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Stability and bifurcation of a simple food chain in a chemostat with removal rates

M.M.A. El-Sheikh *, S.A.A. Mahrouf

Department of Mathematics, Faculty of Science, Menoufia Univerisity, Shebin El-Koom, Egypt

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Abstract

In this paper we consider a model describing predator–prey interactions in a chemostat that incorporates genreal response functions and distinct removal rates. In this case, the conservation law fails. To overcome this problem, we use Liapunov functions in the study of the global stability of equlibria. Mathematical analysis of the model equations with regard to invariance of non-negativity, boundedness of solutions, dissipativity and persistence are studied. Hopf bifurcation theory is applied.

1. Introduction

The chemostat is a laboratory apparatus used for the continuous culture of microorganisms. It can be used to study interactions between different populations of micro-organisms, and has the advantage that the parameters are readily measurable. See ([1–3,6,9,10,12,14,15,17]) for a detailed description of a chemostat and for various mathematical models for analyzing chemostat models. Li and Kuang [11] considered a food chain in a chemostat with one prey and one predator. They assumed that the predator feeds exclusively on the prey, and the prey consumes the nutrient in the chemostat. Also, they obtained results on global stability of boundary equilibria, the positivity and boundedness of solutions and persistence analysis. Here we consider a food chain model in chemostat with two predators and one prey. The model describes the competition occurring among predators of an organism growing on the nutrient in a chemostat that incorporates general response functions and distinct removal rates. This is an interesting practical process both mathematically and biologically. The model of interest is

* Corresponding author.

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$$\begin{aligned}
\frac{dS}{dt} &= (S^\circ - S)D - \frac{1}{\gamma_1}F_1(S)x,\\
\frac{dx}{dt} &= x(F_1(S)x - \overline{D}_1) - \frac{1}{\gamma_2}F_2(x)y,\\
\frac{dy}{dt} &= y(F_2(x)y - \overline{D}_2) - \frac{1}{\gamma_3}F_3(y)z,\\
\frac{dz}{dt} &= z(F_3(y)z - \overline{D}_1),\\
S(0) &= S_\circ > 0, \quad x(0) = x_\circ > 0, \quad y(0) = y_\circ > 0, \quad z(0) = z_\circ > 0,
\end{aligned} \tag{1.1}$$

where $S(t)$ denotes the concentration of nutrient at time $t, x(t)$ denotes the concentration of prey at time $t, y(t)$ and $z(t)$ denote the concentrations of first predator and second predator at time t, respectively. S° denotes the input concentration of the nutrient, γ_1, γ_2 and γ_3 denote the yield constants, $F_1(S)$, $F_2(x)$ and $F_3(y)$ denote the specific per-capita growth rates of $x(t)$, $y(t)$ and $z(t)$, respectively. D is the washout rate of the chemostat, each $\overline{D}_i = D + \epsilon_i,\ i = 1,2,3$, where ϵ_1, ϵ_2 and ϵ_3 denote the specific death rates of the organisms x, y and z, respectively. In our case, organism's death rates are significant, and the removal rate of this organism should be the sum of the washout rate and the death rate. Following [11] we can scale the concentrations of nutrient in units of S°, time in units of $\frac{1}{D}$, a prey $x(t)$ in units of $\gamma_1 S^\circ$, a predator $y(t)$ in units of $\gamma_1\gamma_2 S^\circ$ and a predator $z(t)$ in units of $\gamma_1\gamma_2\gamma_3 S^\circ$, one reduce the number of parameters and obtains the following system of differential equations

$$\begin{aligned}
\frac{dS}{dt} &= 1 - S - f_1(S)x,\\
\frac{dx}{dt} &= x(f_1(S)x - D_1) - f_2(x)y,\\
\frac{dy}{dt} &= y(f_2(x)y - D_2) - f_3(y)z,\\
\frac{dz}{dt} &= z(f_3(y)z - D_3),\\
S(0) &= S_\circ > 0, \quad x(0) = x_\circ > 0, \quad y(0) = y_\circ > 0, \quad z(0) = z_\circ > 0,
\end{aligned} \tag{1.2}$$

where $D_i = \frac{\overline{D}_i}{D}, i = 1,2,3,\ f_1(S) = \frac{F_1(SS^\circ)}{D},\ f_2(x) = \frac{F_2(xS^\circ\gamma_1)}{D},\ f_3(y) = \frac{F_3(yS^\circ\gamma_1\gamma_2)}{D}$. As in [2], we make the following assumptions on the response functions $f_i, i = 1,2,3$.

(i) f_i: $R^+ \to R^+$ and f_i, $i = 1,2,3$ are continuously differentiable functions.
(ii) $f_i(0) = 0$, $i = 1,2,3$.
(iii) $f_1'(S) > 0$ for all $S > 0$, $f_2'(x) > 0$ for all $x > 0$ and $f_3'(y) > 0$ for all $y > 0$.

Our results in this paper are extension to those in [11] where the study if for a simple food chain model (with one predator and one prey) in a chemostat with distinct removal rates. This paper is organized as follows. In Section 2, some elementary properties such as boundedness, invariance of non-negativity, dissipativity and the equilibria and their stabilities investigated. Section 3 is devoted to discuss global stability analysis of subsystems and persistence. In Section 4, we discuss Hopf bifurcation of solutions. Finally a short discussion is given in Section 5.

2. Elementary properties, existence of equilibria and their stabilities

In this section, we present some elementary properties, including boundedness, invariance of non-negativity and dissipativity. Also, we deal with the existence and local stability of the equilibria. First, we consider the elementary properties of system (1.2).

Definition 2.1 ([8, p. 394]). A system of differential equations $X' = F(X)$ is said to be dissipative if there is abounded subset B of R^4 such that for any $X^\circ \in R^4$ there is a time $t_\circ$ which depends on X° and B so that the solution $\phi(t, X^\circ) \in B$ for $t \geqslant t_\circ$.

