Hopf Bifurcation in Three-Species Food Chain Models with Group Defense

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ABSTRACT

Three-species food-chain models, in which the prey population exhibits group defense, are considered. Using the carrying capacity of the environment as the bifurcation parameter, it is shown that the model without delay undergoes a sequence of Hopf bifurcations. In the model with delay it is shown that using a delay as a bifurcation parameter, a Hopf bifurcation can also occur in this case. These occurrences may be interpreted as showing that a region of local stability (survival) may exist even though the positive steady states are unstable. A computer code BIFDD is used to determine the stability of the bifurcation solutions of a delay model.

1. INTRODUCTION

In [32], Rosenzweig considered six different mathematical models of predator–prey or parasite–host interactions and showed that sufficient enrichment (increase of the prey carrying capacity) can cause destabilization of an otherwise stable interior equilibrium. He also integrated the model equations numerically and obtained extinction of the predator by using a truncation for the sake of biological reality. As a consequence he warned that "Man must be careful in attempting to

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enrich ecosystems in order to increase their food yield. There is a real chance that such activity may result in a decimation of the food species that are wanted in greater abundance." This is the so-called paradox of enrichment. Rosenzweig's prediction was criticized by Gilpin [14], May [26], McAllister et al. [27], and Riebesell [31]. However, there is experimental evidence by Huffaker et al. [22], Luckinbill [23], and Schaffer and Rosenzweig [36] indicating that in some situations Rosenzweig's warning is valid.

Freedman and Wolkowicz [13] provided additional support for Rosenzweig's warning for different reasons. They introduced a model of predator–prey interaction in which the prey exhibits group defense. Group defense is a term used to describe the phenomenon whereby predation is decreased or even prevented altogether owing to the ability of the prey to better defend or disguise themselves when their numbers are large. An example of this phenomenon is described by Tener [37]. A lone musk ox can be successfully attacked by wolves. Small herds of musk oxen (2–6 animals) are attacked but with rare success. No successful attacks have been observed in large herds. A second example, described by Holmes and Bethel [21], involves certain insect populations. Apparently, large swarms of the insect make individual identification difficult for their predators. Related examples are considered in Boon and Laudelout [1] and Yang and Humphrey [40].

The model with group defense differs from the classical models of predator–prey interactions in that the predator response function is not a monotone increasing function of prey density, but rather is only monotone increasing until some critical density and then becomes monotone decreasing. Freedman and Wolkowicz [13] showed that for sufficient enrichment there is always a set of initial conditions of positive measure for which extinction of the predator results, and they gave a numerical example to indicate a sequence of bifurcations as the carrying capacity of the environment is increased. Wolkowicz [39] showed that there is actually a threshold of enrichment above which extinction of the predator results for all but a set of initial conditions of measure zero, unless the prey isocline is monotone decreasing for all values of the carrying capacity. In [28] and [29], Mischaikow and Wolkowicz introduced a connection matrix approach to analyze the bifurcation of the predator–prey systems involving group defense.

Freedman and Quan [9] introduced a method whereby the predator is prevented from tending to extinction in the models, namely through interactions of the predator–prey system with a third population. In [35], we consider two Gause-type, three-species food chain models with group defense, one with mutual interference and one without, and derived utilizable criteria for persistence for those models. These persistence criteria depended on the fact that the top predator was also a predator of the bottom prey.

Time delays of one type or another have been incorporated by many authors, (see Cushing [5], Erbe, Freedman and Rao [6], Freedman and Gopalsamy [8], Freedman and Rao [10, 11], Gopalsamy [15], Gopalsamy and Aggarwala [16], MacDonald [24], Thingstad and Langeland [38]). In general it has been found that the introduction of time delays is a destabilizing process, in the sense that increasing the time delay could cause a stable equilibrium to become unstable and/or cause the populations to fluctuate.

In this paper, we first consider a three-species food chain model with group defense given by three autonomous ordinary differential equations. Using the carrying capacity of the environment as the bifurcation parameter, we show that the model undergoes a sequence of Hopf bifurcations. Secondly, we introduce a discrete delay in the model in the top-level predator population. This delay may be regarded as a delay due to gestation, i.e., a time delay in converting predator into prey. We discuss the change of stability and bifurcation of the interior equilibrium.

The biological purpose in both models is to show that in the case of simple food chains with group defense, even though persistence cannot occur (as in [35]), there could be a region (of initial values) of stability in which all three populations would survive, notwithstanding the fact that the positive steady state may itself be unstable.

