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Bifurcation and Stability Analysis of a Food Web in a Chemostat

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Abstract: In this study, a classical model describing a food web in a chemostat involving three species competing for non-reproducing, growth rate-limiting nutrient in which one of the competitors predates on one of the other competitors is considered. Quantitative analyses of non-negativity and boundedness of solution trajectories, dissipativity, behavior around equilibria, global stability and persistence of the model equations are analyzed. We present the global stability of equilibria by constructing a Lyapunov function. Hopf bifurcation theory is applied.

Keywords: Chemostat, Food Web, Global Stability, Hopf Bifurcation, Dissipative

Introduction

In microbiology and population biology, the laboratory device chemostat extensively uses as research technique to culture microorganisms continuously under nutrient limitation in a controlled environment in order to study the general properties of its growth and interaction. Since one can measure the control parameter easily, the device has various applications in ecology and population biology. It can be viewed as a simple lake system in ecology while it serves as a laboratory bio-reactor in chemical engineering used for investigations in genetically altered cell. As for example, the prey (bacteria) consumes nutrient (waste) while the predator (ciliates) feeds on the prey in waste water treatment process. It is of mathematical interest to construct models with chemostat. The dynamics of chemostat model with nutrient uptake is of Monod kinetics play an important role in population ecology. After the first introduction of chemostat the researchers have paid their attention to develop mathematical theories of models in it. Qualitative analyses of predator-prey models in chemostat both from the experimental and the modeling aspect describe by set of differential equations were studied by many authors (Aris and Humphrey, 1977; Butler and Wolkowicz, 1985; Drake and Tsuchiya, 1976; Huang and Zhu, 2005; Hsu *et al.*, 1977; Jost *et al.*, 1973a; Li, 1999; Tsuchiya *et al.*, 1972; Wolkowicz and Lu, 1992; Waltman *et al.*, 1980). For detailed descriptions and the complete mathematical theories for understanding models in a chemostat, we refer Smith and Waltman (1995). Moreover, using chemostat the model describing predation-prey interaction like food chain and food web and their analyses are more interesting problems in the field of mathematical biology (Alhumazi and Ajbar, 2005; Butler and Wolkowicz, 1986; El-Owaidy and Moniem, 2003; Li and Kuang, 2000; Pavlou, 1985; Zhu *et al.*, 2002).

The interactions between species or organisms by using chemostat studied in ecology are predation and competition. In predation, one of the individuals serves as a prey for other individuals but in competition, the individuals compete for the same resources (food supply, water, etc). Competition can occur between individuals of different species or among individuals of the same species. The system comprise of the two interactions (predation and competition) is a food chain or food web. A chemostat type food chain model had been studied in (Tsuchiya *et al.*, 1972; Jost, *et al.*, 1973a; Drake and Tsuchiya, 1976; Butler *et al.*, 1983) and related experiments are described in (Jost *et al.*, 1973b; Drake and Tsuchiya, 1976). They used Michaelis-Menten type functional responses and discharge rates for the both population are equal to the washout rate of the chemostat. In the study (Butler *et al.*, 1983), the authors obtained a global result of their model that show all competing predators coexist which circumvented competitive exclusion principle. But the authors (Li and Kuang, 2000) relaxed the assumptions that the functional responses are general monotone functions and discharge rates for the both population are distinct. They studied a predator-prey food chain model in a chemostat, where

predator feeds on the prey and the prey consumes the nutrient. The authors (El-Owaidy and Moniem, 2003) also studied the same model with the extension that the predator feeds on the prey and the nutrient simultaneously. The paper (Alhumazi and Ajbar, 2005) examined a model describing the dynamic behavior of predator-prey interaction with general growth rates having no restriction on its forms. In general, it is difficult to analyze and study a complete dynamics for tri (or higher)-tropic level food chain models concern with its solutions. Consequently, the persistence or uniformly persistence analysis has been applied to describe the situation when all interacting individuals coexist in a given system. A tri-tropic level food-chain model is considered in (Chiu and Hsu, 1998). They restricted their attentions to study when the prey grows logistically in the absence of predator and the functional responses of predators are of Holling's type II and established the criterion where the top-predator goes extinct globally. The dynamics of a three-level food chain models that incorporate either Michaelis-Menten or general monotone response functions for all trophic levels had been examined by many researchers (Boer *et al.*, 1998; El-Sheikh and Mahrouf, 2005; Freedman and Ruan, 1992; Freedman and Waltman, 1977; Hastings and Powell, 1991; Klebanoff and Hastings, 1994; Ruan and Freedman, 1991; Al-Sheikh, 2008). Bifurcation techniques also used in several studies to explore whether it is possible the coexistence of all trophic levels (Boer *et al.*, 1998; El-Sheikh and Mahrouf, 2005; Freedman and Ruan, 1992; Al-Sheikh, 2008). Persistence analyses of models were carried out in (Butler *et al.*, 1986; Freedman and Waltman, 1984; Ruan and Freedman, 1991).

A food web model describing predator –prey interaction consist of one predator and two competitors with a growth rate- limiting nutrient in which the predator feeds on one of the preys only had been theoretically investigated by (Butler and Wolkowicz, 1986; Wolkowicz, 2006). In (Butler and Wolkowicz, 1986), they considered the general monotone response functions, but in (Wolkowicz, 2006), the response functions that satisfy the law of mass action were assumed. On the other hand, a food web in a chemostat that incorporates one predator and two preys in which the predator predates on both of the preys and the preys consume the nutrient had been studied theoretically by (Nasrin and Rana, 2011), experimentally in lab by (Jost *et al.*, 1973b) and numerically by (Vayenas and Pavlou, 1999). In all of their models, they employed either general monotone functions or Michaelis-Menten kinetics to describe uptake function of nutrient and growth of competitor (prey). In this study, we consider a model in a chemostat comprises of a predator individual and two competitors one of which serves as prey. We

restrict our attention to examine the dynamics of the model (so called food web) where the competitors consume the nutrient and the predator feeds on one of the competitors and nutrient in the chemostat that incorporates general response functions. Our system can be viewed as resulting from the food-chain system (El-Owaidy and Moniem, 2003) by adding another competitor or from the competition system (Li, 1999) by adding a competitor preying upon one of the competitors. In this study we confine our interest to explore the criterion for global stability and persistence of the model for which all the individuals coexists in a steady state for all future time. This model can be viewed as a system experimentally in lab by considering two bacteria as prey, a protozoan as predator and glucose as the limiting nutrient in the chemostat.

This paper is organized as follows. The food web model with general monotonic functional responses is described in section 2. In section 3, the basic properties (boundedness and dissipativity of the system and the existence and the local stability of equilibrium points) are given. Section 4 deals with the global stability of the system around the equilibria. In section 5, Hopf bifurcation theory applied to the system is presented. Finally in section 6, we carried out a short discussion.

Model Equations

Suppose that the concentration of nutrient and populations are all continuous functions of time. Let the concentration of nutrient, the competing populations and the predator population be denoted by $s(t)$, $x_1(t)$, $x_2(t)$ and $y(t)$ respectively at time t. The model equations take the following form (a system of differential equations):

$$s'(t) = \left(s^0 - s(t)\right)D - \sum_{i=1}^{2} \frac{x_i(t)p_i(s(t))}{\eta_i} - \frac{y(t)p_3(s(t))}{\eta_3}$$

$$x_1'(t) = x_1(t)\left(-D + p_1(s(t))\right) - \frac{1}{\gamma}y(t)q(x_1(t)) \qquad (1)$$

$$x_2'(t) = x_2(t)\left(-D + p_2(s(t))\right)$$

$$y'(t) = y(t)\left(-D + p_3(s(t)) + q(x_1(t))\right)$$

with $s(0) = s_0 \geq 0$, $x_i(0) = x_{i0} \geq 0, i = 1, 2$, $y(0) = y_0 \geq 0$ for $s^0 > 0$

In the system (1), s^0 denotes the input nutrient concentration, $p_i(s)$ represent the ith competitor's specific per capita growth rate, η_i are the yield constants and D is the washout rate of the chemostat. In the model equations (1), the population $x_1(t)$ can be treated as both a prey and a competitor. Here, $q(x_1)$ is the predator's growth rate on prey population and γ is the yield factor of predator feeding on prey.

