

Research Article

Dynamical Analysis of a Delayed Reaction-Diffusion Predator-Prey System

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This work deals with the analysis of a delayed diffusive predator-prey system under Neumann boundary conditions. The dynamics are investigated in terms of the stability of the nonnegative equilibria and the existence of Hopf bifurcation by analyzing the characteristic equations. The direction of Hopf bifurcation and the stability of bifurcating periodic solution are also discussed by employing the normal form theory and the center manifold reduction. Furthermore, we prove that the positive equilibrium is asymptotically stable when the delay is less than a certain critical value and unstable when the delay is greater than the critical value.

1. Introduction

The study on the dynamics of predator-prey systems is one of the dominant subjects in ecology and mathematical ecology due to its universal existence and importance [1]. A prototypical predator-prey interaction model is of the following form:

$$\begin{aligned}\frac{du}{dt} &= a(u) - f(u)g(v), \\ \frac{dv}{dt} &= \sigma f(u)g(v) - z(v),\end{aligned}\tag{1.1}$$

where $u(t)$ and $v(t)$ are the densities of the prey and predator at time $t > 0$, respectively.

Furthermore, the function $a(u)$ is growth rate of the prey in the absence of predation, which is given by

$$a(u) = \alpha u \min \left\{ 1, \frac{K-u}{K-\varepsilon} \right\}, \quad \alpha > 0, \varepsilon \geq 0, K > 0. \quad (1.2)$$

If $\varepsilon = 0$, this reduces to the traditional logistic form $a(u) = \alpha u(1 - u/K)$, see [2] and the references therein. Here, the parameter α stands for the specific growth rate of the prey u , and K for carrying capacity of the prey in the absence of predators.

The product $f(u)g(v)$ gives the rate at which prey is consumed, and $f(u)g(v)/v$ is termed as the functional response [3]. In particular, these functions can be defined by

$$f(u) = cu, \quad g(v) = \frac{v}{mv+1}, \quad c > 0, m \geq 0, \quad (1.3)$$

where c denotes the capture rate, and m the half capturing saturation constant.

The proportionality constant σ is the rate of prey consumption. And the function $z(v)$ is given by

$$z(v) = \gamma v + lv^2, \quad \gamma > 0, l \geq 0, \quad (1.4)$$

where γ denotes the natural death rate of the predators, and $l > 0$ can be used to model predator in traspecific competition that is not direct competition for food, such as some type of territoriality, see [2]. In this paper, we discuss the case of $l = 0$, which is used in a much more traditional case. Based on the above discussions, we can obtain the following model:

$$\begin{aligned} \frac{du}{dt} &= \alpha u \left(1 - \frac{u}{K} \right) - \frac{cuv}{mv+1}, \\ \frac{dv}{dt} &= v \left(-\gamma + \frac{c\sigma u}{mv+1} \right). \end{aligned} \quad (1.5)$$

Setting $\beta = \alpha/K$, $b = c\sigma$, model (1.5) leads to the following dimensionless equation:

$$\begin{aligned} \frac{du}{dt} &= u(\alpha - \beta u) - \frac{cuv}{mv+1}, \\ \frac{dv}{dt} &= v \left(-\gamma + \frac{bu}{mv+1} \right), \end{aligned} \quad (1.6)$$

where $b > 0$ denotes conversion rate.

In recent years, the models involving time delay and spatial diffusion have been extensively studied by many authors and many interesting results have been obtained, including the stability, the existence of Hopf bifurcation, and direction of bifurcating periodic solutions,

see [1, 4–18]. In this paper, we mainly focus on the effects of both spatial diffusion and time delay factors on system (1.6) with Neumann boundary conditions as follows:

$$\begin{aligned} \frac{\partial u}{\partial t} &= u(\alpha - \beta u) - \frac{cuv}{mv + 1} + d_1 \Delta u, \quad x \in \Omega, \quad t > 0, \\ \frac{\partial v}{\partial t} &= v \left(-\gamma + \frac{bu(t - \tau)}{mv(t - \tau) + 1} \right) + d_2 \Delta v, \quad x \in \Omega, \quad t > 0, \\ \frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0, \quad x \in \partial\Omega, \quad t > 0, \\ u(x, 0) &= u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, \quad x \in \Omega, \end{aligned} \tag{1.7}$$

where Ω is a bounded open domain in \mathbb{R} with a smooth boundary $\partial\Omega$, and $\Delta = \partial^2/\partial x^2$ denotes the Laplacian operator in \mathbb{R} . $d_1 > 0$ and $d_2 > 0$ denote the diffusion coefficients of the prey u and predator v , respectively. ν is the outward unit normal vector on $\partial\Omega$. $\tau > 0$ can be regarded as the gestation of the predator. System (1.7) includes not only the dispersal processes, but also some of the past states of the system.

Throughout this paper, we restrict ourselves to the one-dimensional spatial domain $\Omega = (0, \pi)$ for the sake of convenience.

The remaining parts of the paper are structured in the following way. In Section 2, we analyze the distribution of the roots of the characteristic equation and give various conditions on the stability of a unique positive equilibrium and the existence of Hopf bifurcation with time delay. In Section 3, applying the normal form theory [19, 20] and the center manifold reduction of partial functional differential equations [21], we derive the explicit algorithm in order to determine the direction of the Hopf bifurcation, the stability, and other properties on bifurcating periodic solutions. Finally, a brief discussion is given.

2. Stability of Positive Equilibrium and Existence of Hopf Bifurcation

In this section, by analyzing the associated characteristic equation of system (1.7) at the positive equilibrium, we investigate the stability of the positive equilibria of system (1.7).

It is straightforward to see that system (1.7) has the following two boundary equilibria:

- (i) $E_1 = (0, 0)$ (total extinct) which is saddle point, hence it is unstable;
- (ii) $E_2 = (\alpha/\beta, 0)$ (extinct of the predator) which is saddle point if $b\alpha > \beta\gamma$, or stable if $b\alpha < \beta\gamma$.

To find the positive equilibrium, we set

$$u(\alpha - \beta u) - \frac{cuv}{mv + 1} = 0, \quad v \left(-\gamma + \frac{bu}{mv + 1} \right) = 0, \tag{2.1}$$

which yields

$$mb\beta u^2 + (c - m\alpha)bu - c\gamma = 0. \tag{2.2}$$

Obviously, system (1.7) has a unique positive equilibrium $E^* = (u^*, v^*)$ with $ba > \beta\gamma$, where

$$u^* = \frac{mba - bc + \sqrt{4mbc\beta\gamma + b^2(m\alpha - c)^2}}{2mb\beta}, \quad v^* = \frac{bu^* - \gamma}{m\gamma}. \quad (2.3)$$

Set $\bar{u} = u - u^*$, $\bar{v} = v - v^*$ and drop the bars for simplicity of notations, then system (1.7) can be transformed into the following equivalent system:

$$\begin{aligned} \frac{\partial u}{\partial t} &= (u + u^*)(\alpha - \beta(u + u^*)) - \frac{c(u + u^*)v}{m(v + v^*) + 1} + d_1 \Delta u, \quad x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} &= (v + v^*) \left(-\gamma + \frac{b(u(t - \tau) + u^*)}{m(v(t - \tau) + v^*) + 1} \right) + d_2 \Delta v, \quad x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0, \quad x \in \partial\Omega, t > 0, \\ u(x, 0) &= u_0(x) - u^* \geq 0, \quad v(x, 0) = v_0(x) - v^* \geq 0, \quad x \in \Omega. \end{aligned} \quad (2.4)$$

Assume that $u_0(x), v_0(x) \in C([-\tau, 0]; X)$ and X is defined by

$$X = \left\{ (u, v) : u, v \in W^{2,2}(\Omega) : \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, x \in \partial\Omega \right\} \quad (2.5)$$

with the inner product $\langle \cdot, \cdot \rangle$.

