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Hopf bifurcation of a delayed diffusive predator-prey model with strong Allee effect

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Abstract

The paper is concerned with a delayed diffusive predator-prey system where the growth of prey population is governed by Allee effect and the predator population consumes the prey according to Beddington-DeAngelis type functional response. The situation of bi-stability and the existence of two coexisting equilibria for the proposed model system are addressed. The stability of the steady state together with its dependence on the magnitude of time delay has been obtained. The conditions that guarantee the occurrence of the Hopf bifurcation in presence of delay are demonstrated. Furthermore, the direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions are determined by the normal form theory and the center manifold theorem. Finally, some numerical simulations have been carried out in order to validate the assumptions of the model.

MSC: 34C23; 34D23

Keywords: predator-prey model; Allee effect; stability; Hopf bifurcation; delay

1 Introduction

In this paper, we consider the following delayed diffusive predator-prey system with Beddington-DeAngelis functional response and strong Allee effect:

$$\begin{cases} \frac{\partial u}{\partial t} = d_1\Delta u + ru(1-\frac{u}{K})(u-m) - \frac{quv(t-\tau)}{a+bu+cv(t-\tau)}, & (x,t)\in\Omega\times(0,+\infty), \\ \frac{\partial v}{\partial t} = d_2\Delta v + v(-d+\frac{eu}{a+bu+cv}), & (x,t)\in\Omega\times(0,+\infty), \\ u(x,t)=u_0(x,t), \qquad v(x,t)=v_0(x,t), & (x,t)\in\Omega\times[-\tau,0], \\ \frac{\partial u(t,x)}{\partial n} = \frac{\partial v(t,x)}{\partial n} = 0, & t>0, x\in\partial\Omega, \end{cases} \tag{1}$$

where $u(x,t)$ represents the population of the prey and $v(x,t)$ represents the population of the predator. The parameters r, K, m, q, a, b, c, d, e, d_1, d_2 are positive constants with d representing the death rate of predator as well as r and K standing for the intrinsic rate of increase and the carrying capacity for the prey population, respectively. The predator consumes the prey with functional response of Beddington-DeAngelis type [1–3]. d_1 and d_2 denote the diffusion coefficients of the prey and the predator,respectively. Δ denotes the Laplacian operator, Ω is a bounded domain, n is the normal vector that goes out of the bounded domain Ω. The homogeneous Neumann boundary conditions indicate that there is no population flux across the boundaries. For the initial conditions, we assume that

$$\psi_j(s,x) \in \mathcal{C} = C\big([-\tau,0],X\big)$$

and X is defined by

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

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

The term

$$ru\left(1 - \frac{u}{K}\right)(u-m)$$

is the growth function considering Allee effect. The so-called Allee effect dates from 1931, Allee reported that the prey growth rate is negative or an increasing function at low population density [4]. The Allee effect is caused by various kinds of biological and environmental factors, such as difficulties in finding mates, low probability of successful mating, depletion in inbreeding rate, anti-predator aggression, predator avoidance due to evolutionary change, etc. [5–8]. Allee effects can be broadly classified into two types: the strong Allee effect and the weak Allee effect [9]. For model (1), the Allee effect is strong or weak as $m > 0$ or $m \leq 0$. In recent years, there have been some excellent papers with the Allee effect in a predator-prey system (see, for example, [10–14]).

It is well known that delays which occur in the interaction between predator and prey play a complicated role in a predator-prey system. Many researchers have incorporated it into biological models [15–22] as delays could affect the stability of a predator-prey system by creating instability, oscillation, and chaos phenomena. The reason for introducing a delay into model (1) is that the predator species may need time τ to possess the ability of predation after it was born.

On the other hand, in real life the species is spatially heterogeneous and hence individuals will tend to migrate towards regions of lower population density to increase the possibility of survival [23]. Hence, in model (1), we consider the factor of diffusion.

In this paper, we will study the Hopf bifurcation of system (1), the direction of Hopf bifurcation and the stability of the bifurcating periodic solutions with the help of the theory of the normal form and center manifold [23].

The remaining part of this paper is organised as follows: In Section 2, we study the existence and boundedness of the system. The existence of possible equilibria are studied in Section 3. The sufficient conditions ensuring linear stability of equilibria and the existence of Hopf bifurcation of the coexisting equilibrium are obtained in Section 4. In Section 5, we investigate the direction and stability of Hopf bifurcation by applying the center manifold method and the normal form theory. Numerical results for the proposed model system are presented in Section 6. Finally, a conclusion is presented in Section 7.

2 Existence and boundedness of solution of system (1)

In this section, we discuss the existence of solution of system (1), and an *a priori* bound of the solution is also established.

Theorem 2.1 *For system* (1), *we have*:

(a) *If* $u_0(x) \geq 0$, $v_0(x) \geq 0$, *then system* (1) *has a unique solution* $(u(t,x), v(t,x))$ *such that* $u(t,x) > 0$, $v(t,x) > 0$ *for* $t \in (0,+\infty)$ *and* $x \in \bar{\Omega}$.

(b) *If* $u_0(x,t) \leq m$ *and* $(u_0, v_0) \not\equiv (m,0)$, *then* $(u(x,t), v(x,t))$ *tends to* $(0,0)$ *uniformly as* $t \to \infty$.

(c) *If* $\frac{K(e-bd)-ad}{cd} < 0$, *then* $(u(x,t), v(x,t))$ *tends to* $(u_s(x), 0)$ *uniformly as* $t \to \infty$, *where* $u_s(x)$ *is a non-negative solution of*

$$d_1 \Delta u + ru\left(1 - \frac{u}{K}\right)(u - m) = 0, \quad x \in \Omega, \frac{\partial u}{\partial \nu} = 0, x \in \partial\Omega. \tag{2}$$

(d) *If* $\frac{K(e-bd)-ad}{cd} > 0$, *then any solution* $(u(x,t), v(x,t))$ *of* (1) *satisfies*

$$\limsup_{t\to+\infty} u(x,t) \leq K, \qquad \limsup_{t\to+\infty} v(x,t) \leq \frac{K(e-bd)-ad}{cd}.$$

Proof

(a) Define

$$f(u,v) = ru\left(1 - \frac{u}{K}\right)(u-m) - \frac{quv(t-\tau)}{a + bu + cv(t-\tau)},$$
$$g(u,v) = v\left(-d + \frac{eu}{a + bu + cv}\right).$$

Then $f_v = -\frac{qu(a+bu)}{(a+bu+cv)^2} \leq 0$ and $g_u = \frac{ev(a+cv)}{(a+bu+cv)^2} \geq 0$ in $\overline{\mathbb{R}^2_+} = \{u \geq 0, v \geq 0\}$. Hence, system (1) is a mixed quasi-monotone system. Consider the following system:

$$\begin{cases} \frac{du}{dt} = r_1 u(1 - \frac{u}{K})(u-m), \\ \frac{dv}{dt} = v(-d + \frac{eu}{a+bu+cv}), \\ u(0) = u_0, \quad v(0) = v_0. \end{cases} \tag{3}$$

Assume $u(t; u_0, v_0)$, $v(t; u_0, v_0)$ is the unique solution to system (3). Let

$$\max_{\bar{\Omega}\times[-\tau,0]} u_0(x,t) = u_M,$$

$$\max_{\bar{\Omega}\times[-\tau,0]} v_0(x,t) = v_M.$$

Obviously, $(\underline{u}(t,x), \underline{v}(t,x)) = (0,0)$ and $(\bar{u}(t), \bar{v}(t)) = (u(t; u_M, v_M), v(t; u_M, v_M))$ are a pair of lower-solution and upper-solution to system (1). Therefore, according to Theorem 8.3.3 in [24] or Theorem 5.3.2 in [25], system (1) has a unique globally defined solution $(u(x,t), v(x,t))$ which satisfies

$$0 \leq u(x,t) \leq u(t; u_M, v_M),$$
$$0 \leq v(x,t) \leq v(t; u_M, v_M).$$

The strong maximum principle implies that $u(x,t), v(x,t) > 0$ when $t > 0$ for all $x \in \bar{\Omega}$.

(b) From the above discussions, we obtain $u(x,t) \leq u(t;u_M,v_M)$ for all $t > 0$. From the ODE satisfied by $u(t;u_M,v_M)$, one can see that $u(t;u_M,v_M) \to 0$ if $u_M < m$ and $u(t;u_M,v_M) \to K$ if $u_M > m$. Thus for any $\varepsilon > 0$, there exists $T_1 > 0$ such that $u(x,t) \leq K + \varepsilon$ in $[T_1,+\infty) \times \bar{\Omega}$.