2. THE MODELS

We first consider the instantaneous model given by the following system of autonomous ordinary differential equations as a food-chain model with group defense:

$$\begin{aligned}
&\dot{x} = xg(x,K) - yp(x),\\
&\dot{y} = y[-r + cp(x)] - zq(y),\\
&\dot{z} = z[-s + dq(y)],\\
&x(0) \geqslant 0, \qquad y(0) \geqslant 0, \qquad z(0) \geqslant 0,
\end{aligned} \tag{2.1}$$

$(\dot{} = \frac{d}{dt})$, where $x(t)$ denotes the prey population, $y(t)$ denotes the intermediate population that feeds upon x and is in turn fed upon by z, and $z(t)$ denotes the top predator population that feeds upon y. We assume that g, p, and q are analytic functions and that K, r, c and d are positive constants.

The function $g(x,K)$ represents the specific growth rate of the prey in the absence of predation. Logistic growth $g(x,K)=r(1-\frac{x}{K})$ is considered as a prototype. $g(x,K)$ is assumed to satisfy the following for any $x>0, K>0$:

$$\begin{aligned} &g(0,K)>0, \qquad g(K,K)=0, \qquad g_x(x,K)\leqslant 0, \\ &g_x(K,K)<0 \qquad g_K(x,K)>0, \qquad g_{xK}(x,K)>0. \end{aligned} \tag{2.2}$$

The function $p(x)$ denotes the predator functional response. To model group defense, it is assumed that there exists $M>0$ such that

$$p'(x)>0 \quad \text{for } 0\leqslant x<M \quad \text{and} \quad p'(x)<0 \quad \text{for } x>M. \tag{2.3}$$

Further, it is assumed that $p(x)$ satisfies

$$p(0)=0,\, p(x)>0 \quad \text{for } x>0 \quad \text{and} \quad p(M)>\frac{r}{c}. \tag{2.4}$$

For technical reasons in the bifurcation analysis it is assumed that

$$p(x)-xp'(x)>0 \quad \text{for all } x>0. \tag{2.5}$$

A function of the form $p(x)=mx/(ax^2+bx+1)$ where m, a, and b are positive constants satisfies these assumptions and approximates Holling-type dynamics for small x (see [20]).

The function $q(y)$ is interpreted as a predator functional response of z on y. Therefore we assume that

$$q(0)=0, \qquad q(y)>0 \quad \text{and} \quad q'(y)>0 \quad \text{for } y>0. \tag{2.6}$$

We have assumed that $p(M)>\frac{r}{c}$, since otherwise the predator y cannot survive on the prey at any density in the absence of the predator z. Therefore, there exists $\lambda<M<K$ such that $p(\lambda)=\frac{r}{c}$. (Note if $\lambda>K$, the group defense has no effect.)

Similar to the analysis of [35], we know that the system has the following equilibria:

$$\begin{aligned} E_0 &= (0,0,0) \\ E_K &= (K,0,0) \\ E_\lambda &= \left(\lambda, \frac{c\lambda}{r} g(\lambda,K), 0\right). \end{aligned}$$

There may also exist an equilibrium of the form

$$E_{\lambda_1} = (\lambda_1, cr^{-1}\lambda_1 g(\lambda_1, K), 0) \quad \text{with } p(\lambda_1) = rc^{-1}, \qquad p'(\lambda_1) < 0.$$

It follows that $M < \lambda_1 < K$, so that E_{λ_1} is a saddle point and hence no Hopf bifurcation can occur at E_{λ_1}.

In general, system (2.1) may or may not possess an interior equilibrium, $E^* = (x^*, y^*, z^*)$. Such an equilibrium, if it exists, is obtained by solving the system

$$\begin{aligned} xg(x,K) - yp(x) &= 0 \\ y[-r + cp(x)] - zq(y) &= 0 \\ -s + dq(y) &= 0. \end{aligned} \tag{2.7}$$

If $x^* < \lambda_1$, there may be a homoclinic bifurcation at E^* (see Chow and Hale [2]). Since we are interested in Hopf bifurcation in this paper, we always assume that system (2.1) has an interior equilibrium $E^* = (x^*, y^*, z^*)$ with

$$\lambda < x^* < M < K. \tag{2.8}$$

The second model is a modification of the first one so as to incorporate a discrete time delay in the gestation of the top level population z. The model now takes the form

$$\begin{aligned} \dot{x} &= xg(x,K) - yp(x) \\ \dot{y} &= y[-r + cp(x)] - zq(y) \\ \dot{z} &= z[-s + dq(y(t-\tau))] \end{aligned} \tag{2.9}$$

with initial conditions given by

$$x(0) = x_0 > 0, \qquad y(t) = y_0(t) > 0, \qquad z(0) = z_0 > 0$$

where $y_0(t)$ is a given continuous function on $-\tau \leqslant t \leqslant 0$. The functions g, p, and q have the same meanings and properties as for system (2.1). Similarly, we assume that system (2.9) possesses an interior equilibrium $E^* = (x^*, y^*, z^*)$ with $\lambda < x^* < M < K$.

