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Research Article

Dynamic Analysis of a Delayed Reaction-Diffusion Predator-Prey System with Modified Holling-Tanner Functional Response

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A predator-prey model with modified Holling-Tanner functional response and time delays is considered. By regarding the delays as bifurcation parameters, the local and global asymptotic stability of the positive equilibrium are investigated. The system has been found to undergo a Hopf bifurcation at the positive equilibrium when the delays cross through a sequence of critical values. In addition, the direction of the Hopf bifurcation and the stability of bifurcated periodic solutions are also studied, and an explicit algorithm is obtained by applying normal form theory and the center manifold theorem. The main results are illustrated by numerical simulations.

1. Introduction

The dynamic relationship between prey and predators has long been and will continue to be one of the dominant subjects in mathematical ecology due to its universal existence and importance [1–12]. In [13, 14], the author proposed the following predator-prey model based on the model in May [15]:

$$\begin{aligned} \frac{du}{dt} &= ru\left(1-\frac{u}{K}\right)-p(u)v, \\ \frac{dv}{dt} &= v\left[s\left(1-\frac{hv}{u}\right)\right], \end{aligned} \tag{1}$$

where u and v denote the population of prey and predator, respectively, and r and s are the intrinsic growth rates of prey and predator, respectively. The parameter K represents the carrying capacity of the prey and the ratio u/h represents the carrying capacity of the predator. It has been assumed that both prey and predator populations grow logistically and that the predator consumes the prey according to a functional $p(u)$.

In recent years, models with time delay have been extensively studied by many authors [5, 16–26]. The authors of [1] discussed model (1) with a discrete delay:

$$\begin{aligned} \frac{du}{dt} &= ru\left(1-\frac{u(t-\tau)}{K}\right)-muv, \\ \frac{dv}{dt} &= v\left[s\left(1-\frac{hv}{u}\right)\right] \end{aligned} \tag{2}$$

and obtained the stability of equilibria, the existence of Hopf bifurcation, and the direction of bifurcating periodic solutions. This paper focuses mainly on the effects of both spatial diffusion and time delay on system (1). It is assumed that the delay affects predation and consumption and that the system has homogeneous Neumann boundary conditions:

$$\begin{aligned} \frac{\partial u}{\partial t} &= d_1\Delta u+ru\left(1-\frac{u}{K}\right)-\frac{mu^2v(t-\tau_1)}{a+u^2}, \quad x\in\Omega,\ t>0, \\ \frac{\partial v}{\partial t} &= d_2\Delta v+v\left[s\left(1-\frac{hv}{u(t-\tau_2)}\right)\right], \quad x\in\Omega,\ t>0, \end{aligned}$$

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0, \quad x = \partial\Omega,\ t > 0,$$
$$u(x,t) = u_0(x,t), \quad x \in \Omega,\ t \in [-\tau_2, 0],$$
$$v(x,t) = v_0(x,t), \quad x \in \Omega,\ t \in [-\tau_1, 0], \tag{3}$$

where d_1 and d_2 are the diffusion coefficients of prey and predator, respectively, $\Delta = \partial^2/\partial x^2$ denotes the Laplacian operator, and n is the outward unit normal vector on $\partial\Omega$. For convenience, it is assumed that $\Omega = (0, l\pi)$, $l > 0$ and that all parameters are positive.

The rest of this paper is structured as follows. In Section 2, the local stability of equilibria is analyzed using the associated characteristic equations, and the occurrence of the Hopf bifurcation with time delays is presented. In Section 3, the global asymptotical stability of the interior equilibrium for any $\tau_1, \tau_2 \geq 0$ is proved by means of the upper-lower solution method. In Section 4, using normal form theory and the center manifold theorem, the stability and direction of bifurcating periodic orbits are investigated. Finally, numerical simulations and a brief discussion are presented.

2. Local Stability and Hopf Bifurcation Analysis

In this section, the local stability of the equilibria of system (3) is analyzed. Denote

$$X = C\left([0, l\pi], R^2\right),$$
$$\langle u, v\rangle = \langle u_1, v_1\rangle + \langle u_2, v_2\rangle, \qquad \tau = \tau_1 + \tau_2, \tag{4}$$

for $u = (u_1, u_2)$, $v = (v_1, v_2) \in X$; then $(X, \langle\cdot,\cdot\rangle)$ is a Hilbert space. In the abstract space $C([-\tau, 0], X)$, system (3) can be regarded as an abstract functional differential equation.

System (3) has two nonnegative equilibria $(K, 0)$ and (u^*, v^*), where

$$v^* = \frac{1}{h}u^*, \tag{5}$$

and u^* is the positive root of the equation

$$rhu^3 + (mK - rhK)u^2 + arhu - arhK = 0. \tag{6}$$

Let $A(u) = rhu^3 + (mK - rhK)u^2 + arhu - arhK$; then $A(0) = -arhK < 0$, $A(K) = mK^3 > 0$, which guarantee the existence of $u^* \in (0, K)$.

From analysis of the characteristic equation of $(K, 0)$, it can easily be determined that it always has a saddle point. To analyze the stability of the positive equilibrium (u^*, v^*), the first step is to linearize system (3) at (u^*, v^*):

$$\frac{\partial U(t)}{\partial t} = d\Delta U(t) + L(U_t), \tag{7}$$

where $d\Delta = (d_1\Delta, d_2\Delta)$,

$$\operatorname{dom}(d\Delta) = \left\{(u, v)^T : u, v \in C^2([0, l\pi], R),\ \frac{\partial u}{\partial x} = \frac{\partial v}{\partial x} = 0, x = 0, l\pi\right\}, \tag{8}$$

and $L : C([-\tau, 0], X) \to X$ is defined as

$$L(\phi) = \begin{pmatrix} \left[r - \dfrac{2ru^*}{K} - \dfrac{2amu^*v^*}{(a + u^{*2})^2}\right]\phi_1(0) - \dfrac{mu^*}{a + u^{*2}}\phi_2(-\tau_1) \\ \dfrac{s}{h}\phi_1(-\tau_2) - s\phi_2(0) \end{pmatrix} \tag{9}$$

for $\phi = (\phi_1, \phi_2)^T \in C([-\tau, 0], X)$.

The characteristic equation of (7) is

$$\lambda y - d\Delta y - L\left(e^{\lambda}y\right) = 0, \quad y \in \operatorname{dom}(d\Delta),\ y \neq 0. \tag{10}$$

Recall that $-\Delta$ under the Neumann boundary condition has eigenvalues $0 = \mu_0 < \mu_1 \leq \mu_2 \leq \cdots \leq \mu_n \leq \mu_{n+1} \leq \cdots$ and $\lim_{i\to\infty}\mu_i = \infty$, with the corresponding eigenfunctions $\psi_n(x)$. Substituting

$$y = \sum_{n=0}^{\infty}\psi_n(x)\begin{pmatrix} y_{1n} \\ y_{2n}\end{pmatrix} \tag{11}$$

into (10), the following expression results:

$$\begin{pmatrix} r - \dfrac{2ru^*}{K} - \dfrac{2amu^*v^*}{(a + u^{*2})^2} - \mu_n d_1 & -\dfrac{mu^*}{a + u^{*2}}e^{-\lambda\tau_1} \\ \dfrac{s}{h}e^{-\lambda\tau_2} & -s - \mu_n d_2 \end{pmatrix}\begin{pmatrix} y_{1n} \\ y_{2n}\end{pmatrix} = \lambda\begin{pmatrix} y_{1n} \\ y_{2n}\end{pmatrix}. \tag{12}$$

Hence, it can be concluded that the characteristic equation (10) is equivalent to the equation

$$\lambda^2 + A_n\lambda + B_n + Ce^{-\lambda\tau} = 0, \quad n = 0, 1, 2, \ldots, \tag{13}$$

where

$$A_n = \mu_n(d_1 + d_2) - r + \frac{2ru^*}{K} + \frac{2amu^*v^*}{(a + u^{*2})^2} + s,$$
$$B_n = \left(r - \frac{2ru^*}{K} - \frac{2amu^*v^*}{(a + u^{*2})^2} - \mu_n d_1\right)(-s - \mu_n d_2), \tag{14}$$
$$C = \frac{s}{h}\frac{mu^*}{a + u^{*2}}, \qquad \tau = \tau_1 + \tau_2.$$