(c) If $\frac{K(e-bd)-ad}{cd} < 0$, then there exists a $\varepsilon > 0$, such that $\frac{(K+\varepsilon)(e-bd)-ad}{cd} < 0$. Therefore, according to the equation of $v(t;u_M,v_M)$, we obtain $0 \leq v(x,t) \leq v(t;u_M,v_M) \to 0$ as $t \to \infty$ uniformly for $x \in \bar{\Omega}$. The limit behavior of $u(x,t)$ is determined by the semiflow generated by the scalar parabolic equation

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 \Delta u + ru(1-\frac{u}{K})(u-m), & (x,t) \in \Omega \times (0,+\infty), \\ \frac{\partial u}{\partial \nu} = 0, & x \in \bar{\Omega}. \end{cases} \tag{4}$$

According to the discussions in [26] and [27], every orbit of (4) converges to a steady state u_s. Therefore, $(u(x,t),v(x,t))$ tends to $(u_s(x),0)$ uniformly as $t \to \infty$.

(d) By the second equation of (1), we easily find that there exists $T_2 \in (0,+\infty)$ such that $v(t,x) \leq \frac{(K+\varepsilon)(e-bd)-ad}{cd}$ in $[T_2,+\infty) \times \Omega$ for an arbitrary constant $\epsilon > 0$. Therefore,

$$\limsup_{t\to+\infty} u(x,t) \leq K, \qquad \limsup_{t\to+\infty} v(x,t) \leq \frac{K(e-bd)-ad}{cd}. \qquad \square$$

3 The existence of equilibria

In this section, we will find all possible non-negative equilibria.

Clearly, system (1) has four feasible non-negative equilibria, namely:

(1) the trivial point $E_0 = (0,0)$;

(2) the boundary equilibrium $E_1 = (m,0)$, representing the state corresponding to the extinction of predator;

(3) the boundary equilibrium $E_2 = (K,0)$, representing the state corresponding to the extinction of predator;

(4) the coexisting equilibrium point(s) $E^* = (u^*,v^*)$.

At the coexisting equilibrium, we must have

$$v = \frac{(e-bd)u-ad}{cd},$$

and u satisfies

$$A_1u^3 + A_1u^2 + A_3u + A_4 = 0, \tag{5}$$

where

$$\begin{aligned} &A_1 = cer; \\ &A_2 = -cer(m+K); \\ &A_3 = K(qe-bdq+cemr); \\ &A_4 = -Kadq. \end{aligned} \tag{6}$$

$A_4 < 0$, so equation (5) has at least a positive root u^*. If $u^* > \frac{ad}{e-bd}$, then system (1) has a coexisting equilibrium $E^* = (u^*,v^*)$.

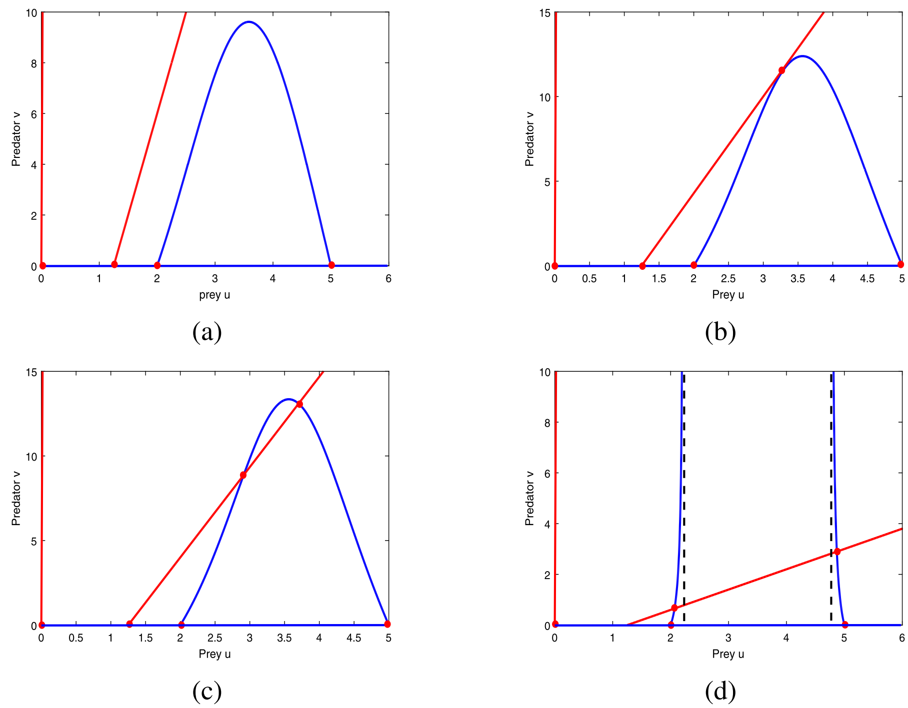


Figure 1 The blue curves are the prey-nullclines and the red lines are the predator-isoclines. The four figures are the possible plots of predator-nullcline for four different values of *c*. (a) For $c = 0.2$, two nullclines do not intersect at any point in the interior of the feasible domain (the prey nullcline is below the predator nullcline), suggesting there is no equilibrium point; **(b)** as we increase the slope of predator-nullcline, the two equilibria approach each other and collide for $c = 0.28$ and consequently, there is one equilibrium point; **(c)** for $c = 0.3$, both the nullclines cross twice, suggesting there are two equilibrium points; **(d)** for $c = 2$, the prey nullcline is unbounded and has two vertical asymptotes $x = x_{\pm}$ shown by black lines. The other parameter values are $r = 0.8$, $K = 5$, $q = 0.2$, $a = 2$, $b = 0.4$, $d = 0.1$, $e = 0.2$, $m = 2$.

The possible number of equilibria can be better analysed by studying the intersections of the nullclines which is one of great feature of planar systems. Let $f(u,v) = 0$ and $g(u,v) = 0$, we show the existence of non-negative equilibria in Figure 1.

4 Local stability and bifurcation

In this section, we discuss the local stability of non-negative equilibria. Before developing our argument, let us set up the following notations.

Notation 4.1 Let $0 = \mu_0 < \mu_1 < \mu_2 < \cdots < \mu_n < \cdots \to \infty$ are the eigenvalues of $-\Delta$ on Ω under homogeneous Neumann boundary condition. We define the following space decomposition:

(i) $S(\mu_n)$ is the space of eigenfunctions corresponding to μ_i for $n = 0, 1, 2, \ldots$;

(ii) $X_{ij} := \{\mathbf{c} \cdot \phi_{ij} : \mathbf{c} \in \mathbb{R}^2\}$, where $\{\phi_{ij}\}$ are orthonormal basis of $S(\mu_n)$ for $j = 1, 2, \ldots, \dim[S(\mu_n)]$;

(iii) $\mathbf{X} := \{\mathbf{u} = (u,v) \in [C^1(\bar{\Omega})]^2 : \frac{\partial u}{\partial \mathbf{v}} = \frac{\partial v}{\partial \mathbf{v}} = 0\}$, and so $\mathbf{X} = \bigoplus_{i=1}^{\infty} \mathbf{X}_i$, where $\mathbf{X}_i = \bigoplus_{j=1}^{\dim[S(\mu_j)]} \mathbf{X}_{ij}$.

The linearization of system (1) at a constant solution $E^* = (u^*, v^*)$ can be expressed by

$$\mathbf{u}_t = (D\Delta + J_1)\mathbf{u} + J_2\mathbf{u}_\tau, \tag{7}$$

where $D = \mathrm{diag}(d_1, d_2)$, $\mathbf{u} = (u(x,t), v(x,t))^T$, and $\mathbf{u}_\tau = (u(x,t-\tau), v(x,t-\tau))$,

$$J_1 = \begin{pmatrix} a_{11} & 0 \\ a_{21} & a_{22} \end{pmatrix}, \qquad J_2 = \begin{pmatrix} 0 & -a_{12} \\ 0 & 0 \end{pmatrix},$$

where

$$\begin{aligned}
a_{11} &= 2\left(r + \frac{rm}{K}\right)u^* - \frac{3r}{K}u^{*2} - mr - \frac{qv^*(a+cv^*)}{(a+bu^*+cv^*)^2}; \\
a_{12} &= \frac{qu^*(a+bu^*)}{(a+bu^*+cv^*)^2}; \qquad a_{21} = \frac{ev^*(a+cv^*)}{(a+bu^*+cv^*)^2}; \\
a_{22} &= -d + \frac{eu^*(a+bu^*)}{(a+bu^*+cv^*)^2}.
\end{aligned} \tag{8}$$

In view of Notation 4.1, we can induce the eigenvalues of system (7) confined on the subspace $\mathbf{X}_i$. If λ is an eigenvalue of (7) on $\mathbf{X}_i$, it must be an eigenvalue of the matrix $-\mu_n D + J^*$ for $\forall\, n \in \{0,1,2,\ldots\} := N_0$, where

$$J^* = \begin{pmatrix} a_{11} & -a_{12}e^{-\lambda\tau} \\ a_{21} & a_{22} \end{pmatrix}.$$

It is easy to see that λ satisfies the following characteristic equation:

$$\lambda^2 + A_n\lambda + B_n + Ce^{-\lambda\tau} = 0, \tag{9}$$

where

$$\begin{aligned}
A_n &= d_1\mu_n + d_2\mu_n - a_{11} - a_{22}, \\
B_n &= (d_1\mu_n - a_{11})(d_2\mu_n - a_{22}), \\
C &= a_{12}a_{21}.
\end{aligned} \tag{10}$$

4.1 Stability of constant steady state as $\tau = 0$

(1) For $E_0 = (0,0)$, the corresponding characteristic equation is

$$(\lambda + d_1\mu_n + mr)(\lambda + d_2\mu_n + d) = 0.$$

Clearly, we obtain

$$\lambda_1 = -mr - d_1\mu_n, \lambda_2 = -d - d_2\mu_n.$$

Hence, E_0 is always stable.

