Stability and bifurcation in a ratio-dependent Holling-III system with diffusion and delay*

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Abstract. A diffusive ratio-dependent predator-prey system with Holling-III functional response and delay effects is considered. Global stability of the boundary equilibrium and the stability of the unique positive steady state and the existence of spatially homogeneous and inhomogeneous periodic solutions are investigated in detail, by the maximum principle and the characteristic equations. Ratio-dependent functional response exhibits rich spatiotemporal patterns. It is found that, the system without delay is dissipative and uniformly permanent under certain conditions, the delay can destabilize the positive constant equilibrium and spatial Hopf bifurcations occur as the delay crosses through some critical values. Then, the direction and the stability of Hopf bifurcations are determined by applying the center manifold reduction and the normal form theory for partial functional differential equations. Some numerical simulations are carried out to illustrate the theoretical results.

Keywords: Hopf bifurcation, ratio-dependent, Holling-type III, delay, diffusion, global stability, uniformly permanent.

1 Introduction

The well-known Lotka–Volterra type prepator-prey system describing predator-prey interactions has long been and will continue to be one of the dominant themes in both ecology and mathematics [1]. Generally, a predator-prey model can take the form

$$\begin{aligned} \frac{\mathrm{d}u}{\mathrm{d}t} &= u(a-bu) - vg(u), \\ \frac{\mathrm{d}v}{\mathrm{d}t} &= -v\left(d - \frac{s}{c}g(u)\right), \end{aligned} \tag{1}$$

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where u, v stand for prey and predator density, respectively. a, a/b, d, s/c are positive constants which denote prey intrinsic growth rate, carrying capacity, predator death rate and conversion rate, respectively. $g(u)$ is the prey-dependent functional response, particularly, $g(u) = cu^2/(m^2 + u^2)$ is so-called Holling-type III, first proposed by Holling [2]. Some biologists have questioned the functional response solely depending on prey density, for example [3–5], especially when predators have to search for food (and therefore, have to share or complete for food). A more suitable predator-prey theory should be the so-called ratio-dependent theory. We replace $g(u)$ by $g(u/v)$. That is, the per capita predator growth rate is a function of the ratio of prey to predator biomass, which is strongly supported by numerous fields and experimental data [3,4]. The ratio-dependent predator-prey system (1) with Holling-type III takes the form

$$\begin{aligned} \frac{\mathrm{d}u}{\mathrm{d}t} &= u(a - bu) - \frac{cu^2 v}{m^2 v^2 + u^2}, \\ \frac{\mathrm{d}v}{\mathrm{d}t} &= -v\left(d - \frac{su^2}{m^2 v^2 + u^2}\right), \end{aligned} \tag{2}$$

where $u^2/(m^2v^2+u^2)$ denotes the predator response function, s stands for the conversion rate.

The above model can produce the richer and more reasonable dynamics biologically [3, 6, 7]. It is well known that the past history and current state can affect the dynamics of models. The effect of gestation delay has been studied by many authors [8–11]. Assuming the reproduction of the predators after eating the prey will be not transient but need some discrete time lag, we introduce a delay to the system (2) to make it close to reality.

Particularly, by using the continuation theorem of coincidence degree theory, Wang and Li [12] investigated the existence of positive periodic solutions for a delayed ratio-dependent predator-prey model with Holling-type III functional response in the following form:

$$\begin{aligned} \frac{\mathrm{d}u(t)}{\mathrm{d}t} &= u(t)\left(a(t) - b(t)\int_{-\infty}^{t} k(t-s)u(s)\,\mathrm{d}s\right) - \frac{c(t)u^2(t)v(t)}{m^2v^2(t) + u^2(t)}, \\ \frac{\mathrm{d}v(t)}{\mathrm{d}t} &= v(t)\left(-d(t) + \frac{su^2(t-\tau)}{m^2v^2(t-\tau) + u^2(t-\tau)}\right), \end{aligned} \tag{3}$$

where $a(t)$, $b(t)$, $c(t)$ and $d(t)$ are all positive ω-period functions, $m > 0$ and