Denote $(u(t), v(t)) = (u(t, x), v(t, x))$ and $U(t) = (u(t), v(t))^T$. Then system (2.4) can be rewritten as an abstract differential equation in the phase space $C([-\tau, 0]; X)$ as follows:

$$\frac{\partial U(t)}{\partial t} = d \Delta U(t) + L(U_t) + F(U_t), \quad (2.6)$$

where $d = \text{diag}(d_1, d_2)$, $U_t(\theta) = U(t + \theta)$, $-\tau \leq \theta \leq 0$, and $L : C([-\tau, 0]; X) \rightarrow X$, $F : C([-\tau, 0]; X) \rightarrow X$ are given by

$$L(\phi) = \begin{pmatrix} -\beta u^* \phi_1(0) - \frac{cu^*}{(mv^* + 1)^2} \phi_2(0) \\ \frac{bv^*}{(mv^* + 1)} \phi_1(-\tau) - \frac{mbu^*v^*}{(mv^* + 1)^2} \phi_2(-\tau) \end{pmatrix}, \quad (2.7)$$

$$F(\phi) = \begin{pmatrix} -\beta \phi_1^2(0) - \frac{c}{(mv^* + 1)^2} \phi_1(0) \phi_2(0) + \frac{cmu^*}{(cm + 1)^3} \phi_2^2(0) \\ \left(\phi_2(0) + \frac{mv^*}{mv^* + 1} \phi_2(-\tau) \right) \left(\frac{b}{mv^* + 1} \phi_1(-\tau) - \frac{bmu^*}{(mv^* + 1)^2} \phi_2(-\tau) \right) \end{pmatrix}, \quad (2.8)$$

respectively, where $\phi(\theta) = U_t(\theta)$, $\phi = (\phi_1, \phi_2)^T \in C([-\tau, 0]; X)$.

The linearization of (2.6) is given by

$$\frac{\partial U(t)}{\partial t} = d\Delta U(t) + L(U_t), \tag{2.9}$$

and its characteristic equation is

$$\lambda y - d\Delta y - L(e^{\lambda \cdot} y) = 0, \tag{2.10}$$

where $y \in \text{dom}(\Delta)$ and $y \neq 0$, $\text{dom}(\Delta) \subset X$.

It is well known that the eigenvalue problem

$$\begin{aligned} -\Delta \psi &= \mu \psi, \quad x \in (0, \pi), \\ \frac{\partial \psi}{\partial x} \Big|_{x=0} &= \frac{\partial \psi}{\partial x} \Big|_{x=\pi} = 0, \end{aligned} \tag{2.11}$$

has eigenvalues $0 = \mu_0 \leq \mu_1 \leq \mu_2 \leq \dots \leq \mu_n \leq \mu_{n+1} \leq \dots$, with the corresponding eigenfunctions $\psi_n(x)$. Substituting

$$y = \sum_{n=0}^{\infty} \psi_n(x) \begin{pmatrix} y_{1n} \\ y_{2n} \end{pmatrix} \tag{2.12}$$

into characteristic equation (2.10), we obtain

$$\begin{pmatrix} -\beta u^* - d_1 \mu_n & -\frac{cu^*}{(mv^* + 1)^2} \\ \frac{bv^*}{mv^* + 1} e^{-\lambda \tau} & -\frac{bmu^* v^*}{(mv^* + 1)^2} e^{-\lambda \tau} - d_2 \mu_n \end{pmatrix} \begin{pmatrix} y_{1n} \\ y_{2n} \end{pmatrix} = \lambda \begin{pmatrix} y_{1n} \\ y_{2n} \end{pmatrix}. \tag{2.13}$$

Hence, we can conclude that the characteristic equation (2.10) is equivalent to the sequence of the following characteristic equations:

$$\lambda^2 + (A_n + De^{-\lambda \tau})\lambda + B_n + C_n e^{-\lambda \tau} = 0 \quad (n = 0, 1, 2, \dots), \tag{2.14}$$

where

$$\begin{aligned} A_n &= \beta u^* + (d_1 + d_2)\mu_n, \\ B_n &= \beta u^* d_2 \mu_n + d_1 d_2 \mu_n^2, \\ C_n &= \frac{bd_1 m \mu_n \beta u^* v^*}{(mv^* + 1)^2} + \frac{bm\beta(u^*)^2 v^*}{(mv^* + 1)^2} + \frac{bcu^* v^*}{(mv^* + 1)^3}, \\ D &= \frac{bmu^* v^*}{(mv^* + 1)^2}. \end{aligned} \tag{2.15}$$

The stability of the positive equilibrium $E^* = (u^*, v^*)$ can be determined by the distribution of the roots of (2.14) ($n = 0, 1, 2, \dots$), that is, the equilibrium $E^* = (u^*, v^*)$ is locally asymptotically stable if all the roots of (2.14) ($n = 0, 1, 2, \dots$) have negative real parts. Note that $\lambda = 0$ is not a root of (2.14) for any $n = 0, 1, 2, \dots$. Next, we analyze the behaviour of system (1.7) in two situations: with/without delay effect.

2.1. Case $\tau = 0$

Equation (2.14) with $\tau = 0$ is equivalent to the following quadratic equation:

$$\lambda^2 + (A_n + D)\lambda + B_n + C_n = 0, \quad (2.16)$$

where A_n, B_n, C_n , and D are defined as (2.15).

Let λ_1 and λ_2 be two roots of (2.16), then for any $n = 0, 1, 2, \dots$, we have

$$\begin{aligned} \lambda_1 + \lambda_2 &= -(A_n + D) < 0, \\ \lambda_1 \lambda_2 &= B_n + C_n > 0. \end{aligned} \quad (2.17)$$

Then we can get the following theorem.

Theorem 2.1. *If $b\alpha > \beta\gamma$ holds, the positive equilibrium $E^* = (u^*, v^*)$ of system (1.7) with $\tau = 0$ is asymptotically stable.*

In the following, we prove that $E^* = (u^*, v^*)$ of system (1.7) is globally stable with $\tau = 0$.

Theorem 2.2. *If $b\alpha > \beta\gamma$ holds, the positive equilibrium $E^* = (u^*, v^*)$ of system (1.7) with $\tau = 0$ is globally asymptotically stable.*

Proof. To prove our statement, we need to construct a Lyapunov function. To this end, we define

$$V(t) = \int_{\Omega} V_1(u, v) dx, \quad (2.18)$$

where

$$V_1(u, v) = \int_{u^*}^u \frac{\xi - u^*}{\xi} d\xi + \frac{c}{b(1 + mv^*)} \int_{v^*}^v \frac{\eta - v^*}{\eta} d\eta. \quad (2.19)$$

We claim that $V_1(u, v)$ is positive definite. In fact, set

$$\frac{\partial V_1}{\partial u} = 1 - \frac{u^*}{u} = 0, \quad \frac{\partial V_1}{\partial v} = \frac{c}{b(1 + mv^*)} \left(1 - \frac{v^*}{v}\right) = 0, \quad (2.20)$$

we can obtain $(u, v) = (u^*, v^*)$. And the Hessian Matrix at (u^*, v^*) is given by

$$H(E)|_{(u^*, v^*)} = \begin{pmatrix} \frac{1}{u^*} & 0 \\ 0 & \frac{c}{bv^*(1 + mv^*)} \end{pmatrix}, \tag{2.21}$$

Hence $H(E)|_{(u^*, v^*)}$ is positive definite, which follows that

$$\min(V_1(u, v)) = V_1(u^*, v^*) = 0. \tag{2.22}$$

The time derivative of V along the solutions of system (1.7) with $\tau = 0$, we have

$$\begin{aligned} \frac{dV}{dt} &= \int_{\Omega} \left(\frac{u - u^*}{u} \frac{\partial u}{\partial t} + \frac{c}{b(1 + mv^*)} \frac{(v - v^*)}{v} \frac{\partial v}{\partial t} \right) dx \\ &= \int_{\Omega} \frac{dV_1}{dt} dx + \int_{\Omega} \left\{ (d_1 \Delta u) \frac{\partial V}{\partial u} + (d_2 \Delta v) \frac{\partial V}{\partial v} \right\} dx \\ &= \int_{\Omega} \left(-\beta(u - u^*)^2 - \frac{cmu^*}{(mv + 1)(mv^* + 1)^2} (v - v^*)^2 \right) dx \\ &\quad - \frac{d_1 u^*}{u^2} \int_{\Omega} \left(\frac{\partial u}{\partial x} \right)^2 dx - \frac{d_2 v^*}{v^2} \int_{\Omega} \left(\frac{\partial v}{\partial x} \right)^2 dx, \end{aligned} \tag{2.23}$$

then, we obtain $dV/dt < 0$.