The basic assumptions on the response functions p_i and q of the model (1) are:

$$p_i, q : \mathbb{R}_+ \to \mathbb{R}_+$$

where, p_i, q are continuously differentiable; $p_i{}'(s) \geq 0$ for all $s \in \mathbb{R}_+$; $q'(x_1) \geq 0$ for all $x_1 \in \mathbb{R}_+$; $p_i(0) = 0$ and $q(0) = 0$.

The model (1) describes four-level predator-prey food web in a chemostat with non-reproducing, growth rate-limiting nutrient, constant dilution rate and input nutrient concentration, negligible death rates and instantaneous growth rates adjustment due to changes in the nutrient concentration. Furthermore, we assume that the uptake rate of nutrient is proportional to conversion rate of prey and similarly uptake rate of prey is proportional to conversion rate of predator. In model (1), the two competitor populations compete exclusively for a single, growth rate-limiting nutrient and the predator population feeds exclusively on one of the competitor population as prey that would be the sole survivor in the absence of the predator population. When all population is present, the full system will be a classical food web. This model is similar to the model (Wolkowicz, 2006).

First we simplify the system (1) by choosing the dimensionless variables. Let:

$$\bar{s} = \frac{s}{s^0}, \bar{x}_i = \frac{x_i}{\eta_i s^0}, i = 1, 2, \bar{y} = \frac{y}{\eta_3 s^0}, \bar{t} = tD, \eta_3 = \gamma \eta_1$$

$$\bar{p}_i(\bar{s}) = \frac{p_i(s^0 \bar{s})}{D}, i = 1, 2, 3, \bar{q}(\bar{x}_1) = \frac{q(\bar{x}_1 \eta_1 s^0)}{D}$$

Then dropping the bars, the system (1) becomes:

$$s'(t) = 1 - s(t) - \sum_{i=1}^{2} x_i(t) p_i(s(t)) - y(t) p_3(s(t))$$
$$x_1'(t) = x_1(t)\big(-1 + p_1(s(t))\big) - y(t) q(x_1(t)) \qquad (2)$$
$$x_2'(t) = x_2(t)\big(-1 + p_2(s(t))\big)$$
$$y'(t) = y(t)\big(-1 + p_3(s(t)) + q(x_1(t))\big)$$

with $s_0 \geq 0$, $x_{i0} \geq 0$, $i = 1, 2$, $y_0 \geq 0$.

The aforesaid assumptions hold good for system (2) also. Therefore, without loss of generality, one can consider the system (2) instead of the system (1) and can always reinterpret their findings in terms of original variables.

Basic Properties

Boundedness and Dissipativity

In this section, we shall prove that the solution trajectories of model (1) initiated in $\mathbb{R}_+^4$ are bounded, positively invariant and dissipative for all future time.

Theorem 1

Let the region Γ be defined by:

$$\Gamma = \left\{ (s, x_1, x_2, y) \in \mathbb{R}_+^4 \;\middle|\; s + \sum_{i=1}^{2} x_i + y = 1 \right\} \qquad (3)$$

Then (i) Γ is positively invariant, (ii) The solution trajectories of the system (2) initiated in $\mathbb{R}_+^4$ are eventually bounded uniformly and enters into Γ and (iii) System (2) is dissipative.

Proof

Let $s_0 > 0$ and consider that $s' = 1 - s - \sum_{i=1}^{2} x_i p_i(s) - y p_3(s) < 1 - s$.

Then:

$$s(t) < 1 - (1 - s_0)e^{-t} \text{ for } s_0 > 0 \text{ and } \limsup_{t \to \infty} s(t) < 1$$

For:

$$x_1' = x_1(-1 + p_1(s)) - yq(x_1) < x_1(-1 + p_1(s)) < \delta_1 x_1$$

where:

$$\delta_1 = \left(-1 + \max_{s \in \Gamma} p_1(s) \right) < 0$$

Then:

$$x_1(t) < x_{10} e^{\delta_1 t}, \delta_1 < 0, \text{ thus } \limsup_{t \to \infty} x_1(t) < x_{10} \text{ for } x_{10} > 0$$

Similarly, we consider the equation:

$$x_2' = x_2(-1 + p_2(s)) < \delta_2 x_2$$

where:

$$\delta_2 = \left(-1 + \max_{s \in \Gamma} p_2(s) \right) < 0$$

Then:

$$x_2(t) < x_{20} e^{\delta_2 t}, \delta_2 < 0, \text{ hence } \limsup_{t \to \infty} x_2(t) < x_{20} \text{ for } x_{20} > 0$$

For the y equation:

$$y' = y(-1 + p_3(s) + q(x_1)) < \delta_3 y$$

where:

$$\delta_3 = \left(-1 + \max_{s \in \Gamma} p_3(s) + \max_{x_1 \in \Gamma} q(x_1) \right) < 0$$

Then:

$$y(t) < y_0 e^{\delta_3 t}, \delta_3 < 0, \text{ hence } \limsup_{t \to \infty} y(t) < y_0 \text{ for } y_0 > 0$$

Finally, we define the function $\Psi(t) = s(t) + x_1(t) + x_2(t) + y(t)$ and taking time derivative along the trajectories of system (2) yields $\Psi'(t) = 1-\Psi(t)$ with $\Psi(0) = s(0) + x_1(0) + x_2(0) + y(0) \geq 0$. Obviously $\Psi(t) = 1 + \Psi(0)e^{-t}$ for $t \geq 0$ and gives that $\lim_{t \to \infty} \Psi(t) = 1$.

Therefore, the trajectories of the system (2) are bounded uniformly and hence the system (2) is dissipative (El-Sheikh and Mahrouf, 2005). This completes the proof.

Equilibria: Existence and their Local Stability

The equilibrium points of the system (2) are the solutions of the following system of equations:

$$\begin{aligned}
1 - s - x_1 p_1(s) - x_2 p_2(s) - y p_3(s) &= 0, \\
x_1(-1 + p_1(s)) - y q(x_1) &= 0, \\
x_2(-1 + p_2(s)) &= 0, \\
y(-1 + p_3(s) + q(x_1)) &= 0,
\end{aligned} \tag{4}$$

with the assumed hypotheses of functions $p_i, q, i = 1,2,3$. The eight possible equilibria of the form $E(s, x_1, x_2, y)$ are given as follows:

- Extinction of all populations: $E_1(1,0,0,0)$
- Survival of population x_1 only: $E_2(\lambda_1, 1-\lambda_1, 0,0)$
- Survival of population x_2 only: $E_3(\lambda_2,0,1-\lambda_2,0)$ where $\lambda_i, i = 1,2$ are the unique solution of $p_i(s)-1 = 0$ (if exists)
- Survival of populations x_1 and x_2 only: $E_4(\bar{s}, \bar{x}_1, \bar{x}_2, 0)$, where $\bar{s}$ is defined by the equations, $p_1(s) = p_2(s) = 1$ with $\bar{s} \in (0,1)$ and $\bar{x}_1, \bar{x}_2$ are the solutions of $x_1 + x_2 = 1 - \bar{s}$
- Survival of population y only: $E_5(\lambda_3,0,0,1-\lambda_3)$, where λ_3 is defined as the unique solution of $p_3(s) -1 = 0$ (if exists)
- Survival of population x_1 and y only: $E_6(\tilde{s}, \tilde{x}_1, 0, \tilde{y})$, where $\tilde{s}$ and $\tilde{x}_1$ are defined as the unique solutions of $p_3(s) + q(x_1) = 1$ and they satisfy the equation:

$$\tilde{s} + \tilde{x}_1 p_1(\tilde{s}) + p_3(\tilde{s}) \frac{\tilde{x}_1(-1 + p_1(\tilde{s}))}{1 - p_3(\tilde{s})} = 1 \tag{5}$$

with $\tilde{s} \in (0,1)$ and $\tilde{y} = \frac{\tilde{x}_1(-1 + p_1(\tilde{s}))}{1 - p_3(\tilde{s})}$.