$$k(s) : R^+ \to R^+$$

is a measurable, ω-periodic, normalized function such that $\int_{-\infty}^{t} k(s)\,\mathrm{d}s = 1$. Clearly, $\int_{-\infty}^{t} k(t-s)u(s)\,\mathrm{d}s = u(t)$ when $k(s) = \delta(s)$, where $\delta(s)$ is Dirac delta function at $s = 0$. In the case that $k(s) = \delta(s)$, and $a(t)$, $b(t)$, $c(t)$ and $d(t)$ are all positive constants,

(3) becomes

$$
\begin{aligned}
\frac{\mathrm{d}u(t)}{\mathrm{d}t} &= u(t)\big(a - bu(t)\big) - \frac{cu^2(t)v(t)}{m^2v^2(t) + u^2(t)},\\
\frac{\mathrm{d}v(t)}{\mathrm{d}t} &= v(t)\left(-d + \frac{su^2(t-\tau)}{m^2v^2(t-\tau) + u^2(t-\tau)}\right).
\end{aligned}
$$

Xu, Gan and Ma [13] studied the global stability of the equilibria of the above system and the existence of Hopf bifurcation. Our work is an extension of the work in [13]. Assuming that predators and preys are in an isolate patch in which the impact of migration, including immigration and emigration, can be neglected, we only consider the diffusion of the spatial domain. It has been shown that the reaction-diffusion system can generate more complex spatiotemporal patterns [14–23]. We consider the ratio-dependent Holling-III predator-prey system with delay and diffusion

$$
\begin{aligned}
&\frac{\partial u(x,t)}{\partial t} = d_1\Delta u(x,t) + u(x,t)\big(a - bu(x,t)\big) - \frac{cu^2(x,t)v(x,t)}{m^2v^2(x,t) + u^2(x,t)},\\
&\quad x \in (0, l\pi),\ t \geqslant 0,\\
&\frac{\partial v(x,t)}{\partial t} = d_2\Delta v(x,t) - v(x,t)\left[d - \frac{su^2(x,t-\tau)}{m^2v^2(x,t-\tau) + u^2(x,t-\tau)}\right],\\
&\quad x \in (0, l\pi),\ t \geqslant 0,\\
&\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, \quad x = 0, l\pi,\ t \geqslant 0,\\
&u(x,t) = \phi(x,t) \geqslant 0, \quad v(x,t) = \psi(x,t) \geqslant 0, \quad (x,t) \in [0, l\pi] \times [-\tau, 0],
\end{aligned}
\tag{4}
$$

where $\Delta = \partial^2/\partial x^2$ denotes the usual Laplacian operator in the one-dimension space, d_1, d_2 denote the diffusion rate of prey and predator, respectively. We assume that $d_1 \geqslant d_2$, which implies that the prey has some hope of escaping. ν is the outward unit normal on $\partial\Omega$, and the homogeneous Neumann boundary conditions imply the closed domain where the populations can not move across the boundary of the domain.

Let $\bar{u}(x,t) = (b/a)u(x,t)$, $\bar{v}(x,t) = (b/a)mv(x,t)$ and $h = c/m$, $\bar{\phi}(x,t) = (b/a)\phi(x,t)$, $\bar{\psi}(x,t) = (b/a)m\psi(x,t)$, and drop the bars for simplicity of notations, then (4) can be transformed into the following system:

$$
\begin{aligned}
&\frac{\partial u(x,t)}{\partial t} = d_1\Delta u(x,t) + au(x,t)\big(1 - u(x,t)\big) - \frac{hu^2(x,t)v(x,t)}{v^2(x,t) + u^2(x,t)},\\
&\quad x \in (0, l\pi),\ t \geqslant 0,\\
&\frac{\partial v(x,t)}{\partial t} = d_2\Delta v(x,t) - v(x,t)\left[d - \frac{su^2(x,t-\tau)}{v^2(x,t-\tau) + u^2(x,t-\tau)}\right],\\
&\quad x \in (0, l\pi),\ t \geqslant 0,\\
&u_x(0,t) = u_x(l\pi,t) = v_x(0,t) = v_x(l\pi,t) = 0, \quad t \geqslant 0,\\
&u(x,t) = \phi(x,t) \geqslant 0, \quad v(x,t) = \psi(x,t) \geqslant 0, \quad (x,t) \in [0, l\pi] \times [-\tau, 0].
\end{aligned}
\tag{5}
$$

