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THE DYNAMICS OF A TRI-TROPHIC FOOD CHAIN IN THE CHEMOSTAT

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Abstract: A tri-trophic food chain in the chemostat is studied and analyzed. The Michaelis-Menten functional response is used for all trophic levels. It is shown that the basic reproductive numbers of the prey and predator affect the dynamics of this model. Also using the dilution rate of the chemostat as a bifurcation parameter it is shown that the model undergoes a sequence of Hopf bifurcations.

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1. Introduction

In this paper the dynamics of a three species food chain model is studied. These dynamics have been examined by many researchers, see for example [1], [3], [5], [6], [7], [9]. It has been shown that these models exhibits a rich set of dynamical behaviors, such as limit cycles and chaos. Most of these studies assumed that the prey population grows logistically in the absence of predators [3]. Several studies used bifurcation analysis to find out if coexistence of all trophic levels is possible [1], [4], [5].

In this paper the tri-trophic food chain is studied. The species at the

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lowest trophic level is called the prey population. Its growth rate depends on the concentration of nutrient subtrate in the chemostat. The Michaelis-Menten functional response is used for all trophic levels.

The aim of this paper is to study the dynamics of the system, in particular, global stability of equilibrium points. Also the dilution rate of the chemostat is used as a bifurcation parameter to show that the model undergoes a sequence of Hopf bifurcations.

The paper is organized as follows. In Section 2 the model of the food chain is described. Section 3 is devoted to discussing the dynamical behavior of the food chain. In Section 4 a Hopf bifurcation of solutions is discussed. Finally a short discussion is given in Section 5.

2. The Model

In this paper we consider the food chain that consists of subtrate $X_o(t)$, prey (trophic level 1) $X_1(t)$, predator (trophic level 2) $X_2(t)$ and top predator (trophic level 3) $X_3(t)$. It is assumed that the uptake of trophic level i is modeled by the Michaelis-Menten kinetic $\frac{M_i X_{i-1}}{A_i + X_{i-1}}$ where M_i is the maximal uptake rate and A_i is the half-saturation constant of trophic level i. The conversion factor from trophic level $i-1$ to trophic level i will be denoted by C_i. The maintenance rate coefficient of trophic level i will be denoted by K_i, see [1]. The specific growth rate of trophic level i is given by $C_i \frac{M_i X_{i-1}}{A_i + X_{i-1}} - K_i$. Our model is given by the following system of ordinary differential equations

$$
\begin{aligned}
X_o'(t) &= (X_r - X_o)D - \frac{M_1 X_o}{A_1 + X_o} X_1 \,, \qquad (2.1)\\
X_1'(t) &= C_1 \frac{M_1 X_o}{A_1 + X_o} X_1 - K_1 X_1 - D X_1 - \frac{M_2 X_1}{A_2 + X_1} X_2 \,,\\
X_2'(t) &= C_2 \frac{M_2 X_1}{A_2 + X_1} X_2 - K_2 X_2 - D X_2 - \frac{M_3 X_2}{A_3 + X_2} X_3 \,,\\
X_3'(t) &= C_3 \frac{M_3 X_2}{A_3 + X_2} X_3 - K_3 X_3 - D X_3 \,,
\end{aligned}
$$

where D is the dilution rate of the chemostat and X_r is the concentration of the input subtrate, and all parameters are positive values.

System (2.1) can be simplified as in [11] by letting

$$
s = X_o, \quad s^o = X_r, \quad x = \frac{X_1}{C_1}, \quad y = \frac{X_2}{C_1 C_2}, \quad z = \frac{X_3}{C_1 C_2 C_3}
$$

to obtain the system

$$\begin{aligned} s'(t) &= (s^o - s)d - \frac{m_1 s}{a_1 + s}x\,, \\ x'(t) &= \frac{m_1 s}{a_1 + s}x - d_1 x - \frac{m_2 x}{a_2 + x}y\,, \\ y'(t) &= \frac{m_2 x}{a_2 + x}y - d_2 y - \frac{m_3 y}{a_3 + y}z\,, \\ z'(t) &= \frac{m_3 y}{a_3 + y}z - d_3 z\,, \end{aligned} \tag{2.2}$$

where s^o, d, m_i, a_i and d_i are all positive and it is assumed that $m_i > d_i$.