3. HOPF BIFURCATION ANALYSIS OF THE INSTANTANEOUS MODEL

In this section we shall vary K in system (2.1) so as to obtain a Hopf bifurcation. To do so, we need to compute the stability of E_λ and E^*.

For general x, y, and z, the variational matrix of system (2.1) has the form

$$V(x,y,z)=\begin{bmatrix} g(x,K)+xg_x(x,K)-yp'(x) & -p(x) & 0 \\ cyp'(x) & -r+cp(x)-zq'(y) & -q(y) \\ 0 & dzq'(y) & -s+dq(y) \end{bmatrix}.$$

The variational matrix at E_λ has the form

$$V_\lambda=\begin{bmatrix} g(\lambda,K)+\lambda g_x(\lambda,K)-\frac{c\lambda}{r}g(\lambda,K)p'(\lambda) & -p(\lambda) & 0 \\ \frac{c^2\lambda}{r}g(\lambda,K)p'(\lambda) & 0 & -q\left(\frac{c\lambda}{r}g(\lambda,K)\right) \\ 0 & 0 & -s+dq\left(\frac{c\lambda}{r}g(\lambda,K)\right) \end{bmatrix}.$$

Hence the characteristic equation is

$$\begin{aligned}\left[y^2-yG_1(\lambda,K)+\frac{c^2\lambda}{r}g(\lambda,K)p(\lambda)p'(\lambda)\right]& \\ \times\left[y+s-dq\left(\frac{c\lambda}{r}g(\lambda,K)\right)\right]&=0 \qquad (3.1)\end{aligned}$$

where

$$\begin{aligned}G_1(\lambda,K)&=-\frac{c\lambda}{r}g(\lambda,K)p'(\lambda)+g(\lambda,K)+\lambda g_x(\lambda,K)\\ &=\frac{c}{r}g(\lambda,K)[p(\lambda)-\lambda p'(\lambda)]+\lambda g_x(\lambda,K).\end{aligned}$$

Equation (3.1) has three roots:

$$y_{1,2}=\frac{1}{2}\left[G_1(\lambda,K)\pm\sqrt{G_1^2(\lambda,K)-\frac{4c^2\lambda}{r}g(\lambda,K)p(\lambda)p'(\lambda)}\right]$$

$$y_3=-s+dq\left(\frac{c\lambda}{r}g(\lambda,K)\right).$$

Clearly y_3 is a real root; y_1 and y_2 are purely imaginary if and only if there is a K_1 such that $G_1(\lambda,K_1)=0$. Further, y_1 and y_2 are complex in a neighborhood of K_1. By (2.2) and (2.5), $g(\lambda,K)>0$, $p(\lambda)-\lambda p'(\lambda)>0$, $g_x(\lambda,K)\leqslant 0$, so there is always a K_1 such that $G_1(\lambda,K_1)=0$ and

$$y_3(K_1)=-s+dq\left(\frac{c\lambda}{r}g(\lambda,K_1)\right)\neq 0.$$

Since $\mathrm{Re}[y_i(K_1)]=0$, $\mathrm{Im}[y_i(K_1)]\neq 0$, $i=1,2$, and by (2.2) and (2.5), $g_K(x,K_1)>0$, $p(\lambda)-\lambda p'(\lambda)>0$, $g_{xK}(\lambda,K_1)>0$, so that

$$\mathrm{Re}\left[\frac{dy_i}{dK}\right]_{K=K_1}=\frac{c}{2r}g_K(\lambda,K_1)[p(\lambda)-\lambda p'(\lambda)]+\frac{\lambda}{2}g_{xK}(\lambda,K_1)>0.$$

Hence there is a Hopf bifurcation at $K=K_1$ (see [25]). We can now formulate the following:

THEOREM 3.1

There is a Hopf bifurcation for system (2.1) *as* K *passes through* K_1 *emanating from the steady state* E_λ *leading to periodic solutions for either* $K>K_1$ *or* $K<K_1$ *or at* $K=K_1$.