It is enough to see that dV/dt satisfies Lyapunov's asymptotic stability theorem, hence the positive equilibrium $E^* = (u^*, v^*)$ of system (1.7) with $\tau = 0$ is globally asymptotically stable. \square

2.2. Case $\tau \neq 0$

In the following, we prove the stability of the positive equilibrium $E^* = (u^*, v^*)$ of system (1.7) and the existence of Hopf bifurcation at the positive equilibrium $E^* = (u^*, v^*)$.

Theorem 2.3. *Assume that $\beta\gamma, A_n^2 - D^2 - 2B_n^2 < 0$ and $B_n^2 - C_n^2 > 0$ hold, then the positive equilibrium $E^* = (u^*, v^*)$ is asymptotically stable for all $\tau \geq 0$.*

Proof. Let $\lambda = \mu(\tau) + i\omega(\tau)$ be a root of the characteristic equation (2.14), then we have

$$\begin{aligned} \mu^2 - \omega^2 + A_n\mu + B_n + (D\omega \sin \omega\tau + (C_n + D\mu) \cos \omega\tau)e^{-\mu\tau} &= 0, \\ 2\mu\omega + A_n\omega - ((C_n + D) \sin \omega\tau + D\omega \cos \omega\tau)e^{-\mu\tau} &= 0, \end{aligned} \tag{2.24}$$

where λ, μ, ω are functions of τ . A necessary condition for the stability of $E^* = (u^*, v^*)$ is that the characteristic equation has a purely imaginary solution $\lambda = i\omega$. Let $\mu(\tau) = 0$ and $\omega(\tau) \neq 0$, then we can reduce (2.24) to

$$\begin{aligned} -\omega^2 + D\omega \sin \omega\tau + C_n \cos \omega\tau + B_n &= 0, \\ A_n\omega + D\omega \cos \omega\tau - C_n \sin \omega\tau &= 0, \end{aligned} \quad (2.25)$$

which lead to

$$\omega^4 + (A_n^2 - D^2 - 2B_n)\omega^2 + (B_n^2 - C_n^2) = 0. \quad (2.26)$$

Since $B_n^2 - C_n^2 > 0$ and $(A_n^2 - D^2 - 2B_n) < 0$, these imply that (2.26) has no positive roots, that is, all roots of (2.14) have negative real parts. \square

Theorem 2.4. Assume that $\beta\alpha > \beta\gamma$, $B_n^2 - C_n^2 < 0$, then there exists a sequence

$$\tau_j^0 = \tau_0^0 + \frac{2j\pi}{\omega_0} \quad (j = 0, 1, 2, \dots), \quad (2.27)$$

where τ_0^0 is defined as (2.32), such that, for system (1.7), the following statements are true.

- (i) If $\tau \in [0, \tau_0^0)$, then the positive equilibrium $E^* = (u^*, v^*)$ is asymptotically stable.
- (ii) If $\tau > \tau_0^0$, then the positive equilibrium $E^* = (u^*, v^*)$ is unstable.
- (iii) $\tau = \tau_0^j$ ($n = 0, 1, 2, \dots$) are Hopf bifurcation values of system (1.7) and these Hopf bifurcations are all spatially homogeneous.

Proof. Let $\lambda = i\omega(\tau)$ be a root of the characteristic equation (2.14). By the same way in Theorem 2.3, then ω satisfies the following equation:

$$\omega^4 + (A_n^2 - D^2 - 2B_n)\omega^2 + (B_n^2 - C_n^2) = 0. \quad (2.28)$$

Since $B_n^2 - C_n^2 < 0$, (2.28) has a unique positive root ω_0 satisfying

$$\omega_0 = \sqrt{\frac{-(A_n^2 - D^2 - 2B_n) + \sqrt{(A_n^2 - D^2 - 2B_n)^2 - 4(B_n^2 - C_n^2)}}{2}} \quad (2.29)$$

and from (2.25) we obtain

$$\begin{aligned} \sin \omega_0\tau &= \frac{D\omega_0^3 + A_n C_n \omega_0 - B_n D \omega_0}{D^2 \omega_0^2 + C_n^2} \triangleq G(\omega_0), \\ \cos \omega_0\tau &= \frac{C_n \omega_0^2 - B_n C_n - A_n D \omega_0^2}{D^2 \omega_0^2 + C_n^2} \triangleq E(\omega_0), \end{aligned} \quad (2.30)$$

then (2.16) has one imaginary root $i\omega_0$ when

$$\tau_j^0 = \tau_0^0 + \frac{2j\pi}{\omega_0}, \quad (j = 0, 1, 2, \dots), \tag{2.31}$$

where τ_0^0 satisfies

$$\tau_0^0 = \begin{cases} \frac{\arccos(E(\omega_0))}{\omega_n}, & \text{if } G(\omega_0) > 0, \\ \frac{\arccos(2\pi - E(\omega_0))}{\omega_0}, & \text{if } G(\omega_0) < 0, \end{cases} \tag{2.32}$$

□

Let $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ be the root of (2.14) satisfying $\alpha(\tau_j^0) = 0$ and $\omega(\tau_j^0) = \omega_0$ when τ is close to τ_j^0 . Now by some simple calculations we obtain

$$\begin{aligned} \left[\frac{d\alpha}{d\tau} \Big|_{\tau=\tau_j^0} \right]^{-1} &= \text{Re} \left[\left(\frac{2\lambda + A_n + De^{-\lambda\tau} - (C_n + D\lambda)\tau e^{-\lambda\tau}}{(C_n + D\lambda)\lambda e^{-\lambda\tau}} \right) \Big|_{\tau=\tau_j^0} \right] \\ &= \frac{2C_n \cos \omega_0\tau + D\omega_0 \sin \omega_0\tau}{C_n^2 + D^2\omega_0^2} - \frac{D^2\omega_n^2}{C_n^2\omega_0^2 + D^2\omega_0^4} \\ &\quad + \frac{A_n\omega_0(-D\omega_n \cos \omega_0\tau + C_n \sin \omega_0\tau)}{C_n^2\omega_0^2 + D^2\omega_0^4}, \end{aligned} \tag{2.33}$$

since $\omega_0^2 = D\omega_n \sin \omega_0\tau + C_n \cos \omega_0\tau$ and $A_n\omega_0 = -D\omega_0 \cos \omega_0\tau + C_n \sin \omega_0\tau$, and from the expression of ω_0^2 in (2.29), we immediately see that

$$\left[\frac{d\alpha}{d\tau} \Big|_{\tau=\tau_j^0} \right]^{-1} = \frac{2\omega_0^2}{C_n^2 + D^2\omega_0^2} + \frac{A_n^2 - D^2}{C_n^2 + D^2\omega_0^2} = \frac{\sqrt{(D^2 - A_n^2)^2 + 4C_n^2}}{C_n^2 + D^2\omega_0^2}. \tag{2.34}$$

Therefore, $\text{sign} [d\alpha/d\tau|_{\tau=\tau_j^0}]^{-1} = 1$, that is, $d\alpha/d\tau|_{\tau=\tau_j^0} > 0$. This implies that all the roots that cross the imaginary axis at $i\omega$ cross from left to right as τ increases.

Hence the transversality condition holds and accordingly Hopf bifurcation occurs at $\tau = \tau_0^0$, and $\tau = \tau_j^0$ ($j = 0, 1, 2, \dots$) are Hopf bifurcation values of system (1.7) and these Hopf bifurcations are all spatially homogeneous. This completes the proof.