The stability of the positive equilibrium (u^*, v^*) can be determined by the distribution of the roots of (13). It is locally asymptotically stable if all the roots of (13) have negative real parts for all $n = 0, 1, 2, \ldots$. Obviously, 0 is not a root of (13) for all $n = 0, 1, 2, \ldots$. When $\tau = 0$ as well as $\tau_1 = \tau_2 = 0$, (13) can be simplified as

$$\lambda^2 + A_n\lambda + B_n = 0. \tag{15}$$

It can be verified that

$$A_n > 0, \quad B_n > 0, \quad \text{if } r - \frac{2ru^*}{K} < 0; \tag{16}$$

that is,

$$u^* > \frac{K}{2}, \tag{17}$$

which requires that

$$A\left(\frac{K}{2}\right) = \frac{m}{4}K^3 - \frac{rh}{8}K^3 - \frac{1}{2}arhK < 0 \tag{18}$$

or

$$2m - rh < 0. \tag{19}$$

Therefore, the following theorem can be stated.

Theorem 1. *If $2m - rh < 0$ holds, the interior equilibrium (u^*, v^*) of system (3) with $\tau_1 = \tau_2 = 0$ is asymptotically stable.*

When $\tau \neq 0$, assume that $\lambda = iw_0$ $(w_0 > 0)$ is a root of (13). Substituting it into (13) yields:

$$\begin{aligned} w_0^2 - B_n &= C\cos w_0\tau, \\ w_0A_n &= C\sin w_0\tau; \end{aligned} \tag{20}$$

that is,

$$w_0^4 + \left(A_n^2 - 2B_n\right)w_0^2 + B_n^2 - C^2 = 0, \tag{21}$$

where

$$\begin{aligned} A_n^2 - 2B_n &= \left(-r + \frac{2ru^*}{K} + \frac{2amu^*v^*}{(a+u^{*2})^2} + \mu_n d_1\right)^2 \\ &\quad + (s + \mu_n d_2)^2, \\ B_n^2 - C^2 &= \left(-r + \frac{2ru^*}{K} + \frac{2amu^*v^*}{(a+u^{*2})^2} + \mu_n d_1\right)^2 \\ &\quad \times (s + \mu_n d_2)^2 - \left(\frac{s}{h}\frac{mu^*}{a+u^{*2}}\right)^2. \end{aligned} \tag{22}$$

This leads to the following theorem.

Theorem 2. *If $2m - rh < 0$ and $B_n^2 - C^2 > 0$ hold for $n = 0, 1, 2, \ldots$, then the interior equilibrium (u^*, v^*) of system (3) is asymptotically stable for all $\tau_1, \tau_2 \geq 0$.*

Proof. If $B_n^2 - C^2 < 0$, then there exists $N_0 \geq 0$ such that, for $0 \leq n \leq N_0$, (20) has a unique positive real root:

$$w_0 = \sqrt{\frac{2B_n - A_n^2 + \sqrt{\left(A_n^2 - 2B_n\right)^2 - 4\left(B_n^2 - C^2\right)}}{2}}. \tag{23}$$

From (20), it follows that

$$\sin w_0\tau = \frac{w_0A_n}{C}, \qquad \cos w_0\tau = \frac{w_0^2 - B_n}{C}. \tag{24}$$

Then (13) has a pair of pure imaginary roots $\pm iw_0$ when

$$\tau = \tau_k = \tau_0 + \frac{2k\pi}{w_0}, \quad k = 0, 1, 2 \ldots, \tag{25}$$

where

$$\tau_0 = \frac{1}{w_0}\left(\arccos\frac{w_0^2 - B_n}{C}\right). \tag{26}$$

Substituting $\lambda(\tau)$ into (13) and taking the derivatives with respect to τ lead to

$$2\lambda\frac{d\lambda(\tau)}{d\tau} + A_n\frac{d\lambda(\tau)}{d\tau} + Ce^{-\lambda\tau}\left(-\lambda - \tau\frac{d\lambda(\tau)}{d\tau}\right) = 0. \tag{27}$$

For $\tau = \tau_0$, considering $Ce^{-iw_0\tau} = w_0^2 - B_n - iw_0A_n$, it follows that

$$\begin{aligned} &\operatorname{sign}\left\{\frac{d\operatorname{Re}(\lambda(\tau))}{d\tau}\right\}\bigg|_{\lambda=iw_0} = \operatorname{sign}\left\{\operatorname{Re}\left(\frac{d\lambda(\tau)}{d\tau}\right)\right\}\bigg|_{\lambda=iw_0} \\ &= \operatorname{sign}\left\{\operatorname{Re}\left(\frac{iCw_0e^{-iw_0\tau_0}}{2w_0i + A_n - C\tau_0e^{-iw_0\tau_0}}\right)\right\} \\ &= \operatorname{sign}\left\{\operatorname{Re}\left(\frac{iw_0^3 - B_nw_0i + w_0^2A_n}{2w_0i + A_n - \tau_0\left(w_0^2 - B_n - iw_0A_n\right)}\right)\right\} \\ &= \operatorname{sign}\left\{\operatorname{Re}\left(\frac{w_0^2A_n + i\left(w_0^3 - B_nw_0\right)}{-\tau_0\left(w_0^2 - B_n\right) + A_n + i\left(\tau_0w_0A_n + 2w_0\right)}\right)\right\} \\ &= \operatorname{sign}\Big\{\left(w_0^2A_n\left[-\tau_0\left(w_0^2 - B_n\right) + A_n\right]\right. \\ &\qquad \left. + \left(w_0^3 - B_nw_0\right)\left(\tau_0w_0A_n + 2w_0\right)\right) \\ &\qquad \times \left(\left[-\tau_0\left(w_0^2 - B_n\right) + A_n\right]^2\right. \\ &\qquad \left. + \left[\tau_0w_0A_n + 2w_0\right]^2\right)^{-1}\Big\} \end{aligned}$$

$$= \operatorname{sign}\left\{\frac{w_0^2\left[A_n^2+2w_0^2-2B_n\right]}{\left[-\tau_0\left(w_0^2-B_n\right)+A_n\right]^2+\left[\tau_0 w_0 A_n+2w_0\right]^2}\right\}$$
$$= \operatorname{sign}\left\{w_0^2\cdot\frac{2B_n-A_n^2+\sqrt{\left(A_n^2-2B_n\right)^2-4\left(B_n^2-C^2\right)}}{2}\times\left(\left[-\tau_0\left(w_0^2-B_n\right)+A_n\right]^2+\left[\tau_0 w_0 A_n+2w_0\right]^2\right)^{-1}\right\}=1. \quad (28)$$

In other words, $(d\lambda/d\tau)|_{\tau=\tau_0}>0$. □

From the above discussion, the following theorem can be stated.

Theorem 3. *If $B_n^2-C^2<0$ holds, then the following statements are true.*

(1) *If $0\le\tau_1+\tau_2<\tau_0$, then the interior equilibrium (u^*,v^*) of system (3) is asymptotically stable.*

(2) *If $\tau_1+\tau_2>\tau_0$, then the interior equilibrium (u^*,v^*) of system (3) is unstable.*

(3) *System (3) undergoes a Hopf bifurcation at the interior equilibrium (u^*,v^*) for $\tau_1+\tau_2=\tau_k$, $k=0,1,2,\ldots$.*

3. Global Stability

This section mainly proves that the interior equilibrium (u^*,v^*) is globally asymptotically stable with the upper-lower solution method in [27, 28]. For simplicity, let $(u_1(t,x),v_1(t,x))>(u_2(t,x),v_2(t,x))$ denote $u_1(t,x)>u_2(t,x)$ and $v_1(t,x)>v_2(t,x)$.

