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Prey - Predator in Chemostat When the Prey Produces Unaffected Inhibitor

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Prey - predator in chemostat when the prey produces unaffected inhibitor is considered. This inhibitor is not lethal to neither predator nor nutrient and results in decrease of growth rate of the prey 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.

1- Introduction

The chemostat is a model of a simple lake but in chemical engineering it also serves as a laboratory model of a bio-reactor used to manufacture products with genetically altered organisms. 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 (9) 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 (2, 3, 4, 5, 6, 7, and 8)). Simple food chain in chemostat when predator produces unaffected toxin is studied by Ashraf (1).

In this work, we consider a model of prey - predator in chemostat when the prey produces unaffected inhibitor. This inhibitor is not lethal to neither predator nor nutrient and results in the decrease of growth rate of the prey at some cost to its reproductive abilities.

The organization of this paper is 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. In final section, discussion, comments and numerical simulation are found.

2- The model

The interest equations are

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

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

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 (4)).

For scaling, let

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

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

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

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 $z = p - \dfrac{k}{1-k}(x + y)$, we find that the system (2.2) is taken the form,

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

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

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

Since the limit plane (3.2) is $\sum: s + x + y = 1$. By dropping the s equation, then the limit system of (3.2) is taken the form

$$x' = x\,((1-k)\,f_1(1-x-y) - 1) - f_2(x)\,y, \qquad (3.3)$$
$$y' = y\,(f_2(x) - 1),$$
$$x(0) > 0, \qquad y(0) > 0.$$

It is easy to show that (3.3) in positive plane. As a consequence, the global attractor of (3.1) lies in the set $z = 0$ and $\sum$ plane where (3.3) is satisfied. When the analysis of (3.3) is completed, the work of Thieme (11), relates the corresponding dynamics of (3.1) and (3.3), and hence of (2.2). We will show that all solutions of (3.3) tend to rest points and hence, using Thieme (10), so do those of (2.2).

The equilibrium point $E_0 = (1,0,0)$, always exists. If $\frac{1}{(1-k)} < f_1(1)$, then there is an equilibrium of (3.3) of the form $E_1 = (\lambda_s, (1-\lambda_s)(1-k), 0)$, where λ_s, is the unique solution of $(1-k)\,f_1(\lambda_s) - 1 = 0$. Similarly, if $1 < f_2((1-\lambda_s)(1-k))$, 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 sol0ution of $f_2(x) - 1 = 0$.

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 $(1-\lambda_s)(1-k) > \lambda_x$. 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 $H(\lambda_s) = 1 - \lambda_s - \frac{1}{(1-k)}\lambda_x$. So $\lambda_s < s^*$, if and only if $(1-\lambda_s)(1-k) > \lambda_x$.

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 $(1-\lambda_s)(1-k) < \lambda_x$ then only E_0 and E_1 exist, E_0 is unstable, and E_1 is locally asymptotically stable. If $\lambda_s < 1$ and $(1-\lambda_s)(1-k) > \lambda_x$ then E_0, E_1, E_2 exist, E_0, E_1, are unstable and E_2, is locally asymptotically stable if

$$\lambda_x\,(1-k)\,f_1'(s^*) + (\lambda_x\,f_2'(\lambda_x) - 1)[(1-k)\,f_1(s^*) - 1] > 0,$$

and there is a periodic solution in $\sum$ (by an application of the Poincare`-Bendixson theorem).

Proof

The Jacobian matrix of (3.3) is taken the form

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

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

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

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

$$\begin{bmatrix} -(1-\lambda_s)(1-k)^2\, f_1'(\lambda_s) & -(1-\lambda_s)(1-k)^2\, f_1'(\lambda_s) - f_2((1-\lambda_s)(1-k)) \\ 0 & f_2((1-\lambda_s)(1-k)) - 1 \end{bmatrix}.$$

The two eigenvalues are $-(1-\lambda_s)(1-k)^2\, f_1'(\lambda_s)$ and $f_2((1-k)(1-\lambda_s)) - 1$. Therefore the predator – free steady state is asymptotically stable if and only if $f_2((1-k)(1-\lambda_s)) - 1 < 0$ or $(1-k)(1-\lambda_s) < \lambda_x$.
The Jacobian matrix at E_2, takes the form