Now for the steady state E^* with $\lambda<x^*<M<K$, we have

$$V^*=\begin{bmatrix} g(x^*,K)+x^*g_x(x^*,K)-y^*p'(x^*) & -p(x^*) & 0 \\ cy^*p'(x^*) & -r+cp(x^*)-z^*q'(y^*) & -q(y^*) \\ 0 & dz^*q'(y^*) & 0 \end{bmatrix}. \tag{3.2}$$

The characteristic equation is given by

$$\det\begin{vmatrix} m_{11}-y & m_{12} & 0 \\ m_{21} & m_{22}-y & m_{23} \\ 0 & m_{32} & -y \end{vmatrix}=0 \tag{3.3}$$

where

$$\begin{aligned}
&m_{11}=g(x^*,K)+x^*g_x(x^*,K)-y^*p'(x^*),\\
&m_{12}=-p(x^*)<0, \qquad m_{21}=cy^*p'(x^*)>0,\\
&m_{22}=cp(x^*)-[r+z^*q'(y^*)],\\
&m_{23}=-q(y^*)<0, \qquad m_{32}=dz^*q'(y^*)>0.
\end{aligned}$$

Hence Equation (3.3) has the form

$$y^3+a_1y^2+a_2y+a_3=0 \tag{3.4}$$

where

$$\begin{aligned}
&a_1=-(m_{11}+m_{22})\\
&a_2=m_{11}m_{22}-(m_{12}m_{21}+m_{23}m_{32})\\
&a_3=m_{11}m_{23}m_{32}.
\end{aligned}$$

By the Routh–Hurwitz criterion, a set of necessary and sufficient conditions for all the roots of (3.4) to have negative real parts is

$$a_1 > 0, \qquad a_3 > 0 \quad \text{and} \quad a_1 a_2 > a_3.$$

Now suppose that $m_{11} < 0$ and $m_{22} \leqslant 0$. Then $a_1 > 0$, $a_2 > 0$, clearly (3.4) has two pure imaginary roots if and only if $a_1 a_2 = a_3$ for some value of K, say $K = K_2$. Since $a_2 > 0$ at $K = K_2$, there is an interval containing K_2, say $(K_2 - \epsilon, K_2 + \epsilon)$ for some $\epsilon > 0$ for which $K_2 - \epsilon > 0$, such that $a_2 > 0$ for $K \in (K_2 - \epsilon, K_2 + \epsilon)$. Thus, for $K \in (K_2 - \epsilon, K_2 + \epsilon)$, the characteristic equation (3.4) cannot have real positive roots. For $K = K_2$, we have

$$(y^2 + a_2)(y + a_1) = 0, \tag{3.5}$$

which has three roots

$$y_1 = i\sqrt{a_2}\,, \qquad y_2 = -i\sqrt{a_2}\,, \qquad y_3 = -a_1.$$

For $K \in (K_2 - \epsilon, K_2 + \epsilon)$, the roots are in general of the form

$$\begin{aligned} y_1(K) &= \alpha(K) + i\beta(K) \\ y_2(K) &= \alpha(K) - i\beta(K) \\ y_3(K) &= -a_1(K). \end{aligned}$$

To apply Hopf's bifurcation theorem as given in [25] to (2.1), we need to verify the transversality condition

$$\operatorname{Re}\left[\frac{dy_j}{dK}\right]_{K=K_2} \neq 0, \qquad j = 1, 2. \tag{3.6}$$

Substituting $y_j(K) = \alpha(K) + i\beta(K)$ into (3.6), and calculating the derivative, we get

$$\begin{aligned} A(K)\alpha'(K) - B(K)\beta'(K) + C(K) &= 0 \\ B(K)\alpha'(K) + A(K)\beta'(K) + D(K) &= 0 \end{aligned} \tag{3.7}$$

where

$$\begin{aligned} A(K) &= 3\alpha^2(K) + 2a_1(K)\alpha(K) + a_2(K) - 3\beta^2(K) \\ B(K) &= 6\alpha(K)\beta(K) + 2a_1(K)\beta(K) \end{aligned}$$

$$C(K) = \alpha^2(K)a_1'(K) + a_2'(K)\alpha(K) + a_3'(K) - a_1'(K)\beta^2(K)$$

$$D(K) = 2\alpha(K)\beta(K)a_1'(K) + a_2'(K)\beta(K).$$

Since

$$B(K_2)D(K_2) + A(K_2)D(K_2) \neq 0,$$

we have

$$\operatorname{Re}\left[\frac{dy_j}{dK}\right]_{K=K_2} = \left.\frac{BK + AC}{2(A^2 + B^2)}\right|_{K=K_2} \neq 0,$$

and $y_3(K_2) = -a_1(K_2) \neq 0$. We summarize the details in the following:

THEOREM 3.2

Suppose $E^* = (x^*, y^*, z^*)$ *exists and* $\lambda < x^* < M < K$, $m_{11} < 0$, $m_{22} \leqslant 0$. *Then system* (2.1) *exhibits a Hopf bifurcation in the first octant leading to a family of periodic solutions that bifurcates from* E^* *for suitable values of* K *in a neighborhood of* K_2.

Using the formula of [25, p. 26], one could establish two lengthy and tedious stability criteria for the bifurcation solutions described in Theorems 3.1 and 3.2. And one also can use the computer code in [19] to determine the stability of those bifurcation solutions. We shall do computer analysis for the delay model in the next section.

We know that solutions of system (2.1) are bounded (see Freedman and So [12]). We also know that the steady state E_K is a saddle point, and by Theorems 3.1 and 3.2, K_1 and K_2 are two bifurcation points; a periodic solution bifurcates from E_λ when K passing through K_1, denoted by $(x(t, K_1), y(t, K_1), z(t, K_1))$; and another periodic solution bifurcates from E^* when K passing through K_2, denoted by $(x(t, K_2), y(t, K_2), z(t, K_2))$. By Rabinowitz's Theorem (see [30]), we have the following:

THEOREM 3.3

There is a continuum (a closed and connected subset) meeting both of the bifurcation solutions $(x(t, K_1), y(t, K_1), z(t, K_2))$ *and* $x(t, K_2)$, $y(t, K_2), z(t, K_2))$.

4. HOPF BIFURCATION ANALYSIS OF THE TIME-DELAY MODEL

In this section, we determine criteria for Hopf bifurcation, using the time delay as the bifurcation parameter. We first derive the characteristic equation for the linearization of system (2.9) near its interior equilibrium $E^* = (x^*, y^*, z^*)$. Let $X(t)$, $Y(t)$, and $Z(t)$ be the respective linearized variables of system (2.9). Then the variational system is

$$\begin{aligned} X'(t) &= m_{11}X(t) + m_{12}Y(t) \\ Y'(t) &= m_{21}X(t) + m_{22}Y(t) + m_{23}Z(t) \\ Z'(t) &= m_{32}Y(t-\tau). \end{aligned} \tag{4.1}$$

where m_{ij} $(i, j = 1,2,3)$ are the same as in Section 3. This leads to the characteristic equation

$$\lambda^3 + \alpha\lambda^2 + \beta\lambda = \delta e^{-\lambda\tau} + \eta\lambda e^{-\lambda\tau} \tag{4.2}$$

where

$$\begin{aligned} \alpha &= -(m_{11} + m_{22}), \\ \beta &= m_{11}m_{22} - m_{12}m_{21}, \\ \delta &= -m_{11}m_{23}m_{32}, \\ \eta &= m_{23}m_{32} < 0. \end{aligned}$$

It is the sign of the real parts of the solutions λ of equation (4.2) that determines the stability of $E^* = (x^*, y^*, z^*)$. Hence we assume as before that $m_{11} < 0$, $m_{22} \leqslant 0$ so that $\operatorname{Re}\lambda < 0$ at $\tau = 0$. Letting $\lambda = \mu + i\nu$ and substituting into (4.2), we obtain the following equations:

$$\begin{aligned} \mu^3 - 3\mu\nu^2 + \alpha(\mu^2 - \nu^2) + \beta\mu &= [(\delta + \eta\mu)\cos\tau\nu + \eta\nu\sin\tau\nu]e^{-\tau\mu}, \\ -\nu^3 + 3\mu^2\nu + 2\alpha\mu\nu + \beta\nu &= [\eta\nu\cos\tau\nu - (\delta + \eta\mu)\sin\tau\nu]e^{-\tau\mu}. \end{aligned} \tag{4.3}$$