Lemma 4 (see [29]). *Assume that $u(t,x)$ is defined by*

$$u_t-d_1\Delta u=ru\left(1-\frac{u}{K}\right),\quad x\in\Omega,\ t>0,$$
$$\frac{\partial u}{\partial n}=0,\quad x\in\partial\Omega, \quad (29)$$
$$u(x,0)=u_0(x)>0,\quad x\in\Omega.$$

Then $\lim_{t\to\infty}u(x,t)=K$.

Theorem 5. *If $r-(m/2\sqrt{a}h)K>0$, then for system (3), the positive equilibrium (u^*,v^*) is globally asymptotically stable.*

Proof. From the maximum principle of parabolic equations, it is known that for any initial value $(u_0(t,x),v_0(t,x))>(0,0)$, the corresponding nonnegative solution $(u(t,x),v(t,x))$ is strictly positive for $t>0$. Because $r-(m/2\sqrt{a}h)K>0$, it is possible to choose ε_0 satisfying

$$0<\varepsilon_0<\left(r-\frac{m}{2\sqrt{a}h}K\right)\left[\frac{m}{2\sqrt{a}h}+\frac{m}{2\sqrt{a}}+\frac{r}{K}(1+h)\right]^{-1}. \quad (30)$$

Because

$$\frac{\partial u}{\partial t}-d_1\Delta u=ru\left(1-\frac{u}{K}\right)-\frac{mu^2v(t-\tau_1)}{a+u^2}\le ru\left(1-\frac{u}{K}\right) \quad (31)$$

according to Lemma 4 and the comparison principle of parabolic equations, there exists $t_1>0$ such that, for any $t>t_1$, $u(x,t)\le K+\varepsilon_0\triangleq\overline{u}$. This in turn implies that

$$\frac{\partial v}{\partial t}-d_1\Delta v=sv\left(1-\frac{hv}{u(t-\tau_2)}\right)\le sv\left(1-\frac{hv}{K+\varepsilon_0}\right) \quad (32)$$

for $t>t_1+\tau_2$.

Hence there exists $t_2>t_1$ such that, for any $t>t_2$,

$$v(x,t)\le\frac{K+\varepsilon_0}{h}+\varepsilon_0\triangleq\overline{v}. \quad (33)$$

Consequently,

$$\begin{aligned}\frac{\partial u}{\partial t}-d_1\Delta u&=ru\left(1-\frac{u}{K}\right)-\frac{mu^2v(t-\tau_1)}{a+u^2}\\&\ge ru\left(1-\frac{u}{K}\right)-\frac{mu^2v(t-\tau_1)}{2\sqrt{a}u}\\&\ge ru\left(1-\frac{u}{K}\right)-\frac{m(K+(h+1)\varepsilon_0)}{2h\sqrt{a}}u\end{aligned} \quad (34)$$

for $t>t_2+\tau_1$.

Because $r-(m/2\sqrt{a}h)K>0$, it can be easily verified that

$$K\left(1-\frac{m(K+(h+1)\varepsilon_0)}{2rh\sqrt{a}}\right)>0,$$
$$K\left(1-\frac{m(K+(h+1)\varepsilon_0)}{2rh\sqrt{a}}\right)-\varepsilon_0>0. \quad (35)$$

Hence, there exists $t_3>t_2$ such that, for any $t>t_3$,

$$u(x,t)\ge K\left(1-\frac{m(K+(h+1)\varepsilon_0)}{2rh\sqrt{a}}\right)-\varepsilon_0\triangleq\underline{u}. \quad (36)$$

This implies that

$$\frac{\partial v}{\partial t}-d_1\Delta v=sv\left(1-\frac{hv}{u(t-\tau_2)}\right)\ge sv-\frac{shv^2}{\underline{u}} \quad (37)$$

for $t>t_3+\tau_2$. Again it can be verified that

$$\frac{\underline{u}}{h}-\varepsilon_0=\frac{K}{h}\left(1-\frac{m(K+(h+1)\varepsilon_0)}{2rh\sqrt{a}}\right)-\frac{\varepsilon_0}{h}-\varepsilon_0>0, \quad (38)$$

and hence there exists $t_4 > t_3$ such that, for any $t > t_4$,

$$v(x,t) \geq \frac{K}{h}\left(1 - \frac{m(K+(h+1)\varepsilon_0)}{2rh\sqrt{a}}\right) - \frac{\varepsilon_0}{h} - \varepsilon_0 \triangleq \underline{v}. \quad (39)$$

Therefore, for $t > t_4$, it is possible to obtain

$$\underline{u} \leq u(x,t) \leq \overline{u}, \qquad \underline{v} \leq v(x,t) \leq \overline{v}, \quad (40)$$

and $\underline{u}, \overline{u}, \underline{v}, \overline{v}$ satisfy

$$\begin{aligned} 0 &\geq r\left(1 - \frac{\overline{u}}{K}\right) - \frac{m\overline{u}\underline{v}}{a+\overline{u}^2}, \qquad 0 \geq s\left(1 - \frac{h\overline{v}}{\overline{u}}\right), \\ 0 &\leq r\left(1 - \frac{\underline{u}}{K}\right) - \frac{m\underline{u}\overline{v}}{a+\underline{u}^2}, \qquad 0 \leq s\left(1 - \frac{h\underline{v}}{\underline{u}}\right). \end{aligned} \quad (41)$$

This implies that $(\overline{u}, \overline{v})$ and $(\underline{u}, \underline{v})$ are a pair of coupled upper and lower solutions of system (3), as in the definition in [29], for the reason that (3) is a mixed quasimonotonic system.

It is clear that there exists $K > 0$ such that, for any $(\underline{u}, \underline{v}) \leq (u_1, v_1)$, $(u_2, v_2) \leq (\overline{u}, \overline{v})$,

$$\begin{aligned} &\left| ru_1\left(1 - \frac{u_1}{K}\right) - \frac{mu_1^2 v_1}{a+u_1^2} - ru_2\left(1 - \frac{u_2}{K}\right) + \frac{mu_2^2 v_2}{a+u_2^2} \right| \\ &\quad \leq K\left(|u_1 - u_2| + |v_1 - v_2|\right), \end{aligned} \quad (42)$$

$$\begin{aligned} &\left| sv_1\left(1 - \frac{hv_1}{u_1}\right) - sv_2\left(1 - \frac{hv_2}{u_2}\right) \right| \\ &\quad \leq K\left(|u_1 - u_2| + |v_1 - v_2|\right). \end{aligned} \quad (43)$$

Define two iteration sequences $(\overline{u}^{(m)}, \overline{v}^{(m)})$ and $(\underline{u}^{(m)}, \underline{v}^{(m)})$ as follows: for $m \geq 1$,

$$\begin{aligned} \overline{u}^{(m)} &= \overline{u}^{(m-1)} + \frac{1}{K}\overline{u}^{(m-1)} \\ &\quad \times \left(r\left(1 - \frac{\overline{u}^{(m-1)}}{K}\right) - \frac{m\overline{u}^{(m-1)}\underline{v}^{(m-1)}}{a + \overline{u}^{(m-1)2}} \right), \\ \overline{v}^{(m)} &= \overline{v}^{(m-1)} + \frac{1}{K}s\overline{v}^{(m-1)}\left(1 - \frac{h\overline{v}^{(m)}}{\overline{u}^{(m)}}\right), \\ \underline{u}^{(m)} &= \underline{u}^{(m-1)} + \frac{1}{K}\underline{u}^{(m-1)} \\ &\quad \times \left(r\left(1 - \frac{\underline{u}^{(m-1)}}{K}\right) - \frac{m\underline{u}^{(m-1)}\overline{v}^{(m-1)}}{a + \underline{u}^{(m-1)2}} \right), \\ \underline{v}^{(m)} &= \underline{v}^{(m-1)} + \frac{1}{K}s\underline{v}^{(m-1)}\left(1 - \frac{h\underline{v}^{(m-1)}}{\underline{u}^{(m-1)}}\right), \end{aligned} \quad (44)$$

where $(\overline{u}^{(0)}, \overline{v}^{(0)}) = (\overline{u}, \overline{v})$, $(\underline{u}^{(0)}, \underline{v}^{(0)}) = (\underline{u}, \underline{v})$.