(2) For $E_1 = (m,0)$, the corresponding characteristic equation is

$$\left(\lambda + d_1\mu_n - mr\left(1 - \frac{m}{K}\right)\right)\left(\lambda + d_2\mu_n + d - \frac{em}{a+bm}\right) = 0.$$

Obviously,

$$\lambda_1 = mr\left(1 - \frac{m}{K}\right) - d_1\mu_n, \qquad \lambda_2 = -d + \frac{em}{a + bm} - d_2\mu_n.$$

Consequently, if $m < K$ or $d < \frac{em}{a+bm}$, then $E_1 = (m, 0)$ is unstable. On the contrary, if $m > K$ and $d > \frac{em}{a+bm}$, then $E_1 = (m, 0)$ is stable.

(3) For $E_2 = (K, 0)$, the corresponding characteristic equation is

$$(\lambda + d_1\mu_n + Kr - mr)\left(\lambda + d_2\mu_n + d - \frac{eK}{a + bK}\right) = 0.$$

Obviously,

$$\lambda_1 = -Kr + mr - d_1\mu_n, \qquad \lambda_2 = -d + \frac{eK}{a + bK} - d_2\mu_n.$$

Therefore, if $m < K$ and $d > \frac{eK}{a+bK}$, then E_2 is stable.

(4) For $E^* = (u^*, v^*)$, when $\tau = 0$, the corresponding characteristic equation is

$$\lambda^2 + (d_1\mu_n + d_2\mu_n - a_{11} - a_{22})\lambda + (d_1\mu_n - a_{11})(d_2\mu_n - a_{22}) + a_{12}a_{21} = 0.$$

Obviously,

$$\lambda_1 + \lambda_2 = a_{11} + a_{22} - d_1\mu_n - d_2\mu_n, \lambda_1\lambda_2 = (d_1\mu_n - a_{11})(d_2\mu_n - a_{22}) + a_{12}a_{21}. \tag{11}$$

All roots of (11) have negative real parts if

$$(\mathrm{H}_1) \quad a_{11} < 0, \qquad a_{22} < 0 \quad \text{and} \quad a_{11}a_{22} + a_{12}a_{21} > 0. \tag{12}$$

Therefore, the coexisting equilibrium $E^* = (u^*, v^*)$ of system (1) is locally asymptotically stable for $\tau = 0$ when condition (12) holds.

4.2 Hopf bifurcation

In this section, we are going to analyze the conditions about the parameters under which the Hopf bifurcation occurs at the coexisting equilibrium.

Assume that $i\omega$ ($\omega > 0$) is a root of equation (9). Then ω should satisfy the following equation for some $n \geq 0$:

$$-\omega^2 + iA_n\omega + B_n + C\big(\cos(\omega\tau) - i\sin(\omega\tau)\big) = 0, \tag{13}$$

which implies that

$$\begin{cases} -\omega^2 + B_n = -C\cos(\omega\tau), \\ A_n\omega = C\sin(\omega\tau). \end{cases} \tag{14}$$

From (14), adding the squared terms for both equations yields

$$\omega^4 + \big(A_n^2 - 2B_n\big)\omega^2 + B_n^2 - C^2 = 0. \tag{15}$$

Let $z = \omega^2$, equation (15) becomes

$$z^2 + \left(A_n^2 - 2B_n\right)z + B_n^2 - C^2 = 0, \tag{16}$$

where

$$\begin{aligned} A_n^2 - 2B_n &= \left(d_1^2 + d_2^2\right)\mu_n^2 - 2(a_{11}d_1 + a_{22}d_2) + a_{11}^2 + a_{22}^2, \\ B_n^2 - C^2 &= (B_n + C)(B_n - C) \\ &= \left(d_1 d_2 \mu_n^2 - (a_{11}d_2 + a_{22}d_1)\mu_n + a_{11}a_{22} + a_{12}a_{21}\right) \\ &\quad \times \left(d_1 d_2 \mu_n^2 - (a_{11}d_2 + a_{22}d_1)\mu_n + a_{11}a_{22} - a_{12}a_{21}\right). \end{aligned} \tag{17}$$

For further discussions, we make the following assumptions:

(H_2) $a_{11}a_{22} - a_{12}a_{21} > 0$;

(H_3) $a_{11}a_{22} - a_{12}a_{21} < 0$.

Theorem 4.1 *If* (H_1) *and* (H_2) *hold, then all roots of equation* (9) *have negative real parts for all* $\tau \geq 0$. *Furthermore, the coexisting equilibrium* E^* *of system* (1) *is asymptotically stable for all* $\tau \geq 0$.

Proof From equation (17), we know that

$$A_n^2 - 2B_n > 0.$$

By (H_1), we get $B_n + C > 0$. Obviously, if (H_1) and (H_2) hold, then

$$B_n - C = d_1 d_2 \mu_n^2 - (a_{11}d_2 + a_{22}d_1)\mu_n + a_{11}a_{22} - a_{12}a_{21} > 0$$

for any $n \geq 0$.

These imply that equation (15) has no positive roots, and hence the characteristic equation (9) has no purely imaginary roots. Therefore, all roots of equation (9) have negative real parts as $\tau \geq 0$. □

Denote

$$\mu^* = \frac{a_{11}d_2 + a_{22}d_1 + \sqrt{(a_{11}d_2 + a_{22}d_1)^2 - 4d_1 d_2(a_{11}a_{22} - a_{12}a_{21})}}{2d_1 d_2}.$$

Thus, there must exist some $N^* \in N_0$, such that $\mu^* = \mu_{N^*}$ or $\mu_{N^*} < \mu^* < \mu_{N^*+1}$. Hence, we have the following lemma.

Lemma 4.1 *If* (H_1) *and* (H_3) *hold, then equation* (9) *has a pair of purely imaginary roots* $\pm i\omega_n$ ($0 \leq n \leq N^*$) *at*

$$\tau = \tau_n^j = \tau_n^0 + \frac{2j\pi}{\omega_n}, \quad j \in N_0, \tag{18}$$

where

$$\tau_n^0 = \frac{1}{\omega_n} \arccos \frac{\omega_n^2 - B_n}{C},$$
$$\omega_n = \sqrt{\frac{2B_n - A_n^2 + \sqrt{(A_n^2 - 2B_n)^2 - 4(B_n^2 - C^2)}}{2}}.$$

Proof From hypothesis (H_3), we know that $B_n + C > 0$. We have

$$B_n - C = d_1 d_2 \mu_n^2 - (a_{11}d_2 + a_{22}d_1)\mu_n + a_{11}a_{22} - a_{12}a_{21}.$$

Hence, equation (16) has no positive roots for $n > N^*$, and $0 \le n \le N^*$ is the necessary condition of equation (16) having positive roots. For $0 \le n \le N^*$ a unique positive root z_n of equation (16) is

$$z_n = \frac{2B_n - A_n^2 + \sqrt{(A_n^2 - 2B_n)^2 - 4(B_n^2 - C^2)}}{2}$$

and

$$\omega_n = \sqrt{\frac{2B_n - A_n^2 + \sqrt{(A_n^2 - 2B_n)^2 - 4(B_n^2 - C^2)}}{2}}$$

is the imaginary part of the purely imaginary root, at

$$\tau = \tau_n^j = \tau_n^0 + \frac{2j\pi}{\omega_n} = \frac{1}{\omega_n} \arccos \frac{\omega_n^2 - B_n}{C} + \frac{2j\pi}{\omega_n}, \quad j \in N_0, \tag{19}$$

equation (9) has a pair of purely imaginary roots $\pm i\omega_n$ $(0 \le n \le N^*)$. □

It is clear from equation (19) that $\tau_n^{j+1} > \tau_n^j$. The following lemma shows that

$$\tau_{N^*}^j \ge \tau_{N^*-1}^j \ge \cdots \ge \tau_1^j > \tau_0^j$$

and hence we have a complete ordering of the bifurcation values τ_n^j.

Lemma 4.2 *If* (H_1) *and* (H_3) *hold, then*

$$\tau_{N^*}^j \ge \tau_{N^*-1}^j \ge \cdots \ge \tau_1^j > \tau_0^j$$

for $j \in N_0$.