3. Dynamical Behavior of the Model

The first step is to show that solutions of system (2.2) are nonnegative and bounded, in other words the system is dissipative.

Theorem 1. *Solutions of (2.2) are nonnegative and bounded.*

Proof. Since $s' \underset{s=0}{|} > 0$, $x' \underset{x=0}{|} = y' \underset{y=0}{|} = z' \underset{z=0}{|} = 0$, solutions remain nonnegative for $t \geq 0$. Furthermore, if $\psi = s + x + y + z$, then $\psi' = s' + x' + y' + z' = (s^o - s)d - d_1 x - d_2 y - d_3 z = s^o d - sd - d_1 x - d_2 y - d_3 z$. Let $\hat{d} = \min\{d, d_1, d_2, d_3\}$, then $\psi' \leq s^o d - \hat{d}\psi$. If $u(t)$ is a solution of $u' = s^o d - \hat{d}u$ with $u(0) = \psi(0)$, then $u(t) = \frac{s^o d}{\hat{d}}(ce^{-\hat{d}t} + 1)$ and $\lim_{t\to\infty} u(t) = \frac{s^o d}{\hat{d}}$. But $\psi(t) \leq u(t)$ which means that $s(t) + x(t) + y(t) + z(t) \leq u(t)$, so we may conclude that $\lim_{t\to\infty} \sup[s(t) + x(t) + y(t) + z(t)] \leq \frac{s^o d}{\hat{d}}$. Therefore solutions of (2.2) are bounded and the system is dissipative. In particular since $s' \underset{s=s_o}{|} \leq 0$, we have $s(t) \leq s^o \ \forall t \geq 0$. This completes the proof. $\square$

The next step is to find equilibria of system (2.2). First we have the trivial solution $E_o = (s^o, 0, 0, 0)$. Secondly, we have the equilibrium point $E_1 = (s_1, x_1, 0, 0)$, where $s_1 = \frac{d_1 a_1}{m_1 - d_1}$ and $x_1 = \frac{d[s^o m_1 - d_1(s^o + a_1)]}{d_1(m_1 - d_1)} = \frac{d(s^o - s_1)(a_1 + s_1)}{m_1 s_1}$.$s_1 > 0$ and $x_1 > 0$ provided that $\frac{s^o m_1}{s^o + a_1} > d_1$. The third equilibrium point, see [1], represents the possibility of coexistence between prey and predator $E_2 = (s_2, x_2, y_2, 0)$, where $x_2 = \frac{d_2 a_2}{m_2 - d_2}$, $d(s^o - s_2) = \frac{m_1 s_2}{a_1 + s_2}x_2$, $y_2 = \frac{a_2 + x_2}{m_2}(\frac{m_1 s_2}{a_1 + s_2} - d_1)$.$s_2 > 0$, $x_2 > 0$ and $y_2 > 0$ provided that $\frac{x_1 m_2}{x_1 + a_2} > d_2$.

The method of linearization is used to study the local stability of these equilibria. To do this we need the Jacobian matrix (variation matrix) J of the system. This matrix is given by

$$J = \begin{bmatrix} -d-\frac{m_1a_1}{(a_1+s)^2}x & -\frac{m_1s}{a_1+s} & 0 & 0 \\ \frac{m_1a_1}{(a_1+s)^2}x & \frac{m_1s}{a_1+s}-d_1-\frac{m_2a_2}{(a_2+x)^2}y & -\frac{m_2x}{a_2+x} & 0 \\ 0 & \frac{m_2a_2}{(a_2+x)^2}y & \frac{m_2x}{a_2+x}-d_2-\frac{m_3a_3}{(a_3+y)^2}z & -\frac{m_3y}{a_3+y} \\ 0 & 0 & \frac{m_3a_3}{(a_3+y)^2}z & \frac{m_3y}{a_3+y}-d_3 \end{bmatrix}.$$