Then, for $m \geq 1$,

$$\begin{aligned} (\underline{u}, \underline{v}) &\leq \left(\underline{u}^{(m)}, \underline{v}^{(m)}\right) \leq \left(\underline{u}^{(m+1)}, \underline{v}^{(m+1)}\right) \\ &\leq \left(\overline{u}^{(m+1)}, \overline{v}^{(m+1)}\right) \leq \left(\overline{u}^{(m)}, \overline{v}^{(m)}\right) \leq (\overline{u}, \overline{v}), \end{aligned} \quad (45)$$

and there exist $(\tilde{u}, \tilde{v}) > (0,0)$ and $(\hat{u}, \hat{v}) > (0,0)$ such that $\lim_{m\to\infty}\overline{u}^{(m)} = \tilde{u}$, $\lim_{m\to\infty}\overline{v}^{(m)} = \tilde{v}$, $\lim_{m\to\infty}\underline{u}^{(m)} = \hat{u}$, $\lim_{m\to\infty}\underline{v}^{(m)} = \hat{v}$, and

$$\begin{aligned} 0 &= \tilde{u}\left(r\left(1 - \frac{\tilde{u}}{K}\right) - \frac{m\tilde{u}\hat{v}}{a+\tilde{u}^2}\right), \qquad 0 = \tilde{v}\left(s\left(1 - \frac{h\tilde{v}}{\tilde{u}}\right)\right), \\ 0 &= \hat{u}\left(r\left(1 - \frac{\hat{u}}{K}\right) - \frac{m\hat{u}\tilde{v}}{a+\hat{u}^2}\right), \qquad 0 = \hat{v}\left(s\left(1 - \frac{h\hat{v}}{\hat{u}}\right)\right). \end{aligned} \quad (46)$$

Because (u^*, v^*) is the unique positive constant equilibrium of system (3), it must hold that $(\tilde{u}, \tilde{v}) = (\hat{u}, \hat{v}) = (u^*, v^*)$.

According to the results of [27, 28], the solution $(u(x,t), v(x,t))$ of system (3) satisfies

$$\lim_{t\to\infty} u(x,t) = u^*, \qquad \lim_{t\to\infty} v(x,t) = v^*, \quad \text{uniformly for } x \in \overline{\Omega}. \quad (47)$$

Hence, the constant equilibrium (u^*, v^*) is globally asymptotically stable. □

4. Direction and Stability of Hopf Bifurcation

Part Two has already shown that system (3) undergoes Hopf bifurcation at the interior equilibrium (u^*, v^*) for $\tau_1 + \tau_2 = \tau_k$, $k = 0, 1, 2, \ldots$. In this section, the direction, stability, and period of the periodic solutions from the steady state will be studied by applying the method introduced by Hassard et al. [30] and the center manifold theorem due to [31–35].

For convenience, let $u' = u(t - \tau_2)$, $v' = v(t)$, $\tau = \tau_1 + \tau_2$. Then system (3) is equal to a single-delay system:

$$\begin{aligned} \frac{\partial u'}{\partial t} &= d_1 \Delta u' + ru\left(1 - \frac{u'}{K}\right) - \frac{mu'^2 v'(t-\tau)}{a + u'^2}, \\ &\qquad x \in (0, l\pi), \quad t > 0, \\ \frac{\partial v'}{\partial t} &= d_1 \Delta v' + v'\left[s\left(1 - \frac{hv'}{u'}\right)\right], \\ &\qquad x \in (0, l\pi), \quad t > 0, \\ \frac{\partial u'}{\partial n} &= \frac{\partial v'}{\partial n} = 0, \quad x = 0,\ l\pi, t > 0. \end{aligned} \quad (48)$$

Let $x(t) = u'(\tau t) - u^*$, $y(t) = v'(\tau t) - v^*$, $\tau = \tau_0 + \mu$. Then $\mu = 0$ is the Hopf bifurcation value of system (48), which can be written as follows:

$$\frac{\partial U(t)}{\partial t} = \tau_0 d\Delta U(t) + \tau_0 L(U_t) + G(U_t), \quad (49)$$

where

$$L(\phi) = \begin{pmatrix} \left[r - \frac{2ru^*}{K} - \frac{2amu^*v^*}{(a+u^{*2})^2}\right]\phi_1(0) - \frac{mu^*}{a+u^{*2}}\phi_2(-1) \\ \frac{s}{h}\phi_1(0) - s\phi_2(0) \end{pmatrix},$$

$$G(\phi,\mu) = \mu d\Delta\phi(0) + \mu L(\phi) + (\mu+\tau_0)F(\phi),$$

$$F(\phi) = \begin{pmatrix} F_1(\phi) \\ F_2(\phi) \end{pmatrix}, \tag{50}$$

with

$$F_1(\phi) = \left[r(\phi_1(0)+u^*)\left(1 - \frac{\phi_1(0)+u^*}{K}\right) - \frac{m(\phi_1(0)+u^*)^2(\phi_2(-1)+v^*)}{a+\phi_1(0)+u^{*2}}\right]\phi_1(0) - \frac{mu^*}{a+u^{*2}}\phi_2(-1), \tag{51}$$

$$F_2(\phi) = s(\phi_2(0)+v^*)\left(1 - \frac{h(\phi_2(0)+v^*)}{\phi_1(0)+u^*}\right) - \frac{s}{h}\phi_1(0) + s\phi_2(0)$$

for $\phi \in C([-1,0],X)$.

From the previous discussion, it is known that $\pm iw_0$ is a pair of simple purely imaginary eigenvalues of the linear system (7) and the following linear functional differential equation:

$$\frac{dz(t)}{dt} = \tau_0 L(zt). \tag{52}$$

By the Riesz representation theorem, there exists a 2×2 matrix function $\eta(\theta,\mu)$ ($\theta \in [-1,0]$), whose elements are bounded variables, such that

$$(\tau_0+\mu)L(\phi) = \int_{-1}^{0} d\eta(\theta,\mu)\phi(\theta), \quad \text{for } \phi \in C\left([-1,0],R^2\right). \tag{53}$$

In fact, it is possible to choose

$$\eta(\theta,\mu) = (\tau_0+\mu)\left(\begin{pmatrix} \left[r - \frac{2ru^*}{K} - \frac{2amu^*v^*}{(a+u^{*2})^2}\right] & 0 \\ \frac{s}{h} & -s \end{pmatrix}\delta(\theta) + \begin{pmatrix} 0 & -\frac{mu^*}{a+u^{*2}} \\ 0 & 0 \end{pmatrix}\delta(\theta+1)\right), \tag{54}$$

where $\delta(\theta)$ is a Dirac delta function satisfying

$$\delta(\theta) = \begin{cases} 1, & \theta = 0, \\ 0, & \theta \neq 0. \end{cases} \tag{55}$$

For $\phi \in C^1([-1,0],R^2)$, define $A(0)$ as

$$A(0)\phi(\theta) = \begin{cases} \frac{d\phi(\theta)}{d\theta}, & \theta \in [-1,0), \\ \int_{-1}^{0} d\eta(\theta,0)\phi(\theta), & \theta = 0, \end{cases}$$
$$R(0)\phi(\theta) = \begin{cases} 0, & \theta \in [-1,0), \\ F(\phi,\mu), & \theta = 0. \end{cases} \tag{56}$$

For $\psi \in C^1([-1,0],(R^2)^*)$, define

$$A^*(\psi(s)) = \begin{cases} -\frac{d\psi(s)}{ds}, & s \in (0,1], \\ \int_{-1}^{0} d\eta(\theta,0)\psi(-\xi), & s = 0. \end{cases} \tag{57}$$