Proof From the above analysis, we know

$$\omega_n^2 = \frac{2B_n - A_n^2 + \sqrt{(A_n^2 - 2B_n)^2 - 4(B_n^2 - C^2)}}{2} = \frac{2}{\sqrt{\frac{(A_n^2 - 2B_n)^2}{(C^2 - B_n^2)^2} + \frac{4}{C^2 - B_n^2}} + \frac{A_n^2 - 2B_n}{C^2 - B_n^2}},$$

where $A_n^2 - B_n$ and $C^2 - B_n^2$ are given in (17). Obviously, $C^2 - B_n^2$ is decreasing in n and $A_n^2 - 2B_n$ is increasing in n. We obtain

$$\omega_{N^*} \le \omega_{N^*-1} \le \cdots \le \omega_1 < \omega_0.$$

Notice that B_n is strictly increasing in n for $0 \le n \le N^*$. Then we find that $\frac{\omega_n^2 - B_n}{C}$ is strictly decreasing in n for $0 \le N \le N^*$. Thus $\tau_n^j = \frac{1}{\omega_n} \arccos \frac{\omega_n^2 - B_n}{C} + \frac{2j\pi}{\omega_n}$ is strictly increasing in n. Namely,

$$\tau_{N^*}^j \ge \tau_{N^*-1}^j \ge \cdots \ge \tau_1^j > \tau_0^j, \quad j \in N_0. \qquad \square$$

From Lemma 4.2, we know that $\tau_0^0 = \min\{\tau_n^j : 0 \le n \le N^*, j \in N_0\}$.

Lemma 4.3 *Let $\lambda_n(\tau) = \alpha_n(\tau) \pm i\omega_n(\tau)$ be the root of* (9) *near $\tau = \tau_n^j$ satisfying $\alpha_n(\tau_n^j) = 0$ for $\omega_n(\tau_n^j) = \omega_n$. Then the following transversality condition holds*:

$$\bigl(\alpha_n'(\tau)\bigr)^{-1} > 0 \tag{20}$$

for $j = 0, 1, 2, \ldots$, and $0 \le n \le N^*$.

Proof Differentiating the two sides of equation (9) with respect to τ yields

$$\frac{d\lambda}{d\tau}\bigl(2\lambda + A_n - C\tau e^{-\lambda\tau}\bigr) = C\lambda e^{-\lambda\tau}.$$

Hence,

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{2\lambda + A_n - C\tau e^{-\lambda\tau}}{C\lambda e^{-\lambda\tau}} = \frac{2}{C}e^{\lambda\tau} + \frac{A_n}{C\lambda}e^{\lambda\tau} - \frac{\tau}{\lambda}.$$

Substituting τ_n^j into the above equation, we obtain

$$\bigl(\alpha_n'(\tau)\bigr)^{-1} = \operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}_{\tau=\tau_n^j} = \frac{2\cos(\omega_n\tau_n^j)}{C} + \frac{A_n \sin(\omega_n\tau_n^j)}{C\omega_n}.$$

Since $C\cos(\omega_n\tau_n^j) = \omega_n^2 - B_n$ and $C\sin(\omega_n\tau_n^j) = A_n\omega_n$ we have

$$\bigl(\alpha_n'(\tau)\bigr)^{-1} = \operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}_{\tau=\tau_n^j} = \frac{\sqrt{(A_n^2 - 2B_n)^2 - 4(B_n^2 - C^2)}}{C^2} > 0. \qquad \square$$

From the above analysis, we have the following conclusion.

Theorem 4.2 *If* (H_1) *and* (H_3) *hold, then the following statements are true*:

(i) *When $\tau \in [0, \tau_0^0)$, the coexisting equilibrium of system* (1) *is locally asymptotically stable.*

(ii) *Hopf bifurcation occurs at $\tau = \tau_0^0$. That is, system* (1) *has a branch of periodic solutions bifurcating from the coexisting equilibrium near $\tau = \tau_0^0$.*

5 Direction and stability of Hopf bifurcation

In the previous section, we have shown that system (1) admits a series of periodic solutions bifurcating from the coexisting equilibrium at the critical value τ_n^j $(n,j \in N_0)$. In this section, we derive explicit formulas to determine the properties of the Hopf bifurcation at the critical value τ_n^j $(n,j \in N_0)$. By using the normal form theory and center manifold reduction for PFDEs developed by [23].

For fixed $n,j \in N_0$, denote τ_n^j by τ^* and introduce the new parameter $\mu = \tau - \tau^*$. Normalizing the delay τ by the time-scaling $t \to t/\tau$. Then (1) can be rewritten as

$$\frac{dU(t)}{dt} = \tau^* D\Delta U(t) + L(\tau^*)(U_t) + F(U_t, \mu), \tag{21}$$

where $L(\mu)(\varphi) : \mathcal{C} \to X$ and $F(\cdot, \mu) : \mathcal{C} \to X$ are given by

$$L(\mu)(\varphi) = \mu \begin{pmatrix} a_{11}\varphi_1(0) - a_{12}\varphi_2(-1) \\ a_{21}\varphi_2(0) + a_{22}\varphi_2(0) \end{pmatrix}, \tag{22}$$

$$F(\varphi, \mu) = \mu D\Delta\varphi(0) + L(\mu)\varphi + f(\varphi, \mu), \tag{23}$$

and

$$f(\varphi, \mu) = (\tau^* + \mu) \begin{pmatrix} b_{11}\varphi_1^2(0) + b_{12}\varphi_1(0)\varphi_2(-1) + b_{22}\varphi_2^2(-1) \\ c_{11}\varphi_1^2(0) + c_{12}\varphi_1(0)\varphi_2(0) + c_{22}\varphi_2^2(0) \end{pmatrix} + h.o.t., \tag{24}$$

where

$$b_{11} = 2\left(r + \frac{rm}{K}\right) - \frac{br}{K}u^* + \frac{2bqv^*(a + cv^*)}{(a + bu^* + cv^*)^3},$$

$$b_{12} = -\frac{aq(a + bu^* + cv^*) + 2qcbu^*v^*}{(a + bu^* + cv^*)^3}, \qquad b_{22} = \frac{2qcu^*(a + bu^*)}{(a + bu^* + cv^*)^3},$$

$$c_{11} = \frac{-2ebv^*(a + cv^*)}{(a + bu^* + cv^*)^3}, \qquad c_{12} = -\frac{ea(a + bu^* + cv^*) + 2ecbu^*v^*}{(a + bu^* + cv^*)^3},$$

$$c_{22} = -\frac{2ecu(a + bu^*)}{(a + bu^* + cv^*)^2},$$

and $\varphi = (\varphi_1, \varphi_2, \varphi_3)^T \in \mathcal{C}$.

Then the linearized system of (21) at $(0, 0)$ is

$$\frac{dU(t)}{dt} = \tau^* D\Delta U(t) + L(\tau^*)(U_t). \tag{25}$$

Based on the discussion in Section 4, we can easily see that, for $\tau = \tau^*$, the characteristic equation of (9) has a pair of simple purely imaginary eigenvalues $\Lambda_0 = \{i\omega_0\tau^*, -i\omega_0\tau^*\}$.

Let $\mathcal{C} := C([-1, 0], \mathbb{R}^2)$, consider the following FDE on $\mathcal{C}$:

$$\dot{z} = L(\tau^*)(z_t). \tag{26}$$

Obviously, $L(\tau^*)$ is a continuous linear function mapping $C([-1, 0], \mathbb{R}^2)$ into $\mathbb{R}^2$. By the Riesz representation theorem, there exists a 2×2 matrix function $\eta(\theta, \tau)$ $(-1 \leq \theta \leq 0)$, whose elements are of bounded variation such that

$$L(\tau^*)(\varphi) = \int_{-1}^{0} \big[d\eta(\theta,\tau^*)\big]\varphi(\theta), \quad \text{for } \varphi \in C. \tag{27}$$

In fact, we can choose

$$\eta(\theta,\tau^*) = \tau^* \begin{pmatrix} a_{11} & 0 \\ a_{21} & a_{22} \end{pmatrix} \delta(\theta) - \tau^* \begin{pmatrix} 0 & -a_{12} \\ 0 & 0 \end{pmatrix} \delta(\theta+1), \tag{28}$$

where δ is the Dirac delta function.

Let $A(\tau^*)$ denote the infinitesimal generator of the semigroup induced by the solutions of (26) and A^* be the formal adjoint of $A(\tau^*)$ under the bilinear pairing

$$\begin{aligned}(\psi,\phi) &= \big(\psi(0),\phi(0)\big) - \int_{-1}^{0}\int_{\xi=0}^{\theta} \psi(\xi-\theta)\,d\eta(\theta)\phi(\xi)\,d\xi \\ &= \big(\psi(0),\phi(0)\big) + \tau^* \int_{-1}^{0} \psi(\theta+1) \begin{pmatrix} 0 & -a_{12} \\ 0 & 0 \end{pmatrix} \phi(\theta)\,d\theta, \end{aligned} \tag{29}$$

for $\phi \in C$, $\psi \in C^* = C([0,1],R^2)$. Then $A(\tau^*)$ and A^* are a pair of adjoint operators. From the discussion in Section 4, we know that $A(\tau^*)$ has a pair of simple purely imaginary eigenvalues $\pm i\omega_0\tau^*$, and they are also eigenvalues of A^* since $A(\tau^*)$ and A^* are a pair of adjoint operators. Let P and P^* be the center spaces, that is, the generalized eigenspaces of $A(\tau^*)$ and A^* associated with Λ_0, respectively. Then P^* is the adjoint space of P and $\dim P = \dim P^* = 2$. Direct computations give the following results.