The Jacobian matrix at the equilibrium point E_o is given by

$$J(E_o) = \begin{bmatrix} -d & -\frac{m_1s^o}{a_1+s^o} & 0 & 0 \\ 0 & \frac{m_1s^o}{a_1+s^o}-d_1 & 0 & 0 \\ 0 & 0 & -d_2 & 0 \\ 0 & 0 & 0 & -d_3 \end{bmatrix},$$

at the equilibrium point E_1 is given by

$$J(E_1) = \begin{bmatrix} -d-\frac{m_1a_1}{(a_1+s_1)^2}x_1 & -\frac{m_1s_1}{a_1+s_1} & 0 & 0 \\ \frac{m_1a_1}{(a_1+s_1)^2}x_1 & 0 & -\frac{m_2x_1}{a_2+x_1} & 0 \\ 0 & 0 & \frac{m_2x_1}{a_2+x_1}-d_2 & 0 \\ 0 & 0 & 0 & d_3 \end{bmatrix}$$

and at the equilibrium point E_2 is given by

$$J(E_2) = \begin{bmatrix} -d-\frac{m_1a_1}{(a_1+s_2)^2}x_2 & -\frac{m_1s_2}{a_1+s_2} & 0 & 0 \\ \frac{m_1a_1}{(a_1+s_2)^2}x_2 & \frac{m_1s_2}{a_1+s_2}-d_1-\frac{m_2a_2}{(a_2+x_2)^2}y_2 & -\frac{m_2x_2}{a_2+x_2} & 0 \\ 0 & \frac{m_2a_2}{(a_2+x_2)^2}y_2 & 0 & -\frac{m_3y_2}{a_3+y_2} \\ 0 & 0 & 0 & \frac{m_3y_2}{a_3+y_2}-d_3 \end{bmatrix}.$$

Studying $J(E_o)$ and $J(E_1)$ we can easily determine the eigenvalues and therefore the following results are found:

E_o is locally asymptotically stable if $\frac{m_1s^o}{a_1+s^o} < d_1$ which implies that $x_1 < 0$ and therefore E_1 does not exist.

E_1 is locally asymptotically stable if $\frac{m_2x_1}{a_2+x_1} < d_2$ which implies that E_2 does not exist.

But for the equilibrium point E_2 the case is not as easy. The eigenvalues of $J(E_2)$ are $\lambda_1 = \frac{m_3y_2}{a_3+y_2} - d_3$, the rest of the eigenvalues satisfy the equation given by

$$\det \begin{vmatrix} j_{11}-\lambda & j_{12} & 0 \\ j_{21} & j_{22}-\lambda & j_{23} \\ 0 & j_{32} & -\lambda \end{vmatrix} = 0, \tag{3.1}$$

where

$$j_{11} = -d - \frac{m_1 a_1}{(a_1+s_2)^2} x_2, \quad j_{12} = -\frac{m_1 s_2}{a_1+s_2},$$

$$j_{21} = \frac{m_1 a_1}{(a_1+s_2)^2} x_2, \quad j_{22} = \frac{m_1 s_2}{a_1+s_2} - d_1 - \frac{m_2 a_2}{(a_2+x_2)^2} y_2,$$

$$j_{23} = -\frac{m_2 x_2}{a_2+x_2}, \quad j_{32} = \frac{m_2 a_2}{(a_2+x_2)^2} y_2.$$

Hence equation (3.1) has the form

$$\lambda^3 + \alpha_1 \lambda^2 + \alpha_2 \lambda + \alpha_3 = 0\,, \tag{3.2}$$

where

$$\alpha_1 = -\left(j_{11} + j_{22}\right), \quad \alpha_2 = j_{11} j_{22} - \left(j_{12} j_{21} + j_{23} j_{32}\right), \quad \alpha_3 = j_{11} j_{23} j_{32}\,.$$

By the Routh-Hurwitz criterion, a set of necessary and sufficient conditions for all roots of (3.2) to have negative real parts is that $\alpha_1 > 0$, $\alpha_3 > 0$ and $\alpha_1 \alpha_2 > \alpha_3$.

Suppose that $\frac{m_1 s_2}{a_1+s_2} < d_1$, then all three conditions are satisfied and the roots will have negative real parts. Therefore, E_2 is locally asymptotically stable if $\frac{m_3 y_2}{a_3+y_2} < d_3$ and $\frac{m_1 s_2}{a_1+s_2} < d_1$.