- Survival of population x_2 and y only: $E_7(\hat{s}, 0, \hat{x}_2, \hat{y})$, where $\hat{s}$ is defined by the equations, $p_1(s) = p_2(s) = $

1 with $\hat{s} \in (0,1)$ and $\hat{x}_2, \hat{y}$ are the solutions of $x_2 + y = 1 - \hat{s}$
- Survival of all three populations: $E_8(\lambda_2, \bar{x}_1, \bar{x}_2, \bar{y})$, where $\bar{x}_1$ is defined as the unique solution of

$$q(x_1) = 1 - p_3(\lambda_2), \qquad \bar{y} = \frac{\bar{x}_1(-1 + p_1(\lambda_2))}{q(\bar{x}_1)} \quad \text{and}$$

$$\bar{x}_2 = 1 - \lambda_2 - \bar{x}_1 p_1(\lambda_2) - \bar{y} p_3(\lambda_2)$$

The values λ_i represent the break-even concentration of nutrient.

Now we say that an equilibrium point will exist if its components are non-negative. The washout equilibrium point $E_1(1,0,0,0)$ always exists. Since p_i is increasing with $p_i(0) = 0$, λ_i exist and satisfying:

$$0 < \lambda_i < 1 \text{ and } p_i(\lambda_i) = 1 \Leftrightarrow p_i(1) > 1 \tag{6}$$

In this case, there are equilibrium points E_2, E_3 and E_5 respectively, otherwise, no such equilibrium points exist. Now E_4 is a equilibrium point provided $\bar{x}_1 > 0, \bar{x}_2 > 0$ with $\bar{s} \in (0,1)$. Similar conditions hold for E_7. In case of the equilibrium point E_6, since p_3, q are increasing with $p_3(0) = q(0) = 0$, $\tilde{s}$ and $\tilde{x}_1$ exist and satisfy:

$$\begin{aligned}
p_3(\tilde{s}) + q(\tilde{x}_1) &= 1 \\
\Leftrightarrow p_3(1) + \lim_{x_1 \to \infty} q(x_1) &> 1
\end{aligned} \tag{7}$$

For the existence of E_6, we have two cases as in (El-Owaidy and Moniem, 2003):

Case 1: $1 - p_3(\tilde{s}) = q(\tilde{x}_1) > 0$, then no condition is necessary

Case 2: $-1 + p_1(\tilde{s}) > 0 \Rightarrow \tilde{s} > \lambda_1$

Note that $F(s) = 1 - s - \tilde{x}_1 p_1(s) - p_3(s) \frac{\tilde{x}_1(-1 + p_1(s))}{1 - p_3(s)}$ is decreasing in s with $F(0) = 1, F(\tilde{s}) = 0$ and $F(\lambda_1) = 1 - \lambda_1 - \tilde{x}_1$. So $\tilde{s} > \lambda_1$ if and only if $\tilde{x}_1 < 1 - \lambda_1$. Therefore, E_6 exists if and only if:

$$\lambda_1 < 1 \text{ and } \tilde{x}_1 < 1 - \lambda_1 \tag{8}$$

Finally, the feasibility conditions for the mixed culture (interior) equilibrium point E_8 are $\bar{x}_1 > 0, \bar{x}_2 > 0, \bar{y} > 0$. In order for $\bar{x}_1 > 0$, we require $\lambda_3 > \lambda_2$. Similar calculations show that $\bar{y} > 0 \Rightarrow \lambda_2 > \lambda_1$ and $\bar{x}_2 > 0 \Rightarrow \lambda_2 < 1$. Therefore, E_8 exists if and only if:

$$\lambda_3 > \lambda_2 > \lambda_1 > 0 \text{ and } \lambda_2 < 1 \tag{9}$$

Next, the local stability analysis of the eight equilibrium points will be investigated by finding the eigenvalues of the associated Jacobian matrices. The Jacobian matrix due to the linearization of (2) about an arbitrary equilibrium $E(s, x_1, x_2, y) \in \mathbb{R}_+^4$ is given by:

$$J(E) = \left[J_{ij} \right]_{4 \times 4} \tag{10}$$

where:

$$J_{11} = -1 - x_1 p_1{}'(s) - x_2 p_2{}'(s) - y p_3{}'(s),$$
$$J_{12} = -p_1(s), J_{13} = -p_2(s), J_{14} = -p_3(s),$$
$$J_{21} = x_1 p_1{}'(s), J_{22} = -1 + p_1(s) - y q'(x_1), J_{23} = 0,$$
$$J_{24} = -q(x_1), J_{31} = x_2 p_2{}'(s), J_{32} = 0, J_{33} = -1 + p_2(s),$$
$$J_{34} = 0, J_{41} = y p_3{}'(s), J_{42} = y q'(x_1), J_{43} = 0,$$
$$J_{44} = -1 + p_3(s) + q(x_1).$$

The dynamic behavior of plane equilibria E_1, E_2, E_3, E_4, E_5 and E_7 have been stated in the form of Theorems [2-7] respectively. We left the proofs as these directly follow from the Routh-Hurwitz criteria.

Theorem 2

If $\lambda_i > 1, i = 1, 2, 3$, then the washout equilibrium point E_1 is Locally Asymptotically Stable (LAS) that is, hyperbolic sink and hyperbolic saddle if otherwise.

Theorem 3

Suppose $\lambda_1 < 1$. (i) If $1 - \tilde{x}_1 < \lambda_1 < \lambda_2$, then E_2 is LAS (hyperbolic sink). (ii) If $1 - \tilde{x}_1 > \lambda_1 > \lambda_2$, then E_2 is hyperbolic saddle and is repelling locally in both directions of x_2 and y. In particular, the stable manifold W^+ and the unstable manifold W^- both are of dimensions two and given by $Dim W^+(E_2(\lambda_1, 1 - \lambda_1, 0, 0)) = 2$, $Dim W^-(E_2(\lambda_1, 1 - \lambda_1, 0, 0)) = 2$.

Theorem 4

Suppose $\lambda_2 < 1$. (i) If $\lambda_2 < \min\{\lambda_1, \lambda_3\}$, then the equilibrium point E_3 is hyperbolic sink. (ii) If $\lambda_2 > \max\{\lambda_1, \lambda_3\}$, then E_3 is a hyperbolic saddle and is repelling locally in both directions of x_1 and y. In particular, $Dim W^+(E_3) = 2$, $Dim W^-(E_3) = 2$.

Theorem 5

Suppose $\lambda_3 < 1$. (i) If $\lambda_3 < \lambda_2$ and $p_1(\lambda_3) - (1 - \lambda_3)q'(0) < 1$, then the equilibrium point E_5 is hyperbolic sink. (ii) If the inequalities in (i) are reversed, then E_5 is a hyperbolic saddle point and is repelling locally in both directions of x_1 and x_2.