Theorem 2.1. *Let Γ be the region defined by*

$$\Gamma = \left\{(S,x,y,z) \in R^4_+ : \frac{1}{D_{\max}} - k \leqslant S + x + y + z \leqslant \frac{1}{D_{\min}} + k\right\}, \tag{2.1}$$

where $D_{max} = \max\{1, D_1, D_2, D_3\}, D_{min} = \min\{1, D_1, D_2, D_3\}$ and k is a positive constant. Then

(i) *Γ is positively invariant.*
(ii) *All solutions of system (1.2) with initial values in R^4_+ are eventually uniformly bounded and attracted into the region Γ.*
(iii) *System (1.2) is dissipative.*

Proof. Let $S_\circ > 0$. Consider

$$\frac{dS}{dt} = 1 - S - f_1(S)x < 1 - S.$$

Then

$$S(t) < 1 - \frac{e^{-t}}{1 - S_\circ} \text{ for } S_\circ > 0$$

and

$$\lim_{t\to\infty} \sup S(t) < 1 \text{ for } S_\circ > 0.$$

For

$$\frac{dx}{dt} = x(f_1(S)x - D_1) - f_2(x)y < x(f_1(S)x - D_1) < \delta_1 x,$$

where $\delta_1 = \left(\max_{S\in\Gamma} f_1(s) - D_1\right) < 0$. Then

$$x(t) < x_\circ e^{\delta_1 t}, \ \delta_1 < 0,$$

thus

$$\lim_{t\to\infty} \sup x(t) < x_\circ \text{ for } x_\circ > 0.$$

Similarly we consider the equation

$$\frac{dy}{dt} = y(f_2(x)y - D_2) - f_3(y)z < y(f_2(x)y - D_2) < \delta_2 y,$$

where $\delta_2 = \left(\max_{S\in\Gamma} f_2(x) - D_2\right) < 0$. Then

$$y(t) < y_\circ e^{\delta_2 t}, \ \delta_2 < 0,$$

hence

$$\lim_{t\to\infty} \sup y(t) < y_\circ \quad \text{for } y_\circ > 0.$$

For the z equation

$$\frac{dz}{dt} = z(f_3(y)z - D_3) < z\left(\max_{y\in\Gamma} f_3(y) - D_3\right) < \delta_3 z,$$

where $\delta_3 = \left(\max_{y\in\Gamma} f_3(-y) - D_3\right) < 0$. Then

$$z(t) < z_\circ e^{\delta_3 t}, \ \delta_3 < 0,$$

hence

$$\lim_{t\to\infty} \sup z(t) < z_\circ \text{ for } z_\circ > 0.$$

Thus the solutions of system (1.2) are uniformly bounded and the dissipativity of system (1.2) follows from Definition 2.1. This completes the proof. □

Now, we discuss the existence and local stability of the equilibria of system (1.2). The washout equilibrium point (no prey or predators organisms) for the system (1.2) is denoted by $P_0(1,0,0,0)$. The variational matrix due to linearization of (1.2) is given by

$$J = \begin{pmatrix} -1-\frac{\partial f_1(S)}{\partial S}x & -f_1(S) & 0 & 0 \\ \frac{\partial f_1(S)}{\partial S}x & f_1(S)-D_1-y\frac{\partial f_2(x)}{\partial x} & -f_2(x) & 0 \\ 0 & y\frac{\partial f_2(x)}{\partial x} & f_2(x)-D_2-z\frac{\partial f_3(y)}{\partial y} & -f_3(y) \\ 0 & 0 & z\frac{\partial f_3(y)}{\partial y} & f_3(y)-D_3 \end{pmatrix}. \tag{2.2}$$

The variational matrix J at the trivial equilibrium point $P_0(1,0,0,0)$ is given by

$$J_{P_0(1,0,0,0)} = \begin{pmatrix} -1 & -f_1(1) & 0 & 0 \\ 0 & f_1(1)-D_1 & 0 & 0 \\ 0 & 0 & -D_2- & 0 \\ 0 & 0 & 0 & -D_3 \end{pmatrix}. \tag{2.3}$$

The eigenvalues of the matrix $J_{P_{0(1,0,0,0)}}$ are $\lambda_1 = -1 < 0$, $\lambda_2 = f_1(1) - D_1, \lambda_3 = -D_2 < 0$ and $\lambda_4 = -D_3 < 0$. Thus the eigenvalues of the matrix $J_{P_{0(1,0,0,0)}}$ have negative real parts if $f_1(1)-D_1 < 0$ which leads to the following result.

Theorem 2.2. *If*

$$f_1(1) - D_1 < 0,$$

then the trivial equilibrium point $P_{0(1,0,0,0)}$ is locally asymptotically stable.

Proof. Since all the eigenvalues of the variational matrix $J_{P_{0(1,0,0,0)}}$ have negative real parts if $f_1(1)-D_1 < 0$ holds, then the result follows (see [16, p. 85]). □

Now the non-trivial equilibria of system (1.2) are obtained by solving the system of equations

$$\begin{aligned} &1 - S - f_1(S)x = 0, \\ &x(f_1(s)x - D_1) - f_2(x)y = 0, \\ &y(f_2(x)y - D_2) - f_3(y)z = 0, \\ &z(f_3(y)z - D_3) = 0, \end{aligned} \tag{2.4}$$

subject to the hypotheses of the functions f_i, $i = 1, 2, 3$. The possible equilibria are given as follows:

(i) $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ where S_1 is defined as the unique solution of $f_1(S) - D_1 = 0$.
(ii) $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$ where x_2 is the unique solution of $f_2(x_2) - D_2 = 0$ and S_2 is the unique solution of $f_1(S)x_2 + S = 1$.
(iii) $P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3}y_3)$ where y_3 is defined as the unique solution of $f_3(y) - D_3 = 0$,x_2 is defined as the unique solution of $x = \frac{f_2(x)y_3}{(f_1(S_3)-D_1)}$ and S_3 is defined as the unique solution of $f_1(S)x_3 + S = 1$.

2.1. Existence and local stability of $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$

Consider the system (1.2) restricted to R^+_{Sx} as represented by

$$\begin{aligned} &\frac{dS}{dt} = 1 - S - f_1(S)x, \\ &\frac{dx}{dt} = x(f_1(S) - D_1), \\ &S(0) = S_\circ > 0, x(0) = x_\circ > 0. \end{aligned} \tag{2.5}$$

The following lemma shows the existence of equilibrium point $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$.

Lemma 2.3. *Suppose that there exists* $(S_1, x_1) \in R^+_{Sx}$ *such that*

$$S_1 + x_1 D_1 - 1 = 0 \text{ as } t \to \infty.$$

Then the equilibrium point $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ *exists.*

Proof. By equating the right-hand side of system (2.5) to zero, we have the two surfaces

$$1 - S - f_1(S)x = 0,$$

$$xf_1(S) - xD_1 = 0.$$

Then

$$1 - S = f_1(S)x,$$

$$xD_1 = xf_1(S).$$

Thus $1 - S = xD_1$. □

Now, we discuss the local linearized stability of system (1.2) restricted to a neighborhood of the equilibrium point $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$. The variational matrix due to the linearization of system (1.2) about $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ is given by

$$J_{P_1} = \begin{pmatrix} -1 - \frac{(1-S_1)}{D_1} f_1'(S_1) & f_1(S_1) & 0 & 0 \\ \frac{(1-S_1)}{D_1} f_1'(S_1) & 0 & -f_2\left(\frac{1-S_1}{D_1}\right) & 0 \\ 0 & 0 & f_2\left(\frac{1-S_1}{D_1}\right) - D_2 & 0 \\ 0 & 0 & 0 & -D_3 \end{pmatrix}. \tag{2.6}$$

Henceforth we let J_{22} defines the matrix

$$J_{22} = \begin{pmatrix} -1 - \frac{(1-S_1)}{D_1} f_1'(S_1) & f_1(S_1) \\ \frac{(1-S_1)}{D_1} f_1'(S_1) & 0 \end{pmatrix}. \tag{2.7}$$

The eigenvalues of J_{P_1} are given by $\lambda_1 = f_2(\frac{1-S_1}{D_1}) - D_2$, $\lambda_2 = -D_3 < 0$ and λ_3, λ_4 are the eigenvalues of J_{22} which are given by the quadratic equation

$$\lambda^2 - (\mathrm{Trace}\, J_{22})\lambda + \det J_{22} = 0.$$

By the Routh–Hurwitz criteria (see [16, pp. 84–86]), the eigenvalues of J_{22} have negative real parts if *Trace* $J_{22} < 0$ and $\det J_{22} > 0$. Thus we have the following results.