Define the numbers $R_o = \frac{m_1 s^o}{d_1(a_1+s^o)}$, $R_1 = \frac{m_2 x_1}{d_2(a_2+x_1)}$, $R_2 = \frac{m_3 y_2}{d_3(a_3+y_2)}$ and $R_3 = \frac{m_1 s_2}{d_1(a_1+s_2)}$.

Theorem 2. *(i) If $R_o < 1$ then E_o is locally asymptotically stable and E_1 does not exist.*

(ii) If $R_1 < 1$ then E_1 is locally asymptotically stable and E_2 does not exist.

(iii) If $R_2 < 1$ and $R_3 < 1$ then E_2 is locally asymptotically stable.

Now we study global behavior of solutions of (2.2)

Theorem 3. *If $R_o < 1$ and $R_1 < 1$ then E_o is the only equilibrium point and solutions of (2.2) converge to E_o.*

Proof. Assume that $R_o < 1$ and $R_1 < 1$ then by Theorem 2 E_1 and E_2 don't exist. If (2.2) has a positive equilibrium point $(\overline{s}, \overline{x}, \overline{y}, \overline{z})$, then from the second equation of (2.2) $\frac{m_1 \overline{s}}{a_1+\overline{s}} > d_1$ which implies that $s^o < \overline{s}$, an impossible situation. Hence $(\overline{s}, \overline{x}, \overline{y}, \overline{z})$ does not exist. Therefore, E_o is the only equilibrium point.

Now to prove that E_o is globally asymptotically stable assume that $u(t) = (s(t), x(t), y(t), z(t))$ is a solution of (2.2). Then $s(t) \le s^o$ $\forall t \ge 0$, and therefore $x'(t) \le \left(\frac{m_1 s^o}{a_1+s^o} - d_1\right) x(t)$ for t large. If $R_o < 1$ then $x'(t) \le 0$

for t large and $\lim_{t\to\infty} x(t) = x^* \geq 0$ and $\lim_{t\to\infty} x'(t) = 0$. If $x^* > 0$, then $\lim_{t\to\infty} x'(t) \leq \left(\frac{m_1 s^o}{a_1+s^o} - d_1\right) x^* < 0$ which is a contradiction. Hence $\lim_{t\to\infty} x(t) = 0$. Consequently $\lim_{t\to\infty} y(t) = \lim_{t\to\infty} z(t) = 0$. $\lim_{t\to\infty} s'(t) = \left(s^o - \lim_{t\to\infty} s(t)\right) d$, therefore $\lim_{t\to\infty} s(t) = s^o$. Hence E_o is globally asymptotically stable and the theorem is proved. □

Theorem 3 shows that if $R_o < 1$, then the prey population cannot survive, and consequently the predator and top predator become extinct. So we may think of R_o as the basic reproductive number of the prey.

When $R_o < 1$ and $R_1 > 1$ then E_o and E_2 both exist. If $R_o > 1$ then E_1 exists and E_o becomes unstable. Recall that when $R_1 < 1$, E_1 is locally asymptotically stable. The next theorem shows that under these conditions E_1 becomes globally asymptotically stable. The method is similar to the method used in [2], [8].

Theorem 4. *If $R_o > 1$ and $R_1 < 1$ then E_o and E_1 are the only equilibria. Furthermore, if $\frac{m_3 y}{a_3+y} < d_3\ \forall y > 0$, then solutions $(s(t), x(t), y(t), z(t))$ of (2.2) with $x(0) > 0$ converge to E_1.*

Proof. First we prove that E_o and E_1 are the only equilibria. E_2 does not exist by Theorem 2. Now assume that $(\overline{s}, \overline{x}, \overline{y}, \overline{z})$ is a positive equilibrium point, then the second equation of (2.2) implies that $\overline{s} > \frac{a_1 d_1}{m_1 - d_1} = s_1$ and from the first equation of (2.2) we get $\overline{x} = \frac{(s_o - \overline{s}) d (a_1 + \overline{s})}{m_1 \overline{s}} < \frac{(s_o - s_1) d (a_1 + s_1)}{m_1 s_1} = x_1$. The third equation of (2.2) tells us that $\frac{m_2 \overline{x}}{a_2 + \overline{x}} - d_2 > 0$, i.e., $\frac{m_2 \overline{x}}{a_2 + \overline{x}} > d_2$. But we see by the assumption $R_1 < 1$ that $\frac{m_2 x_1}{a_2 + x_1} < d_2$ which means that $x_1 < \overline{x}$ and we get a contradiction. Hence (2.2) has no positive equilibrium point and therefore E_o and E_1 are the only equilibria.