Theorem 6

Suppose E_4 exists. Let $\breve{a}_1 > 0, \breve{a}_2 > 0$ and $\breve{a}_1 \breve{a}_2 > \breve{a}_3$. (i) If $p_3(\bar{s}) + q(\bar{x}_1) < 1$, then E_4 is hyperbolic sink. (ii) If $p_3(\bar{s}) + q(\bar{x}_1) > 1$, then E_4 is a hyperbolic saddle point and is repelling locally in direction of y.

Theorem 7

Suppose E_7 exists. Let $\hat{a}_1 > 0, \hat{a}_2 > 0$, $\hat{a}_1 \hat{a}_2 > \hat{a}_3$. (i) If $p_1(\hat{s}) - \hat{y}q'(0) < 1$, then E_7 is hyperbolic sink. (ii) If $p_1(\hat{s}) - \hat{y}q'(0) > 1$, then E_7 is a hyperbolic saddle point and is repelling locally in direction of x_1.

Next, we perform the linearized stability analyses for the rest point E_6. The Jacobian matrix due to linearization of system (2) around E_6 is given by:

$$J(E_6) = \begin{bmatrix} m_{11} & m_{12} & m_{13} & m_{14} \\ m_{21} & m_{22} & 0 & m_{24} \\ 0 & 0 & m_{33} & 0 \\ m_{41} & m_{42} & 0 & 0 \end{bmatrix} \tag{11}$$

where:

$$m_{11} = -1 - \tilde{x}_1 p_1{}'(\tilde{s}) - \tilde{y} p_3{}'(\tilde{s}), m_{12} = -p_1(\tilde{s}),$$
$$m_{13} = -p_2(\tilde{s}), m_{14} = -p_3(\tilde{s}), m_{21} = \tilde{x}_1 p_1{}'(\tilde{s}),$$
$$m_{22} = -1 + p_1(\tilde{s}) - \tilde{y}q'(\tilde{x}_1), m_{24} = -q(\tilde{x}_1), \tag{12}$$
$$m_{33} = -1 + p_2(\tilde{s}), m_{41} = \tilde{y} p_3{}'(\tilde{s}),$$
$$m_{42} = \tilde{y}q'(\tilde{x}_1)$$

The eigenvalues of the matrix $J(E_6)$ are given by:

$$r_1 = m_{33} = -1 + p_2(\tilde{s})$$

and r_2, r_3, r_4 satisfy the equation:

$$r^3 + \tilde{a}_1 r^2 + \tilde{a}_2 r + \tilde{a}_3 = 0$$

where:

$$\tilde{a}_1 = -m_{11} - m_{22},$$
$$\tilde{a}_2 = -m_{24}m_{42} + m_{11}m_{22} - m_{12}m_{21} - m_{14}m_{41}, \tag{13}$$
$$\tilde{a}_3 = m_{11}m_{24}m_{42} - m_{12}m_{24}m_{41} - m_{14}m_{21}m_{42} + m_{14}m_{22}m_{41}.$$

We summarize above discussion as follows.

Theorem 8

Suppose (8) holds. (i) If $\tilde{s} > \lambda_2$ and $\tilde{a}_1 > 0, \tilde{a}_3 > 0$, $\tilde{a}_1 \tilde{a}_2 > \tilde{a}_3$, then E_6 is a hyperbolic saddle and is repelling locally in direction of x_2. (ii) The equilibrium point E_6 is hyperbolic sink, if $\tilde{s} < \lambda_2$ and $\tilde{a}_1 > 0, \tilde{a}_3 > 0$, $\tilde{a}_1 \tilde{a}_2 > \tilde{a}_3$ hold concurrently. In particular, the stable manifold

$W^+(E_6 = (\tilde{s}, \tilde{x}_1, 0, \tilde{y}))$ is the $s - x_1 - y$ space and the unstable manifold $W^-(E_6)$ is the x_2 direction, that is $DimW^+(E_6) = 3$, $DimW^-(E_6) = 1$.

Finally, when the interior equilibrium point $E_8(\overline{s}, \overline{x}_1, \overline{x}_2, \overline{y})$ exists, the Jacobian matrix at E_8 is given by:

$$J(E_8) = \begin{bmatrix} n_{11} & n_{12} & n_{13} & n_{14} \\ n_{21} & n_{22} & 0 & n_{24} \\ n_{31} & 0 & 0 & 0 \\ n_{41} & n_{42} & 0 & 0 \end{bmatrix} \tag{14}$$

where:

$$
\begin{aligned}
&n_{11} = -1 - \overline{x}_1 p_1'(\lambda_2) - \overline{x}_2 p_2'(\lambda_2) - \overline{y} p_3'(\lambda_2), \\
&n_{12} = -p_1(\lambda_2), n_{13} = -1, n_{14} = -p_3(\lambda_2), \\
&n_{21} = \overline{x}_1 p_1'(\lambda_2), n_{22} = -1 + p_1(\lambda_2) - \overline{y} q'(\overline{x}_1), \\
&n_{24} = -q(\overline{x}_1), n_{31} = \overline{x}_2 p_2'(\lambda_2), n_{41} = \overline{y} p_3'(\lambda_2), \\
&n_{42} = \overline{y} q'(\overline{x}_1)
\end{aligned}
\tag{15}
$$

The eigenvalues of $J(E_8)$ satisfy the equation:

$$r^4 + \overline{a}_1 r^3 + \overline{a}_2 r^2 + \overline{a}_3 r + \overline{a}_4 = 0$$

where:

$$
\begin{aligned}
&\overline{a}_1 = -TraceJ(E_8) = -n_{11} - n_{22} \\
&\overline{a}_2 = -n_{12}n_{21} - n_{24}n_{42} + n_{11}n_{22} - n_{14}n_{41} + n_{31} \\
&\overline{a}_3 = -n_{22}n_{31} + n_{11}n_{24}n_{42} - n_{12}n_{24}n_{41} - n_{14}n_{21}n_{42} + n_{14}n_{22}n_{41} \\
&\overline{a}_4 = \det J(E_8) = -n_{24}n_{31}n_{42}
\end{aligned}
\tag{16}
$$

Therefore by Routh-Hurwitz criteria E_8 will be LAS if and only if $\overline{a}_1 > 0, \overline{a}_2 > 0, \overline{a}_3 > 0, \overline{a}_4 > 0$, $\overline{a}_1 \overline{a}_2 > \overline{a}_3$ and $\overline{a}_1 \overline{a}_2 \overline{a}_3 > \overline{a}_3^2 + \overline{a}_4 \overline{a}_1^2$.

Thus we summarize above result in the following theorem.

Theorem 9

Suppose (9) holds. Then E_8 is LAS if $\overline{a}_1 > 0, \overline{a}_2 > 0, \overline{a}_3 > 0, \overline{a}_4 > 0$, $\overline{a}_1 \overline{a}_2 > \overline{a}_3$ and $\overline{a}_1 \overline{a}_2 \overline{a}_3 > \overline{a}_3^2 + \overline{a}_4 \overline{a}_1^2$, otherwise unstable.

Global Stability Analysis

In the last section, we showed the existence of all equilibria and their local stability. Here, we shall present the global stability analysis of system (2) around the equilibria.

Theorem 10

If $\lambda_i > 1$, then the solution trajectories of the system (2) satisfy $\lim_{t \to +\infty} (s(t), x_1(t), x_2(t), y(t)) = (1, 0, 0, 0)$.

Proof

The proof is very straightforward and similar to (Li and Kuang, 2000; Nasrin and Rana, 2011).