Then $A(0)$ and A^* are adjoint operators under the bilinear form:

$$(\psi(s),\phi(\theta))_0 = \overline{\psi}(0)\phi(0) - \int_{-1}^{0}\int_{0}^{\theta} \overline{\psi}(\xi-\theta)\,d\eta(0,\theta)\phi(\xi)\,d\xi. \tag{58}$$

Therefore, $\pm iw_0$ are eigenvalues of $A(0)$ as well as A^*. Next, the eigenvectors of $A(0)$ and A^* corresponding to the eigenvalues iw_0 and $-iw_0$ can be calculated. Let

$$q(\theta) = \begin{pmatrix} 1 \\ C \end{pmatrix} e^{iw_0\tau_0\theta}. \tag{59}$$

Under the condition $A(0)q(0) = iw_0\tau_0 q(0)$, that is,

$$\tau_0 \begin{pmatrix} r - \frac{2ru^*}{K} - \frac{2amu^*v^*}{(a+u^{*2})^2} - iw_0 & -\frac{mu^*}{a+u^{*2}}e^{-iw_0\tau_0} \\ \frac{s}{h} & -s - iw_0 \end{pmatrix} \begin{pmatrix} 1 \\ C \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \tag{60}$$

it follows that

$$C = \frac{s}{h(s+iw_0)}. \tag{61}$$

Similarly, let $q^*(s) = E(1 \quad D)e^{iw_0\tau_0 s}$, and with $A^*q^*(0) = -iw_0\tau_0 q^*(0)$, that is,

$$\tau_0 \begin{pmatrix} r - \frac{2ru^*}{K} - \frac{2amu^*v^*}{(a+u^{*2})^2} + iw_0 & \frac{s}{h} \\ -\frac{mu^*}{a+u^{*2}}e^{-iw_0\tau_0} & -s + iw_0 \end{pmatrix} \begin{pmatrix} 1 \\ D \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \tag{62}$$

it is possible to obtain

$$D = \frac{-h\left(r - 2ru^*/K - 2amu^*v^*/\left(a+u^{*2}\right)^2 + iw_0\right)}{s}. \quad (63)$$

According to the conditions $(q^*, q) = 1$ and $(q^*, \overline{q}) = 0$,

$$\begin{aligned}(q^*, q) &= \overline{q^*}(0)\, q(0) - \int_{-1}^{0}\int_{\xi=0}^{\theta} \overline{q^*}(\xi-\theta)\, d\eta(0,\theta)\, q(\xi)\, d\xi \\ &= \overline{E}\begin{pmatrix}1 & \overline{D}\end{pmatrix}\begin{pmatrix}1\\ C\end{pmatrix} - \int_{-1}^{0}\int_{\xi=0}^{\theta} \overline{E}\begin{pmatrix}1 & \overline{D}\end{pmatrix} e^{-iw_0\tau_k(\xi-\theta)} d\eta(\theta) \\ &\qquad \times \begin{pmatrix}1\\ C\end{pmatrix} e^{iw_0\tau_k\xi} d\xi \\ &= \overline{E}\left\{1 + \overline{D}C - \int_{-1}^{0} \theta\begin{pmatrix}1 & \overline{D}\end{pmatrix} d\eta(0,\theta)\begin{pmatrix}1\\ C\end{pmatrix} e^{iw_0\tau_k\theta}\right\} \\ &= \overline{E}\left\{1 + \overline{D}C + \begin{pmatrix}1 & \overline{D}\end{pmatrix}\tau_0\begin{pmatrix}0 & -\dfrac{mu^*}{a+u^{*2}}\\ 0 & 0\end{pmatrix}\right. \\ &\qquad \left. \times \begin{pmatrix}1\\ C\end{pmatrix} e^{-iw_0\tau_k}\right\} \\ &= \overline{E}\left\{1 + \overline{D}C + \tau_0 C\left(-\frac{mu^*}{a+u^{*2}}\right) e^{-iw_0\tau_k}\right\}.\end{aligned} \quad (64)$$

Therefore,

$$E = \frac{1}{1 + D\overline{C} + \tau_0\overline{C}\left(-mu^*/\left(a+u^{*2}\right)\right) e^{iw_0\tau_k}}. \quad (65)$$

Let $\Phi = (q(\theta), \overline{q}(\theta))$, $\Psi = (q^*(s), \overline{q}^*(s))^T$, $I = \begin{pmatrix}1 & 0\\ 0 & 1\end{pmatrix}$; then

$$(\Psi, \Phi)_0 = I. \quad (66)$$

Therefore, the center subspace of system (52) is $P = \operatorname{span}\{q(\theta), \overline{q}(\theta)\}$, and the adjoint subspace is $P^* = \operatorname{span}\{q^*(s), \overline{q}^*(s)\}$. Let $f_0 = (f_0^1, f_0^2)$, where

$$f_0^1 = \begin{pmatrix}1\\ 0\end{pmatrix}, \qquad f_0^2 = \begin{pmatrix}0\\ 1\end{pmatrix}. \quad (67)$$

Using the notion from [30], it is also possible to define

$$c \cdot f_0 = c_1 f_0^1 + c_2 f_0^2 \quad (68)$$

for $c = (c_1, c_2)^T \in C^2$.

Define $(\psi \cdot f_0)(\theta) = \psi(\theta) \cdot f_0$ for $\psi(\theta) \in [-1, 0]$ and

$$\langle u, v\rangle = \frac{1}{l\pi}\int_0^{l\pi} u_1\overline{v}_1 dx + \frac{1}{l\pi}\int_0^{l\pi} u_2\overline{v}_2 dx \quad (69)$$

for $u = (u_1, u_2)$, $v = (v_1, v_2) \in C([0, l\pi], R^2)$.

Hence,

$$\langle \phi, f_0\rangle = \left(\left\langle \phi, f_0^1\right\rangle, \left\langle \phi, f_0^2\right\rangle\right)^T \quad (70)$$

for $\phi \in C([-1, 0], X)$. Then the center subspace of linear system (7) is given by $P_{CN}\mathrm{C}$, where

$$\begin{aligned}P_{CN}\phi &= \Phi\left(\Psi, \langle\phi, f_0\rangle\right)_0 \cdot f_0, \quad \phi \in \mathrm{C}, \\ P_{CN}\mathrm{C} &= \left\{\left(q(\theta)z + \overline{q}(\theta)\overline{z}\right) \cdot f_0 : z \in C\right\},\end{aligned} \quad (71)$$

and $\mathrm{C} = P_{CN}\mathrm{C} \oplus P_S\mathrm{C}$, where $P_S\mathrm{C}$ is a stable subspace.

According to [30], it is known that the infinitesimal generator A_U of linear system (7) satisfies

$$A_U\psi = \dot{\psi}(\theta). \quad (72)$$

Moreover, $\psi \in \operatorname{dom}(A_U)$ if and only if

$$\begin{aligned}&\dot{\psi}(\theta) \in \mathrm{C}, \qquad \psi(0) \in \operatorname{dom}(\Delta), \\ &\dot{\psi}(\theta)(0) = \tau_0\Delta\psi(0) + \tau_0 L_0(\psi).\end{aligned} \quad (73)$$

Setting $\mu = 0$ in (49), the center manifold

$$W(z, \overline{z}) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta) z\overline{z} + W_{02}(\theta)\frac{\overline{z}^2}{2} + \cdots \quad (74)$$

can be obtained in $P_S\mathrm{C}$. The flow of system (49) can be written as

$$u_t = \Phi(z(t), \overline{z}(t))^T \cdot f_0 + W(z(t), \overline{z}(t)), \quad (75)$$

where

$$\begin{aligned}\dot{z}(t) &= iw_0\tau_0 z(t) + \overline{q^*}(0) \\ &\quad \times \left\langle G\left(\Phi(z(t), \overline{z}(t))^T \cdot f_0 + W(z, \overline{z}), 0\right), f_0\right\rangle \\ &\triangleq iw_0\tau_0 z(t) + g(z, \overline{z}),\end{aligned} \quad (76)$$

$$\begin{aligned}g(z, \overline{z}) &= \overline{q^*}(0) \\ &\quad \times \left\langle G\left(\Phi(z(t), \overline{z}(t))^T \cdot f_0 + W(z, \overline{z}), 0\right), f_0\right\rangle \\ &= g_{20}(\theta)\frac{z^2}{2} + g_{11}(\theta) z\overline{z} + g_{02}(\theta)\frac{\overline{z}^2}{2} \\ &\quad + g_{21}(\theta)\frac{z^2\overline{z}}{2} + \cdots.\end{aligned} \quad (77)$$