Lemma 5.1 *Let*

$$\alpha = \frac{a_{21}}{i\omega - a_{22}}, \qquad \alpha^* = \frac{i\omega - a_{11}}{a_{21}}. \tag{30}$$

Then

$$p_1(\theta) = e^{i\omega_0\tau^*\theta}(1,\alpha)^T, \qquad p_2(\theta) = \bar{p}_1(\theta), \quad -1 \le \theta \le 0, \tag{31}$$

is a basis of P associated with Λ_0 and

$$q_1(s) = \big(1,\alpha^*\big)^T e^{-i\omega_0\tau^* s}, \qquad q_2(s) = \bar{q}_1(s), \quad 0 \le s \le 1, \tag{32}$$

is a basis of Q associated with Λ_0.

Let $\Phi = (\Phi_1,\Phi_2)$ and $\Psi^* = (\Psi_1^*,\Psi_2^*)^T$ with

$$\begin{aligned}\Phi_1(\theta) &= \frac{p_1(\theta)+p_2(\theta)}{2} = \begin{pmatrix} \operatorname{Re}\{e^{i\omega_0\tau^*\theta}\} \\ \operatorname{Re}\{\alpha e^{i\omega_0\tau^*\theta}\} \end{pmatrix} = \begin{pmatrix} \cos\omega_0\tau^*\theta \\ -\frac{a_{21}(a_{22}\cos(\omega\tau^*\theta)-\omega\sin(\omega\tau^*\theta))}{(\omega^2+a_{22}^2)} \end{pmatrix}, \\ \Phi_2(\theta) &= \frac{p_1(\theta)-p_2(\theta)}{2i} = \begin{pmatrix} \operatorname{Im}\{e^{i\omega_0\tau^*\theta}\} \\ \operatorname{Im}\{\alpha e^{i\omega_0\tau^*\theta}\} \end{pmatrix} = \begin{pmatrix} \sin\omega_0\tau^*\theta \\ -\frac{a_{21}(a_{22}\omega\cos(\omega\tau^*\theta)+a_{22}\sin(\omega\tau^*\theta))}{(\omega^2+a_{22}^2)} \end{pmatrix},\end{aligned}$$

for $\theta \in [-1,0]$, and

$$\Psi_1^*(s) = \frac{q_1(s)+q_2(s)}{2} = \begin{pmatrix} \operatorname{Re}\{e^{-i\omega_0\tau^* s}\} \\ \operatorname{Re}\{\alpha^* e^{-i\omega_0\tau^* s}\} \end{pmatrix} = \begin{pmatrix} \cos\omega_0\tau^* s \\ \frac{\omega_0\sin(s\tau\omega_0)-a_{11}\cos(\omega_0\tau^* s)}{a_{21}} \end{pmatrix},$$
$$\Psi_2^*(s) = \frac{q_1(s)-q_2(s)}{2i} = \begin{pmatrix} \operatorname{Im}\{e^{-i\omega_0\tau^* s}\} \\ \operatorname{Im}\{\alpha e^{-i\omega_0\tau^* s}\} \end{pmatrix} = \begin{pmatrix} -\sin\omega_0\tau^* s \\ \frac{\omega_0\cos(s\tau\omega_0)+a_{11}\sin(\omega_0\tau^* s)}{a_{21}} \end{pmatrix},$$

for $s \in [0,1]$. From (29), we can obtain (Ψ_1^*,Φ_1) and (Ψ_1^*,Φ_2). Note that

$$(q_1,p_1) = \bigl(\Psi_1^*,\Phi_1\bigr) - \bigl(\Psi_2^*,\Phi_2\bigr) + i\bigl[\bigl(\Psi_1^*,\Phi_2\bigr) + \bigl(\Psi_2^*,\Phi_1\bigr)\bigr]$$

and

$$(q_1,p_1) = 1 + \alpha\alpha^* - a_{12}\alpha\tau^* e^{-i\omega_0\tau^*} := D^*.$$

Therefore, we have

$$\bigl(\Psi_1^*,\Phi_1\bigr) - \bigl(\Psi_2^*,\Phi_2\bigr) = \operatorname{Re}\bigl\{D^*\bigr\},$$
$$\bigl(\Psi_1^*,\Phi_2\bigr) + \bigl(\Psi_2^*,\Phi_1\bigr) = \operatorname{Im}\bigl\{D^*\bigr\}.$$

Now, we define $(\Psi^*,\Phi) = (\Psi_j^*,\Phi_k)$ $(j,k=1,2)$ and construct a new basis ψ for Q by

$$\Psi = (\Psi_1,\Psi_2)^T = \bigl(\Psi^*,\Phi\bigr)^{-1}\Psi^*.$$

Obviously, $(\Psi,\Phi) = I_{2\times 2}$, the second order identity matrix. In addition, define $f_0 = (\xi_0^1,\xi_0^2)$, where

$$\xi_0^1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \qquad \xi_0^2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}.$$

Let $c\cdot f_0$ be defined by

$$c\cdot f_0 = c_1\xi_0^1 + c_2\xi_0^2$$

for $c = (c_1,c_2)^T$, $c_j \in R$ $(j=1,2)$.

Then the center space of linear equation (25) is given by $P_{CN}\mathcal{C}$, where

$$P_{CN}\varphi = \Phi\bigl(\Psi,\langle\varphi,f_0\rangle\bigr)\cdot f_0, \quad \varphi \in c, \tag{33}$$

and $\mathcal{C} = P_{CN}\mathcal{C} \oplus P_S\mathcal{C}$, here $P_S\mathcal{C}$ denotes the complementary subspace of $P_{CN}\mathcal{C}$.

Let A_{τ^*} be defined by

$$A_{\tau^*}\varphi(\theta) = \dot\varphi(\theta) + X_0(\theta)\bigl[\tau^* D\Delta\varphi(0) + L\bigl(\tau^*\bigr)\bigl(\varphi(\theta)\bigr) - \dot\varphi(0)\bigr], \quad \varphi \in B\mathcal{C},$$

where $X_0 : [-1,0] \to B(X,X)$ is given by

$$X_0(\theta) = \begin{cases} 0, & -1 \leq \theta < 0, \\ I, & \theta = 0. \end{cases} \tag{34}$$

Then A_{τ^*} is the infinitesimal generator induced by the solution of (25) and (21) can be rewritten as the following operator differential equation:

$$\dot{U}_t = A_{\tau^*} U_t + X_0 F(U_t, \mu). \tag{35}$$

Using the decomposition $\mathcal{C} = P_{CN}\mathcal{C} \oplus P_S\mathcal{C}$ and (33), the solution of (21) can be rewritten as

$$U_t = \Phi \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix} \cdot f_0 + h(x_1, x_2, \mu), \tag{36}$$

where

$$\begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix} = \bigl(\Psi, \langle U_t, f_0 \rangle\bigr), \tag{37}$$

and $h(x_1, x_2, \mu) \in P_s c$ with $h(0,0,0) = Dh(0,0,0) = 0$. In particular, the solution of (21) on the center manifold is given by

$$U_t^* = \Phi \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix} \cdot f_0 + h(x_1, x_2, 0). \tag{38}$$

Setting $z = x_1 - ix_2$ and noticing that $p_1 = \Phi_1 + i\Phi_2$, then (38) can be rewritten as

$$U_t^* = \frac{1}{2}\Phi \begin{pmatrix} z + \bar{z} \\ i(z - \bar{z}) \end{pmatrix} \cdot f_0 + w(z, \bar{z}) = \frac{1}{2}(p_1 z + \bar{p_1}\bar{z}) \cdot f_0 + W(z, \bar{z}), \tag{39}$$

where $W(z,\bar{z}) = h(\frac{z+\bar{z}}{2}, -\frac{z-\bar{z}}{2i}, 0)$. Moreover, by [23], z satisfies

$$\dot{z} = i\omega_0 \tau^* z + g(z, \bar{z}), \tag{40}$$

where

$$g(z, \bar{z}) = \bigl(\Psi_1(0) - i\Psi_2(0)\bigr)\bigl\langle F\bigl(U_t^*, 0\bigr), f_0\bigr\rangle. \tag{41}$$

Let

$$W(z, \bar{z}) = W_{20}\frac{z^2}{2} + W_{11} z\bar{z} + W_{02}\frac{\bar{z}^2}{2} + \cdots \tag{42}$$

and

$$g(z, \bar{z}) = g_{20}\frac{z^2}{2} + g_{11} z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + \cdots. \tag{43}$$