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

If the determinant of this matrix is positive and its trace is negative, then E_2 is locally asymptotically stable, it means that $\lambda_x\, (1-k)\, f_1'(s^*) + (\lambda_x\, f_2'(\lambda_x) - 1)[(1-k)\, f_1(s^*) - 1] > 0.$

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 $x(t) < e^{-(1-(1-k)\, f_1(1))\, t}$, 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

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

and

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

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:

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

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

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

First the term $x\,[(1-k) f_1(s) - 1]\,[1 - \dfrac{(1-\lambda_s)(1-k)\ f_1(s)}{(1-s)}]$ 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 $x\,[(1-k) f_1(s) - 1]\ C'(x)$ is nonpositive for $s \in [0,1)$.
Define

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

If $0 < x \le (1-\lambda_s)(1-k)$, then

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

and

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

Use the definition of η, we find that $h(s,x,y) \le 0$.

If $(1-\lambda_s)(1-k) < x < \lambda_x$, 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 $x = (1-\lambda_s)(1-k)$. 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 $X_1 = \{(s,x,y) : s \in [0,1],\ \ x,y \in (0,1]\}$,

X_2 represents $sx-plane$: $0 \le s, x \le 1$,

X_3 represents $sy-plane$: $0 \le s, y \le 1$,

and $X = X_2 \cup X_3$.

We want to show that X is a uniformly strong repeller for X_1. Since E_0 and E_1 are the only steady states in X. 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 X_1. The stable manifold structures of E_0 and E_1 imply that they are not cyclically chained to each other on the boundary X. Therefore X is a uniform strong repeller for X_1 (see proposition (1.2) of Thieme (11)).

So, there are $\delta_1 > 0$ and $\delta_2 > 0$ such that $\liminf_{t\to\infty} x(t) > \delta_1$ and $\liminf_{t\to\infty} y(t) > \delta_2$ with δ_1 and δ_2 are not depending on the initial values in X_1. By proposition (2.2) of Thieme (11) to the first equation of (3.2) yields that there is $\delta_3 > 0$: $\liminf_{t\to\infty} s(t) > \delta_3$ with δ_3 is not depending on the initial values in X_1. Proof is completed.

Conclusion and Numerical Simulation

In this paper, we consider a food chain with one prey and one predator in the chemostat, when the prey produces unaffected toxin. This inhibitor is not lethal to neither predator nor nutrient and results in decrease of growth rate of the prey 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 $\lambda_s + \dfrac{\lambda_x}{(1-k)} > 1$. We also showed that E_2 is locally asymptotically if

$\lambda_x(1-k)\, f_1'(s^*) + (\lambda_x\, f_2'(\lambda_x) - 1)[(1-k)\, f_1(s^*) - 1] > 0,$ and exists in the sense that the system is uniformly persistent. A numerical simulation is described by eight iterative examples. They are presented here to show the influence of changing the parameter k on the dynamical behavior. In all examples, parameters values of (3.2) are as follows:

$$(s(0), x(0), y(0)) = (0.1, 0.7, 0.8),\ m_1 = 12.0,\ m_2 = 11.0,\ a_1 = 0.8,\ a_2 = 0.7.$$

At $k \in]0, 0.3]$, 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.

Also, at $k \in]0.3, 0.75]$, 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 and 6b).

For $k \in]0.75, 0.8[$, the solution approaches the predator-free steady state. E_0 is unstable and E_1 is globally asymptotically stable (see figs. 7a and 7b).

Finally, at $k \in]0.8, 1[$, the solution approaches the washout steady state E_0 and therefore it 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.