Since $R_o > 1$, E_o is stable only in the $s-y-z$ space. We will apply the Dulac criterion to show that E_1 is globally asymptotically stable in the $s-x$ plane. Let $B(s,x) = \frac{1}{x}$ for $s \geq 0$ and $x > 0$. Then $\frac{\partial (Bs')}{\partial s} + \frac{\partial (Bx')}{\partial x} = -\frac{d}{x} - \frac{m_1 a_1}{(a_1+s)^2} < 0$ (i.e., does not change sign and is not identically zero) for $s \geq 0$ and $x > 0$. Hence there are no periodic solutions on the $s-x$ plane, and E_1 is globally asymptotically stable in the $s-x$ plane.

Now assuming that $\frac{m_3 y}{a_3+y} < d_3\ \forall y > 0$ we will prove that E_1 is a global attractor for system (2.2). Let $H(s) = \frac{d(s^o - s)(a_1 + s)}{m_1 s}$. Then $\lim_{s\to 0^+} H(s) = +\infty$, $\lim_{s\to\infty} H(s) = -\infty$, $H(s^o) = 0$, $H(s_1) = \frac{d(s^o - s_1)(a_1 + s_1)}{m_1 s_1} = x_1$ and $H'(s) =$

$\frac{-d\left(s^2+a_1 s^o\right)}{m_1 s^2}<0.$

Let $G(s)=\int\limits_{s_1}^{s}\frac{\frac{m_1 u}{a_1+u}-d_1}{\frac{m_1 u}{a_1+u}}du=\frac{m_1-d_1}{m_1}\left[s-s_1-s_1\ln\left(\frac{s}{s_1}\right)\right]$. Then $G(s_1)=0$, $\lim\limits_{s\to 0^+}G(s)=+\infty$, and $G(s)>0$ for $s>0$, $s\neq s_1$.

Let $F(s)=\frac{x_1-H(s)}{G(s)}$. Since $H'(s)<0$ and $H(s_1)=x_1$ then $F(s)<0$ for $0<s<s_1$ and $F(s)>0$ for $s_1<s<s^o$. Moreover, $\lim\limits_{s\to 0^+}F(s)=0$, $\lim\limits_{s\to s_1^-}F(s)=-\infty$ and $\lim\limits_{s\to s_1^+}F(s)=+\infty$. Let $\theta>0$ satisfies $\theta<\min\limits_{s_1<s\leq s^o}F(s)$, then $F(s)<\theta$ for $0<s<s_1$ and $F(s)>\theta$ for $s_1<s<s^o$. We are going to use the Liapunov function used in [2], [8] on the region

$$\Omega=\left\{(s,x,y,z)\in R_+^4:0<s\leq s^o,x>0\right\},$$

$$V(s,x,y,z)=\frac{1}{\theta+1}\left[x^{\theta+1}-x_1^{\theta+1}\right]-\frac{x_1}{\theta}\left[x^{\theta}-x_1^{\theta}\right]+x^{\theta}\int\limits_{s_1}^{s}\frac{\frac{m_1 u}{a_1+u}-d_1}{\frac{m_1 u}{a_1+u}}du+cy+ez\,,$$

where $c>0$ and $e>0$ will be defined later. Then $V\geq 0$ on $\overline{\Omega}$ and $V=0$ iff $s=s_1$, $x=x_1$, $y=0$ and $z=0$.