Now we show that the system (2) is persistent by showing that a positive equilibrium point of any 3-dimensional subspace of $\mathrm{R}^+_{sx_1x_2y}$, is globally asymptotically stable with respect to trajectories originating from the interior of it. First we establish criterion for the global stability of $E_2(\lambda_1, 1 - \lambda_1, 0, 0)$.

Consider system (2) restricted to $\mathrm{R}^+_{sx_1}$:

$$
\begin{aligned}
&s'(t) = 1 - s - x_1 p_1(s) \\
&x_1'(t) = x_1(-1 + p_1(s))
\end{aligned}
\tag{17}
$$

We have shown that $\overline{E}_2(\lambda_1, 1 - \lambda_1)$ and consequently $E_2(\lambda_1, 1 - \lambda_1, 0, 0)$ exists if $\lambda_1 < 1$. For any point in $\mathrm{R}^+_{sx_1}$, let G be a neighborhood of it. In $\mathrm{R}^+_{sx_1}$, we choose the Liapunov function V such that:

$$V(s, x_1) = \frac{1}{2} c_1 (s - \hat{s})^2 + \frac{1}{2} c_2 (x_1 - \hat{x}_1)^2 \tag{18}$$

where, $c_1, c_2 \in \mathrm{R}_+$ and $\hat{s} = \lambda_1, \hat{x}_1 = 1 - \lambda_1$ are solutions of (17). Then V is a positive definite in $\mathrm{R}^+_{sx_1}$ and also a Liapunov function for (17) in G.

Now:

$$V' = c_1(s - \hat{s})(1 - s - x_1 p_1(s)) + c_2(x_1 - \hat{x}_1)x_1(-1 + p_1(s)) \tag{19}$$

along the trajectories of (17) in $\mathrm{R}^+_{sx_1}$.

But from (17), we have $1 - \hat{s} - \hat{x}_1 p_1(\hat{s}) = 0$, $-1 + p_1(\hat{s}) = 0$.

Thus:

$$
\begin{aligned}
V' &= c_1(s - \hat{s})(\hat{s} + \hat{x}_1 p_1(\hat{s}) - s - x_1 p_1(s)) \\
&\quad + c_2(x_1 - \hat{x}_1)x_1(-p_1(\hat{s}) + p_1(s)) \\
&= -c_1(s - \hat{s})^2 + c_1(s - \hat{s})(\hat{x}_1 p_1(\hat{s}) - x_1 p_1(s)) \\
&\quad + c_2(x_1 - \hat{x}_1)x_1(p_1(s) - p_1(\hat{s})) \\
&= c_{11}(s - \hat{s})^2 + \frac{1}{2} c_{12}(s - \hat{s})(x_1 - \hat{x}_1) \\
&\quad + \frac{1}{2} c_{21}(s - \hat{s})(x_1 - \hat{x}_1) + c_{22}(x_1 - \hat{x}_1)^2
\end{aligned}
\tag{20}
$$

where:

$$
c_{11} = -c_1 < 0, c_{12} = c_{21} = c_1 \frac{(\hat{x}_1 p_1(\hat{s}) - x_1 p_1(s))}{(x_1 - \hat{x}_1)},
$$

$$
c_{22} = \frac{x_1(p_1(s) - p_1(\hat{s}))}{(x_1 - \hat{x}_1)}
$$

In particular:

$$V' = X^t C X = \langle CX, X \rangle \qquad (21)$$

where:

$$X = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = \begin{pmatrix} s - \hat{s} \\ x_1 - \hat{x}_1 \end{pmatrix} \ and \ C = \begin{pmatrix} c_{11} & \frac{1}{2}c_{12} \\ \frac{1}{2}c_{12} & c_{22} \end{pmatrix}$$

It is clear that C is a real symmetric matrix and $C = \frac{1}{2}(C^t + C)$ where t stands for transpose.

Let $\Gamma_0 = \left\{ (s, x_1) \in \mathbb{R}^+_{sx_1} \,\middle|\, s > 0, x_1 > 0, s + x_1 = 1 \right\}$.

Define two sets as:

$$S_1 = \left\{ (s, x_1) \in \Gamma_0 \cap \mathrm{int}\, \mathbb{R}^+_{sx_1} \,\middle|\, V(s, x_1) = 0 \right\},$$
$$S_2 = \left\{ (s, x_1) \in \mathrm{int}\, \mathbb{R}^+_{sx_1} \,\middle|\, s = \hat{s}, x_1 = \hat{x}_1 \right\}$$

Then it is obvious that the sets are identical, i.e., $S_1 \equiv S_2$.

Next we define the set $\mathbb{E}$ as $\mathbb{E} = \left\{ (s, x_1) \in \mathbb{R}^+_{sx_1} \,\middle|\, V' = 0 \right\} \cap \bar{G}$.

Then $E_2(\lambda_1, 1 - \lambda_1, 0, 0)$ is the largest invariant set in $\mathbb{E}$ restricted to $\mathbb{R}^+_{sx_1}$.

Hence we conclude from LaSalle's Invariant Principle (LaSalle and Lefchetz, 1961) that $\bar{E}_2(\lambda_1, 1 - \lambda_1)$ or consequently $E_2(\lambda_1, 1 - \lambda_1, 0, 0)$ is globally asymptotically stable with respect to trajectories originating from $\mathrm{int}\, \mathbb{R}^+_{sx_1}$ if the matrix C is a negative definite.

Theorem 11

The equilibrium point $E_2(\lambda_1, 1 - \lambda_1, 0, 0)$ in $\mathbb{R}^+_{sx_1}$ is globally asymptotically stable with respect to solution trajectories originating from $\mathrm{int}\, \mathbb{R}^+_{sx_1}$ if:

$$(i)\, c_{22} < 0 \quad (ii)\, c_{11}c_{22} - \frac{1}{4}c^2_{12} > 0.$$

Proof

The proof is very straightforward and similar to (Nani and Freedman, 2000).

Now, we shall deduce the global asymptotic stability criteria of $E_6(\tilde{s}, \tilde{x}_1, 0, \tilde{y})$ with respect to solution trajectories initiating from $\mathrm{int}\, \mathbb{R}^+_{sx_1y}$.

For the system (2) restricted in $\mathbb{R}^+_{sx_1y}$, we choose the Liapunov function:

$$W(s, x_1, y) = s - \tilde{s} - \tilde{s}\ln\left(\frac{s}{\tilde{s}}\right) + \frac{1}{2}k_1(x_1 - \tilde{x}_1)^2 + \frac{1}{2}k_2(y - \tilde{y})^2 \qquad (22)$$

where, $k_i \in \mathbb{R}_+$ for $i = 1, 2$.

Then:

$$W' = \left(\frac{s - \tilde{s}}{s}\right)(1 - s - x_1 p_1(s) - y p_3(s))$$
$$+ k_1(x_1 - \tilde{x}_1)(x_1(-1 + p_1(s)) - yq(x_1)) \qquad (23)$$
$$+ k_2(y - \tilde{y})y(-1 + p_3(s) + q(x_1))$$

along the trajectories of the system (2) restricted in $\mathbb{R}^+_{sx_1y}$.

But we have $1 - \tilde{s} - \tilde{x}_1 p_1(\tilde{s}) - \tilde{y}p_3(\tilde{s}) = 0$, $\tilde{x}_1(-1 + p_1(\tilde{s})) - \tilde{y}q(\tilde{x}_1) = 0$, $-1 + p_3(\tilde{s}) + q(\tilde{x}_1) = 0$.