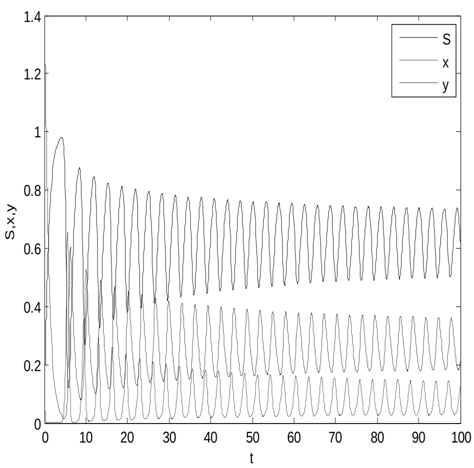

Fig.(1a). k = 0.1

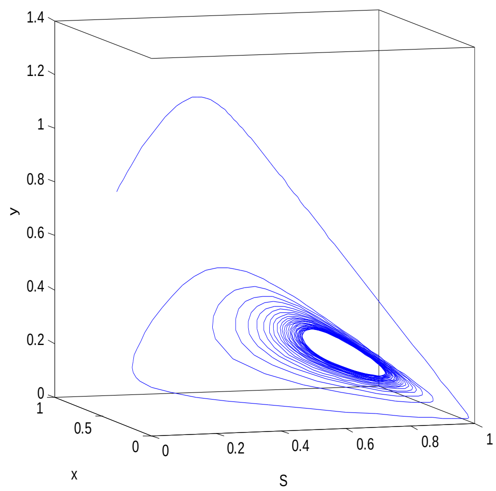

Fig.(1b). k = 0.1

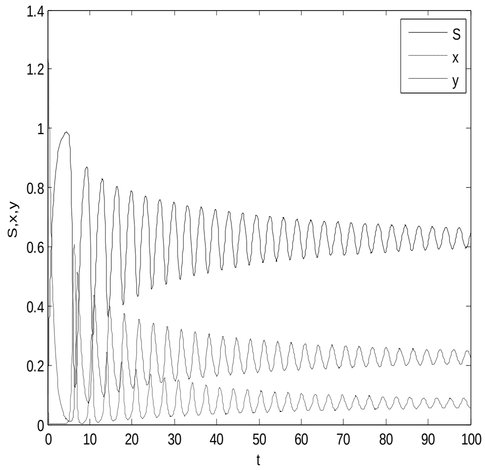

Fig.(2a). k = 0.2

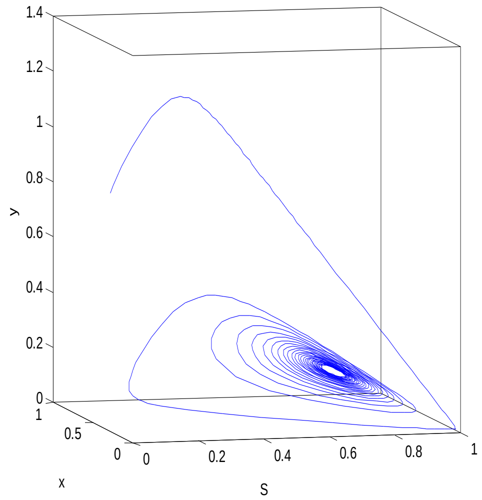

Fig.(2b). k = 0.2

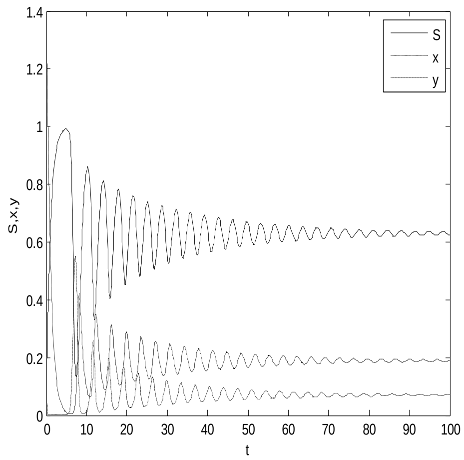

Fig.(3a). k = 0.3

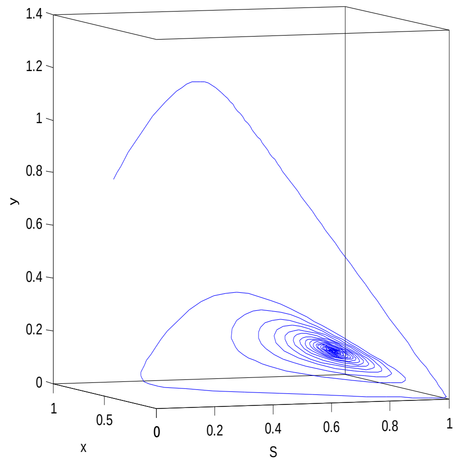