In addition, what is more important in ecosystem is whether the species would survive in the long run. That is, whether the system is permanent. In the present paper, we aim to study the uniform permanence and dissipativeness and investigate the effects of the delay and diffusion on system (5). The main results are that, the boundary equilibrium is globally asymptotically stable if $s < d$ and $2a > h$, and unstable if $s > d$ for all $\tau \geqslant 0$. The delay and diffusion have no effects on the stability of the boundary equilibrium. In addition, the system without delay is dissipative when $s > d$ and is uniformly permanent when $s > d$, $2a > h$. And, if $s > d$, there is $\tilde{\tau} > 0$ such that the positive constant equilibrium is stable for $\tau \in [0, \tilde{\tau})$ and unstable for $\tau \in (\tilde{\tau}, +\infty)$. And a family of homogeneous, as well as inhomogeneous periodic solutions, may bifurcate from the positive constant steady state under some certain conditions, by virtue of the effects of diffusion and delay.

The rest of the paper is organized as follows. In Section 2, the global stability of the boundary equilibrium and the stability of the positive coexistence of system (5) are studied in detail. And the dissipativeness and uniform permanence of the system without delay are investigated by the comparison principle. And we also consider the existence of Hopf bifurcations as the delay τ crosses a sequence of critical values. In Section 3, the direction and stability of the Hopf bifurcations are given. Some numerical simulations are carried out to illustrate the theoretical results in Section 4.

2 Some dynamical behaviors of the system

Firstly, we make the following assumptions:

(H1) d_1, d_2, a, h, d and s are all positive constants, and $d_1 > d_2$.

(H2) $s > d$ and $h\sqrt{(s-d)d} < as$.

It is easy to check that system (5) always has a unique boundary equilibrium point $E_1(1,0)$. And the system has a unique positive constant steady state $E(u^*, v^*)$ if and only if (H2) holds, where $u^* = 1 - h/(as)\sqrt{(s-d)d} > 0$, $v^* = as/(hd)u^*(1-u^*) > 0$. Next, we study the stability of the boundary equilibrium.

2.1 Global stability analysis of the boundary equilibrium

The linearized equations of system (5) at $E_1(1,0)$ are given by

$$\begin{aligned} \frac{\partial u}{\partial t} &= d_1 \Delta u - au(x,t) - hv(x,t), \\ \frac{\partial v}{\partial t} &= d_2 \Delta v + (s-d)v(x,t). \end{aligned} \tag{6}$$

From the properties of the Laplacian operator defined on the bounded domain the operator on X has the eigenvalues $-n^2/l^2$ with the relative eigenfunctions

$$\beta_n^1 = \begin{pmatrix} \cos\frac{n}{l}x \\ 0 \end{pmatrix}, \quad \beta_n^2 = \begin{pmatrix} 0 \\ \cos\frac{n}{l}x \end{pmatrix}, \quad n = 0, 1, 2, \dots,$$

where
$$X = \left\{ u, v \in W^{2,2}(\Omega)\colon\ \frac{\partial u(x,t)}{\partial x} = \frac{\partial v(x,t)}{\partial x} = 0,\ x \in \partial\Omega \right\}$$
and $\Omega = (0, l\pi)$.

The characteristic equations of the linearized equations (6) are given by
$$\left(\lambda + \frac{d_1 n^2}{l^2} + a\right)\left(\lambda + \frac{d_2 n^2}{l^2} + d - s\right) = 0, \quad n = 0, 1, 2, \dots.$$
That is, $\lambda_1 = -d_1 n^2/l^2 - a < 0$, $\lambda_2 = -d_2 n^2/l^2 + s - d \leqslant s - d$, $n = 0, 1, 2, \dots$.