Theorem 2.4. *If*

(i) $f_2(\frac{1-S_1}{D_1}) - D_2 < 0$,
(ii) $\mathrm{Trace}\, J_{22} < 0$ *and* $\det J_{22} > 0$.

Then the equilibrium point $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ *is locally asymptotically stable.*

Proof. The proof follows by properties of the eigenvalues of the variational matrix for$P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ and Theorem 3.5.1 in [16]. □

Theorem 2.5. *Suppose*

(i) $f_2(\frac{1-S_1}{D_1}) - D_2 < 0$,
(ii) $\mathrm{Trace}\, J_{22} < 0$ *and* $\det J_{22} > 0$.

Then the equilibrium point $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ *is a hyperbolic saddle point and is repelling in both y and z directions locally. In particular, the dimension of the stable manifold* W^+ *and the unstable manifold* W^- *are given by*

$$\mathrm{Dim} W^+\left(P_1\left(S_1, \frac{(1-S_1)}{D_1}, 0, 0\right)\right) = 2, \ \mathrm{Dim} W^-\left(P_1\left(S_1, \frac{(1-S_1)}{D_1}, 0, 0\right)\right) = 2.$$

Proof. The proof is similar to the proof of Theorem 2.5 so it is omitted. □

Existence and local stability of $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$. Consider the system (1.2) restricted to R^+_{Sxy} as represented by

$$\begin{aligned}
\frac{\mathrm{d}S}{\mathrm{d}t} &= 1 - S - f_1(S)x, \\
\frac{\mathrm{d}x}{\mathrm{d}t} &= x(f_1(S) - D_1), -f_2(x)y, \\
\frac{\mathrm{d}y}{\mathrm{d}t} &= y(f_2(x) - D_2), \\
S(0) &= S_\circ > 0, \quad x(0) = x_\circ > 0, \quad y(0) = y_\circ > 0.
\end{aligned} \tag{2.8}$$

The possible equilibria in R^+_{Sxy} are $\overline{P}_1(S_2, \frac{(1-S_2)}{D_1}, 0)$ and $\overline{P}_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2)$.

Using method similar to Lemma 2.3, we can show that $\overline{P}_1(S_2, \frac{(1-S_2)}{D_1}, 0)$ exists in R^+_{Sxy} if there exists S_2 and x_2 such that $S_2 + x_2 D_1 - 1 = 0$ as $t \to \infty$.

We now linearized system (2.8) in the neigbourhood of $\overline{P}_1(S_2, \frac{(1-S_2)}{D_1}, 0)$. The variational matrix is given by

$$J_{\overline{P}_1} = \begin{pmatrix} -1 - \frac{(1-S_1)}{D_1} f_1'(S_1) & f_1(S_1) & 0 \\ \frac{(1-S_1)}{D_1} f_1'(S_1) & 0 & -f_2\left(\frac{1-S_1}{D_1}\right) \\ 0 & 0 & f_2\left(\frac{1-S_1}{D_1}\right) - D_2 \end{pmatrix}.$$

The eigenvalues of $J_{\overline{P}_1}$ are given by $\lambda_1 = f_2(\frac{1-S_1}{D_1}) - D_2$, λ_2 and λ_3 are satisfy the quadratic equation

$$\lambda^2 - (\mathrm{Trace}\, J_{22})\lambda + \det J_{22} = 0,$$

where J_{22} is defined as in Eq. (2.7), with S_1 replaced by S_2. Note that if $\mathrm{Trace}\, J_{22} < 0$ and $\det j_{22} > 0$, then $\mathrm{Re}\,\lambda_2 < 0$ and $\mathrm{Re}\,\lambda_3 < 0$. This leads the following results.

Theorem 2.6. *The equilibrium point* $\overline{P}_1(S_2, \frac{(1-S_2)}{D_1}, 0) \in R^+_{Sxy}$ *is*

(i) *a hyperbolic saddle point if* $f_2(\frac{1-S_1}{D_1}) - D_2 < 0$, *and* $\mathrm{Trace}\, J_{22} < 0$ *with* $\det J_{22} > 0$. *In particular*, $\overline{P}_1$ *is repelling in the y-direction.*
(ii) *asymptotically stable (sink) if* $f_2(\frac{1-S_1}{D_1}) - D_2 < 0$, *and* $\mathrm{Trace}\, J_{22} > 0$ *with* $\det J_{22} < 0$.

Proof. The proof follows directly by inspection of the eigenvalues of the variational matrix for $\overline{P}_1(S_2, \frac{(1-S_2)}{D_1}, 0)$ and by Theorem 3.5.1 of Rao [16]. □

The following theorem proves the existence of the equilibrium point $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$ which will be shown by persistence analysis.

Theorem 2.7. *Suppose*

(i) *Lemma* 2.3 *holds*,
(ii) $\overline{P}_1(S_2, \frac{(1-S_2)}{D_1}, 0)$ *is a unique hyperbolic rest point in* R^+_{Sxy} *and repelling locally in y-direction (See Theorem* 2.6*)*.
(iii) *No periodic nor homoclinic orbits exist in the planes of* R^+_{Sxy}.