The derivative of V along trajectories of (2.2) is given by

$$\begin{aligned} V' &= x^{\theta}x'-x_1x^{\theta-1}x'+\theta x^{\theta-1}G(s)\,x'+x^{\theta}G'(s)\,s'+cy'+ez' \\ &= x^{\theta}G'(s)\,s'+x^{\theta-1}\left[x-x_1+\theta G(s)\right]x'+cy'+ez'\,, \end{aligned}$$

where

$$\begin{aligned} G'(s)\,s' &= \left[\tfrac{m_1 s}{a_1+s}-d_1\right]\frac{s'}{\frac{m_1 s}{a_1+s}}=\left[\tfrac{m_1 s}{a_1+s}-d_1\right]\left[\tfrac{(a_1+s)(s^o-s)d}{m_1 s}-x\right] \\ &= \left[\tfrac{m_1 s}{a_1+s}-d_1\right]\left[H(s)-x\right]. \end{aligned}$$

Therefore,

$$\begin{aligned} V' &= x^{\theta}\left[\tfrac{m_1 s}{a_1+s}-d_1\right]\left[H(s)-x\right]+x^{\theta-1}\left[x-x_1+\theta G(s)\right]\left[\tfrac{m_1 s}{a_1+s}x-d_1x-\tfrac{m_2x}{a_2+x}y\right] \\ &\quad+c\left[\tfrac{m_2x}{a_2+x}y-d_2y-\tfrac{m_3y}{a_3+y}z\right]+e\left[\tfrac{m_3y}{a_3+y}z-d_3z\right] \\ &= x^{\theta}\left[\tfrac{m_1 s}{a_1+s}-d_1\right]\left[H(s)-x_1+\theta G(s)\right]+c\left[\tfrac{m_2x_1}{a_2+x_1}-d_2\right]y-\theta x^{\theta-1}G(s)\tfrac{m_2x}{a_2+x}y \\ &\quad+\left[c\left(\tfrac{m_2x}{a_2+x}-\tfrac{m_2x_1}{a_2+x_1}-\tfrac{m_3z}{a_3+z}\right)-x^{\theta-1}(x-x_1)\tfrac{m_2x}{a_2+x}\right]y+e\left[\tfrac{m_3y}{a_3+y}-d_3\right]z \\ &= I+II+III+IV\,. \end{aligned}$$

The first part, $I=x^{\theta}\left[\frac{m_1 s}{a_1+s}-d_1\right]\left[H(s)-x_1+\theta G(s)\right]$. By the definition of θ

we have $H(s) - x_1 + \theta G(s) > 0$ for $0 < s < s_1$ and $H(s) - x_1 + \theta G(s) < 0$ for $s_1 < s < s_o$. Also $\frac{m_1 s}{a_1+s} - d_1 < \frac{m_1 s_1}{a_1+s_1} - d_1 = 0$ for $0 < s < s_1$ and $\frac{m_1 s}{a_1+s} - d_1 > \frac{m_1 s_1}{a_1+s_1} - d_1 = 0$ for $s_1 < s < s^o$. Therefore $I < 0$ for $s \neq s_1$ and $I = 0$ iff $s = s_1$.

The second part, $II = c\left[\frac{m_2 x_1}{a_2+x_1} - d_2\right] y - \theta x^{\theta-1} G(s) \frac{m_2 x}{a_2+x} y \leq 0$ since $R_1 < 1$ and $II = 0$ iff $y = 0$.

The third part,

$$III = \left[c\left(\frac{m_2 x}{a_2+x} - \frac{m_2 x_1}{a_2+x_1} - \frac{m_3 z}{a_3+z}\right) - x^{\theta-1}(x - x_1)\frac{m_2 x}{a_2+x}\right] y\,,$$

$$c\left(\frac{m_2 x}{a_2+x} - \frac{m_2 x_1}{a_2+x_1} - \frac{m_3 z}{a_3+z}\right) \leq \frac{c m_2 a_2 (x - x_1)}{(a_2+x)(a_2+x_1)}.$$

Thus

$$III \leq \left[\frac{c m_2 a_2 (x - x_1)}{(a_2+x)(a_2+x_1)} - x^{\theta-1}(x - x_1)\frac{m_2 x}{a_2+x}\right] y$$
$$= \frac{m_2 (x - x_1)}{a_2+x}\left[\frac{c a_2}{a_2+x_1} - x^{\theta}\right] y.$$

Let $c = \frac{a_2+x_1}{a_2} x_1^{\theta}$, then $III \leq \frac{m_2(x-x_1)}{a_2+x}\left[x_1^{\theta} - x^{\theta}\right] y \leq 0$ and $III = 0$ iff $y = 0$.