3. Direction and Stability of Hopf Bifurcation

In the previous section, we have already obtained that system (1.7) undergoes Hopf bifurcation at the positive equilibrium $E^* = (u^*, v^*)$ when τ crosses through the critical value τ_j^0 ($j = 0, 1, 2, \dots$). In this section, we will study the direction of the Hopf bifurcation and the stability

of the bifurcating periodic solutions by employing the normal form method [19, 20] as well as center manifold theorem [21] for partial differential equations with delay. Then we compute the direction and stability of the Hopf bifurcation when $\tau_0 = \tau_j^0$ for fixed $j \in \{0, 1, 2, \dots\}$.

Without loss of generality, we denote the critical value of τ by τ_0 and set $\tau = \tau_0 + \mu$, then $\mu = 0$ is the Hopf bifurcation value of system (2.6). Rescaling the time by $t \rightarrow t/\tau$ to normalize the delay, system (2.6) can be written in the following form:

$$\frac{\partial U(t)}{\partial t} = \tau_0 d\Delta U(t) + \tau_0 L(U_t) + G(U_t, \mu), \quad (3.1)$$

where

$$L(\phi) = \begin{pmatrix} -\beta u^* \phi_1(0) - \frac{cu^*}{(mv^* + 1)^2} \phi_1(0) \\ \frac{bv^*}{(mv^* + 1)} \phi_2(-1) - \frac{bmu^* v^*}{(mv^* + 1)^2} \phi_2(-1) \end{pmatrix},$$

$$G(\phi, \mu) = \mu d\Delta \phi(0) + \mu L(\phi) + (\tau_0 + \mu) F(\phi, \mu), \quad (3.2)$$

$$F(\phi, \mu) = \begin{pmatrix} -\beta \phi_1^2(0) - \frac{c}{(mv^* + 1)^2} \phi_1(0) \phi_2(0) + \frac{cmu^*}{(cm + 1)^3} \phi_2^2(0) \\ \left(\phi_2(0) - \frac{mv^*}{mv^* + 1} \phi_2(-1) \right) \left(\frac{b}{mv^* + 1} \phi_1(-1) - \frac{bmu^*}{(mv^* + 1)^2} \phi_2(-1) \right) \end{pmatrix}$$

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

From Section 2, we know that $\pm i\omega_0 \tau_0$ are a pair of simple purely imaginary eigenvalues of the linear system

$$\frac{\partial U(t)}{\partial t} = \tau_0 d\Delta U(t) + \tau_0 L(U_t), \quad (3.3)$$

and the following linear functional differential equation:

$$\dot{U}(t) = \tau_0 L(U_t). \quad (3.4)$$

By the Riesz representation theorem, there exists a 2×2 matrix function $\eta(\theta, \tau_0)$ of bounded variation for $\theta \in [-1, 0]$, such that

$$(\tau_0 + \mu) L(\tau_0)(\phi) = \int_{-1}^0 d\eta(\theta, \tau_0) \phi(\theta) \quad \text{for } \phi \in C([-1, 0], \mathbb{R}^2). \quad (3.5)$$

In fact, we can choose

$$\eta(\theta, \tau_0) = (\tau_0 + \mu) H_1 \delta(\theta) + (\tau_0 + \mu) H_2 \delta(\theta + 1), \quad (3.6)$$

where

$$H_1 = \begin{pmatrix} -\beta u^* & -\frac{cu^*}{(mv^* + 1)^2} \\ 0 & 0 \end{pmatrix}, \quad H_2 = \begin{pmatrix} 0 & 0 \\ \frac{bv^*}{mv^* + 1} & -\frac{bmu^*v^*}{(mv^* + 1)^2} \end{pmatrix}, \quad (3.7)$$

and δ is the Dirac delta function.

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

$$A(0)\phi(\theta) = \begin{cases} \frac{d}{d\theta}\phi(\theta), & \theta \in [-1, 0), \\ \int_{-1}^0 d\eta(\theta, \tau_0)\phi(\theta), & \theta = 0, \end{cases} \quad (3.8)$$

$$R(0)\phi(\theta) = \begin{cases} 0, & \theta \in [-1, 0), \\ F(\phi, \mu), & \theta = 0. \end{cases}$$

For $\psi = (\psi_1, \psi_2) \in C^1([-1, 0], (\mathbb{R}^2)^*)$, we define

$$A^*(\psi(s)) = \begin{cases} -\frac{d}{ds}\psi(s), & s \in (0, 1], \\ \int_{-1}^0 \psi(-\xi)d\eta(\theta, 0), & s = 0. \end{cases} \quad (3.9)$$

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

$$\langle \psi(s), \phi(\theta) \rangle = \bar{\psi}(0)\phi(0) - \int_{-1}^0 \int_{\xi=0}^{\theta} \bar{\psi}(\xi - \theta)d\eta(0, \theta)\phi(\xi)d\xi, \quad (3.10)$$

where $\eta(\theta) = \eta(0, \theta)$.

We note that $\pm i\omega_0\tau_0$ are the eigenvalues of $A(0)$. Since $A(0)$ and A^* are two adjoint operators, $\pm i\omega_0\tau_0$ are also eigenvalues of A^* . We will first try to obtain eigenvector of $A(0)$ and A^* corresponding to the eigenvalue $i\omega_0\tau_0$ and $-i\omega_0\tau_0$, respectively.

Let $q(\theta) = (1, \rho)^T e^{i\omega_0\tau_0\theta}$, ($\theta \in [-1, 0]$) be the eigenvector of $A(0)$ corresponding to the eigenvalue $i\omega_0\tau_0$. Then we have $A(0)q(\theta) = i\omega_0\tau_0q(\theta)$ by the definition of eigenvector. Therefore, from (3.6), (3.10), and the definition of $A(0)$, we can get

$$\tau_0 \begin{pmatrix} -\beta u^* - i\omega_0 & -\frac{cu^*}{(mv^* + 1)^2} \\ \frac{bv^*}{mv^* + 1} e^{-i\omega_0\tau_0} & -\frac{bmu^*v^*}{(mv^* + 1)^2} e^{-i\omega_0\tau_0} - i\omega_0 \end{pmatrix} \begin{pmatrix} 1 \\ \rho \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad (3.11)$$

here,

$$\rho = -\frac{(mv^* + 1)^2(\beta u^* + i\omega_0)}{cu^*}. \quad (3.12)$$

On the other hand, suppose that $q^*(S) = D(1, r)e^{i\omega_0\tau_0 S}$ is the eigenvector of A^* corresponding to the eigenvalue $-i\omega_0\tau_0$. By the definition of A^* , we have

$$\tau_0 \begin{pmatrix} -\beta u^* + i\omega_0 & \frac{bv^*}{mv^* + 1} e^{-i\omega_0\tau_0} \\ \frac{cu^*}{(mv^* + 1)^2} & -\frac{bmu^*v^*}{(mv^* + 1)^2} e^{-i\omega_0\tau_0} + i\omega_0 \end{pmatrix} \begin{pmatrix} D \\ Dr \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad (3.13)$$

where

$$r = -\frac{mv^*}{mv^* + 1} - \frac{m\beta u^*v^*(mv^* + 1) + cu^*}{\omega_0(mv^* + 1)^2} i, \quad (3.14)$$

and we also assume that $\langle q^*(S), q(\theta) \rangle = 1$. To obtain the value of D , from (3.10) we have

$$\begin{aligned} \langle q^*(S), q(\theta) \rangle &= \bar{D} \left\{ (1, \bar{r})(1, \rho)^T - \int_{-1}^0 \int_{\xi=0}^{\theta} (1, \bar{r}) e^{-i(\xi-\theta)\omega_0\tau_0} d\eta(\theta) (1, \rho)^T e^{i\xi\omega_0\tau_0} d\xi \right\} \\ &= \bar{D} \left\{ 1 + \rho\bar{r} - \int_{-1}^0 (1, \bar{r}) \theta e^{i\theta\omega_0\tau_0} d\eta(\theta) (1, \rho)^T \right\} \\ &= \bar{D} \left\{ 1 + \rho\bar{r} + \frac{b\bar{r}\tau_0 v^*}{mv^* + 1} \left(\frac{m\rho u^*}{mv^* + 1} - 1 \right) e^{-i\omega_0\tau_0} \right\}. \end{aligned} \quad (3.15)$$