From Taylor's formula,

$$\begin{aligned}f(u, v) &= \frac{m(u+u^*)^2(v+v^*)}{a + (u+u^*)^2} \\ &= \frac{mu^{*2}v^*}{a+u^{*2}} + \frac{2amu^*v^*}{(a+u^*)^2}u + \frac{mu^{*2}}{a+u^{*2}}v + b_{20}u^2 \\ &\quad + b_{11}uv + b_{30}u^3 + b_{21}u^2v + O(4),\end{aligned}$$

$$g(u,v) = \frac{sh(v+v^*)^2}{u+u^*} = sh\left(\frac{v^*}{h} - \frac{1}{h^2}u + \frac{2}{h}v + \frac{1}{h^2u^*}u^2 + \frac{1}{u^*}v^2 - \frac{2}{hu^*}uv + \frac{2}{h^2u^{*2}}u^2v - \frac{1}{h^2u^{*2}}u^3 + O(4)\right), \tag{78}$$

where

$$\begin{aligned} b_{11} &= \frac{2amu^*}{(a+u^*)^2}, \\ b_{20} &= \frac{amv^*\left(a^2+2au^{*2}+u^{*4}\right) - 4amu^{*2}v^*\left(a+u^{*2}\right)}{\left(a+u^{*2}\right)^4}, \\ b_{21} &= \frac{am\left(a+u^{*2}\right) - 4amu^{*2}\left(a+u^{*2}\right)}{\left(a+u^{*2}\right)^3}, \\ b_{30} &= \left[-8amu^*v^*\left(a+u^{*2}\right) - 8amv^* \times\left(3u^{*2}-2au^*\right) + 64amu^{*3}v^*\right] \times\left(a+u^{*2}\right)\left((a+u^*)^2\right)^{-1}, \\ O(4) &= O\left(\|(u,v)\|^4\right). \end{aligned} \tag{79}$$

Let $G(\phi,0) = \tau_0(G_1,G_2)^T$, where

$$\begin{aligned} G_1 &= \left(-\frac{r}{K} - b_{20}\right)\phi_1^2(0) - b_{11}\phi_1(0)\phi_2(-1) - b_{30}\phi_1^3(0) - b_{21}\phi_1^2(0)\phi_2(-1) + O(4), \\ G_2 &= -\frac{s}{hu^*}\phi_1^2(0) - \frac{sh}{u^*}\phi_2^2(0) + \frac{2s}{u^*}\phi_1(0)\phi_2(0) - \frac{2s}{hu^{*2}}\phi_1^2(0)\phi_2(0) + \frac{s}{hu^{*2}}\phi_1^3(0) + O(4). \end{aligned} \tag{80}$$

From (77),

$$\begin{aligned} g_{20} &= 2\overline{E}\tau_0\left[\left(-\frac{r}{K} - b_{20}\right) - b_{11}Ce^{-iw_0\tau_0}\right] + 2\overline{E}\tau_0\overline{D}\left[-\frac{s}{hu^*} - \frac{sh}{u^*}C^2 + \frac{2s}{u^*}C\right], \\ g_{11} &= \overline{E}\tau_0\left[2\left(-\frac{r}{K} - b_{20}\right) - b_{11}\left(Ce^{-iw_0\tau_0} + \overline{C}e^{iw_0\tau_0}\right)\right] + \overline{E}\tau_0\overline{D}\left[-\frac{2s}{hu^*} - \frac{2sh}{u^*}C\overline{C} + \frac{2s}{u^*}\left(C+\overline{C}\right)\right], \\ g_{02} &= 2\overline{E}\tau_0\left[\left(-\frac{r}{K} - b_{20}\right) - b_{11}\overline{C}e^{iw_0\tau_0}\right] + 2\overline{E}\tau_0\overline{D}\left[-\frac{s}{hu^*} - \frac{sh}{u^*}\overline{C}^2 + \frac{2s}{u^*}\overline{C}\right], \end{aligned}$$

$$\begin{aligned} g_{21} &= 2\overline{E}\tau_0\left[\left(-\frac{r}{K} - b_{20}\right) - \overline{D}\frac{s}{hu^*}\right] \times \frac{1}{l\pi}\int_0^{l\pi}\left(W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)\right)dx \\ &\quad - 2\overline{E}\tau_0\overline{D}\frac{sh}{u^*}\frac{1}{l\pi}\int_0^{l\pi}\left(W_{20}^{(1)}(0)\overline{C} + 2W_{11}^{(1)}(0)C\right)dx \\ &\quad - E\tau_0 b_{11}\frac{1}{l\pi}\int_0^{l\pi}\left(W_{20}^{(1)}(0)\overline{C}e^{iw_0\tau_0} + 2W_{11}^{(1)}(0)Ce^{-iw_0\tau_0} + W_{20}^{(2)}(-1) + 2W_{11}^{(2)}(-1)\right)dx \\ &\quad + \overline{E}\tau_0\overline{D}\frac{2s}{u^*}\frac{1}{l\pi}\int_0^{l\pi}\left(W_{20}^{(1)}(0)\overline{C} + 2W_{11}^{(1)}(0)C + W_{20}^{(2)}(0) + 2W_{11}^{(2)}(0)\right)dx \\ &\quad - 2\overline{E}\tau_0 b_{21}\left(\overline{C}e^{iw_0\tau_0} + 2Ce^{-iw_0\tau_0}\right) \\ &\quad - 2\overline{E}\tau_0\overline{D}\frac{2s}{hu^{*2}}\left(\overline{C} + 2C\right) \\ &\quad - 6\overline{E}\tau_0 b_{30} + 6\overline{E}\tau_0\overline{D}\frac{s}{hu^{*2}}. \end{aligned} \tag{81}$$

In the last formula, $W_{20}(0)$, $W_{20}(-1)$, $W_{11}(0)$, and $W_{11}(-1)$ are still unknown. Therefore, it is necessary to compute $W_{20}(\theta)$ and $W_{11}(\theta)$, as described below.

From (74), it is possible to obtain

$$\begin{aligned} \dot{W} &= W_{20}z\dot{z} + W_{11}\overline{z}\dot{z} + W_{11}z\dot{\overline{z}} + W_{02}\overline{z}\dot{\overline{z}} + \cdots, \\ A_U W &= A_U W_{20}\frac{z^2}{2} + A_U W_{11}z\overline{z} + W_{02}A_U\frac{\overline{z}^2}{2} + \cdots. \end{aligned} \tag{82}$$

In addition, $W(z,\overline{z})$ satisfies

$$\begin{aligned} \dot{W} &= A_U W + X_0 G\left(\Phi(z,\overline{z})^T\cdot f_0 + W(z,\overline{z}),0\right) - \Phi\left(\Psi,\left\langle X_0 G\left(\Phi(z,\overline{z})^T\cdot f_0 + W(z,\overline{z}),0\right),f_0\right\rangle\right)_0\cdot f_0 \\ &\triangleq A_U W + H_{20}\frac{z^2}{2} + H_{11}z\overline{z} + H_{02}\frac{\overline{z}^2}{2} + \cdots. \end{aligned} \tag{83}$$

Therefore,

$$\begin{aligned} 2iw_0\tau_0 W_{20} &= A_U W_{20} + H_{20}, \\ -A_U W_{11} &= H_{11}, \\ -2iw_0\tau_0 W_{02} &= A_U W_{02} + H_{02}. \end{aligned} \tag{84}$$