From (39), we have

$$
\begin{aligned}
&\langle F(U_t^*,0),f_0\rangle \\
&\quad= \frac{\tau^* z^2}{4}\begin{pmatrix} b_{11}+b_{12}\alpha e^{-i\omega_0\tau^*}+b_{22}\alpha^2 e^{-2i\omega_0\tau^*} \\ c_{11}+c_{12}\alpha+c_{22}\alpha^2\end{pmatrix} \\
&\qquad+\frac{\tau^* z\bar z}{4}\begin{pmatrix} 2b_{11}+b_{12}(\bar\alpha e^{i\omega_0\tau^*}+\alpha e^{-i\omega_0\tau^*})+2b_{22}\alpha\bar\alpha \\ 2c_{11}+c_{12}(\bar\alpha+\alpha)+2c_{22}\alpha\bar\alpha\end{pmatrix} \\
&\qquad+\frac{\tau^* \bar z^2}{4}\begin{pmatrix} b_{11}+b_{12}\bar\alpha e^{i\omega_0\tau^*}+b_{22}\bar\alpha^2 e^{2i\omega_0\tau^*} \\ c_{11}+c_{12}\bar\alpha+c_{22}\bar\alpha^2\end{pmatrix} \\
&\qquad+\frac{\tau^*}{4}\begin{pmatrix} \langle b_{11}(4w_{11}^{(1)}(0)+2w_{20}^{(1)}(0))+b_{12}(w_{20}^{(2)}(-1)+2w_{11}^{(2)}(-1)+2\alpha e^{i\omega\tau^*}w_{11}^{(1)}(0) \\ +\bar\alpha e^{i\omega\tau^*}w_{20}^{(1)}(0))+b_{22}(2\bar\alpha e^{i\omega\tau^*}w_{20}^{(2)}(-1)+4\alpha e^{-i\omega\tau^*}w_{11}^{(2)}(-1)),1\rangle \\ \langle c_{11}(4w_{11}^{(1)}(0)+2w_{20}^{(1)}(0))+c_{12}(2w_{11}^{(2)}(0)+w_{11}^{(2)}(0)+2\alpha w_{11}^{(1)}(0)+\bar\alpha w_{20}^{(1)}(0)) \\ +c_{22}(2\bar\alpha w_{20}^{(2)}(0)+4\alpha w_{11}^{(2)}(0)),1\rangle \end{pmatrix} \\
&\qquad\times z^2\bar z+\cdots,
\end{aligned}
$$

where

$$\langle W_{ij}^n(\theta),1\rangle=\frac{1}{\pi}\int_0^\pi W_{ij}^n(\theta)(x)\,dx,\quad i+j=2,n\in\mathbb{N}.$$

Let $(\psi_1,\psi_2,\psi_3)=\Psi_1(0)-i\Psi_2(0)$. Then by (41), (42) and (43), we can obtain the following quantities:

$$
\begin{aligned}
g_{20}&=\frac{\tau^*}{2}\big[\big(b_{11}+b_{12}\alpha e^{-i\omega_0\tau^*}+b_{22}\alpha^2e^{-2i\omega_0\tau^*}\big)\psi_1+\big(c_{11}+c_{12}\alpha+c_{22}\alpha^2\big)\psi_2\big],\\
g_{11}&=\frac{\tau^*}{4}\big[\big(2b_{11}+b_{12}\big(\bar\alpha e^{i\omega_0\tau^*}+\alpha e^{-i\omega_0\tau^*}\big)+2b_{22}\alpha\bar\alpha\big)\psi_1\\
&\quad+\big(2c_{11}+c_{12}(\bar\alpha+\alpha)+2c_{22}\alpha\bar\alpha\big)\psi_2\big],\\
g_{02}&=\frac{\tau^*}{2}\big[\big(b_{11}+b_{12}\bar\alpha e^{i\omega_0\tau^*}+b_{22}\bar\alpha^2e^{2i\omega_0\tau^*}\big)\bar\psi_1+\big(c_{11}+c_{12}\bar\alpha+c_{22}\bar\alpha^2\big)\bar\psi_2\big],\\
g_{21}&=\frac{\tau^*}{2}\big[\big\langle b_{11}\big(4w_{11}^{(1)}(0)+2w_{20}^{(1)}(0)\big)+b_{12}\big(w_{20}^{(2)}(-1)+2w_{11}^{(2)}(-1)+2\alpha e^{i\omega\tau^*}w_{11}^{(1)}(0)\\
&\quad+\bar\alpha e^{i\omega\tau^*}w_{20}^{(1)}(0)\big)+b_{22}\big(2\bar\alpha e^{i\omega\tau^*}w_{20}^{(2)}(-1)+4\alpha e^{-i\omega\tau^*}w_{11}^{(2)}(-1)\big),1\big\rangle\psi_1+\big\langle c_{11}\big(4w_{11}^{(1)}(0)\\
&\quad+2w_{20}^{(1)}(0)\big)+c_{12}\big(2w_{11}^{(2)}(0)+w_{11}^{(2)}(0)+2\alpha w_{11}^{(1)}(0)+\bar\alpha w_{20}^{(1)}(0)\big)+c_{22}\big(2\bar\alpha w_{20}^{(2)}(0)\\
&\quad+4\alpha w_{11}^{(2)}(0)\big),1\big\rangle\psi_2\big].
\end{aligned}
$$

Since $W_{20}(\theta)$, $W_{11}(\theta)$ for $\theta\in[-1,0]$ appear in g_{21}, we still need to compute them. It follows easily from (42) that

$$\dot W(z,\bar z)=W_{20}z\dot z+W_{11}(\dot z\bar z+z\dot{\bar z})+W_{02}\bar z\dot{\bar z}+\cdots \tag{44}$$

and

$$A_{\tau^*}W=A_{\tau^*}W_{20}\frac{z^2}{2}+A_{\tau^*}W_{11}z\bar z+A_{\tau^*}W_{02}\frac{\bar z^2}{2}+\cdots. \tag{45}$$

In addition, by [23], $W(z(t),\bar{z}(t))$ satisfy

$$\dot{W} = A_{\tau^*}W + H(z,\bar{z}), \tag{46}$$

where

$$\begin{aligned} H(z,\bar{z}) &= H_{20}\frac{z^2}{2} + H_{11}z\bar{z} + H_{02}\frac{\bar{z}^2}{2} + \cdots \\ &= X_0F\left(U_t^*,0\right) - \Phi\left(\Psi,\left\langle X_0F\left(U_t^*,0\right),f_0\right\rangle\right)\cdot f_0, \end{aligned} \tag{47}$$

with $H_{ij} \in P_S\mathcal{C}$, $i+j=2$.

Thus, from (39) and (44)-(46), we obtain

$$\begin{cases} (2i\omega_0\tau^* - A_{\tau^*})W_{20} = H_{20}, \\ -A_{\tau^*}W_{11} = H_{11}. \end{cases} \tag{48}$$

Notice that A_{τ^*} has only two eigenvalues $\pm i\omega_0\tau^*$ with zero real parts, therefore, (46) has the unique solution W_{ij} $(i+j=2)$ in $P_S\mathcal{C}$ given by

$$\begin{cases} W_{20} = (2i\omega_0\tau^* - A_{\tau^*})^{-1}H_{20}, \\ W_{11} = -A_{\tau^*}^{-1}H_{11}. \end{cases} \tag{49}$$

From (47), we know that, for $-1 \le \theta < 0$,

$$\begin{aligned} H(z,\bar{z}) &= -\Phi(\theta)\Psi(0)\left\langle F\left(U_t^*,0\right),f_0\right\rangle\cdot f_0, \\ &= -\left(\frac{p_1(\theta)+p_2(\theta)}{2},\frac{p_1(\theta)-p_2(\theta)}{2i}\right)\left(\Psi_1(0)\Psi_2(0)\right)\times\left\langle F\left(U_t^*,0\right),f_0\right\rangle\cdot f_0, \\ &= -\frac{1}{2}\left[p_1(\theta)\left(\Psi_1(0)-i\Psi_2(0)\right)+p_2(\theta)\left(\Psi_1(0)+i\Psi_2(0)\right)\right]\times\left\langle F\left(U_t^*,0\right),f_0\right\rangle\cdot f_0, \\ &= -\frac{1}{4}\left[g_{20}p_1(\theta)+\bar{g}_{02}p_2(\theta)\right]z^2\cdot f_0 - \frac{1}{2}\left[g_{11}p_1(\theta)+\bar{g}_{11}p_2(\theta)\right]z\bar{z}\cdot f_0 + \cdots. \end{aligned}$$