Then

$$\lim_{t\to\infty} \inf S(t) > 0,$$
$$\lim_{t\to\infty} \inf x(t) > 0,$$
$$\lim_{t\to\infty} \inf y(t) > 0.$$

In particular, the subsystem in R^+_{Sxy} *exhibits uniform persistence and consequently, the equilibrium point* $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$ *exists.*

Proof. The proof follows from the definition of uniform persistence by Freedman and Ruan [5] with Theorem 4.3 of [11]. □

Now we discuss the local stability of the equilibrium point $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$. The variational matrix due to linearization around the equilibrium point P_2 is

$$J_{P_2} = \begin{pmatrix} -1 - f_1'(S_2)x_2 & -f_1(S_2) & 0 & 0 \\ f_1'(S_2)x_2 & C_1 & 0 & 0 \\ 0 & C_2 & -D_2 & C_3 \\ 0 & 0 & 0 & C_3 - D_3 \end{pmatrix}, \tag{2.9}$$

where

$$C_1 = (1 - \frac{x_2}{D_2} f_2'(x_2))(f_1(S_2) - D_1),$$
$$C_2 = \frac{x_2}{D_2} f_2'(x_2)(f_1(S_2) - D_1),$$
$$C_3 = f_3\left(\frac{x_2}{D_2}(f_1(S_2) - D_1)\right).$$

The corresponding eigenvalues of the variational matrix for $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$ are $\lambda_1 = f_3\left(\frac{x_2}{D_2}(f_1(S_2) - D_1)\right) - D_3, \lambda_2, \lambda_3$ and λ_4 are satisfied the cubic equation

$$\lambda^3 + n_1\lambda^2 + n_2\lambda + n_3 = 0, \tag{2.10}$$

where

$$\begin{aligned} n_1 &= 1 + f_1'(S_2)x_2 + \left(\frac{x_2}{D_2} f_2'(x_2) - 1\right)(f_1(S_2) - D_1), \\ n_2 &= (1 + f_1'(S_2)x_2)\left(\frac{x_2}{D_2} f_2'(x_2) - 1\right)(f_1(S_2) - D_1) + f_1(S_2) f_2'(S_2)x_2 + f_1'(x_2)(f_1(S_2) - D_1)x_2, \\ n_3 &= (1 + f_1'(S_2)x_2)(f_1(S_2) - D_1) f_2'(x_2)x_2. \end{aligned} \tag{2.11}$$

The above discussion leads to the following results.

Theorem 2.8. *Suppose*

(i) $f_3\left(\frac{x_2}{D_2}(f_1(S_2) - D_1)\right) < D_3$,
(ii) $n_1 > 0$ *and* $n_1 n_2 > n_3$, *where* n_1, n_2 *and* n_3 *are defined as in* (2.11).

Then the equilibrium point $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$ *is asymptotically stable.*

Proof. The proof follows immediately by the Routh–Hurwitz criteria and Theorem 3.5.1 in [16]. □

Theorem 2.9. *Let the assumption* (ii) *of Theorem* 2.9 *be satisfied and* $f_3\left(\frac{x_2}{D_2}(f_1(S_2) - D_1)\right) > D_3$. *Then the equilibrium point* $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$ *is a hyperbolic saddle point which is repelling in the z-direction locally. In particular, the stable manifold* $W^+\left(P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)\right)$ *is the* $S - x - y$ *space and the unstable manifold* $W^-\left(P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)\right)$ *is the z-direction with Dim* $W^-(P_2) = 1$.

Proof. The proof is similar to that of Theorem 2.6 so it is omitted. □

3. Global analysis and uniform persistence

In this section we shall deduce sufficient conditions for the existence of a positive equilibrium point $P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3}y_3)$. This will be done by proving that system (1.2) is uniformly persistent (see [13], p. 182). An important condition to show the uniform persistence is:

(H_1) If an equilibrium exists in the interior of any 3-dimensional subspace of R^+_{Sxyz}, it must be globally asymptotically stable with respect to orbits initiating in that interior.

We now derive criteria for the global stability condition (H_1) to be valid. First criterion is concerned with the global asymptotic stability of the equilibrium point $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$. Consider system (1.2) restricted to R^+_{Sx} as depicted by (2.5). We have shown that the 2-dimensional equilibrium $\overline{P}_1(S_1, \frac{(1-S_1)}{D_1})$ exists where Lemma 2.3 holds. Let G be a neighbourhood of any point in R^+_{Sx}. We choose the Liapunov function

$$V(S,x) = \frac{1}{2}c_1(S-S_1)^2 + \frac{1}{2}c_2\left(x - \frac{(1-S_1)}{D_1}\right)^2, \tag{3.1}$$

where c_1 and c_2 are positive constants. Note that V is positive definite with respect to $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ in R^+_{Sx} and a Liapunov function for system (2.5) in G. Now, the derivative of (3.1) along the solution curves of (2.5) in R^+_{Sx} is given by

$$\frac{dV}{dt} = c_1(S-S_1)(1-S-f_1(S)x) + c_2(x-x_1)x(f_1(S)-D_1), \tag{3.2}$$

where $x_1 = \frac{(1-s_1)}{D_1}$. But from (2.5), we have

$$1 = S_1 + f_1(S_1)x_1 \quad \text{and} \quad D_1 = f_1(S_1).$$

Then (3.2) can be written in the following form:

$$\begin{aligned}\frac{dV}{dt} &= c_1(S-S_1)(S_1+f_1(S_1)x_1 - S - f_1(S)x) + c_2(x-x_1)x(f_1(S)-f_1(S_1))\\ &= -c_1(S-S_1)^2 + c_1(S-S_1)(f_1(S_1)x_1 - f_1(S)x) + c_2(x-x_1)x(f_1(S)-f_1(S_1))\\ &= c_{11}(S-S_1)^2 + \frac{1}{2}c_{12}(S-S_1)(x-x_1) + \frac{1}{2}c_{21}(S-S_1)(x-x_1) + c_{22}(x-x_1)^2,\end{aligned} \tag{3.3}$$

where

$$\begin{aligned} c_{11} &= -c_1^2 < 0,\\ c_{12} &= c_{21} = c_1\frac{(f_1(S_1)x_1 - f_1(S)x)}{(x-x_1)},\\ c_{22} &= c_2\frac{x(f_1(S)-f_1(S_1))}{(x-x_1)}.\end{aligned}$$

It is clear from Eq. (3.3) that, the derivative $\frac{dV}{dt}$ can be written in the following form:

$$\frac{dV}{dt} = X^{\mathrm{T}}CX = \langle CX, X\rangle, \tag{3.4}$$

where

$$X = \begin{pmatrix} S-S_1 \\ x-x_1\end{pmatrix} \quad \text{and} \quad C = \begin{pmatrix} c_{11} & \frac{1}{2}c_{12} \\ \frac{1}{2}c_{21} & c_{22}\end{pmatrix}.$$

In particular, C is symmetric and real matrix such that $C = \frac{1}{2}(C^{\mathrm{T}} + C)$ where 'T' denotes transpose.