Fig.(3b). k = 0.3

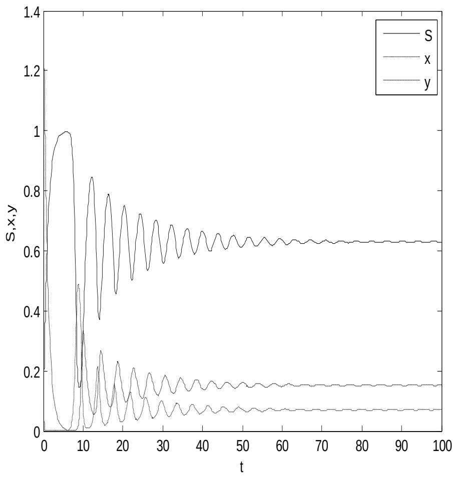

Fig.(4a). k = 0.4

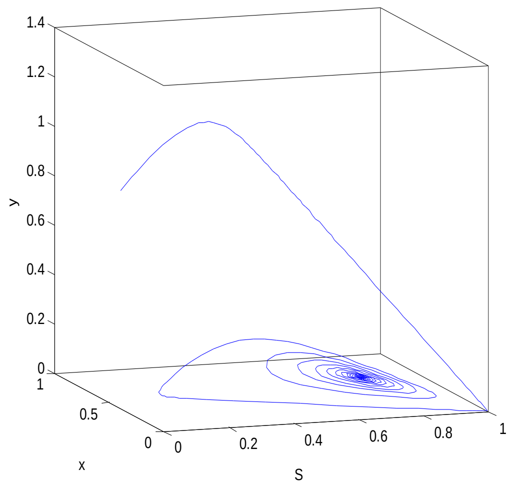

Fig.(4b). k = 0.4

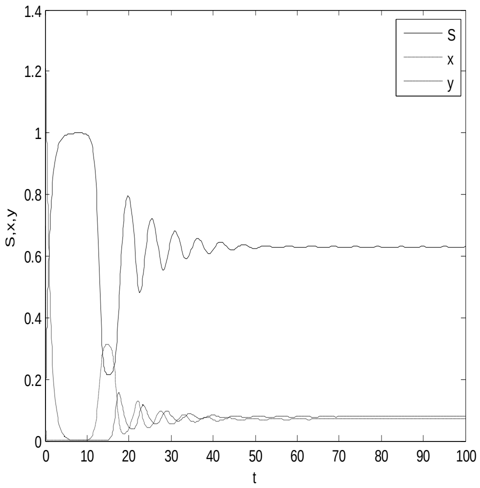

Fig.(5a). k = 0.6

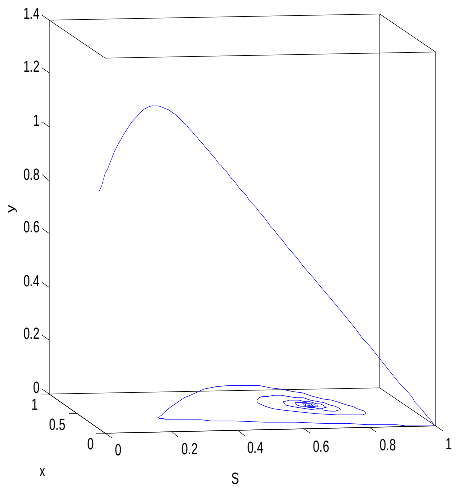

Fig.(5b). k = 0.6

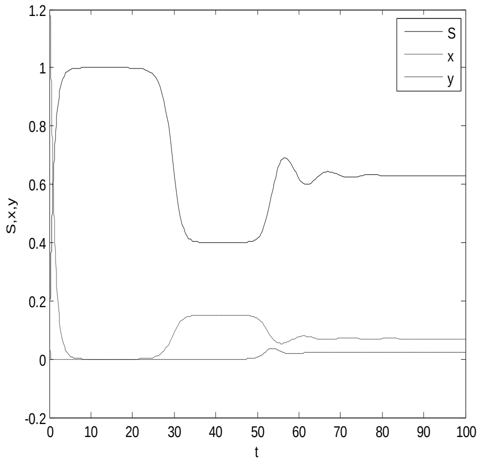

Fig.(6a). k = 0.75