Therefore, for $-1 \le \theta < 0$,

$$H_{20}(\theta) = -\frac{1}{2}\left[g_{20}p_1(\theta)+\bar{g}_{02}p_2(\theta)\right]\cdot f_0, \tag{50}$$

$$H_{11}(\theta) = -\frac{1}{2}\left[g_{11}p_1(\theta)+\bar{g}_{11}p_2(\theta)\right]\cdot f_0, \tag{51}$$

and

$$\begin{aligned} &H(z,\bar{z})(0) = F\left(U_t^*,0\right) - \Phi\left(\Psi,\left\langle F\left(U_t^*,0\right),f_0\right\rangle\right)\cdot f_0, \\ &H_{20}(0) = \frac{\tau^*}{2}\begin{pmatrix} b_{11}+b_{12}\alpha e^{-i\omega_0\tau^*}+b_{22}\alpha^2e^{-2i\omega_0\tau^*} \\ c_{11}+c_{12}\alpha+c_{22}\alpha^2 \end{pmatrix} - \frac{1}{2}\left[g_{20}p_1(0)+\bar{g}_{02}p_2(0)\right]\cdot f_0, \end{aligned} \tag{52}$$

$$\begin{aligned} H_{11}(0) = {}&\frac{\tau^*}{4}\begin{pmatrix} 2b_{11}+b_{12}(\bar{\alpha}e^{i\omega_0\tau^*}+\alpha e^{-i\omega_0\tau^*})+2b_{22}\alpha\bar{\alpha} \\ 2c_{11}+c_{12}(\bar{\alpha}+\alpha)+2c_{22}\alpha\bar{\alpha} \end{pmatrix} \\ &- \frac{1}{2}\left[g_{11}p_1(0)+\bar{g}_{11}p_2(0)\right]\cdot f_0. \end{aligned} \tag{53}$$

By the definition of A_{τ^*}, we get from (49)

$$\dot{W}_{20}(\theta) = 2i\omega_0\tau^* W_{20}(\theta) + \frac{1}{2}\bigl[g_{20}p_1(\theta) + \bar{g}_{02}p_2(\theta)\bigr]\cdot f_0, \quad -1 \le \theta < 0.$$

Noting that $p_1(\theta) = p_1(0)e^{i\omega_0\tau^*}$, $-1 \le \theta \le 0$. Hence

$$W_{20}(\theta) = \frac{i}{2}\left[\frac{g_{20}}{\omega_0\tau^*}p_1(\theta) + \frac{\bar{g}_{02}}{3\omega_0\tau^*}p_2(\theta)\right]\cdot f_0 + Ee^{2i\omega_0\tau^*\theta} \tag{54}$$

and

$$E = W_{20}(0) - \frac{i}{2}\left[\frac{g_{20}}{\omega_0\tau^*}p_1(0) + \frac{\bar{g}_{02}}{3\omega_0\tau^*}p_2(0)\right]\cdot f_0. \tag{55}$$

Using the definition of A_{τ^*}, and combining (49) and (55), we get

$$\begin{aligned}
&2i\omega_0\tau^*\left[\frac{ig_{20}}{2\omega_0\tau^*}p_1(0)\cdot f_0 + \frac{i\bar{g}_{02}}{6\omega_0\tau^*}p_2(0)\cdot f_0 + E\right] \\
&\quad - \tau^* D\Delta\left[\frac{ig_{20}}{2\omega_0\tau^*}p_1(0)\cdot f_0 + \frac{i\bar{g}_{02}}{6\omega_0\tau^*}p_2(0)\cdot f_0 + E\right] \\
&\quad - L(\tau^*)\left[\frac{ig_{20}}{2\omega_0\tau^*}p_1(\theta)\cdot f_0 + \frac{i\bar{g}_{02}}{6\omega_0\tau^*}p_2(\theta)\cdot f_0 + Ee^{2i\omega_0\tau^*\theta}\right] \\
&\ = \frac{\tau^*}{2}\begin{pmatrix} b_{11} + b_{12}\alpha e^{-i\omega_0\tau^*} + b_{22}\alpha^2 e^{-2i\omega_0\tau^*} \\ c_{11} + c_{12}\alpha + c_{22}\alpha^2 \end{pmatrix} - \frac{1}{2}\bigl[g_{20}p_1(0) + \bar{g}_{02}p_2(0)\bigr]\cdot f_0.
\end{aligned}$$

Notice that

$$\begin{cases} \tau^* D\Delta[p_1(0)\cdot f_0] + L(\tau^*)[p_1(\theta)\cdot f_0] = i\omega_0\tau^* p_1(0)\cdot f_0, \\ \tau^* D\Delta[p_2(0)\cdot f_0] + L(\tau^*)[p_2(\theta)\cdot f_0] = -i\omega_0\tau^* p_2(0)\cdot f_0. \end{cases}$$

Then we have

$$2i\omega_0\tau^* E - \tau^* D\Delta E - L(\tau^*)\bigl(Ee^{2i\omega_0\tau^*\theta}\bigr) = \frac{\tau^*}{2}\begin{pmatrix} b_{11} + b_{12}\alpha e^{-i\omega_0\tau^*} + b_{22}\alpha^2 e^{-2i\omega_0\tau^*} \\ c_{11} + c_{12}\alpha + c_{22}\alpha^2 \end{pmatrix}.$$

From the above expression, we can see easily that

$$E = \frac{1}{2}\begin{pmatrix} 2i\omega_0 - a_{11} & a_{12}e^{-2i\omega_0\tau^*} \\ -a_{21} & 2i\omega_0 - a_{22} \end{pmatrix}^{-1} \times \begin{pmatrix} b_{11} + b_{12}\alpha e^{-i\omega_0\tau^*} + b_{22}\alpha^2 e^{-2i\omega_0\tau^*} \\ c_{11} + c_{12}\alpha + c_{22}\alpha^2 \end{pmatrix}.$$

In a similar way, we have

$$\dot{W}_{11}(\theta) = \frac{1}{2}\bigl[g_{11}p_1(\theta) + \bar{g}_{11}p_2(\theta)\bigr]\cdot f_0, \quad -1 \le \theta < 0,$$

and

$$W_{11}(\theta) = \frac{i}{2\omega_0\tau^*}\bigl[-g_{11}p_1(\theta) + \bar{g}_{11}p_2(\theta)\bigr]\cdot f_0 + F.$$

Similar to the above, we obtain

$$F = \frac{1}{4}\begin{pmatrix} -a_{11} & a_{12} \\ -a_{21} & -a_{22} \end{pmatrix}^{-1} \times \begin{pmatrix} 2b_{11} + b_{12}(\bar{\alpha}e^{i\omega_0\tau^*} + \alpha e^{-i\omega_0\tau^*}) + 2b_{22}\alpha\bar{\alpha} \\ 2c_{11} + c_{12}(\bar{\alpha} + \alpha) + 2c_{22}\alpha\bar{\alpha} \end{pmatrix}.$$

So far, $W_{20}(\theta)$ and $W_{11}(\theta)$ have been expressed by the parameters of system (1). Therefore, g_{21} can be expressed explicitly.

Theorem 5.1 *System* (1) *has the following Poincaré normal form*:

$$\dot{\xi} = i\omega_0\tau^*\xi + c_1(0)\xi|\xi|^2 + o(|\xi|^5),$$

where

$$c_1(0) = \frac{i}{2\omega_0\tau^*}\left[g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right] + \frac{g_{21}}{2},$$

so we can compute the following results:

$$\begin{aligned} \sigma_2 &= -\frac{\operatorname{Re}(c_1(0))}{\operatorname{Re}(\lambda'(\tau^*))}, \\ \beta_2 &= 2\operatorname{Re}(c_1(0)), \\ T_2 &= -\frac{\operatorname{Im}(c_1(0)) + \sigma_2 \operatorname{Im}(\lambda'(\tau^*))}{\omega_0\tau^*}, \end{aligned}$$

which determine the properties of bifurcating periodic solutions at the critical values τ^*, i.e., σ_2 determines the directions of the Hopf bifurcation: *if $\sigma_2 > 0$ ($\sigma_2 < 0$), then the Hopf bifurcation is supercritical* (*subcritical*) *and the bifurcating periodic solutions exist for $\tau > \tau^*$; β_2 determines the stability of the bifurcating periodic solutions*: *the bifurcating periodic solutions on the center manifold are stable* (*unstable*), *if $\beta_2 < 0$ ($\beta_2 > 0$); and T_2 determines the period of the bifurcating periodic solutions*: *the period increases* (*decreases*), *if $T_2 > 0$ ($T_2 < 0$).*

6 Numerical results and discussions

In this section we present results of the numerical simulations to facilitate the interpretation of our mathematical findings in system (1) proved in the previous sections.

6.1 Stability of the interior equilibrium for all $\tau \geq 0$

Consider system (1) with the following parameters: $r = 0.8$, $K = 5$, $q = 0.2$, $a = 2$, $b = 0.4$, $d = 0.2$, $e = 0.2$, $m = 2$ and $c = 0.3$. Choose $\Omega = (0,\pi)$ and the diffusion coefficients $d_1 = 0.2$, $d_2 = 0.6$. According to the discussions in Section 4.1, $E_0 = (0,0)$ and $E_1 = (5,0)$ are both stable, and $E_2 = (2,0)$ is unstable. In addition, by a direct calculation, we find that system (1) has a coexisting equilibrium $E^* = (4.7296, 2.7926)$. Clearly, the conditions (H_1) and (H_2) hold, according to Theorem 4.1, system (1) is locally asymptotically stable at E^* for all $\tau \geq 0$. The corresponding phase portrait of system (1) with $\tau = 10$, is shown in Figure 2.