Theorem 3.1. *The equilibrium point* $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ *is globally asymptotically stable with respect to solution trajectories emanating from* $\mathrm{Int}\,R^+_{Sx}$ *if*

(i) $c_{22} < 0$ *and*
(ii) $c_{11}c_{22} - \frac{1}{4}c_{12}^2 > 0$, *hold.*

Proof. The proof follows from computing the leading principal minors of the matrix C and using Forbenius theorem [13, pp. 177–178]. □

Now, we discuss global asymptotic stability of the equilibrium point $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$ by studying the global asymptotic stability of the rest point $\overline{P}_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2)$, with respect to solutions initiating from $\mathrm{Int}\,R^+_{Sxy}$. Consider the Liapunov function

$$W(S,x,y) = S - S_2 - S_2 \ln\frac{S}{S_2} + \frac{1}{2}k_1(x-x_2)^2 + \frac{1}{2}k_2(y-y_2)^2, \tag{3.5}$$

where $y_2 = \frac{(f_1(S_2)-D_1)}{D_2}x_2$ and k_1 and k_2 are positive constants. The derivative of (3.5) along the solution curves of (2.8) in $\operatorname{Int} R^+_{Sx}$ is given by the expression

$$\frac{dW}{dt} = \frac{(S-S_2)}{S}(1 - S - f_1(S)x) + k_1(x-x_2)(x(f_1(S)-D_1) - f_2(x)y) + k_2(y-y_2)y(f_2(x)-D_2). \tag{3.6}$$

Using (2.8) we have $1 = S_2 + f_1(S_2)x_2, D_1 = f_1(S_2) - \frac{y_2}{x_2}f_2(x_2)$ and $D_2 = f_2(x_2)$. Then (3.6) becomes

$$\begin{aligned}\frac{dW}{dt} &= \frac{(S-S_2)}{S}(S_2 + f_1(S_2)x_2 - S - f_1(S)x) + k_1(x-x_2)\left(x\left(f_1(S) - f_1(S_2) + \frac{y_2}{x_2}f_2(x_2)\right) - f_2(x)y\right)k_2(y-y_2)\\ &\quad \times (f_2(x) - f_2(x_2))y = -\frac{(S-S_2)^2}{S} + \frac{(f_1(S_2)x_2 - f_1(S)x)}{S(S-S_2)}(S-S_2)(x-x_2) - k_1\frac{(f_1(S_2)-f_1(S)y)}{(S-S_2)}(S-S_2)\\ &\quad \times (x-x_2) + k_1\frac{\left(\frac{y_2}{x_2}f_2(x_2) - f_2(x)y\right)}{(x-x_2)}(x-x_2)^2 + k_2\frac{y(f_2(x)-f_2(x_2))}{(y-y_2)}(y-y_2)^2.\end{aligned} \tag{3.7}$$

Let $X = \begin{pmatrix} v_1 \\ v_2 \\ v_3 \end{pmatrix}$ such that $\begin{pmatrix} v_1 = S - S_2 \\ v_2 = x - x_2 \\ v_3 = y - y_2 \end{pmatrix}$ and set $b_{11} = \frac{-1}{S} < 0$, $b_{23} = 0$, $b_{12} = \frac{(f_1(S_2)x_2 - f_1(S)x)}{S(S-S_2)} - k_1\frac{(f_1(S_2)-f_1(S)y)}{S(S-S_2)}$, $b_{22} = k_1\frac{\left(\frac{y_2}{x_2}f_2(x_2) - f_2(x)y\right)}{(x-x_2)}$ and $b_{33} = k_2\frac{y(f_2(x)-f_2(x_2))}{y-y_2}$.

Then (3.7) can be written in the following quadratic form:

$$\frac{dW}{dt} = X^T B X, \tag{3.8}$$

where $B = \begin{pmatrix} b_{11} & \frac{1}{2}b_{12} & \frac{1}{2}b_{13} \\ \frac{1}{2}b_{12} & b_{22} & \frac{1}{2}b_{23} \\ \frac{1}{2}b_{13} & \frac{1}{2}b_{23} & b_{33} \end{pmatrix}$, $b_{ij} = b_{ji},\ i,j = 1, 2, 3$ and B is a symmetric and real matrix such that $B = \frac{1}{2}(B^T + B)$.

The eigenvalues of B are given by the cubic equation

$$\lambda^3 + m_1\lambda^2 + m_2\lambda + m_3 = 0, \tag{3.9}$$

where

$$\begin{aligned} m_1 &= \operatorname{Trace} B = -(b_{11} + b_{22} + b_{33}),\\ m_2 &= b_{11}b_{22} + b_{11}b_{33} - \frac{1}{4}b_{12}^2,\\ m_3 &= \det B = b_{33}\left(b_{11}b_{22} - \frac{1}{4}b_{12}^2\right). \end{aligned} \tag{3.10}$$

Hence by the Routh–Hurwitz criteria and Lemma 6.1 of Nani and Freedman [13], the matrix B is negative definite if

$m_1 > 0,\ m_3 > 0$ and $m_1 m_2 > m_3$.

The previous discussion leads to the following result.

Theorem 3.2. *The rest point* $\overline{P}_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2) \in R^+_{Sxy}$ *is globally asymptotically stable with respect to solutions trajectories initiating from* $\operatorname{Int} R^+_{Sxy}$ *if*

(i) $b_{22} < 0, b_{33} < 0$,
(ii) $b_{11}b_{22} - \frac{1}{4}b_{12}^2 > 0$.

Proof. The proof is similar to the proof of Theorem 3.1, so it is omitted. □

Now, we present some results about Persistence, uniform persistence and finally give sufficient conditions for the existence of the positive interior equilibrium point $P_3(S_3, x_3, y_3\frac{(f_2(x_3)-D_2)}{D_3}y_3)$. We first state the following lemma of Butler–McGehee [4] which will be needed for our result.

Lemma 3.3 ([4, p. 227]). *Let P be an isolated hyperbolic equilibrium point in the omega limit set $\Omega(X)$ of an orbit $v(X)$. Then $\Omega(X) = P$ or there exit points Q^+ and Q^- in $\Omega(X)$ with $Q^+ \in W^+(P)$ and $Q^- \in W^-(P)$.*

Theorem 3.4. *Assume system (1.2) is such that*

(i) $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ *is a hyperbolic saddle point and is repelling in both y and z directions locally (see Theorem 2.5).*
(ii) $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$ *is a hyperbolic saddle point which is repelling in the z-direction locally (see Theorem 2.19 (i)).*
(iii) *System (1.2) is dissipative and solutions initiating in R^+_{Sxy} are eventually uniformly bounded (see Theorem 2.2).*
(iv) *The equilibria $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ and $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$ are globally asymptotically stable with respect to R^+_{Sx} and R^+_{Sxy}, respectively.*

Then system (1.2) is uniformly persistence.

