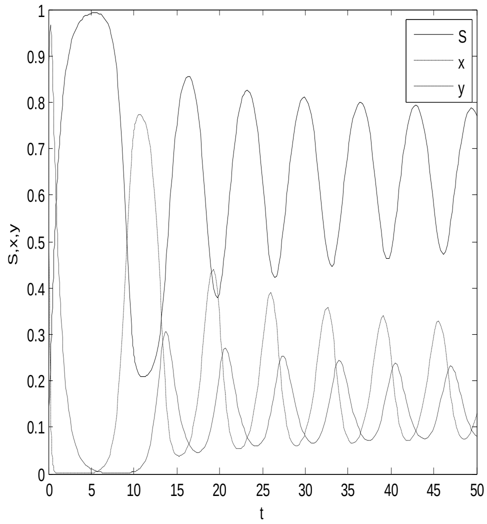


Fig.(1a). k = 0.1 Fig.(1b). k = 0.1



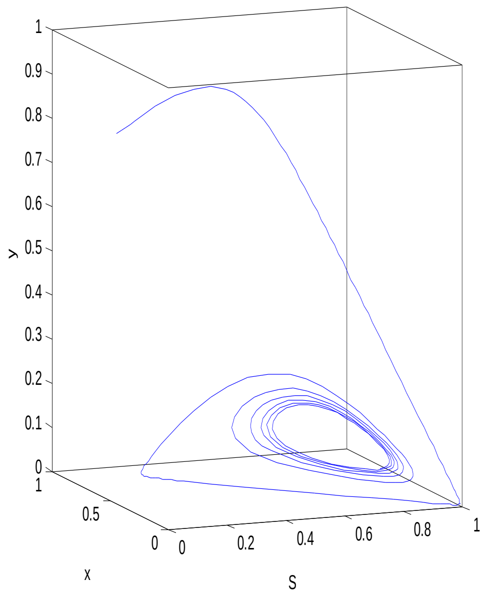
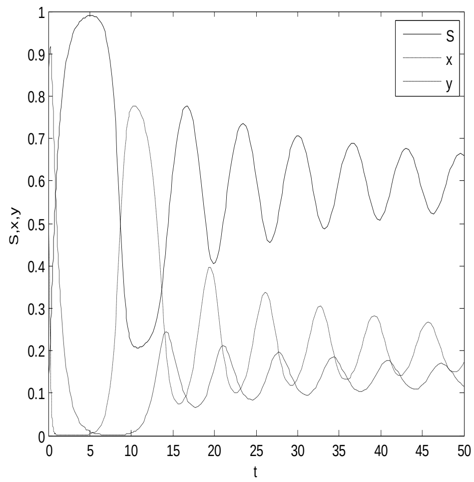