For $-1 \le \theta < 0$,

$$H_{20}\frac{z^2}{2} + H_{11}z\overline{z} + H_{02}\frac{\overline{z}^2}{2} + \cdots = -\Phi\left(\Psi,\left\langle X_0 G\left(\Phi(z,\overline{z})^T\cdot f_0 + W(z,\overline{z}),0\right),f_0\right\rangle\right)_0\cdot f_0, \tag{85}$$

and therefore

$$H_{20}(\theta) = -\left[g_{20}q(\theta) + \overline{g}_{02}\overline{q}(\theta)\right] \cdot f_0, \qquad H_{11}(\theta) = -\left[g_{11}q(\theta) + \overline{g}_{11}\overline{q}(\theta)\right] \cdot f_0. \tag{86}$$

From (84) and (86),

$$\dot{W}_{20}(\theta) = 2iw_0\tau_0 W_{20}(\theta) + \left[g_{20}q(\theta) + \overline{g}_{02}\overline{q}(\theta)\right] \cdot f_0. \tag{87}$$

Solving for $W_{20}(\theta)$,

$$W_{20}(\theta) = \frac{ig_{20}q(\theta)}{w_0\tau_0} \cdot f_0 + \frac{i\overline{g}_{02}\overline{q}(\theta)}{3w_0\tau_0} \cdot f_0 + E_1 e^{2iw_p\tau_0\theta}. \tag{88}$$

Similarly,

$$W_{11}(\theta) = \frac{-ig_{11}q(\theta)}{w_0\tau_0} \cdot f_0 + \frac{i\overline{g}_{11}\overline{q}(\theta)}{w_0\tau_0} \cdot f_0 + E_2, \tag{89}$$

where E_1 and E_2 are both two-dimensional vectors and can be determined as follows.

For $\theta = 0$, according to the definition of A_U and the first two equations of (84),

$$\begin{aligned} 2iw_0\tau_0 W_{20}(0) &= \int_{-1}^{0} d\eta(\theta, 0) W_{20}(\theta) + H_{20}(0) \\ &- \int_{-1}^{0} d\eta(\theta, 0) W_{11}(\theta) = H_{11}(0). \end{aligned} \tag{90}$$

Then

$$H_{20}(0) = -\left[g_{20}q(0) + \overline{g}_{02}\overline{q}(0)\right] \cdot f_0 + 2\tau_0 \times \begin{pmatrix} -\frac{r}{K} - b_{20} - b_{11}Ce^{-iw_0\tau_0} \\ -\frac{s}{hu^*} - \frac{sh}{u^*}C^2 + \frac{2s}{u^*}C \end{pmatrix}. \tag{91}$$

Note that

$$\begin{aligned} \int_{-1}^{0} d\eta(\theta, 0) e^{iw_0\tau_0\theta} q(0) &= iw_0\tau_0 q(0), \\ \int_{-1}^{0} d\eta(\theta, 0) e^{-iw_0\tau_0\theta} \overline{q}(0) &= -iw_0\tau_0 \overline{q}(0). \end{aligned} \tag{92}$$

It follows that

$$\begin{aligned} &2\tau_0 \begin{pmatrix} -\frac{r}{K} - b_{20} - b_{11}Ce^{-iw_0\tau_0} \\ -\frac{s}{hu^*} - \frac{sh}{u^*}C^2 + \frac{2s}{u^*}C \end{pmatrix} \\ &= g_{20}q(0) + \overline{g}_{02}\overline{q}(0) + 2iw_0\tau_0 W_{20}(0) - \int_{-1}^{0} d\eta(\theta, 0) W_{20}(\theta) \\ &= -g_{20}q(0) + \frac{\overline{g}_{02}\overline{q}(0)}{3} + 2iw_0\tau_0 E_1 - \int_{-1}^{0} d\eta(\theta, 0) \left[\frac{ig_{20}q(\theta)}{w_0\tau_0} + \frac{i\overline{g}_{02}\overline{q}(\theta)}{3w_0\tau_0} + E_1 e^{2iw_p\tau_0\theta}\right] \\ &= \left(2iw_0\tau_0 I - \int_{-1}^{0} d\eta(\theta, 0) e^{2iw_p\tau_0\theta}\right) E_1 \\ &= \left[2iw_0\tau_0 \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} - \tau_0 \times \begin{pmatrix} r - \frac{2ru^*}{K} - \frac{2amu^*v^*}{(a+u^{*2})^2} & -\frac{mu^*}{a+u^{*2}} e^{-2iw_0\tau_0} \\ \frac{s}{h} & -s \end{pmatrix}\right] E_1 \\ &= \tau_0 \begin{pmatrix} 2iw_0 - r + \frac{2ru^*}{K} + \frac{2amu^*v^*}{(a+u^{*2})^2} & \frac{mu^*}{a+u^{*2}} e^{-2iw_0\tau_0} \\ -\frac{s}{h} & 2iw_0 + s \end{pmatrix} E_1. \end{aligned} \tag{93}$$

Therefore, it is possible to obtain

$$E_1 = E_{11} \cdot E_{12}, \tag{94}$$

where

$$\begin{aligned} E_{11} &= \begin{pmatrix} 2iw_0 - r + \frac{2ru^*}{K} + \frac{2amu^*v^*}{(a+u^{*2})^2} & \frac{mu^*}{a+u^{*2}} e^{-2iw_0\tau_0} \\ -\frac{s}{h} & 2iw_0 + s \end{pmatrix}^{-1}, \\ E_{12} &= 2 \begin{pmatrix} -\frac{r}{K} - b_{20} - b_{11}Ce^{-iw_0\tau_0} \\ -\frac{s}{hu^*} - \frac{sh}{u^*}C^2 + \frac{2s}{u^*}C \end{pmatrix}. \end{aligned} \tag{95}$$

Similarly,

$$H_{11}(0) = -\left[g_{11}q(0) + \overline{g}_{11}\overline{q}(0)\right] \cdot f_0 + \tau_0 \times \begin{pmatrix} 2\left(-\frac{r}{K} - b_{20}\right) - b_{11}\left(Ce^{-iw_0\tau_0} + \overline{C}e^{iw_0\tau_0}\right) \\ -\frac{2s}{hu^*} - \frac{2sh}{u^*}C\overline{C} + \frac{2s}{u^*}\left(C + \overline{C}\right) \end{pmatrix}. \tag{96}$$

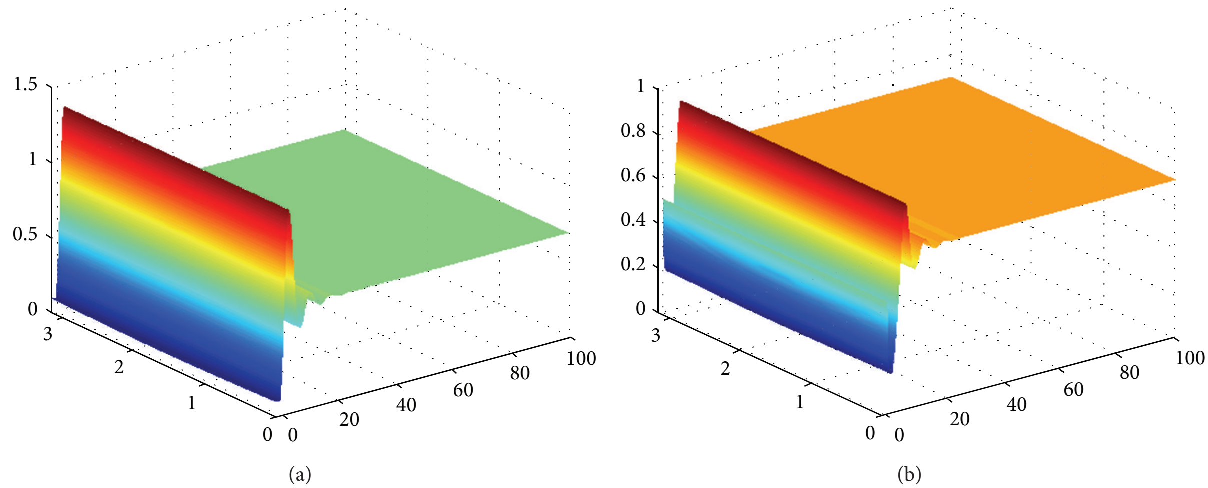

FIGURE 1: Convergence to positive equilibrium. Here the parameters are assumed to be $\tau_1 = 0$, $\tau_2 = 1.5$, and the initial values are $u(x,t) = 0.1 + 0.01t\sin x$, $v(x,t) = 0.5 + 0.01t\cos x$, and $t \in [-1.5, 0]$, $x \in [0, \pi]$.