Thus, we can choose

$$\bar{D} = \left(1 + \rho\bar{r} + \frac{b\bar{r}\tau_0 v^*}{mv^* + 1} \left(\frac{m\rho u^*}{mv^* + 1} - 1 \right) \right)^{-1} e^{i\omega_0\tau_0}, \quad (3.16)$$

such that $\langle q^*(S), q(\theta) \rangle = 0$ and $\langle q^*(S), q(\theta) \rangle = 1$, that is to say that let $\phi = (q(\theta), \bar{q}(\theta))$, $\psi = (q^*(S), \bar{q}^*(S))^T$, then $(\psi, \phi) = I$, where I is the unit matrix. Then the center subspace of system (3.4) is $P = \text{span}\{q(\theta), \bar{q}(\theta)\}$, and the adjoint subspace $P^* = \text{span}\{q^*(S), \bar{q}^*(S)\}$. Let $f_0 = (f_0^1, f_0^2)$, where

$$f_0^1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \quad f_0^2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}, \quad (3.17)$$

by using the notation from [20], we also define

$$cf_0 = c_1 f_0^1 + c_2 f_0^2, \quad (3.18)$$

for $c = \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} \in \mathcal{C} = C([-1, 0], X)$.

And the center subspace of linear system (3.4) is given by $P_{CN}\mathcal{C}$, where

$$\begin{aligned} P_{CN}\phi &= \phi(\psi, \langle \phi, f_0 \rangle)_0 \cdot f_0, \quad \phi \in \mathcal{C}, \\ P_{CN}\mathcal{C} &= (q(\theta)z + \bar{q}(\theta)\bar{z}) \cdot f_0, \quad z \in \mathcal{C}, \end{aligned} \quad (3.19)$$

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

Following Wu [20], we know that the infinitesimal generator A_U of linear system (3.4) satisfies

$$\dot{U}(t) = A_U U \quad (3.20)$$

moreover, $U \in \text{dom}(A_U)$ if and only if

$$\dot{U}(t) \in \mathcal{C}, \quad U(0) \in \text{dom}(\Delta), \quad \dot{U}(0) = \tau_0 \Delta U(0) + \tau_0 L(U(0)). \quad (3.21)$$

As the formulas to be developed for the bifurcation direction and stability are all relative to $\mu = 0$ only, we set $\mu = 0$ in system (3.4) and can obtain the center manifold

$$W(z, \bar{z}) = W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + \dots \quad (3.22)$$

with the range in $P_S\mathcal{C}$. The flow of system (3.4) in the center manifold can be written as follows:

$$U_t = \phi(z(t), \bar{z}(t))^T \cdot f_0 + W(z(t), \bar{z}(t)), \quad (3.23)$$

where

$$\dot{z}(t) = i\omega_0 \tau_0 z(t) + q^*(0) \left\langle G(\phi(z(t), \bar{z}(t)))^T \cdot f_0 + W(z, \bar{z}, 0), f_0 \right\rangle. \quad (3.24)$$

We rewrite (3.24) as

$$\dot{z}(t) = i\omega_0 \tau_0 z(t) + g(z(t), \bar{z}(t)), \quad (3.25)$$

with

$$\begin{aligned} g(z(t), \bar{z}(t)) &= q^*(0) \left\langle G(\phi(z(t), \bar{z}(t)))^T \cdot f_0 + \omega(z, \bar{z}, 0), f_0 \right\rangle \\ &= g_{20} \frac{z^2}{2} + g_{11} z\bar{z} + g_{02} \frac{\bar{z}^2}{2} + g_{21} \frac{\bar{z}^2 \bar{z}}{2}. \end{aligned} \quad (3.26)$$

Denote $G(\phi, 0) = \tau_0(G_1, G_2)^T$, and let

$$\begin{aligned} f^1(u, v) &= (u + u^*)(\alpha - \beta(u + u^*)) - \frac{c(u + u^*)v}{m(v + v^*) + 1}, \\ f^2(u, v) &= (v + v^*) \left(-r + \frac{b(u(t - \tau) + u^*)}{m(v(t - \tau) + v^*) + 1} \right). \end{aligned} \quad (3.27)$$

Afterwards, from Taylor formula, we have

$$\begin{aligned} G_1 &= -\beta\phi_1^2(0) - \frac{c}{(mv^* + 1)^2} \phi_1(0)\phi_2(0) + \frac{cmu^*}{(mv^* + 1)^3} \phi_2^2(0) \\ &\quad + \frac{cm}{(mv^* + 1)^3} \phi_1(0)\phi_2^2(0) - \frac{cm^2u^*}{(mv^* + 1)^4} \phi_2^3(0), \\ G_2 &= \frac{b}{mv^* + 1} \left(\phi_2(0) - \frac{mv^*}{mv^* + 1} \phi_2(-1) \right) \left(\phi_1(-1) - \frac{mu^*}{mv^* + 1} \phi_2(-1) \right) \left(1 - \frac{m}{mv^* + 1} \phi_2(-1) \right). \end{aligned} \quad (3.28)$$

From (3.26) and (3.28), we have

$$\begin{aligned} g_{20} &= 2\bar{D}\tau_0 \left[-\beta - \frac{c\rho}{(mv^* + 1)^2} + \frac{cm\rho^2u^*}{(mv^* + 1)^3} \right] \\ &\quad + 2\bar{D}\bar{r}\tau_0 \left[\frac{b\rho}{mv^* + 1} e^{-i\omega_0\tau_0} + \frac{bm\rho v^*}{(mv^* + 1)^2} \left(\frac{m\rho u^*}{mv^* + 1} - 1 \right) e^{-2i\omega_0\tau_0} \right], \\ g_{11} &= \bar{D}\tau_0 \left[-2\beta + \left(\frac{2m\bar{\rho}\rho u^*}{(mv^* + 1)^3} - \frac{\bar{\rho} + \rho}{(mv^* + 1)^2} \right) (c + bmv^*) \right] \\ &\quad + \bar{D}\tau_0 \left[\frac{b\bar{r}}{mv^* + 1} (\bar{\rho} e^{-i\omega_0\tau_0} + \rho e^{i\omega_0\tau_0}) \right], \\ g_{02} &= 2\bar{D}\tau_0 \left[-\beta - \frac{c\bar{\rho}}{(mv^* + 1)^2} + \frac{cm\bar{\rho}^2u^*}{(mv^* + 1)^3} \right] \\ &\quad + 2\bar{D}\bar{r}\tau_0 \left[\frac{bm^2\bar{\rho}^2u^*v^*}{(mv^* + 1)^3} e^{2i\omega_0\tau_0} - \frac{mb\bar{\rho}v^*}{(mv^* + 1)^2} e^{2i\omega_0\tau_0} + \frac{b\bar{\rho}}{mv^* + 1} e^{i\omega_0\tau_0} \right], \end{aligned}$$

$$\begin{aligned}
g_{21} = & 2\bar{D}\tau_0 \left[-\beta \left(2W_{11}^1(0) + W_{20}^2(0) \right) \right] \\
& + 2\bar{D}\tau_0 \left[-\frac{c}{(mv^* + 1)^2} \left(\rho W_{11}^1(0) + \frac{1}{2}\bar{\rho}W_{20}^1(0) + \frac{1}{2}W_{20}^2(0) + W_{11}^2(0) \right) \right] \\
& + 2\bar{D}\tau_0 \left[\frac{cmu^*}{(mv^* + 1)^3} \left(2\rho W_{11}^2(0) + \bar{\rho}W_{20}^2(0) \right) \right] \\
& + 2\bar{D}\tau_0 \left[\frac{b\bar{r}}{mv^* + 1} \left(\rho W_{11}^1(-1) + \frac{1}{2}\bar{\rho}W_{20}^1(-1) \right) \right] \\
& + 2\bar{D}\tau_0 \left[\frac{b\bar{r}}{mv^* + 1} \left(\frac{1}{2}W_{20}^2(0)e^{i\omega_0\tau_0} + W_{11}^2(0)e^{-i\omega_0\tau_0} \right) \right] \\
& + 2\bar{D}\tau_0 \left[-\frac{mbv^*\bar{r}}{(mv^* + 1)^2} e^{-i\omega_0\tau_0} \left(W_{11}^2(-1) + \rho W_{11}^1(-1) \right) \right] \\
& + 2\bar{D}\tau_0 \left[-\frac{mbv^*\bar{r}}{2(mv^* + 1)^2} e^{i\omega_0\tau_0} \left(W_{20}^2(-1) + \bar{\rho}W_{20}^1(-1) \right) \right] \\
& + 2\bar{D}\tau_0 \left[\frac{m^2bu^*\bar{v}^*\bar{r}}{(mv^* + 1)^3} \left(2W_{11}^2(-1)\rho e^{-i\omega_0\tau_0} + W_{20}^2(-1)\bar{\rho}e^{i\omega_0\tau_0} \right) \right].
\end{aligned} \tag{3.29}$$