Fig.(2a). k = 0.2 Fig.(2b). k = 0.2



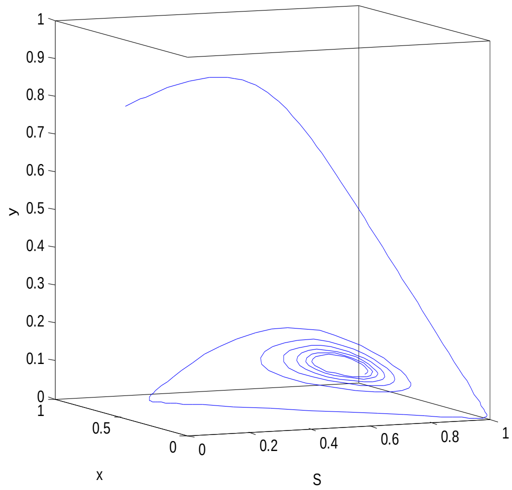


Fig.(3a). k = 0.3 Fig.(3b). k = 0.3

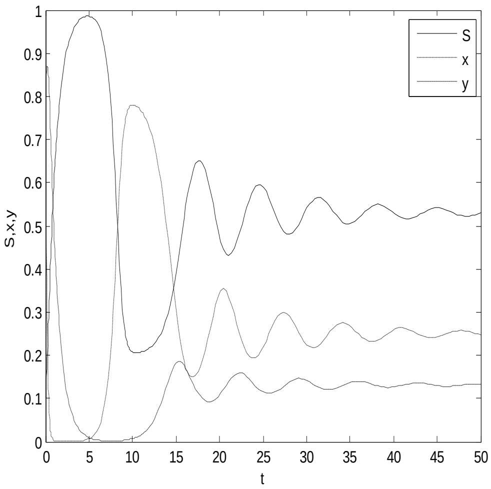


Fig.(4a). k = 0.4

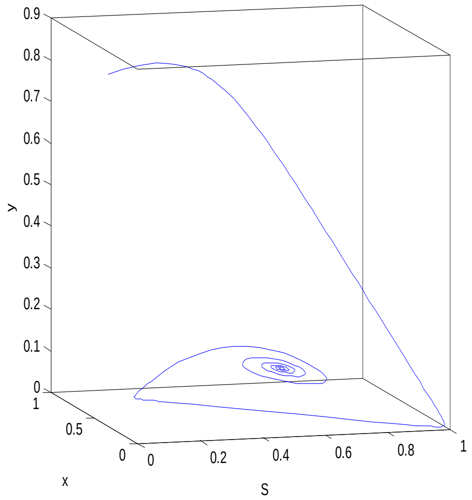


Fig.(4b). k = 0.4

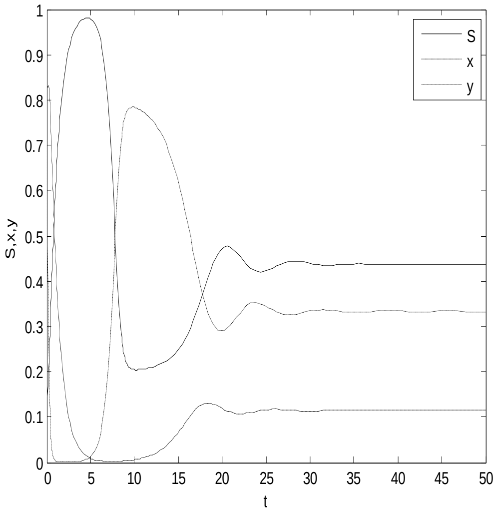


Fig.(5a). k = 0.5

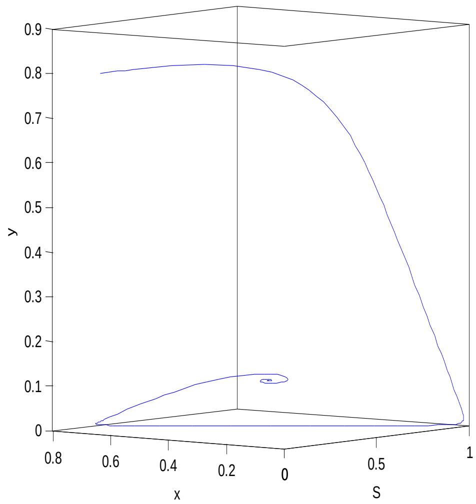


Fig.(5b). k = 0.5

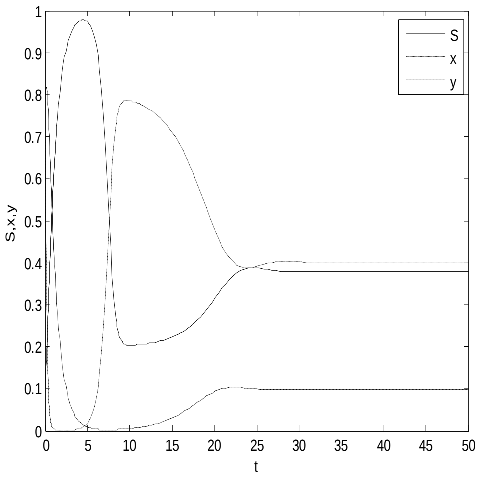