We consider λ and hence μ and ν as functions of the delay τ, and we will be interested in the change of stability of E^*, which will occur at any values of τ for which $\mu = 0$. If $\mu = 0$, then $\nu \neq 0$, and hence we assume that $\delta \neq 0$. Let $\hat{\tau}$ be such that $\mu(\hat{\tau}) = 0$. Then equations (4.3) reduce to

$$\begin{aligned} -\alpha\hat{\nu}^2 &= \delta\cos\hat{\tau}\hat{\nu} + \eta\hat{\nu}\sin\hat{\tau}\hat{\nu}, \\ -\hat{\nu}^3 + \beta\hat{\nu} &= \eta\hat{\nu}\cos\hat{\tau}\hat{\nu} - \delta\sin\hat{\tau}\hat{\nu}. \end{aligned} \tag{4.4}$$

Squaring and adding the equations of (4.4) and simplifying, gives an equation for $\hat{\nu}$ of the form

$$\hat{\nu}^6 + (\alpha^2 - 2\beta)\hat{\nu}^4 + (\beta^2 - \eta^2)\hat{\nu}^2 - \delta^2 = 0. \tag{4.5}$$

This is a cubic equation in $\hat{\nu}^2$ that has one or more real roots, $\hat{\nu}_0^2$, since when $\hat{\nu} = 0$, the left side of (4.5) is negative, and for sufficiently large values of $\hat{\nu}$, it is positive.

Then from (4.4) we can solve for $\hat{\tau}$, which is of the form

$$\hat{\tau}_n = \frac{1}{\hat{\nu}_0} \arcsin \frac{\hat{\nu}_0\left(\delta\hat{\nu}_0^2 - \alpha\eta\hat{\nu}_0^2 - \beta\delta\right)}{\eta^2\hat{\nu}_0^2 + \delta^2} + \frac{2n\pi}{\hat{\nu}_0}, \qquad n = 0, 1, 2, \cdots \tag{4.6}$$

This implies that as τ "bifurcates" from $\tau = 0$, infinitely many branches of $\mu(\tau)$ appear, of which one crosses $\mu = 0$ at each $\hat{\tau}_n$.

To establish Hopf bifurcation at $\tau = \hat{\tau}$, we need to show that $\frac{d}{d\tau}\mu(\hat{\tau}) \neq 0$. From (4.3), differentiating with respect to τ and setting $\tau = \hat{\tau}$, $\nu = \hat{\nu}$, $\mu = 0$, and solving for $\frac{d\mu}{d\tau}$ and $\frac{d\nu}{d\tau}$, we get for $\frac{d\mu}{d\tau}$,

$$\frac{d\mu(\hat{\tau})}{d\tau} = \frac{AC - BD}{A^2 + B^2} \tag{4.7}$$

where

$$\begin{aligned} A &= 3\hat{\nu}^2 - \beta - \eta\hat{\tau}\hat{\nu}\sin\hat{\tau}\hat{\nu} + (\eta - \delta\hat{\tau})\cos\hat{\tau}\hat{\nu}, \\ B &= 2\alpha\hat{\nu} + (\eta - \delta\hat{\tau})\sin\hat{\tau}\hat{\nu} + \eta\hat{\tau}\hat{\nu}\cos\hat{\tau}\hat{\nu}, \\ C &= \delta\hat{\tau}\sin\hat{\tau}\hat{\nu} - \eta\hat{\nu}^2\cos\hat{\tau}\hat{\nu}, \\ D &= \eta\hat{\nu}^2\sin\hat{\tau}\hat{\nu} + \delta\hat{\nu}\cos\hat{\tau}\hat{\nu}. \end{aligned} \tag{4.8}$$

We note, using (4.4) that

$$AC - BD = \hat{\nu}^2\left[3\hat{\nu}^4 + 2(\alpha^2 - 2\beta)\hat{\nu}^2 + (\beta^2 - \eta^2)\right]. \tag{4.9}$$

Suppose we let

$$\Phi(z) = z^3 + (\alpha^2 - 2\beta)z^2 + (\beta^2 - \eta^2)z - \delta^2,$$

which is the left side of (4.5) with $z = \hat{\nu}^2$. Then we may note that from (4.7) and (4.9),

$$\frac{d\mu(\hat{\tau})}{d\tau} = \frac{\hat{\nu}^2}{A^2 + B^2}\frac{d\Phi}{dz}(\hat{\nu}^2).$$

Hence if $\hat{\nu}_0$ is the first positive root of (4.5),

$$\frac{d\mu(\hat{\tau}_{\tau_0})}{d\tau} > 0.$$

From the preceding, the following are valid.

THEOREM 4.1.

Let $m_{11} < 0$, $m_{22} \leqslant 0$. Let $\hat{\nu}_0$ be the first positive root of Equation (4.5). *Then a Hopf bifurcation occurs as τ passes through $\hat{\tau}_0$.*

THEOREM 4.2.