Since $W_{11}(\theta)$ and $W_{20}(\theta)$ for $\theta \in [-1, 0]$ appear in g_{21} , we need to compute them. It follows from (3.26) that

$$\begin{aligned}
\dot{W}(z, \bar{z}) = & W_{20}z\dot{z} + W_{11}z\dot{\bar{z}} + W_{11}z\dot{\bar{z}} + W_{20}\bar{z}\dot{\bar{z}}, \dots, \\
A_U W = & A_U W_{20} \frac{z^2}{2} + A_U W_{11} z\bar{z} + A_U W_{20} \frac{\bar{z}^2}{2} + \dots.
\end{aligned} \tag{3.30}$$

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

$$\dot{W} = A_U W + H(z, \bar{z}), \tag{3.31}$$

where

$$\begin{aligned}
H(z, \bar{z}) = & H_{20} \frac{z^2}{2} + H_{11} z\bar{z} + H_{02} \frac{\bar{z}^2}{2} + \dots \\
= & X_0 G(U_t, 0) - \phi(\psi, \langle X_0 G(U_t, 0), f_0 \rangle) \cdot f_0.
\end{aligned} \tag{3.32}$$

Thus, from (3.24) and (2.18), we can get

$$\begin{aligned} [2i\omega_0\tau_0 - A_U]W_{20} &= H_{20}, \\ -A_U W_{11} &= H_{11}, \\ [-2i\omega_0\tau_0 - A_U]W_{02} &= H_{02}. \end{aligned} \quad (3.33)$$

Note that A_U has only two eigenvalues $\pm i\omega_0\tau_0$, therefore, (3.33) has unique solution W_{ij} in Q given by

$$\begin{aligned} W_{20} &= [2i\omega_0\tau_0 - A_U]^{-1}H_{20}, \\ W_{11} &= -A_U^{-1}H_{11}, \\ W_{02} &= [-2i\omega_0\tau_0 - A_U]^{-1}H_{02}. \end{aligned} \quad (3.34)$$

From (2.18), we know that for $\theta \in [-1, 0)$

$$\begin{aligned} H(z, \bar{z}) &= -\phi(\theta)\psi(0)\langle G(U_t, f_0) \rangle \cdot f_0 \\ &= -[q(\theta)q^*(0) + \bar{q}(\theta)\bar{q}^*(0)]\langle G(U_t, f_0) \rangle \cdot f_0 \\ &= -[q(\theta)g(z, \bar{z}) + \bar{q}(\theta)\bar{g}(z, \bar{z})] \cdot f_0. \end{aligned} \quad (3.35)$$

Therefore, for $\theta \in [-1, 0)$

$$H_{20}(\theta) = -[g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta)] \cdot f_0, \quad (3.36)$$

$$H_{11}(\theta) = -[g_{11}q(\theta) + \bar{g}_{11}\bar{q}(\theta)] \cdot f_0. \quad (3.37)$$

From (3.34), (3.36), and the definition of A_U , it follows that

$$W_{20}(\theta) = 2i\omega_0\tau_0 W_{20}(\theta) + [g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta)] \cdot f_0. \quad (3.38)$$

Noting that $q(\theta) = q(0)e^{i\omega_0\tau_0\theta}$, $\theta \in [-1, 0)$, we have

$$W_{20}(\theta) = \frac{ig_{20}}{\omega_0\tau_0}q(0)e^{i\omega_0\tau_0\theta} \cdot f_0 + \frac{i\bar{g}_{20}}{3\omega_0\tau_0}\bar{q}(0)e^{-i\omega_0\tau_0\theta} \cdot f_0 + E'_1 e^{2i\omega_0\tau_0\theta}. \quad (3.39)$$

Similarly, from (3.34) and (3.37), we obtain

$$W_{11}(\theta) = -\frac{ig_{11}}{\omega_0\tau_0}q(0)e^{i\omega_0\tau_0\theta} \cdot f_0 + \frac{i\bar{g}_{11}}{\omega_0\tau_0}\bar{q}(0)e^{-i\omega_0\tau_0\theta} \cdot f_0 + E'_2. \quad (3.40)$$

In what follows, we will seek appropriate E'_1 and E'_2 in (3.39) and (3.40). From the definition of A_U and (3.33), we have

$$\int_{-1}^0 \eta(\theta)W_{20}(\theta) = 2i\omega_0\tau_0W_{20}(\theta) - H_{20}(\theta), \tag{3.41}$$

$$\int_{-1}^0 \eta(\theta)W_{11}(\theta) = -H_{11}(0), \tag{3.42}$$

where $\eta(\theta) = \eta(0, \theta)$, then

$$H_{20} = -[g_{20}q(0) + \bar{g}_{02}\bar{q}(0)] \cdot f_0 + 2\tau_0 \left(\begin{array}{c} -\beta - \frac{c\rho}{(mv^* + 1)^2} + \frac{cm\rho^2u^*}{(mv^* + 1)^3} \\ \frac{b\rho}{mv^* + 1} e^{-i\omega_0\tau_0} + \frac{bm\rho v^*}{(mv^* + 1)^2} \left(\frac{m\rho u^*}{mv^* + 1} - 1 \right) e^{-2i\omega_0\tau_0} \end{array} \right). \tag{3.43}$$

Substituting (3.43) into (3.41), note that

$$\begin{aligned} \left(i\omega_0\tau_0 - \int_{-1}^0 e^{i\omega_0\tau_0} d\eta(\theta) \right) \bar{q}(0) &= 0, \\ \left(-i\omega_0\tau_0 - \int_{-1}^0 e^{i\omega_0\tau_0} d\eta(\theta) \right) q(0) &= 0, \end{aligned} \tag{3.44}$$

then we deduce

$$\begin{aligned} & 2\tau_0 \left(\begin{array}{c} -\beta - \frac{c\rho}{(mv^* + 1)^2} + \frac{cm\rho^2u^*}{(mv^* + 1)^3} \\ \frac{b\rho}{mv^* + 1} e^{-i\omega_0\tau_0} + \frac{bm\rho v^*}{(mv^* + 1)^2} \left(\frac{m\rho u^*}{mv^* + 1} - 1 \right) e^{-2i\omega_0\tau_0} \end{array} \right) \\ &= g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta) + 2i\omega_0\tau_0W_{20}(\theta) - \int_{-1}^0 d\eta(\theta)W_{20}(\theta) \\ &= -g_{20}q(0) + \frac{\bar{g}_{02}\bar{q}(0)}{3} + 2i\omega_0\tau_0E \\ &\quad - \int_{-1}^0 d\eta(\theta) \left[\frac{ig_{20}}{\omega_0\tau_0} q(0)e^{i\omega_0\tau_0\theta} + \frac{i\bar{g}_{20}}{3\omega_0\tau_0} \bar{q}(0)e^{i\omega_0\tau_0\theta} + Ee^{2i\omega_0\tau_0\theta} \right] \\ &= \left(2i\omega_0\tau_0I - \int_{-1}^0 d\eta(\theta)e^{2i\omega_0\tau_0\theta} \right) E \end{aligned}$$

$$\begin{aligned}
&= \left[2i\omega_0\tau_0 \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} - \tau_0 \begin{pmatrix} -\beta u^* & -\frac{cu^*}{(mv^*+1)^2} \\ \frac{bv^*}{(mv^*+1)} e^{-2i\omega_0\tau_0} & -\frac{bmu^*v^*}{(mv^*+1)^2} e^{-2i\omega_0\tau_0} \end{pmatrix} \right] E \\
&= \tau_0 \begin{pmatrix} 2i\omega_0 + \beta u^* & \frac{cu^*}{(mv^*+1)^2} \\ -\frac{bv^*}{(mv^*+1)} e^{-2i\omega_0\tau_0} & 2i\omega_0 + \frac{bmu^*v^*}{(mv^*+1)^2} e^{-2i\omega_0\tau_0} \end{pmatrix} E.
\end{aligned} \tag{3.45}$$