Then we know that all the characteristic roots of the linearization of system (5) at $E_1(1,0)$ are negative if $s < d$. And there is at least one positive characteristic root, if $s > d$. Combining the stability theory, we can obtain the following result.

Theorem 1. *Suppose* (H1) *is satisfied. Then the boundary equilibrium $E_1(1,0)$ of system* (5) *is locally asymptotically stable if $s < d$ and unstable if $s > d$ for all $\tau \geqslant 0$.*

In the following, we shall apply the comparison method in [6, 22, 23] to obtain that, $E_1(1,0)$ is globally asymptotically stable for all $\tau \geqslant 0$ under the certain conditions.

Theorem 2. *Suppose that* (H1)*, $s < d$ and $2a > h$ are satisfied. Then for any initial value $\phi(x,\theta) > 0$, $\psi(x,\theta) \geqslant 0$, $\theta \in [-\tau, 0]$, the corresponding solution $(u(x,t), v(x,t))$ of system* (5) *converges uniformly to $E_1(1,0)$ as $t \to +\infty$. Thus, the equilibrium $E_1(1,0)$ is globally asymptotically stable.*

Proof. It is easy to see that all the solutions $(u(x,t), v(x,t))$ of system (5) are nonnegative by the maximum principle. And since $\phi(x,t) > 0$, $u(x,t)$ is strictly positive for $t > 0$. It is well known that if $\omega(x,t)$ satisfies
$$\begin{aligned}
&\frac{\partial \omega}{\partial t} - d\Delta\omega = \omega(a - b\omega), \quad x \in \Omega,\ t > 0,\\
&\frac{\partial \omega}{\partial \mu} = 0, \quad x \in \partial\Omega,\ t > 0,\\
&\omega(x,0) \geqslant 0\ (\not\equiv 0), \quad x \in \Omega,
\end{aligned}$$
where $d, a, b > 0$, then $\omega(x,t) \to a/b$ as $t \to +\infty$ uniformly in $x \in \bar{\Omega}$.

By the second equation of system (5), we know that
$$\frac{\partial v}{\partial t} - d_2\Delta v = -dv + \frac{s u^2(x, t-\tau) v(x,t)}{u^2(x, t-\tau) + v^2(x, t-\tau)} \leqslant (s - d)v.$$
By the comparison principle of parabolic equations, we obtain that
$$\limsup_{t\to+\infty} \max_{x\in[0,l\pi]} v(x,t) \leqslant 0, \quad \text{since } s - d < 0.$$
Thus
$$v(x,t) \to 0 \quad \text{as } t \to +\infty \text{ uniformly in } \Omega. \tag{7}$$

By the first equation of system (5), we have

$$\begin{aligned}\frac{\partial u}{\partial t} - d_1 \Delta u(x,t) &= u(x,t)\left(a - au(x,t) - \frac{hu(x,t)v(x,t)}{u^2(x,t)+v^2(x,t)}\right)\\ &\geqslant u\left(a - \frac{h}{2} - au\right), \quad x \in (0, l\pi),\end{aligned}$$

according to $uv/(u^2+v^2) \leqslant 1/2$.

From the maximum principle

$$\liminf_{t\to+\infty} \min_{x\in[0,l\pi]} u(x,t) \geqslant 1 - \frac{h}{2a} \triangleq u_0 > 0, \quad \text{since } 2a > h. \tag{8}$$

By (7) and (8), we have that

$$\lim_{t\to+\infty} \frac{hu(x,t)v(x,t)}{u^2(x,t)+v^2(x,t)} = 0 \quad \text{uniformly in } \Omega.$$

Then, for all $\epsilon \in (0, a)$, there exists $T(\epsilon) > 0$ such that

$$\frac{hu(x,t)v(x,t)}{u^2(x,t)+v^2(x,t)} < \epsilon \quad \forall t > T(\epsilon),\ x \in \Omega.$$