Then

$$\begin{aligned}
&\tau_0 \begin{pmatrix} 2\left(-\frac{r}{K} - b_{20}\right) - b_{11}\left(Ce^{-iw_0\tau_0} + \overline{C}e^{iw_0\tau_0}\right) \\ -\frac{2s}{hu^*} - \frac{2sh}{u^*}C\overline{C} + \frac{2s}{u^*}\left(C + \overline{C}\right) \end{pmatrix} \\
&= g_{11}q(0) + \overline{g}_{11}\overline{q}(0) - \int_{-1}^{0} d\eta(\theta, 0) W_{11}(\theta) \\
&= g_{11}q(0) + \overline{g}_{11}\overline{q}(0) \\
&\quad - \int_{-1}^{0} d\eta(\theta, 0)\left[\frac{-ig_{11}q(\theta)}{w_0\tau_0} + \frac{i\overline{g}_{11}\overline{q}(\theta)}{w_0\tau_0} + E_2\right] \\
&= -\int_{-1}^{0} d\eta(\theta, 0) E_2 \\
&= \tau_0 \begin{pmatrix} -r + \frac{2ru^*}{K} + \frac{2amu^*v^*}{(a + u^{*2})^2} & \frac{mu^*}{a + u^{*2}} \\ -\frac{s}{h} & s \end{pmatrix} E_2.
\end{aligned} \tag{97}$$

Therefore, it is possible to obtain

$$E_2 = E_{21} \cdot E_{22}, \tag{98}$$

where

$$\begin{aligned}
E_{21} &= \begin{pmatrix} -r + \frac{2ru^*}{K} + \frac{2amu^*v^*}{(a + u^{*2})^2} & \frac{mu^*}{a + u^{*2}} \\ -\frac{s}{h} & s \end{pmatrix}^{-1}, \\
E_{22} &= \begin{pmatrix} 2\left(-\frac{r}{K} - b_{20}\right) - b_{11}\left(Ce^{-iw_0\tau_0} + \overline{C}e^{iw_0\tau_0}\right) \\ -\frac{2s}{hu^*} - \frac{2sh}{u^*}C\overline{C} + \frac{2s}{u^*}\left(C + \overline{C}\right) \end{pmatrix}.
\end{aligned} \tag{99}$$

Then g_{21} is expressed by the parameters. Therefore, the following values can be computed:

$$\begin{aligned}
c_1(0) &= \frac{i}{2w_0\tau_0}\left(g_{20}g_{11} - 2\left|g_{11}\right|^2 - \frac{\left|g_{02}\right|^2}{3}\right) + \frac{g_{21}}{2}, \\
\mu_2 &= -\frac{\operatorname{Re}\left(c_1(0)\right)}{\operatorname{Re}\lambda'(\tau_0)}, \\
\beta_2 &= 2\operatorname{Re}\left(c_1(0)\right), \\
T_2 &= -\frac{\operatorname{Im}\left\{c_1(0)\right\} + \mu_2 \operatorname{Im}\left\{\lambda'(\tau_0)\right\}}{w_0\tau_0}.
\end{aligned} \tag{100}$$

Theorem 6. *If μ_2, β_2, and T_2 are defined as above, then the following are true:*

(i) *if $\mu_2 > 0$ ($\mu_2 < 0$), then the Hopf bifurcation is supercritical (subcritical);*

(ii) *if $\beta_2 < 0$ ($\beta_2 > 0$), then the periodic solutions are stable (unstable);*

(iii) *if $T_2 > 0$ ($T_2 < 0$), then the period of the bifurcating periodic solutions of system (3) increases (decreases).*

Remark 7. The direction and stability of the Hopf bifurcation have already been computed when $\tau = \tau_0$. The other Hopf bifurcation value τ_k can be analyzed using the same procedure.

5. Simulations and Discussion

This paper has considered a delayed predator-prey model with modified Holling-Tanner functional response. The effect of time delays on the positive equilibrium of system (3) has been investigated. The results obtained here show that the time delay plays an important role in determining system stability. Theorem 3 shows that the time delay can cause a stable equilibrium to become unstable or, in other words, that

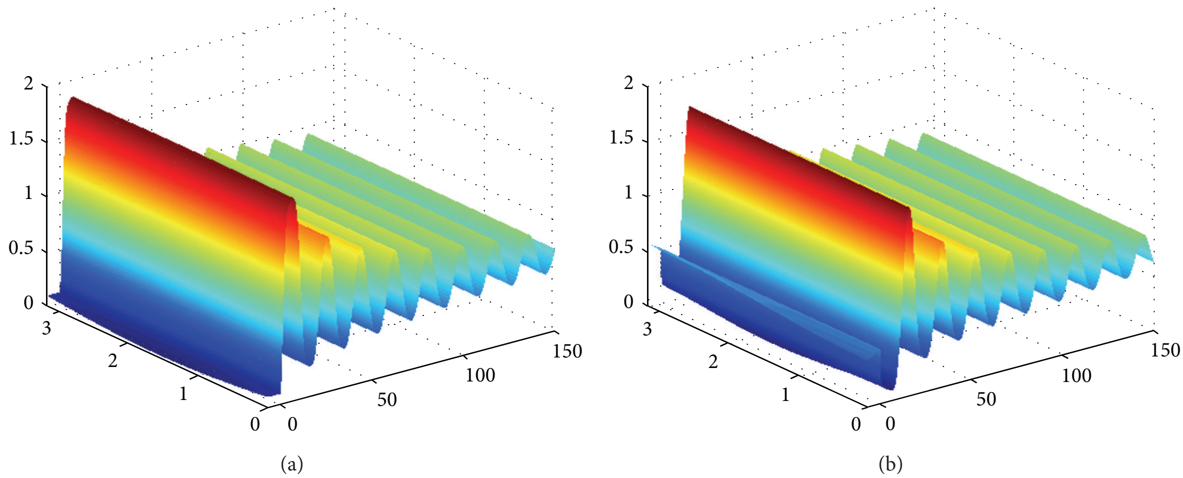

FIGURE 2: Convergence to positive equilibrium. Here the parameters are assumed to be $\tau_1 = 0$, $\tau_2 = 7$, and the initial values $u(x,t) = 0.1 + 0.01t \sin x$, $v(x,t) = 0.5 + 0.01t \cos x$, and $t \in [-7, 0]$, $x \in [0, \pi]$.

there is a critical value τ_0, such that, for $0 \le \tau_1 + \tau_2 < \tau_0$, equilibrium (u^*, v^*) is stable; when $\tau_1 + \tau_2$ approaches τ_0, equilibrium (u^*, v^*) bifurcates into periodic solutions; and when $\tau_1 + \tau_2 > \tau_0$, the equilibrium becomes unstable.

Numerical simulations are performed to illustrate the dynamic behavior of system (3). Assume that $r = 1$, $a = 1$, $h = 1$, $K = 2$, $s = 1$, $m = 4$, $d_1 = 0.1$, $d_2 = 0.2$, and $l = 1$. In this case, $\tau_0 = 2.201$. As shown in Figure 1, the positive equilibrium is stable when $\tau_1 + \tau_2 < \tau_0$, and the predators and prey tend to a steady state. However, if $\tau_1 + \tau_2 > \tau_0$, the positive equilibrium loses its stability and Hopf bifurcation occurs, leading to oscillatory behavior. These results are identical to the numerical results illustrated in Figure 2.

In both figures, the upper diagram represents the prey and the lower diagram represents the predator.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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