If at $\tau = \tau_1$, E^* is unstable, then E^* is unstable for all $\tau > \tau_1$.

COROLLARY 4.3.

E^* is unstable for $\tau > \hat{\tau}_0$.

Now we use a computer code BIFDD developed by Hassard (cf [18]) to discuss the stability of the bifurcation solutions. Let

$$\begin{aligned} g(x,K) &= 1 - \frac{x}{K}, \\ p(x) &= xe^{-x}, \\ q(y) &= y. \end{aligned}$$

Obviously, $g(x, K)$, $p(x)$ and $q(y)$ satisfy all the conditions in (2.2)–(2.6). For the parameter values

$$K = 1.2, \qquad r = 0.2, \qquad c = 1, \qquad s = 0.6, \qquad d = 0.6678$$

and the steady state

$$(x^*, y^*, z^*) = (0.62, 0.8985, 0.1335),$$

we found

$$\begin{aligned} \hat{\tau}_0 &= 1.57, & \mu_2 &= 4.2441, \\ \tau_2 &= 3.0556, & \beta_2 &= -2.448. \end{aligned}$$

Since $\mu_2 > 0$, a Hopf bifurcation occurs and a family of small amplitude periodic orbits exists for values of τ slightly greater than the critical value $\hat{\tau}_0$. Since $\beta_2 < 0$, the individual periodic orbits are locally attracting. Since $\tau_2 > 0$, the period of the solutions increases with τ.

5. DISCUSSION

The notion of "paradox of enrichment" leading to possible extinction of predators, introduced by Rosenzweig, was shown to be a real possibility in [13] in predator–prey systems with group defense.

Here we have considered simple food-chain models where the prey exhibits group defense. Since the predator is faced with possible extinction in the absence of the superpredator, the question arises as to whether there is any chance of its survival when the superpredator is present.

Of course, persistence in this case is impossible. However, we have shown that there may be a stable region in the neighborhood of an interior steady state, whether or not the steady state itself is stable. This was done by obtaining conditions for a Hopf bifurcation that could lead to the introduction of stable periodic solutions when the environment or time delay changes so as to destabilize the steady state.

A computer code BIFDD is applied to analyze Hopf bifurcations in a delay model; for some parameter values, the critical value $\hat{\tau}_0$ of delay is found and the stability of the bifurcation solutions is determined.

Applying a computer code BIFDD to determine the stability of the bifurcation solutions was suggested by the referees. The code was provided by Dr. J. W. H. So, Theorem 3.3 was inspired by a talk with Dr. S. Busenberg. The authors are grateful to all of them. The second author also thanks Mr. H. Xia for helpful discussions.

REFERENCES

1 B. Boon and H. Laudelout, Kinetics of intrite oxydation by *Nitrobacter Winogrodski Biochem. J.* 85:440–447 (1962).
2 S. N. Chow and J. K. Hale, *Methods of Bifurcation*, Springer-Verlag, Heidelberg, 1982.
3 K. L. Cooke and Z. Grossman, Discrete delay, distributed delay and stability switches, *J. Math. Anal. Appl.* 86:592–627 (1982).
4 K. L. Cooke and P. Van den Driessche, On zeros of some transcendental equations, *Funkcial. Ekvac.* 29:77–90 (1986).
5 J. M. Cushing, *Integrodifferential Equations and Delay Models in Population Dynamics*, Springer-Verlag, Heidelberg, 1977.
6 L. H. Erbe, H. I. Freedman and V. S. H. Rao, Three species food chain models with mutual interference and time delays, *Math. Biosci.* 80:57–80 (1986).
7 H. I. Freedman, *Deterministic Mathematical Models in Population Ecology*, HIFR Consulting Ltd., Edmonton, 1986.
8 H. I. Freedman and K. Gopalsamy, Nonoccurrence of stability switching in systems with discrete delays, *Canad. Math. Bull.* 31:52–58 (1988).
9 H. I. Freedman and H. Quan, Interactions leading to persistence in predator–prey systems with group defense, *Bull. Math. Biol.* 50:517–530 (1988).
10 H. I. Freedman and V. S. H. Rao, The trade-off between mutual interference and time lags in predator–prey systems, *Bull. Math. Biol.* 45:991–1004 (1983).
11 H. I. Freedman and V. S. H. Rao, Stability criteria for a system involving two time delays, *SIAM J. Appl. Math.* 46:552–560 (1986).
12 H. I. Freedman and J. W. H. So, Global stability and persistence of simple food chains, *Math. Biosci.* 76:69–86 (1985).
13 H. I. Freedman and G. Wolkowicz, Predator–prey systems with group defense: the paradox of enrichment revised, *Bull. Math. Biol.* 48:493–508 (1986).
14 M. E. Gilpin, Enriched predator–prey systems: theoretical stability, *Science* 177:902–904 (1972).