Thus (23) reduces to:

$$W' = \left(\frac{s - \tilde{s}}{s}\right)(\tilde{s} + \tilde{x}_1 p_1(\tilde{s}) + \tilde{y}p_3(\tilde{s}) - s - x_1 p_1(s) - y p_3(s))$$
$$+ k_1(x_1 - \tilde{x}_1)\left(x_1\left(-p_1(\tilde{s}) + \frac{\tilde{y}q(\tilde{x}_1)}{\tilde{x}_1} + p_1(s)\right) - yq(x_1)\right)$$
$$+ k_2(y - \tilde{y})y(-p_3(\tilde{s}) - q(\tilde{x}_1) + p_3(s) + q(x_1)).$$
$$= -\frac{(s - \tilde{s})^2}{s} + \left\{\frac{\tilde{x}_1 p_1(\tilde{s}) - x_1 p_1(s)}{s(x_1 - \tilde{x}_1)}\right\}(s - \tilde{s})(x_1 - \tilde{x}_1)$$
$$+ \left\{\frac{\tilde{y}p_3(\tilde{s}) - y p_3(s)}{s(y - \tilde{y})}\right\}(s - \tilde{s})(y - \tilde{y}_1)$$
$$+ \left\{-k_1 \frac{x_1(p_1(\tilde{s}) - p_1(s))}{(s - \tilde{s})}\right\}(s - \tilde{s})(x_1 - \tilde{x}_1)$$
$$+ \left\{k_1 \frac{x_1 \frac{\tilde{y}q(\tilde{x}_1)}{\tilde{x}_1} - yq(x_1)}{(x_1 - \tilde{x}_1)}\right\}(x_1 - \tilde{x}_1)^2$$
$$+ \left\{-k_2 y \frac{p_3(\tilde{s}) - p_3(s)}{(s - \tilde{s})}\right\}(s - \tilde{s})(y - \tilde{y})$$
$$+ \left\{-k_2 y \frac{q(\tilde{x}_1) - q(x_1)}{(y - \tilde{y})}\right\}(y - \tilde{y})^2 \qquad (24)$$

Let $X = \begin{pmatrix} v_1 \\ v_2 \\ v_3 \end{pmatrix}$ such that $\begin{array}{l} v_1 = s - \tilde{s} \\ v_2 = x_1 - \tilde{x}_1 \\ v_3 = y - \tilde{y} \end{array}$ and set:

$$b_{11} = -\frac{1}{s} < 0, \quad b_{12} = b_{21} = \frac{\tilde{x}_1 p_1(\tilde{s}) - x_1 p_1(s)}{s(x_1 - \tilde{x}_1)} - k_1 \frac{x_1(p_1(\tilde{s}) - p_1(s))}{(s - \tilde{s})},$$

$$b_{22} = k_1 \frac{x_1 \frac{\tilde{y}q(\tilde{x}_1)}{\tilde{x}_1} - yq(x_1)}{(x_1 - \tilde{x}_1)},$$

$$b_{13} = b_{31} = \frac{\tilde{y}p_3(\tilde{s}) - y p_3(s)}{s(y - \tilde{y})} - k_2 y \frac{p_3(\tilde{s}) - p_3(s)}{(s - \tilde{s})},$$

$$b_{33} = -k_2 y \frac{q(\tilde{x}_1) - q(x_1)}{(y - \tilde{y})}, \quad b_{23} = b_{32} = 0$$

Then:

$$V' = b_{11}v_1^2 + b_{22}v_2^2 + b_{33}v_3^2 + b_{12}v_1v_2 + b_{13}v_1v_3 \qquad (25)$$

where, $b_{ij} = b_{ji}$ with $b_{23} = b_{32} = 0$. Therefore, we write:

$$V' = X^t BX = \langle BX, X \rangle \qquad (26)$$

where:

$$B = \begin{pmatrix} b_{11} & \frac{1}{2}b_{12} & \frac{1}{2}b_{13} \\ \frac{1}{2}b_{12} & b_{22} & \frac{1}{2}b_{23} \\ \frac{1}{2}b_{13} & \frac{1}{2}b_{23} & b_{33} \end{pmatrix}$$

It is clear that B is a real symmetric matrix such that $B = \frac{1}{2}(B^t + B)$ where t stands for transpose. The eigenvalues of B satisfy the equation:

$$r^3 + m_1 r^2 + m_2 r + m_3 = 0 \qquad (27)$$

where, $m_1 = -traceB = -(b_{11} + b_{22} + b_{33})$:

$$m_2 = \det \begin{vmatrix} b_{22} & \frac{1}{2}b_{23} \\ \frac{1}{2}b_{23} & b_{33} \end{vmatrix} + \det \begin{vmatrix} b_{11} & \frac{1}{2}b_{13} \\ \frac{1}{2}b_{13} & b_{33} \end{vmatrix} + \det \begin{vmatrix} b_{11} & \frac{1}{2}b_{12} \\ \frac{1}{2}b_{12} & b_{22} \end{vmatrix},$$

$$m_3 = -\det(B)$$

These reduce with $b_{23} = b_{32} = 0$ to:

$$m_1 = -(b_{11} + b_{22} + b_{33}),$$

$$m_2 = b_{22}b_{33} + \left(b_{11}b_{33} - \frac{1}{4}b_{13}^2\right) + \left(b_{11}b_{22} - \frac{1}{4}b_{12}^2\right),$$

$$m_3 = \frac{1}{4}b_{13}^2 b_{22} - b_{33}\left(b_{11}b_{22} - \frac{1}{4}b_{12}^2\right)$$

Thus B is negative definite if:

$$m_1 > 0, m_3 > 0, m_1 m_2 > m_3 \qquad (28)$$

Follows from the Routh-Hurwitz criteria and Lemma 6.1 of (Nani and Freedman, 2000).

Using Lemma 6.2 (Nani and Freedman, 2000), the criteria (28) gives the following result.

Theorem 12

The equilibrium point $\bar{E}_6(\tilde{s}, \tilde{x}_1, \tilde{y}) \in \mathbb{R}^+_{sx_1y}$ is globally asymptotically stable if:

(i) $\quad b_{11} < 0, b_{22} < 0, b_{33} < 0$

(ii) $\quad b_{11}b_{33} - \frac{1}{4}b_{13}^2 > 0$

(iii) $\quad b_{33}\left(b_{11}b_{22} - \frac{1}{4}b_{12}^2\right) < \frac{1}{4}b_{13}^2 b_{22}$ with $b_{11}b_{22} - \frac{1}{4}b_{12}^2 > 0$

Proof

We left the proof as it is very straightforward and similar to (Nani and Freedman, 2000).

Hopf-Andronov-Poincare Bifurcation

In this section, we shall show that the system (2) undergoes a Hopf-Andronov-Poincare bifurcation by using μ as a bifurcation real parameter. Without loss of generality, suppose that p_1 is a function of s and μ. Then system (2) becomes:

$$\begin{aligned} s'(t) &= 1 - s - x_1 p_1(s; \mu) - x_2 p_2(s) - y p_3(s) \\ x_1'(t) &= x_1(-1 + p_1(s; \mu)) - y q(x_1) \\ x_2'(t) &= x_2(-1 + p_2(s)) \\ y'(t) &= y(-1 + p_3(s) + q(x_1)) \end{aligned} \qquad (29)$$

with $s_0 \geq 0, x_{i0} \geq 0, i = 1, 2, y_0 \geq 0$.