Finally, we arrive at

$$E = 2E'_1 \begin{pmatrix} -\beta - \frac{c\rho}{(mv^*+1)^2} + \frac{cm\rho^2 u^*}{(mv^*+1)^3} \\ \frac{b\rho}{mv^*+1} e^{-i\omega_0\tau_0} + \frac{bmv\rho v^*}{(mv^*+1)^2} \left(\frac{m\rho u^*}{mv^*+1} - 1 \right) e^{-2i\omega_0\tau_0} \end{pmatrix}, \tag{3.46}$$

where

$$E'_1 = \begin{pmatrix} 2i\omega_0 + \beta u^* & \frac{cu^*}{(mv^*+1)^2} \\ -\frac{bv^*}{(mv^*+1)} e^{-2i\omega_0\tau_0} & 2i\omega_0 + \frac{bmu^*v^*}{(mv^*+1)^2} e^{-2i\omega_0\tau_0} \end{pmatrix}^{-1}, \tag{3.47}$$

and from the above equation we can find the value of E^1 and E^2 .

Following the similar steps, we also get

$$\begin{aligned}
H_{11} &= -[g_{20}q(0) + \bar{g}_{02}\bar{q}(0)] \cdot f_0 \\
&+ \tau_0 \begin{pmatrix} -2\beta + \left(\frac{2m\bar{\rho}\rho u^*}{(mv^*+1)^3} - \frac{\bar{\rho} + \rho}{(mv^*+1)^2} \right) (c + bmv^*) \\ \frac{b\bar{r}}{mv^*+1} (\bar{\rho}e^{-i\omega_0\tau_0} + \rho e^{i\omega_0\tau_0}) \end{pmatrix},
\end{aligned} \tag{3.48}$$

then

$$\begin{aligned}
&\tau_0 \begin{pmatrix} -2\beta + \left(\frac{2m\bar{\rho}\rho u^*}{(mv^*+1)^3} - \frac{\bar{\rho} + \rho}{(mv^*+1)^2} \right) (c + bmv^*) \\ \frac{b\bar{r}}{mv^*+1} (\bar{\rho}e^{-i\omega_0\tau_0} + \rho e^{i\omega_0\tau_0}) \end{pmatrix} \\
&= g_{11}q(0) + \bar{g}_{11}\bar{q}(0) - \int_{-1}^0 d\eta(\theta)W_{11}(\theta)
\end{aligned}$$

$$\begin{aligned}
 &= g_{11}q(0) + \bar{g}_{11}\bar{q}(0) - \int_{-1}^0 d\eta(\theta) \left[\frac{ig_{11}}{\omega_0\tau_0}q(0)e^{i\omega_0\tau_0\theta} + \frac{i\bar{g}_{11}}{\omega_0\tau_0}\bar{q}(0)e^{i\omega_0\tau_0\theta} + E' \right] \\
 &= \int_{-1}^0 d\eta(\theta)E' = \tau_0 \begin{pmatrix} \beta u^* & \frac{cu^*}{(mv^* + 1)^2} \\ -\frac{bv^*}{mv^* + 1} & \frac{bmu^*v^*}{(mv^* + 1)^2} \end{pmatrix} E'.
 \end{aligned}
 \tag{3.49}$$

Finally, we arrive at

$$E' = E'_2 \begin{pmatrix} -2\beta + \left(\frac{2m\bar{\rho}\rho u^*}{(mv^* + 1)^3} - \frac{\bar{\rho} + \rho}{(mv^* + 1)^2} \right) (c + bmv^*) \\ \frac{b\bar{r}}{mv^* + 1} (\bar{\rho}e^{-i\omega_0\tau_0} + \rho e^{i\omega_0\tau_0}) \end{pmatrix},
 \tag{3.50}$$

where

$$E'_2 = \begin{pmatrix} \beta u^* & \frac{cu^*}{(mv^* + 1)^2} \\ -\frac{bv^*}{mv^* + 1} & \frac{bmu^*v^*}{(mv^* + 1)^2} \end{pmatrix}^{-1}.
 \tag{3.51}$$

In a similar manner, we can calculate E'^1 and E'^2 . Then g_{21} can be expressed. Based on the above analysis, it is enough to see that each g_{ij} is determined by the parameters. Thus, we can compute the following values which determine the direction and stability of the following bifurcating periodic orbits:

$$\begin{aligned}
 C_1(0) &= \frac{i}{2\omega_0\tau_0} \left(g_{11}g_{22} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3} \right) + \frac{g_{21}}{2}, \\
 \mu_2 &= -\frac{\text{Re}(C_1(0))}{\text{Re}(\lambda'(\tau_0))}, \\
 \beta_2 &= 2 \text{Re}(C_1(0)), \\
 T_2 &= -\frac{\text{Im}(C_1(0)) + \mu_2 \text{Im}(\lambda'(\tau_0))}{\omega_0\tau_0}.
 \end{aligned}
 \tag{3.52}$$

Theorem 3.1. For system (1.7),

- (i) μ_2 determines the directions of the Hopf bifurcation: if $\mu_2 > 0$ (< 0), the direction of the Hopf bifurcation is forward (backward), that is, the bifurcating periodic solutions exist for $\tau > \tau_0 = \tau_j^0$ ($\tau < \tau_0 = \tau_j^0$);

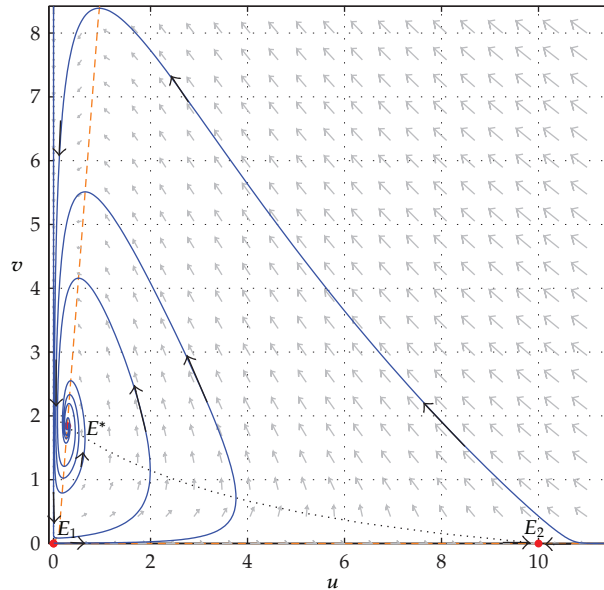


Figure 1: The phase portrait of model (1.7) without the diffusion and delay effects, that is, $\tau = 0$, $d_1 = d_2 = 0$. The other parameters are taken as $\alpha = 2$, $\beta = 0.2$, $\gamma = 0.5$, $b = 2$, and $c = 3$, $m = 1$. In this case, $E_1 = (0, 0)$ and $E_2 = (10, 0)$ are saddle points; the unique positive equilibrium $E^* = (0.6623, 1.6491)$ is globally asymptotically stable. The dashed curve is the u -nullcline $u(\alpha - \beta u) - cuv/(mv + 1) = 0$, and the dotted curve is the v -nullcline $v(-r + bu/(mv + 1)) = 0$.