15 K. Gopalsamy, Delayed responses and stability in two-species systems, *J. Austral. Math. Soc. Ser. B* 25:473–500 (1984).

16 K. Gopalsamy and B. D. Aggarwala, Limit cycles in two-species competition with time delays, *J. Austral. Math. Soc. Ser. B* 22:148–160 (1980).

17 J. K. Hale, *Theory of Functional Differential Equations*, Springer-Verlag, New York, 1977.

18 B. D. Hassard, A code for Hopf bifurcation analysis of autonomous delay-differential systems, in *Oscillation, Bifurcation and Chaos, CMS Conference Proceedings*, 1986, pp. 447–463.

19 B. D. Hassard, N. D. Kazarinoff and Y. H. Wan, *Theory and Applications of Hopf Bifurcation*, Cambridge University Press, Cambridge, 1981.

20 C. S. Holling, The functional response of predators to prey density and its role in mimicry and population regulation, *Mem. Entomology. Soc. Canada* 45:3–60 (1965).

21 J. C. Holmes and W. M. Bethel, Modification of intermediate host behavior by parasites, *Zoolog. J. Linear. Soc. Suppl. 1* 51:123–149 (1972).

22 C. B. Huffaker, K. P. Shea and S. G. Herman, Experimental studies on predation: complex dispersion and levels of food in an alarine predator–prey interaction, *Hilgardia* 34:305–429 (1963).

23 L. S. Luckinbill, Coexistence in laboratory populations of *Paramecium Aurelia* and its predator *Didinium Nasutium Ecology* 54:1320–1327 (1973).

24 N. MacDonald, *Time Lays in Biological Models*, Springer-Verlag, Heidelberg, 1978.

25 J. E. Marsden and M. McKracken, *The Hopf Bifurcation and its Applications*, Springer-Verlag, New York, 1976.

26 R. M. May, Limit cycles in predator-prey communities, *Science* 177:900–902 (1972).

27 C. D. McAllister, R. J. Lebrasseur and T. R. Parsons, Stability of enriched aquatic ecosystems, *Science* 175: 564–565 (1972).

28 K. Mischaikow and G. Wolkowicz, A connection matrix approach illustrated by means of a predator–prey model involving group defense, in *Mathematical Ecology*, T. G. Hallam, L. J. Gross, and S. A. Levin, Eds., World Scientific Publishing, Singapore, 1988, pp. 682–716.

29 K. Mischaikow and G. Wolkowicz, A predator–prey system involving group defense: a connection matrix approach, *Nonlin. Anal. Th. Math. Appl.* 14:955–969 (1990).

30 P. H. Rabinowitz, Some global results for nonlinear eigenvalue problems, *J. Functional Anal.* 7:487–513 (1971).

31 J. F. Riebesell, Paradox of enrichment in competitive systems, *Ecology* 55:183–187 (1974).

32 M. L. Rosenzweig, Paradox of enrichment: destabilization of exploitation ecosystems in ecological time, *Science* 171:385–387 (1971).

33 M. L. Rosenzweig, Reply to McCallister et al., *Science* 175:564–565 (1972).

34 M. L. Rosenzweig, Reply to Gilpin, *Science* 177:904 (1972).

35 S. Ruan and H. I. Freedman, Persistence in three-species food chain models with group defense, *Math. Biosci.* 107:111–125 (1991).

36 W. H. Schaffer and M. L. Rosenzweig, Homage to the red queen. Part I. Coevolution of predators and their victims, *Theoret. Pop. Biol.* 14:135–157 (1978).

37 J. S. Tener, *Muskoxen*, Queen's Printer, Ottawa, 1965.
38 T. F. Thingstad and T. I. Langeland, Dynamics of a chemostat culture: the effect of a delay in a cell response, *J. Theor. Biol.* 48:149–159 (1974).
39 G. Wolkowicz, Bifurcation analysis of a predator–prey system involving group defense, *SIAM J. Appl. Math.* 48:1–15 (1988).
40 R. D. Yang and A. E. Humphrey, Dynamics and steady state studies of phenal biodegradation in pure and mixed cultures, *Biotechnol. Bioeng.* 17:1121–1235 (1975).