Now system (29) can be written as:

$$x'(t) = F(x; \mu), x(0) = x_0 \qquad (30)$$

where, $x = (s, x_1, x_2, y)^t \in \mathbb{R}^4$, $x_0 = (s_0, x_{10}, x_{20}, y_0)^t$ and $\mu \in \mathbb{R}$ is the bifurcation real parameter. The function $F(x; \mu)$ is a $C^r (r \geq 5)$ on an open set in $\mathbb{R}^4 \times \mathbb{R}$. Let:

$$P_\mu = \begin{cases} E_2(\lambda_1, 1 - \lambda_1, 0, 0; \mu), E_3(\lambda_2, 0, 1 - \lambda_2, 0; \mu), \\ E_4(\bar{s}, \bar{x}_1, \bar{x}_2, 0; \mu), E_5(\lambda_3, 0, 0, 1 - \lambda_3; \mu), \\ E_6(\tilde{s}, \tilde{x}_1, 0, \tilde{y}; \mu), E_7(\hat{s}, 0, \hat{x}_2, \hat{y}; \mu), \\ E_8(\lambda_2, \bar{x}_1, \bar{x}_2, \bar{y}; \mu) \end{cases}$$

be the set of equilibria of system (29). Suppose that G is a sufficiently large open set containing $E_i \in P_\mu$ such that $F(P_\mu) = 0$ for $\mu \in \mathbb{R}$. We are now interested to vary μ in order to observe the qualitative changes of solution trajectories near P_μ.

Corollary 1

Assume that Theorems [3-7] are hold. Then there is no Hopf bifurcation at E_2, E_3, E_4, E_5 and E_7.

Proof

If Theorems [3-7] hold respectively, then E_2, E_3, E_4, E_5 and E_7 are repeller and their stable manifolds lie along an axis.

Next we need to compute stability of $E_6(\tilde{s}, \tilde{x}_1, 0, \tilde{y}; \mu)$ and $E_8(\lambda_2, \bar{x}_1, \bar{x}_2, \bar{y}; \mu)$ and then vary μ so as to obtain a desired Hopf bifurcation at $\mu = \mu_1^*$ and $\mu = \mu_2^*$ around E_6 and E_8 respectively.

Firstly, Hopf bifurcation analysis for $E_6(\tilde{s}, \tilde{x}_1, 0, \tilde{y}; \mu)$:

The linearization of system (29) about $E_6(\tilde{s}, \tilde{x}_1, 0, \tilde{y}; \mu)$ for any values of μ is given by:

$$\zeta' = J_\mu(E_6)\zeta, \zeta \in \mathbb{R}^4$$

where, $J_\mu(E_6)$ is defined as in (11) and its nonzero elements are defined as in (12), with $p_1(\tilde{s})$ and $p_1'(\tilde{s})$ replaced by $p_1(\tilde{s}; \mu)$ & $p_1'(\tilde{s}; \mu)$ respectively.

The eigenvalues of the matrix $J_\mu(E_6)$ are $r_1 = m_{33} = -1 + p_2(\tilde{s})$ and $r_i, i = 2,3,4$ satisfy the equation

$$r^3 + b_1 r^2 + b_2 r + b_3 = 0 \tag{31}$$

where, $b_i = \tilde{a}_i, i = 1,2,3$ are defined as in (13).

By the Routh-Hurwitz criteria, all the roots of (31) will have negative real parts if:

$$R_1 : b_1 > 0, b_3 > 0 \text{ and } R_2 : b_1 b_2 > b_3$$

It is required for a Hopf bifurcation that either R_1 or R_1 must be violated. Suppose that $b_1 > 0$, $b_3 > 0$, then clearly (31) has two purely imaginary roots if and only if

$$b_1 b_2 = b_3 \tag{32}$$

for some values of μ, say μ_1^*. Since $b_2 > 0$ at $\mu = \mu_1^*$, there is an open interval containing μ_1^*, say $(\mu_1^* - \varepsilon, \mu_1^* + \varepsilon)$ for some $\varepsilon > 0$ for which $\mu_1^* - \varepsilon > 0$, such that $b_2 > 0$ for $\mu \in (\mu_1^* - \varepsilon, \mu_1^* + \varepsilon)$. Thus for $\mu \in (\mu_1^* - \varepsilon, \mu_1^* + \varepsilon)$, the characteristic equation (31) cannot have positive real roots. For $\mu = \mu_1^*$, we have (Freedman and Ruan, 1992, p.80):

$$(r^2 + b_2)(r + b_1) = 0 \tag{33}$$

The roots of (33) are $r_2 = i\sqrt{b_2}$, $r_3 = -i\sqrt{b_2}$, $r_4 = -b_1$.

For $\mu \in (\mu_1^* - \varepsilon, \mu_1^* + \varepsilon)$, we write the roots in the general form:

$$r_2(\mu) = \alpha(\mu) + i\beta(\mu), r_3(\mu) = \alpha(\mu) - i\beta(\mu)$$
$$\text{and } r_4(\mu) = -b_1(\mu)$$

For the application of Hopf's bifurcation theory to the system (29) (Marsden and Mckracken, 1976), it is required to satisfy the transversality condition:

$$\text{Re}\left[\frac{dr_i}{d\mu}\right]_{\mu=\mu_1^*} \neq 0, i = 2,3 \tag{34}$$

Substituting $r_2(\mu) = \alpha(\mu) + i\beta(\mu)$ and $r_3(\mu) = \alpha(\mu) + i\beta(\mu)$ into (31) and calculating the derivatives with respect to μ, we obtain:

$$K(\mu)\alpha'(\mu) - L(\mu)\beta'(\mu) + M(\mu) = 0,$$
$$L(\mu)\alpha'(\mu) + K(\mu)\beta'(\mu) + N(\mu) = 0, \tag{35}$$

where:

$$K(\mu) = 3\alpha^2(\mu) + 2b_1(\mu)\alpha(\mu) + b_2(\mu) - 3\beta^2(\mu)$$
$$L(\mu) = 6\alpha(\mu)\beta(\mu) + 2b_1(\mu)\beta(\mu)$$
$$M(\mu) = b_1'(\mu)\left(\alpha^2(\mu) - \beta^2(\mu)\right) + b_2'(\mu)\alpha(\mu) + b_3'(\mu)$$
$$N(\mu) = 2b_1'(\mu)\alpha(\mu)\beta(\mu) + b_2'(\mu)\beta(\mu)$$

Since $K(\mu_1^*)M(\mu_1^*) + L(\mu_1^*)N(\mu_1^*) \neq 0$, we have:

$$\text{Re}\left[\frac{dr_i}{d\mu}\right]_{\mu=\mu_1^*} = \alpha'(\mu)\Big|_{\mu=\mu_1^*}$$
$$= -\frac{K(\mu)M(\mu) + L(\mu)N(\mu)}{K^2(\mu) + L^2(\mu)}\Bigg|_{\mu=\mu_1^*} \neq 0, i = 2,3$$

and $r_4(\mu_1^*) = -b_1(\mu_1^*) \neq 0$.

Hence there is a Hopf bifurcation at $\mu = \mu_1^*$. We have the following result:

Theorem 13

Suppose R_1 holds. Then the system (29) undergoes a Hopf bifurcation when μ passes through μ_1^* emanating from the steady state $E_6(\tilde{s}, \tilde{x}_1, 0, \tilde{y})$ leading to periodic solutions trajectories for either $\mu > \mu_1^*$ (supercritical bifurcation), or $\mu < \mu_1^*$ (sub-critical-bifurcation) or at $\mu = \mu_1^*$.

Next, Hopf bifurcation at $E_8(\lambda_2, \bar{x}_1, \bar{x}_2, \bar{y}; \mu)$:

The Jacobian matrix corresponding to $E_8(\lambda_2, \bar{x}_1, \bar{x}_2, \bar{y}; \mu)$ is given by:

$$J_\mu(E_8) = \left[n_{ij}\right]_{4\times4} \tag{36}$$

where, $J_\mu(E_8)$ and its nonzero elements n_{ij} are defined as in (14) and (15) with $p_1(\tilde{s})$ and $p_1'(\tilde{s})$ replaced by $p_1(\tilde{s}; \mu)$ and $p_1'(\tilde{s}; \mu)$ respectively.