Finally, $VI = e\left[\frac{m_3 y}{a_3+y} - d_3\right] z < 0$ by assumption and $IV = 0$ iff $z = 0$.

We conclude that $V' \leq 0$ on $\overline{\Omega}$ and $V' = 0$ iff $s = s_1$, $y = 0$ and $z = 0$. Hence E_1 is a global attractor for system (2.2) and this completes the proof. □

Theorem 4 shows that if $R_1 < 1$, then the prey population cannot support the predator or the top predator, and consequently the predator and the top predator become extinct. So we may think of R_1 as the basic reproductive number of the predator.

When $R_o > 1$ and $R_1 > 1$ the three equilibria E_o, E_1 and E_2 exist, E_o and E_1 become unstable

4. Bifurcation Analysis

In this section using the dilution rate d as a bifurcation parameter, we show that our model undergoes a sequence of Hopf bifurcations. Clearly there is no Hopf bifurcation at any of the equilibria E_o or E_1. So we are going to vary d in system (2.2) to obtain a Hopf bifurcation at the equilibrium point E_2. We have the following result.

Theorem 5. *Assume that* $0 < j_{22} < |j_{11}|$ *and* $j_{11}j_{22} > j_{12}j_{21} + j_{23}j_{32}$, *then there is a positive number* d^* *such that system (2.2) exhibits a Hopf bifurcation leading to a family of periodic solutions that bifurcates from the equilibrium point* E_2 *for suitable values of* d *in a neighborhood of* d^*.

Proof. First recall that the Jacobian matrix at E_2 is given by

$$J(E_2) = \begin{bmatrix} -d - \frac{m_1 a_1}{(a_1+s_2)^2}x_2 & -\frac{m_1 s_2}{a_1+s_2} & 0 & 0 \\ \frac{m_1 a_1}{(a_1+s_2)^2}x_2 & \frac{m_1 s_2}{a_1+s_2} - d_1 - \frac{m_2 a_2}{(a_2+x_2)^2}y_2 & -\frac{m_2 x_2}{a_2+x_2} & 0 \\ 0 & \frac{m_2 a_2}{(a_2+x_2)^2}y_2 & 0 & -\frac{m_3 y_2}{a_3+y_2} \\ 0 & 0 & 0 & \frac{m_3 y_2}{a_3+y_2} - d_3 \end{bmatrix}.$$

As we mentioned in Section 3, the eigenvalues of $J(E_2)$ are $\lambda_1 = \frac{m_3 y_2}{a_3+y_2} - d_3$ which is a real number, the rest of the eigenvalues λ_2, λ_3 and λ_4 satisfy equation (3.2). Assume that $0 < j_{22} < |j_{11}|$ and $j_{11}j_{22} > j_{12}j_{21} + j_{23}j_{32}$, then $\alpha_1 > 0$ and $\alpha_2 > 0$.

Recall that:

$\alpha_1 = -(j_{11} + j_{22})$,

$\alpha_2 = j_{11}j_{22} - (j_{12}j_{21} + j_{23}j_{32})$,

$\alpha_3 = j_{11}j_{23}j_{32}$.

Clearly (3.2) will have two pure imaginary roots if and only if $\alpha_1\alpha_2 = \alpha_3$, i.e., if and only if $j_{11}j_{22}(j_{11} + j_{22}) = j_{11}j_{12}j_{21} + j_{22}j_{12}j_{21} + j_{22}j_{23}j_{32}$ for some value of d, say $d = d^*$, see [4], [5].