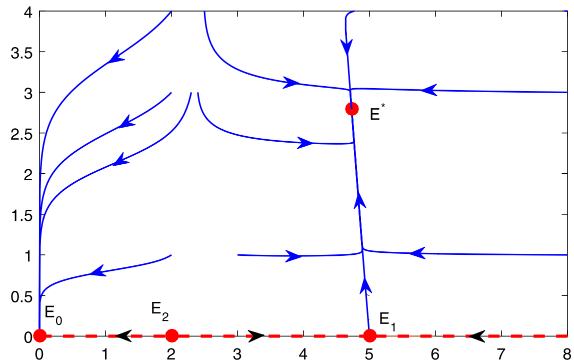


Figure 2 Phase portraits of the model system (1). $E_0 = (0,0)$, $E_1 = (5,0)$ and $E^* = (4.7296, 2.7926)$ are all locally asymptotically stable for all $\tau \geq 0$.

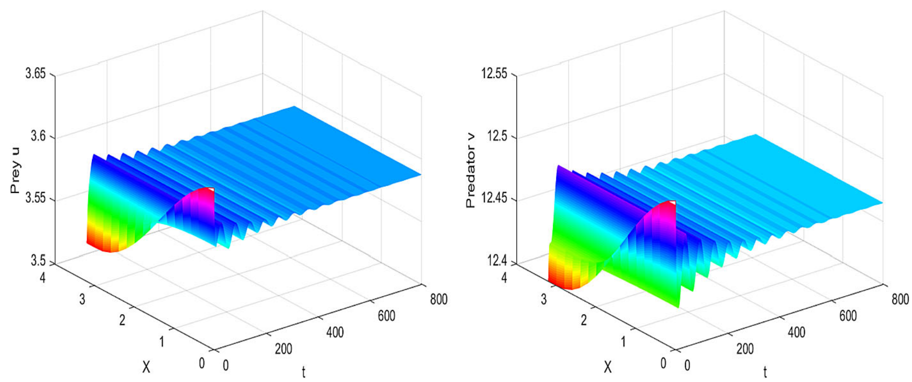


Figure 3 The coexisting equilibrium E^* is locally stable where $\tau = 3 < \tau_0$.

6.2 Hopf bifurcation

Let the parameters be the same as above except $d = 0.1$ and $m = 2.05$. Choose $\Omega = (0, \pi)$ and the diffusion coefficients $d_1 = 0.2$, $d_2 = 0.6$. According to the discussions in Section 4.1, $E_0 = (0,0)$ is stable yet, but $E_1 = (5,0)$ and $E_2 = (2,0)$ become unstable. By a direct calculation, we find that system (1) has two the coexisting equilibria $E_1^* = (3.5871, 12.4646)$ and $E_2^* = (3.0866, 9.7950)$. For E_2^*, condition (H_1) is not satisfied. Therefore, E_2^* is unstable. For $E_1^* = (3.5871, 12.4646)$, by simple calculation, we find that the critical value is $\tau_0^0 = 4.1981$. According to Theorem 4.2, system (1) is locally asymptotically stable for $\tau = 3 \in [0, \tau_0^0)$, as shown in Figure 3 and Figure 4. As τ increases through the critical value τ_0^0, the coexisting equilibrium E_1^* loses its stability permanently and a family of periodic solutions bifurcate from the coexisting equilibrium E_1^* caused by the phenomenon of Hopf bifurcation, as shown in Figure 4.

In addition, when $\tau = \tau_0^0 = 4.1981$, we get $c_1(0) = -0.0126 + 0.0675i$, $\sigma_2 = -\frac{\mathrm{Re}(c_1(0))}{\mathrm{Re}(\lambda'(\tau^*))} = 0.0104 > 0$, $\beta_2 = 2\,\mathrm{Re}(c_1(0)) = -0.0252 < 0$. According to Theorem 5.1 in Section 5, the bifurcated periodic solutions of system (1) when $\tau_0^0 = 4.1981$ in the whole phase space are both orbitally asymptotically stable, and the Hopf bifurcations are supercritical for $\sigma_2 > 0$.

However, as τ increases further, with the same initial values, the solution converges to E_0, as shown in Figure 5. All this suggests that the increasing delay may cause the prey and predator to go extinct.

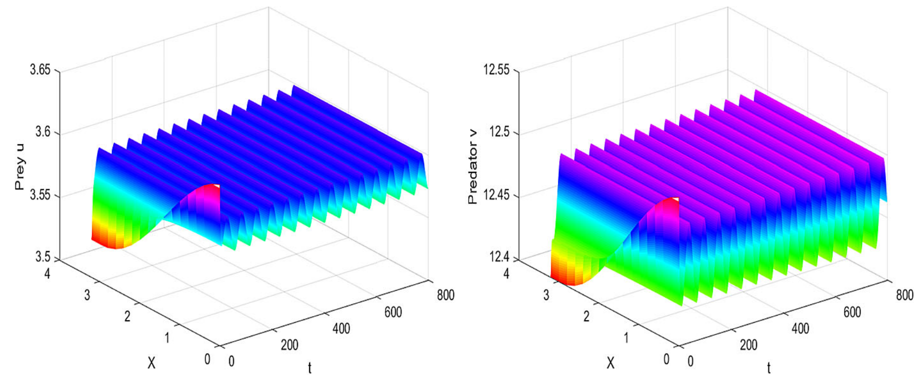


Figure 4 The periodic solutions bifurcating from the coexisting equilibrium E^* where $\tau = 4.2 > \tau_0$.

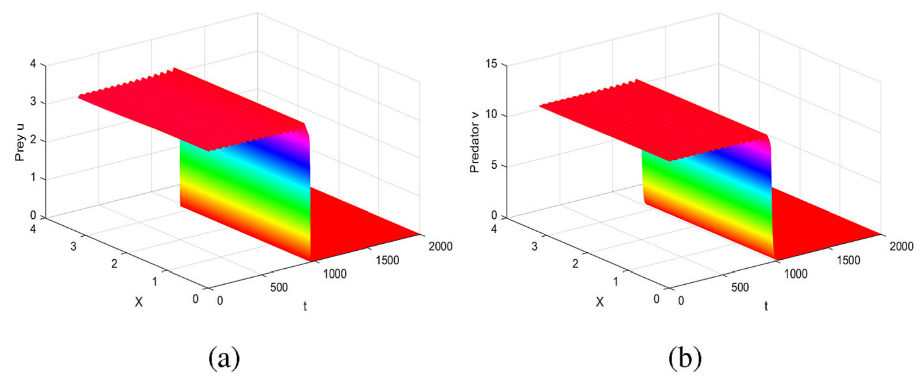
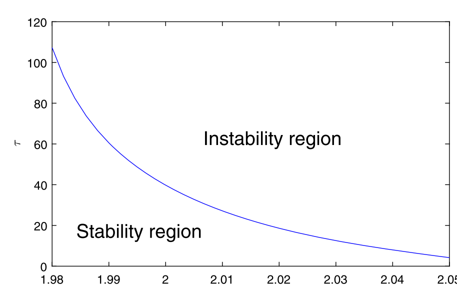


Figure 5 The solution of system (1) converges to E_0 with $\tau = 4.5 > \tau_0$.

Figure 6 Stability region exploring the dynamics of the system in the (m, τ) parameter space.



6.3 The effect of Allee effect

In order to investigate the effect of Allee effect, we let the parameters be the same as above except for m varying in $[1.98, 2.05]$. The stability and instability regions of the solution of the system (1) is shown by plotting the Allee threshold m versus the critical value of the time delay τ in Figure 6. Figure 6 depicts also show the locus of the Hopf bifurcation changes with the change of the two parameters m and τ. We see that as the Allee threshold m increases from 1.98 to 2.05, the Hopf bifurcation is achieved for lower critical values of τ.

7 Conclusion

In this paper, we considered a delayed diffusive predator-prey system with Beddington-DeAngelis functional response and strong Allee effect. With delay τ as a bifurcation parameter, we showed that a Hopf bifurcation occurs at the critical value τ_0^0. The bifurcating periodic solutions were analyzed in light of the normal form and center manifold. Theoretical analysis shows that with the strong Allee effect in prey, extinction for both species is always a locally stable equilibrium. If $u_0(x,t) < m$, then both prey and the predator are destined to go extinct (Theorem 2.1(b)) and if $\frac{K(e-bd)-ad}{cd} < 0$, then the predator is destined to go extinct (Theorem 2.1(c)). Theoretical analysis and numerical simulations also show that that the increasing delay may cause the prey and predator to go extinct. However, there are still many problems about model (1) that need to be studied, such as Turing stability, spatiotemporal patterns.

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Competing interests
The authors declare that they have no competing interests.

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