The characteristic equation corresponding to $J_\mu(E_8)$ obeys:

$$r^4 + d_1 r^3 + d_2 r^2 + d_3 r + d_4 = 0 \tag{37}$$

where the coefficients $d_i = \bar{a}_i, i = 1,2,3,4$ are defined as in (16).

By the Routh-Hurwitz criteria, all the roots of (37) will have negative real parts if:

$$R_3 : d_1 > 0, d_3 > 0, d_4 > 0, d_1 d_2 > d_3$$
$$and\ R_4 : d_1 d_2 d_3 > d_3^2 + d_4 d_1^2.$$

It is required for a Hopf bifurcation that either R_3 or R_4 must be violated. Suppose $d_i > 0, i = 1,2,3,4$ such that:

- $d_1 d_2 > d_3$
- R_4 is violated such that $d_1 d_2 d_3 = d_3^2 + d_4 d_1^2$

$$\Leftrightarrow d_2 d_3 = \frac{d_3^2}{d_1} + d_1 d_4 > d_4$$

In factor form, the Equation 37 can be written as:

$$\left(r^2 + \theta_1\right)\left(r + \theta_2\right)\left(r + \theta_3\right) = 0,$$
$$\theta_i > 0, i = 1,2,3$$

where:

$$d_1 = \theta_2 + \theta_3, d_2 = \theta_2 \theta_3 + \theta_1,$$
$$d_3 = \theta_1\left(\theta_2 + \theta_3\right) \text{and } d_4 = \theta_1 \theta_2 \theta_3 \tag{38}$$

In particular, Equation 37 leads the following set of roots:

$$\sigma\left(J_\mu(E_8)\right) = \left\{ i\sqrt{\theta_1}, -i\sqrt{\theta_1}, -\theta_2, -\theta_3 \right\}$$

where, $\theta_i, i = 1,2,3$ are solution of (38).

It shows that Equation 37 has two pure imaginary roots for some value of μ, say μ_2^*. Therefore, there is an open interval containing μ_2^*, say $\left(\mu_2^* - \varepsilon, \mu_2^* + \varepsilon\right)$ for some $\varepsilon > 0$, the equation (37) cannot have positive real roots. But for $\mu \in \left(\mu_2^* - \varepsilon, \mu_2^* + \varepsilon\right)$, the roots are in general of the form:

$$r_1(\mu) = \alpha(\mu) + i\beta(\mu), r_2(\mu) = \alpha(\mu) - i\beta(\mu),$$
$$r_3(\mu) = -\theta_2(\mu) \text{ and } r_4(\mu) = -\theta_3$$

Now we apply Hopf's transversality condition (34) so as to obtain the desired conditions for Hopf bifurcation to occur for system (29). Substituting $r_1(\mu) = \alpha(\mu) + i\beta(\mu)$ and $r_2(\mu) = \alpha(\mu) - i\beta(\mu)$ into (37) and computing the derivatives with respect to μ, we get:

$$\bar{K}(\mu)\alpha'(\mu) - \bar{L}(\mu)\beta'(\mu) + \bar{M}(\mu) = 0,$$
$$\bar{L}(\mu)\alpha'(\mu) + \bar{K}(\mu)\beta'(\mu) + \bar{N}(\mu) = 0, \tag{39}$$

where:

$$\bar{K}(\mu) = 4\alpha\left(\alpha^2 - \beta^2\right) - 8\alpha\beta^2 + 3d_1\left(\alpha^2 - \beta^2\right) + 2d_2\alpha + d_3$$
$$\bar{L}(\mu) = 4\beta\left(\alpha^2 - \beta^2\right) + 8\alpha^2\beta + 6d_1\alpha\beta + 2d_2\beta$$
$$\bar{M}(\mu) = d_1'\left[\alpha\left(\alpha^2 - \beta^2\right) - 2\alpha\beta^2\right] + d_2'\left(\alpha^2 - \beta^2\right) + d_3'\alpha + d_4'$$
$$\bar{N}(\mu) = d_1'\left[\beta\left(\alpha^2 - \beta^2\right) + 2\alpha^2\beta\right] + 2d_2'\alpha\beta + d_3'\beta$$

Since $\bar{K}\left(\mu_2^*\right)\bar{M}\left(\mu_2^*\right) + \bar{L}\left(\mu_2^*\right)\bar{N}\left(\mu_2^*\right) \neq 0$, we have:

$$Re\left[\frac{dr_i}{d\mu}\right]_{\mu = \mu_2^*} = \alpha'(\mu)\Big|_{\mu = \mu_2^*}$$
$$= -\frac{\bar{K}(\mu)\bar{M}(\mu) + \bar{L}(\mu)\bar{N}(\mu)}{\bar{K}^2(\mu) + \bar{L}^2(\mu)}\Bigg|_{\mu = \mu_2^*} \neq 0, i = 1,2$$

and $r_3\left(\mu_2^*\right) = -\theta_2\left(\mu_2^*\right) \neq 0$, $r_4\left(\mu_2^*\right) = -\theta_3\left(\mu_2^*\right) \neq 0$. Hence there is a Hopf bifurcation at $\mu = \mu_2^*$. We summarize above discussion in the following result.

Theorem 14

Suppose (i) $E_8(\lambda_2, \bar{x}_1, \bar{x}_2, \bar{y})$ exists (ii) $d_i > 0, i = 1,2,3,4$, $d_1 d_2 > d_3$ and R_4 is violated. Then system (29) exhibits a Hopf bifurcation in the first orthant, leading to a family of periodic solutions trajectories that bifurcate from E_8 when μ varies in a small neighborhood of $\mu = \mu_2^*$.

Discussion and Conclusion

We showed a detailed mathematical analysis of a classical food web model describing three species interaction competing for a single nutrient in which one of the competitors predates on one of the other competitors. We assumed general monotone response functions for the nutrient uptake of the competitors and growth rate for predator. The considered model is more general and its analysis extends the works of the system (El-Owaidy and Moniem, 2003; Li and Kuang, 2000; Butler and Wolkowicz, 1986; Wolkowicz, 2006). We proved that the trajectories of system (2) are bounded for all future time. We showed that the equilibria for system (2) are LAS if exist by using Routh-Hurwitz criterion. We found that all the species cannot persist if break-even concentrations of the preys are close to one. This happens when E_1 is a global attractor of system (2). We proved that if exists the equilibria E_2 and E_6 are globally asymptotically stable by using Liapunov functions as in (Nani and Freedman, 2000) showing that the predator will be die out in the chemostat whatever be the initial concentrations of prey and predator. Next, when E_8 exists then all the species (predator-preys) coexist,

that is, the system (2) is persistent uniformly and circumvented the conservation principle. We applied the similar technique as in (Freedman and Waltman, 1984) and presented that the system (2) passes though a Hopf bifurcation at E_6 leading to periodic solutions. Finally, we established theoretical criteria for which the system (2) undergoes a Hopf Andronov-Poincare bifurcation at the equilibrium point E_8 and possesses a family of periodic solutions that bifurcates from E_8. Therefore, we can conclude that the results obtained in this study partially generalize and improve to the works done by (Butler and Wolkowicz, 1986; El-Owaidy and Moniem, 2003; Li and Kuang, 2000; Nasrin and Rana, 2011; Wolkowicz, 2006).

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Ethics

This article is original and contains unpublished material. The author confirms that he has read and approved the manuscript and no ethical issues involved.

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