On the one hand,

$$\begin{aligned}\frac{\partial u}{\partial t} - d_1 \Delta u(x,t) &= u(x,t)\left(a - au(x,t) - \frac{hu(x,t)v(x,t)}{u^2(x,t)+v^2(x,t)}\right)\\ &\leqslant au(x,t)\bigl(1 - u(x,t)\bigr),\end{aligned}$$

and

$$\begin{aligned}\frac{\partial u}{\partial t} - d_1 \Delta u(x,t) &= u(x,t)\left(a - au(x,t) - \frac{hu(x,t)v(x,t)}{u^2(x,t)+v^2(x,t)}\right)\\ &\geqslant u(x,t)\bigl(a - \epsilon - au(x,t)\bigr).\end{aligned}$$

Again from the comparison principle, we can obtain that

$$\limsup_{t\to+\infty} \max_{x\in[0,l\pi]} u(x,t) \leqslant 1, \qquad \liminf_{t\to+\infty} \min_{x\in[0,l\pi]} u(x,t) \geqslant 1 - \frac{\epsilon}{a}.$$

Let $\epsilon \to 0$, we have $u(x,t) \to 1$ as $t \to +\infty$ uniformly in Ω. The result is derived. □

2.2 Dissipativeness and uniform permanence of the system without delay

In this subsection, we analyze the dynamical behavior of the system. We assume that the initial value $v(x,0) > 0$ for all $x \in [0, l\pi]$. The system (5) with $\tau = 0$ is the following form:

$$
\begin{aligned}
&\frac{\partial u(x,t)}{\partial t} = d_1\Delta u(x,t) + au(x,t)\big(1-u(x,t)\big) - \frac{hu^2(x,t)v(x,t)}{v^2(x,t)+u^2(x,t)},\\
&\quad x\in(0,l\pi),\ t\geqslant 0,\\
&\frac{\partial v(x,t)}{\partial t} = d_2\Delta v(x,t) - dv(x,t) + \frac{su^2(x,t)v(x,t)}{v^2(x,t)+u^2(x,t)},\\
&\quad x\in(0,l\pi),\ t\geqslant 0,\\
&u_x(0,t)=u_x(l\pi,t)=v_x(0,t)=v_x(l\pi,t)=0, \quad t\geqslant 0,\\
&u(x,0)=\phi(x)\geqslant 0\ (\not\equiv 0), \quad v(x,0)=\psi(x)>0, \quad x\in[0,l\pi].
\end{aligned}
\tag{9}
$$

In order to obtain the main result, we first give a lemma.

Lemma 1. *Consider the ordinary differential equation*

$$
\frac{\mathrm{d}x}{\mathrm{d}t} = xf(x), \qquad x(t_0)=x_0>0. \tag{10}
$$

Suppose $f(x)$ is continuously differentiable with respect to x,

$$
f(a)=0 \quad \textit{and} \quad (x-a)f(x)<0
$$

for a constant $a>0$. Then the solution of (10)*, $x(t)$, satisfies $\lim_{t\to+\infty} x(t)=a$.*

Note that the system (10) has only two fixed points $x\equiv 0$ and $x\equiv a$. Then one can prove the conclusion by the uniqueness of the solution. So we omit the detailed proof here.

Theorem 3. *Suppose* (H1) *is satisfied. Then the system* (9) *is dissipative if $s>d$.*

Proof. Standard maximum principle of parabolic equations shows the solutions of system (9) always exist and are nonnegative. And since $\psi(x,0)>0$, $v(x,t)$ is strictly positive for $t>0$.

By the first equation of (9),

$$
\frac{\partial u}{\partial t} - d_1\Delta u(x,t) \leqslant au(x,t)\big(1-u(x,t)\big).
$$

From the comparison principle we know that $\limsup_{t\to+\infty}\max_{x\in[0,l\pi]} u(x,t)\leqslant 1$.