- (ii) β_2 determines the stability of the bifurcating periodic solutions on the center manifold: if $\beta_2 < 0$ (> 0), the bifurcating periodic solutions are orbitally asymptotically stable (unstable);
- (iii) T_2 determines the period of the bifurcating periodic solutions: the period increases (decreases) if $T_2 > 0$ (< 0).

4. Conclusions and Remarks

In this paper, under homogeneous Neumann boundary conditions, we have analyzed dynamical behaviors of the diffusion predator-prey system (1.7) with and without delay. The value of this study lies in two aspects. First, it presents the stability of positive equilibrium $E^* = (u^*, v^*)$ of system (1.7) with and without delay, and the existence of Hopf bifurcation, which indicates that the dynamical behaviors become rich and complex with delay. Second, it shows the analysis of stability of Hopf bifurcation, from which one can find that small sufficiently delays cannot change the stability of the positive equilibrium and large delays cannot only destabilize the positive equilibrium but also induce an oscillation near the positive equilibrium.

Next, numerical simulations are performed to illustrate results with respect to the theoretical facts under the special example. When τ and d_i ($i = 1, 2$) are all equal 0, we demonstrate that the positive equilibrium E^* is globally asymptotically stable (see, Figure 1), which means that if the intraspecific competitions of the prey and the predator dominate

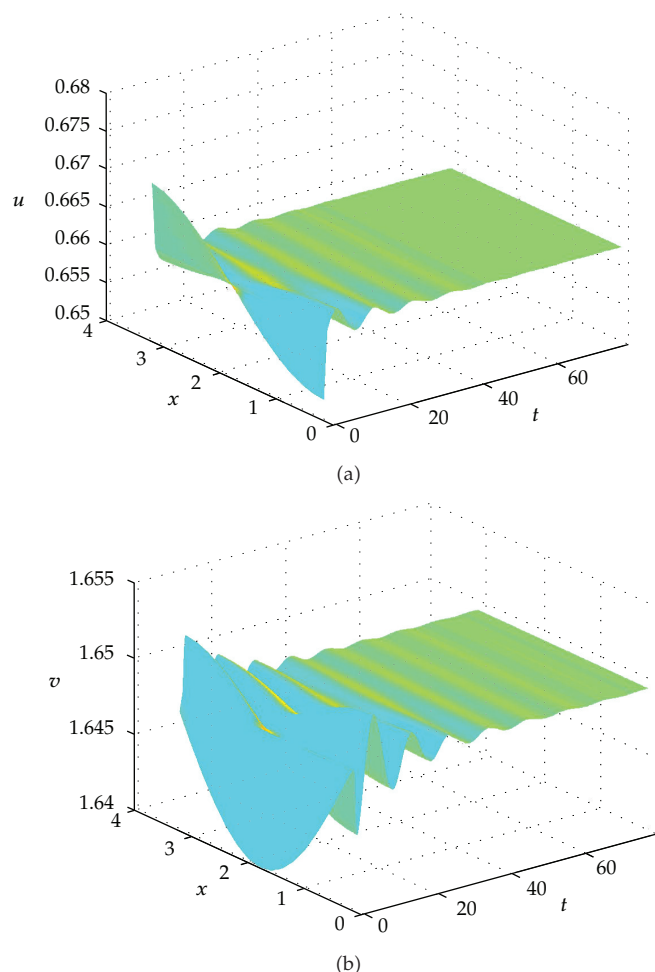


Figure 2: The solution of system (1.7) tends to the positive equilibrium E^* . The parameters are taken as $\alpha = 2, \beta = 0.2, \gamma = 0.5, b = 2, c = 3, m = 1, d_1 = 0.01, d_2 = 0.1, \tau = 0.9$, and the initial values $u(x, t) = 0.662 + 0.01t \cos x, v(x, t) = 1.649 + 0.01t \sin x, t \in [-0.9, 0], x \in [0, \pi]$. In this case, $\tau < \tau_0^0 = 1.0289$.

the inter-specific interaction between the prey and the predator, then both the prey and the predator populations are permanent [14].

In addition, we consider the dynamics of system (1.7) affecting by both spatial diffusion and time-delay factors with fixed parameters $d_1 = 0.01$ and $d_2 = 0.1$. In this case, $\tau_0^0 = 1.0289, \text{Re}(C_1(0)) = -0.6689 < 0$. If $\tau < \tau_0^0$, the positive equilibrium E^* is remain stability (see Figure 2), which indicates that the predators and preys can coexist in stable conditions.

While if $\tau > \tau_0^0$, the positive equilibrium E^* losses its stability and Hopf bifurcation occurs, which means that a family of stable periodic solutions bifurcate from E^* since $\mu_2 = 0.5515 > 0, \beta_2 = -0.1338 < 0$ (see Figure 3). The numerical result indicates that the predator coexists with the prey with oscillatory behaviors.

In the present paper, we incorporate time delay into biological system due to the gestation of the predator, which causes stable equilibrium to become unstable and causes the populations to oscillate via Hopf bifurcation. That is to say that the effect of delay for

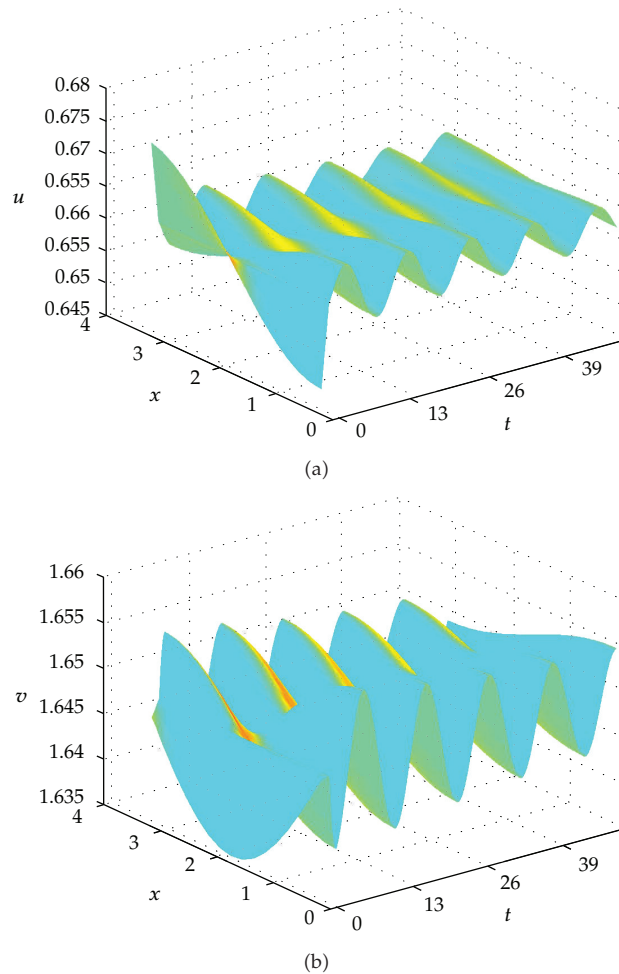


Figure 3: The solution of system (1.7) tends to aperiodic orbit. The parameters are taken as $\alpha = 2$, $\beta = 0.2$, $\gamma = 0.5$, $b = 2$, $c = 3$, $m = 1$, $d_1 = 0.01$, $d_2 = 0.1$, $\tau = 1.3$, and the initial values $u(x, t) = 0.662 + 0.01t \cos x$, $v(x, t) = 1.649 + 0.01t \sin x$, and $t \in [-1.3, 0]$, $x \in [0, \pi]$. In this case, $\tau > \tau_0^0 = 1.0289$.

the population dynamics is tremendous. From a biological perspective, the time delay of species may be related to the gestation of the predator, mature stage from juvenile to adult, the interaction time between prey and predator and others. In these cases, the methods and results in the present paper may provide a favorable value on controlling ecological population. It would be more accurate to describe the growth rate of population.

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