Fig.(6a). k = 0.55

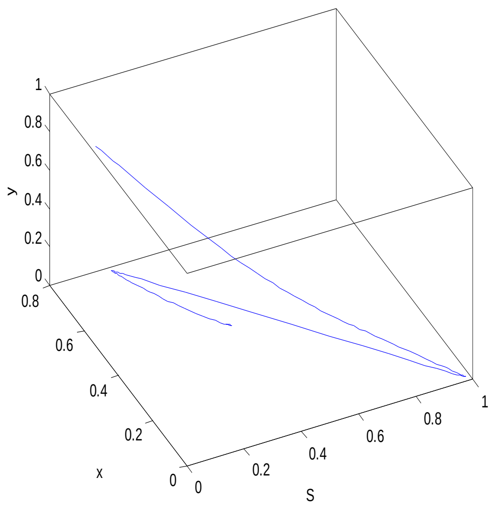


Fig.(6b). k = 0.55

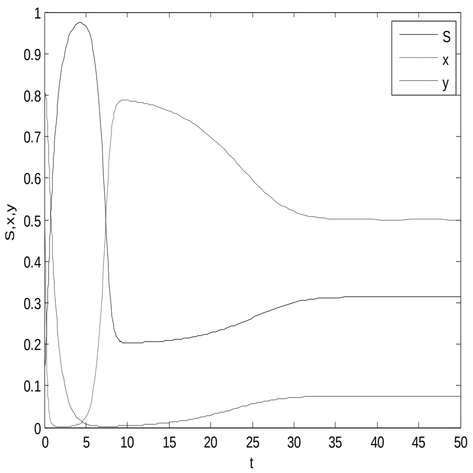


Fig.(7a). k = 0.6

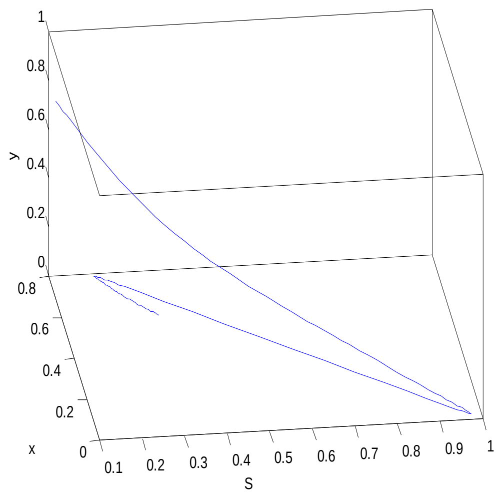


Fig.(7b). k = 0.6

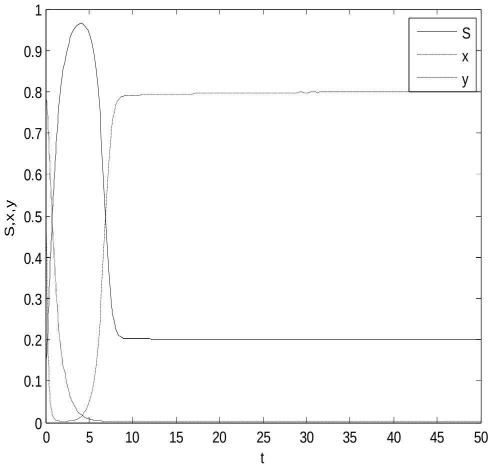


Fig.(8a). k = 0.7

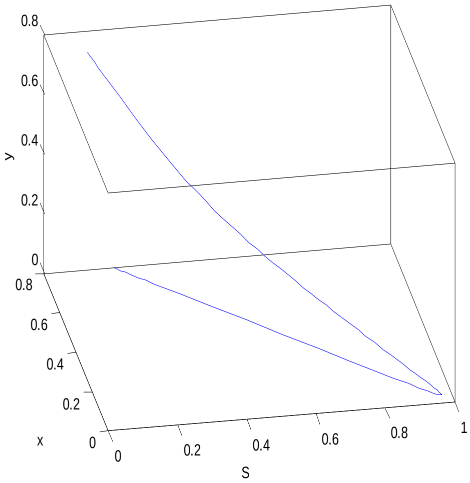


Fig.(8b). k = 0.7

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