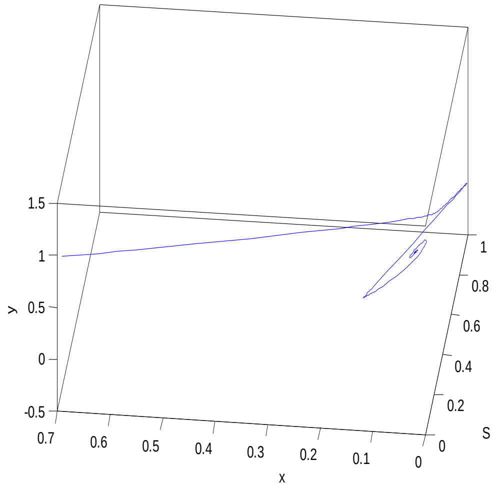

Fig.(6b). k = 0.75

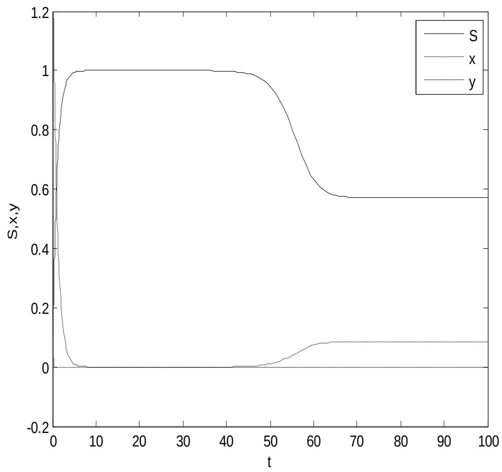

Fig.(7a). k = 0.8

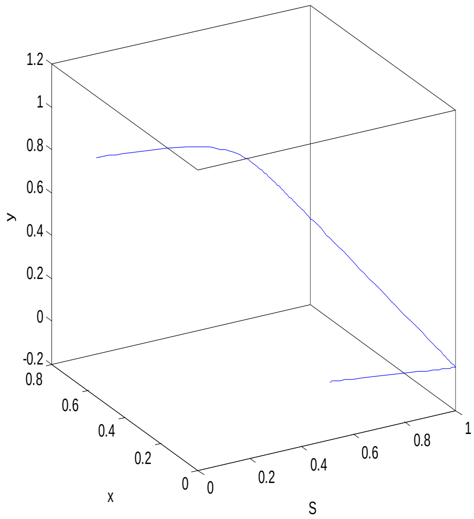

Fig.(7b). k = 0.8

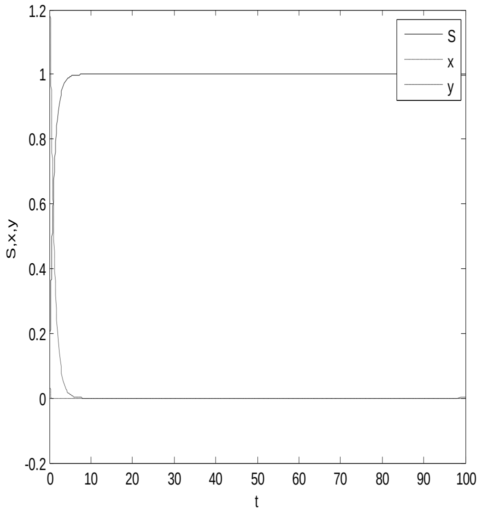

Fig.(8a). k = 0.83

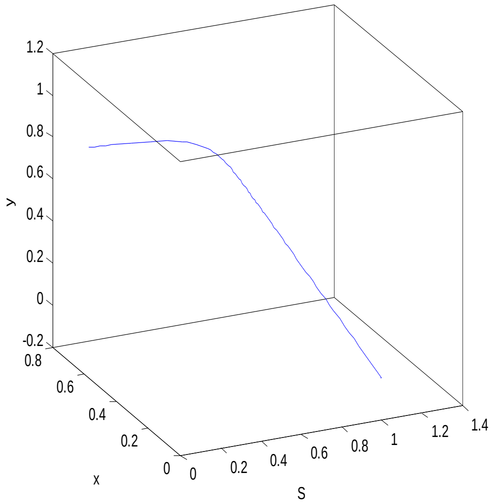

Fig.(8b). k = 0.83

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