Proof. The proof depends on Lemma 3.3. Let Γ be the region defined as in Theorem 2.2. We have shown in Theorem 2.2 that Γ is positively invariant and any solution of system (1.2) initiating at a point in R^4_+ is eventually uniformly bounded. However, $P_1 = P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ and $P_2 = P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0)$ are the only compact invariant sets on ∂R^4_+. Let $M = P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3}y_3)$ be such that $M \in \mathrm{Int}\, R^4_+$. The proof is completed by showing that no point $Q_i \in \partial R^4_+$ belongs to the omega limit set $\Omega(M)$ First, we prove that $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0) \notin \Omega(M)$. Suppose that the inverse is true, that is, $P_1 \in \Omega(M)$ then by Lemma 3.3, there exists a point $Q_1^+ \in W^+(P_1) \setminus \{P_1\}$ such that $Q_1^+ \in \Omega(M)$. But $W^+(P_1) \cap (R^4_+ \setminus \{P_1\}) = \phi$. This contradicts the positive invariance property of $\Gamma \subset R^4_+$. Thus $P_1 \in \Omega(M)$. Second, we show that $P_2 \notin \Omega(M)$. If $P_2 \in \Omega(M)$, then there exists a point $Q_2^+ \in W^+(P_2) \setminus \{P_2\}$such that $Q_2^+ \in \Omega(M)$ by Lemma 3.3. But $W^+(P_2) \cap (InR^4_+) = \phi$ and P_2 is globally asymptotically stable with respect to R^+_{Sxy}. This implies that the closure of the orbit $\overline{O(Q_2^+)}$ through Q_2^+ either contains P_2 or unbounded This is contradiction. Hence $P_2 \notin \Omega(M)$. Third, we prove that $\partial R^4_+ \cap \Omega(M) = \phi$. Suppose that $\partial R^4_+ \cap \Omega(M) \neq \phi$. Let $Q \in \partial R^4_+$ and $Q \in \Omega(M)$. Then the closure $\overline{O(Q)}$ of the orbit Q, must either contain P_1 and P_2 or unbounded This gives a contradiction. Hence $\partial R^4_+ \cap \Omega(M) = \phi$. Finally, we see that if P_1 is unstable, then $W^+(P_1) \cap (R^4_+ \setminus \{P_1\}) = \phi$, and $W^-(P_1) \cap (R^4_+ \setminus \{P_1\}) \neq \phi$. Similarly if P_2 is unstable, then $W^+(P_2) \cap (\mathrm{Int}\, R^4_+) = \phi$ and $W^-(P_2) \cap (\mathrm{Int}\, R^4_+) \neq \phi$. Then the uniform persistence follows since $\Omega(M)$ must be in $\mathrm{Int}\, R^4_+$. This completes the proof. □

Remark 1. The global asymptotic stability of the equilibria P_1 and P_2 with respect to R^+_{Sx} and R^+_{Sxy}, respectively, implies that the boundary flow is isolated and a cyclic with respect to Γ. The uniform persistent of system (1.2) implies that a positive interior equilibrium of the form $P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3}y_3)$ exists (See [5]).

4. Bifurcation analysis

In this section, we discuss Hopf Andronov–Poncare bifurcation theory for system (1.2) with a bifurcation real parameter μ. In particular, μ is chosen such that the per-capita growth rate function f_1 is a function of S and μ. Then we have

$$\begin{aligned}
\frac{dS}{dt} &= 1 - S - f_1(S;\mu)x,\\
\frac{dx}{dt} &= x(f_1(S;\mu)x - D_1) - f_2(x)y,\\
\frac{dy}{dt} &= y(f_2(x)y - D_2) - f_3(y)z,\\
\frac{dz}{dt} &= z(f_3(y)z - D_1),\\
S(0) &= S_\circ > 0, \quad x(0) = x_\circ > 0, \quad y(0) = y_\circ > 0, \quad z(0) = z_\circ > 0.
\end{aligned} \tag{4.1}$$

The system (4.1) can be recast into the form

$$X^{\cdot} = F(X;\mu), X(0) = X_\circ > 0, \tag{4.2}$$

where $X = \begin{pmatrix} S \\ x \\ y \\ z \end{pmatrix}$, $X_\circ = \begin{pmatrix} S_\circ \\ x_\circ \\ y_\circ \\ z_\circ \end{pmatrix}$ and μ is a bifurcation parameter. The function $F(X;\mu)$ is a $C^r(r \geqslant 5)$ on an open set in $R^4_+ \times R$. Let $P_\mu = \left\{P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0; \mu), P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0; \mu), P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3}y_3; \mu)\right\}$, be the set of equilibria of system (4.1) such that $F(P_\mu) = 0$ for some $\mu \in R$ on sufficiently large open set G containing each member of P_μ. We are interested in studying how the orbit structure near P_μ changes as μ varied. The following result shows that the Hopf bifurcation cannot occur at the equilibrium point $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$.

Corollary 4.1. *Assume that Theorem* 2.6 *is satisfied. Then the Hopf bifurcation cannot occur at* $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$.

Proof. The proof follows from the fact that when Theorem 2.6 holds, then P_1 is a hyperbolic saddle point and its stable manifold lies along one axis. □

Now, we must obtain stability properties of the equilibria $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0; \mu)$ and $P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3}y_3; \mu)$ and then vary μ in order to compute the desired Hopf bifurcation for $\mu = \mu_1^*$ and $\mu = \mu_2^*$ around P_2 and P_3, respectively. First we consider Hopf bifurcation analysis for $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0; \mu)$. The linearization of system (4.1) about P_2 for any values of μ is given by

$$\Psi^{\cdot} = J_\mu(P_2)\Psi, \Psi \in R^+,$$

where

$$J_\mu(P_2) = \begin{pmatrix} -1 - f_1'(S_2;\mu)x_2 & -f_1(S_2;\mu) & 0 & 0 \\ +f_1'(S_2;\mu)x_2 & A_1 & 0 & 0 \\ 0 & A_2 & -D_2 & A_3 \\ 0 & 0 & 0 & A_3 - D_3 \end{pmatrix} \tag{4.3}$$

and

$$\begin{aligned} A_1 &= \left(1 - \frac{x^2}{D_2}f_2'(x_2)(f_1(S_2;\mu) - D_1\right), \\ A_2 &= \frac{x_2}{D_2}f_2'(x_2)(f_1(S_2;\mu) - D_1), \\ A_3 &= f_3\left(\frac{x_2}{D_2}(f_1(S_2;\mu) - D_1)\right). \end{aligned} \tag{4.4}$$

The eigenvalues of the matrix $J_\mu(P_2)$ are $\lambda_1 = f_3\left(\frac{x_2}{D_2}(f_1(S_2;\mu) - D_1)\right) - D_3$, λ_i, $i = 2,3,4$ satisfy the cubic equation

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \tag{4.5}$$

where

$$\begin{aligned} a_1 &= 1 + f_1'(S_2;\mu)x_2 + \left(\frac{x^2}{D_2}f_2'(x_2) - 1\right)(f_1(S_2;\mu) - D_1), \\ a_2 &= (1 + f_1'(S_2;\mu)x_2)\left(\frac{x^2}{D_2}f_2'(x_2) - 1\right)(f_1(S_2;\mu) - D_1) + f_1(S_2;\mu)f_1'(S_2;\mu)x_2 + f_2'(x_2)(f_1(S_2;\mu) - D_1)x_2, \\ a_3 &= (1 + f_1'(S_2;\mu)x_2)(f_1(S_2;\mu) - D_1)f_2'(x_2)x_2. \end{aligned}$$

By the Routh–Hurwitz criteria (See [16], p. 185) necessary and sufficient conditions for all the roots of (4.5) to have negative real parts are

$$a_1 > 0, \quad a_3 > 0 \quad \text{and} \quad a_1a_2 > a_3. \tag{4.6}$$

It is clear as in [2], that the constant term is positive because of $S_1 < S_2$. Now assume that the following hypothesis (H_2) $f_2'(x_2)x_2 > D_2$ and $f_1(S_2;\mu) > D_1$ holds.