Since $\alpha_2 > 0$ at $d = d^*$, there is an interval containing d^*, say $(d^* - \varepsilon, d^* + \varepsilon)$ for some value of $\varepsilon > 0$ for which $d^* - \varepsilon > 0$ such that $\alpha_2 > 0$ for $d \in (d^* - \varepsilon, d^* + \varepsilon)$. Thus for $d \in (d^* - \varepsilon, d^* + \varepsilon)$, equation (3.2) has no positive real roots. For $d = d^*$, equation (3.2) becomes

$$\left(\lambda^2 + \alpha_2\right)(\lambda + \alpha_1) = 0\,. \tag{4.1}$$

Equation (4.1) has one negative real root and two pure imaginary roots, $\lambda_2 = -\alpha_1$, $\lambda_3 = i\sqrt{\alpha_2}$ and $\lambda_4 = -i\sqrt{\alpha_2}$. For $d \in (d^* - \varepsilon, d^* + \varepsilon)$ the roots have the form

$$\begin{aligned} \lambda_2(d) &= -\alpha_1(d)\,, \\ \lambda_3(d) &= \gamma(d) + i\beta(d)\,, \\ \lambda_4(d) &= \gamma(d) - i\beta(d)\,. \end{aligned}$$

Substituting $\lambda_i(d)$, $i = 3, 4$ into equation (3.2) we get the equation

$$\gamma^3(d) - 3\gamma(d)\beta^2(d) + \alpha_1(d)\gamma^2(d) - \alpha_1(d)\beta^2(d) + \alpha_2(d)\gamma(d) + \alpha_3(d) = 0$$
$$3\gamma^2(d)\beta(d) - \beta^3(d) + 2\alpha_1(d)\gamma(d)\beta(d) + \alpha_2(d)\beta(d) = 0 \tag{4.2}$$

Differentiating (4.2) with respect to d we get

$$\begin{aligned} A(d)\gamma'(d) - B(d)\beta'(d) + C(d) &= 0\,, \\ B(d)\gamma'(d) + A(d)\beta'(d) + D(d) &= 0\,, \end{aligned} \tag{4.3}$$

where

$$\begin{aligned} A(d) &= 3\gamma^2(d) - 3\beta^2(d) + 2\alpha_1(d)\gamma(d) + \alpha_2(d)\ , \\ B(d) &= 6\gamma(d)\beta(d) + 2\alpha_1(d)\beta(d)\ , \\ C(d) &= \alpha_1'(d)\gamma^2(d) - \alpha_1'(d)\beta^2(d) + \alpha_2'(d)\gamma(d) + \alpha_3'(d)\ , \\ D(d) &= 2\alpha_1'(d)\gamma(d)\beta(d) + \alpha_2'(d)\beta(d)\ . \end{aligned}$$

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

$$\mathrm{Re}\left[\lambda_i'(d)\right]_{d=d^*} = \frac{A(d)C(d) + B(d)D(d)}{A^2(d) + B^2(d)}\Big|_{d=d^*} \neq 0\,.$$

Therefore, we can apply Hopf Bifurcation Theorem [10] to prove that the system (2.2) exhibits a Hopf bifurcation at E_2 leading to a family of periodic solutions that bifurcates from the equilibrium point E_2 for some $d \in (d^* - \varepsilon, d^* + \varepsilon)$. This completes the proof. □

5. Discussion

A tri-trophic food chain model in the chemostat with the Michaelis-Menten functional response is studied in this paper. The dynamics of this model depends on the numbers R_o, R_1 and R_2. If $R_o < 1$ and $R_1 < 1$ then $E_o = (s^o, 0, 0, 0)$ is the only equilibrium point, solutions of (2.2) converges to E_o and the prey population cannot survive which leads to the extinction of the predator and top predator population. If $R_o < 1$ and $R_1 > 1$ then the system has two equilibria E_o and $E_2 = (s_2, x_2, y_2, 0)$. If $R_o > 1$, $R_1 < 1$ and $\frac{m_3 y}{a_3 + y} < d_3\ \forall y > 0$ then E_o and $E_1 = (s_1, x_1, 0, 0)$ are the only equilibria, solutions $(s(t), x(t), y(t), z(t))$ of (2.2) with $x(0) > 0$ converge to E_1 and the prey population cannot support the predator or the top predator, and consequently the predator and top predator become extinct. When $R_o > 1$ and $R_1 > 1$ the three equilibria E_o, E_1 and E_2 exist, but E_o and E_1 become unstable.

We then use d. The dilution rate of the chemostat, as a bifurcation parameter. We conclude that Hopf bifurcation occur, under certain conditions, at the equilibrium point E_2 leading to periodic solutions bifurcating from E_2.

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