Then $a_1 > 0$ and $a_3 > 0$. Clearly (4.5) has two pure imaginary roots if and only if

$$a_1a_2 = a_3 \tag{4.7}$$

for some values of μ say, μ_1^*. Since at $\mu = \mu_1^*$ there is an interval containing μ_1^*, say $(\mu_1^* - \varepsilon, \mu_1^* + \varepsilon)$ for some $\varepsilon > 0$ for which $\mu \in (\mu_1^* - \varepsilon, \mu_1^* + \varepsilon)$. Thus for $\mu \in (\mu_1^* - \varepsilon, \mu_1^* + \varepsilon)$ the characteristic equation (4.5) cannot have positive real roots. For $\mu = \mu_1^*$ we have (see [6, p. 80])

$$(\lambda^2 + a_2)(\lambda + a_1) = 0, \tag{4.8}$$

which has three roots $\lambda_1 = i\sqrt{a_2}$, $\lambda_2 = -i\sqrt{a_2}$ and $\lambda_3 = -a_1$. For $\mu \in (\mu_1^* - \varepsilon, \mu_1^* + \varepsilon)$ the roots λ_1, λ_2 and λ_3 have in general the form

$$\begin{aligned} \lambda_1(\mu) &= \alpha(\mu) + i\beta(\mu), \\ \lambda_2(\mu) &= \alpha(\mu) - i\beta(\mu), \\ \lambda_3(\mu) &= -a_1(\mu). \end{aligned}$$

To apply Hopf bifurcation theorem to (4.1) (see [7], p. 185) we need to verify the transversality condition

$$Re\left[\frac{d\lambda_i}{d\mu}\right]_{\mu=\mu_1^*} \neq 0, \ i = 1, 2, 3. \tag{4.9}$$

Substituting $\lambda_1(\mu) = \alpha(\mu) + i\beta(\mu)$, and $\lambda_2(\mu) = \alpha(\mu) - i\beta(\mu)$ into (4.5), and calculating the derivative, we obtain

$$\begin{aligned} A(\mu)\alpha'(\mu) - B(\mu)\beta'(\mu) + C(\mu) &= 0, \\ B(\mu)\alpha'(\mu) + A(\mu)\beta'(\mu) + D(\mu) &= 0, \end{aligned} \tag{4.10}$$

where

$$\begin{aligned} A(\mu) &= 3\alpha^2(\mu) + 2a_1(\mu)\alpha(\mu) + a_2(\mu) - 3\beta^2(\mu), \\ B(\mu) &= 6\alpha(\mu)\beta(\mu) + 2a_1(\mu)\beta(\mu), \\ C(\mu) &= \alpha^2(\mu)a_1'(\mu) + a_2'(\mu)\alpha(\mu) + a_3'(\mu) - a_1'(\mu)\beta^2(\mu), \\ D(\mu) &= 2\alpha(\mu)\beta(\mu)a_1'(\mu) + a_2'(\mu)\beta(\mu). \end{aligned} \tag{4.11}$$

Since $A(\mu)C(\mu) + B(\mu)D(\mu) \neq 0$, we have

$$\text{Re}\left[\frac{d\lambda_i}{d\mu}\right]_{\mu=\mu_1^*} = \frac{A(\mu)C(\mu) + B(\mu)D(\mu)}{A^2(\mu) + B^2(\mu)} \neq 0, \ i = 1, 2, 3 \quad \text{and} \quad \lambda_3(\mu_1^*) = -a_1(\mu_1^*) \neq 0.$$

We summarize the above discussion in the following result.

Theorem 4.2. *Assume that $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2}x_2, 0; \mu)$ exists and the assumption (H_2) holds. Then system (4.1) exhibits a Hopf bifurcation in the first octant leading to a family of periodic solutions that bifurcates from P_2 for suitable values of μ in the neighbourhood of μ_1^*.*

Now we study the Hopf bifurcation at the equilibrium point $P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3}y_3; \mu)$. The variational matrix corresponding to $P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3}y_3; \mu)$ is given by

$$J_\mu(P_3) = \begin{pmatrix} a_{11} & a_{12} & 0 & 0 \\ a_{21} & a_{22} & a_{23} & 0 \\ 0 & a_{32} & a_{33} & a_{34} \\ 0 & 0 & a_{43} & 0 \end{pmatrix}, \tag{4.12}$$

where

$$a_{11} = -1 - f_1'(S_3; \mu)x_3, \quad a_{12} = f_1(S_3; \mu), \quad a_{21} = f_1'(S_3; \mu)x_3,$$

$$a_{22} = \left(1 - \frac{f_2'(x_3)}{f_2(x_3)}x_3\right)(f_1(S_3; \mu) - D_1), \quad a_{23} = -f_2(x_3), \quad a_{32} = y_3 f_2'(x_3),$$

$$a_{33} = \left(1 - \frac{y_3}{D_3}f_3'(y_3)\right)(f_2(x_3) - D_2), \quad a_{34} = -f_3(y_3) \quad \text{and} \quad a_{43} = \frac{y_3}{D_3}(f_2(x_3) - D_2).$$

The characteristic equation corresponding to $J_\mu(P_3)$ obeys

$$\lambda^4 + d_1\lambda^3 + d_2\lambda^2 + d_3\lambda + d_4 = 0. \tag{4.13}$$

The coefficients d_i, $i = 1,2,3,4$ are given by

$$d_1 = -\mathrm{Trace}\,J_\mu(P_3) = -(a_{11} + a_{22} + a_{33}),$$

$$d_2 = a_{22}a_{33} + a_{11}a_{33} + a_{11}a_{22} - a_{34}a_{43} - a_{12}a_{21} - a_{23}a_{32},$$

$$d_3 = a_{12}a_{21}a_{33} + a_{34}a_{43}a_{11} + a_{23}a_{32}a_{11} + a_{34}a_{43}a_{22} - a_{11}a_{22}a_{33},$$

$$d_4 = a_{12}a_{21}a_{34}a_{43} - a_{11}a_{22}a_{34}a_{43}.$$

By the Routh–Hurwitz criteria [16] the roots of (4.13) have negative real parts if and only if the following hypotheses:

(H_3) $d_1 > 0$, $d_3 > 0$, $d_4 > 0$,
(H_4) $d_1 d_2 d_3 > (d_3)^2 + (d_1)^2 d_4$, hold.

In order to apply Hopf bifurcation theory, we must violate either (H_3) and (H_4) The characteristic equation (4.13) can be factored into the form

$$(\lambda^2 + \theta_1)(\lambda + \theta_2)(\lambda + \theta_3) = 0, \theta_i > 0, \; i = 1, 2, 3,$$

where

$$d_1 = \theta_2 + \theta_3,$$

$$d_2 = \theta_2\theta_3 + \theta_1,$$

$$d_3 = \theta_1(\theta_2 + \theta_3),$$

$$d_4 = \theta_1\theta_2\theta_3,$$

which implies

$$\theta_1 = \frac{d_4}{d_1}, \quad \theta_2 = \frac{d_1(d_2d_3 - d_4)}{d_2d_4} \quad \text{and} \quad \theta_3 = \frac{d_1d_4}{d_2d_3 - d_4}.$$

In particular, the set of roots of (4.13) is given by $P_3(\mu) = \{i\sqrt{\theta_1}, -i\sqrt{\theta_1}, -\theta_2, -\theta_3\}$. Then Eq. (4.13) has two pure imaginary roots for some value of μ say $\mu = \mu_2^*$. But for $\mu \in (\mu_2^* - \varepsilon, \mu_2^* + \varepsilon)$ the roots are in general form

$$\lambda_1(\mu) = \alpha(\mu) + i\beta(\mu),$$
$$\lambda_2(\mu) = \alpha(\mu) - i\beta(\mu),$$
$$\lambda_3(\mu) = -\theta_3,$$
$$\lambda_4(\mu) = -\theta_4.$$

Now, we apply Hopf bifurcation theorem for system (4.1) by satisfying Hopf transversality condition (4.9). Substituting $\lambda_1(\mu) = \alpha(\mu) + i\beta(\mu)$ and $\lambda_2(\mu) = \alpha(\mu) - i\beta(\mu)$ into Eq. (4.13) and computing the derivatives with respect to μ, we get

$$\begin{aligned} &\overline{A}(\mu)\alpha'(\mu) - \overline{B}(\mu)\beta'(\mu) + \overline{C}(\mu) = 0, \\ &\overline{B}(\mu)\alpha'(\mu) + \overline{A}(\mu)\beta'(\mu) + \overline{D}(\mu) = 0, \end{aligned} \tag{4.14}$$

where

$$\overline{A}(\mu) = 4\alpha(\alpha^2 - \beta^2) - 8\alpha\beta^2 + 3d_1(\alpha^2 - \beta^2) + 2\alpha d_1 + d_4,$$

$$\overline{B}(\mu) = 4\beta(\alpha^2 - \beta^2) - 8\alpha^2\beta + 6\alpha\beta d_1 + 2\beta d_2,$$

$$\overline{C}(\mu) = d_1'[\alpha(\alpha^2 - \beta^2) - 2\alpha\beta^2] + d_2'(\alpha^2 - \beta^2) + \alpha d_3' + d_4',$$

$$\overline{D}(\mu) = d_1'[\beta(\alpha^2 - \beta^2) - 2\alpha^2\beta] + 2\alpha\beta d_2' + \beta d_3'.$$

Thus

$$Re\left[\frac{d\lambda_i}{d\mu}\right]_{\mu=\mu_1^*} = \alpha'(\mu_2^*) = \left|\frac{\overline{A}(\mu)\overline{C}(\mu) + \overline{B}(\mu)\overline{D}(\mu)}{(\overline{A}(\mu))^2 + (\overline{B}(\mu))^2}\right|_{\mu=\mu_2^*} \neq 0,$$

since $\overline{A}(\mu_2^*)\overline{C}(\mu_2^*) + \overline{B}(\mu_2^*)\overline{D}(\mu_2^*) \neq 0$. The above discussion leads to the following result.

Theorem 4.3. *Suppose*

(i) *System (4.1) is uniformly persistent.*
(ii) $P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3} y_3)$ *exists.*
(iii) $d_i > 0$, $i = 1, 2, 3, 4$ *and* $d_2 d_3 > d_4$, *be satisfied.*

Then system (4.1) exhibits a Hopf Andronov–Poincare bifurcation in the first orthant, leading to a family of periodic solutions bifurcates from P_3 for suitable values of μ in the neighborhood of $\mu = \mu_2^*$.

5. Discussion

In this paper, we used a food chain system with one prey $x(t)$ and two predators $y(t)$ and $z(t)$ in the chemostat. In this case, the prey consumes the nutrient and the predator $y(t)$ consumes the prey but the predator $y(t)$ does not consumes the nutrient. Also, the predator $z(t)$ consumes the predator $y(t)$ but the predator $z(t)$ does not consume the nutrient or the prey. A general monotone response functions are considered and removal rates are different. The considered system is extended to the system of [2], which is more general and realistic than the system used in [11]. The main difficulty is that a conservation law is lost due to the different removal rates. In this case, the system can not be reduced to 3-dimensional system and therefore we must study the full system. We found that the trivial equilibrium $P_0(1, 0, 0, 0)$ (no predator or prey organisms) of system (1.2) is locally asymptotically stable if $f_1(1) > D_1$ holds. Also, we introduced sufficient conditions for the existence and local stability of the equilibria $P_1(S_1, \frac{(1-S_1)}{D_1}, 0, 0)$ and $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2} x_2, 0$ for system (1.2).

We constructed Liapunov functions on the base of those of Nani and Freedman [13], to show that the rest points $\overline{P}(S_1, \frac{(1-S_1)}{D_1})$ and $\overline{P}_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2} x_2)$ are globally asymptotically stable. The global asymptotic stability of $\overline{P}_1$ and $\overline{P}_2$ implies that the predators will be washout in the chemostat regardless of the initial density levels of prey and predators. Next, when $P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3} y_3)$ exists then the prey and predators coexist in the sense that the system (1.2) is uniformly persistent. The technique used in this result is similar to the technique of Freedman [4]. We presented generalized criteria as in Freedman [6] for Hopf bifurcation to occur at $P_2(S_2, x_2, \frac{(f_1(S_2)-D_1)}{D_2} x_2, 0)$ leading to periodic orbits. After that, we introduced theoretical criteria under which Hopf Andronov–Poincare bifurcation occur leading to a family of periodic solutions bifurcates form the interior of the equilibrium point $P_3(S_3, x_3, y_3, \frac{(f_2(x_3)-D_2)}{D_3} y_3)$. We claim that our obtained results improve and partially generalize some those given in [2] and [11].

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