Then, for all $\epsilon>0$, there is $T>0$ such that $u(x,t)<1+\epsilon$ for all $t>T$, $x\in[0,l\pi]$. By the second equation of (9),

$$
\begin{aligned}
\frac{\partial v(x,t)}{\partial t} - d_2\Delta v(x,t) &= v(x,t)\left(-d+\frac{su^2(x,t)}{v^2(x,t)+u^2(x,t)}\right)\\
&\leqslant v(x,t)\left(-d+\frac{s(1+\epsilon)^2}{(1+\epsilon)^2+v^2(x,t)}\right)\\
&= v(x,t)\frac{(s-d)(1+\epsilon)^2-dv^2(x,t)}{(1+\epsilon)^2+v^2(x,t)} \quad \text{for } t>T.
\end{aligned}
$$

Consider the corresponding initial value problem

$$\frac{\mathrm{d}z}{\mathrm{d}t} = z(t)\frac{(s-d)(1+\epsilon)^2 - dz^2(t)}{(1+\epsilon)^2 + z^2(t)}, \qquad z(T) = \max_{[0,l\pi]} v(x,T) > 0.$$

By Lemma1, we know that $\lim_{t\to+\infty} z(t) = \sqrt{(s-d)/d}(1+\epsilon)$. Again from the comparison principle it follows

$$\limsup_{t\to+\infty} \max_{x\in[0,l\pi]} v(x,t) \leqslant \sqrt{\frac{s-d}{d}}(1+\epsilon).$$

Let $\epsilon \to 0$,

$$\limsup_{t\to+\infty} \max_{x\in[0,l\pi]} v(x,t) \leqslant \sqrt{\frac{s-d}{d}}.$$

Hence, system (9) is dissipative. □

Theorem 4. *Suppose that* (H1) *is satisfied. Then system* (9) *is uniformly permanent if* $s > d$ *and* $2a > h$.

Proof. By (8), there exists $T > 0$ such that $\min_{x\in[0,l\pi]} u(x,t) \geqslant u_0/2 > 0$ for all $t > T$. Then, for $t > T$,

$$\begin{aligned}\frac{\partial v(x,t)}{\partial t} - d_2\Delta v(x,t) &= v(x,t)\left(-d + \frac{su^2(x,t)}{u^2(x,t)+v^2(x,t)}\right)\\ &\geqslant v(x,t)\left(-d + \frac{s(\frac{u_0}{2})^2}{(\frac{u_0}{2})^2 + v^2(x,t)}\right)\\ &= v(x,t)\frac{(s-d)u_0^2 - 4dv^2(x,t)}{u_0^2 + 4v^2(x,t)}.\end{aligned}$$

Consider the corresponding initial value problem

$$\frac{\mathrm{d}z}{\mathrm{d}t} = z(t)\frac{(s-d)u_0^2 - 4dz^2(t)}{u_0^2 + 4z^2(t)}, \qquad z(T) = \max_{[0,l\pi]} v(x,T) > 0.$$

By virtue of Lemma1, we obtain that $\lim_{t\to+\infty} z(t) = \sqrt{(s-d)/(4d)}u_0$. Again from the maximum principle, we have that

$$\liminf_{t\to+\infty} \min_{x\in[0,l\pi]} v(x,t) \geqslant \sqrt{\frac{s-d}{4d}}u_0 > 0. \tag{11}$$

By (8) and (11), system (9) is uniformly permanent. □

2.3 Stability of $E(u^*, v^*)$ and existence of Hopf bifurcation

In this section, under the assumption $s > d$, we study the stability of the equilibrium $E(u^*, v^*)$ and the existence of Hopf bifurcation, by analyzing the distribution of the eigenvalues.

Let $\tilde{u} = u - u^*$, $\tilde{v} = v - v^*$ and drop the tildes for the sake of simplicity. Then (5) becomes

$$\begin{aligned}
\frac{\partial u(x,t)}{\partial t} &= d_1\Delta u(x,t) + a\big(u(x,t)+u^*\big)\big(1-u(x,t)-u^*\big) \\
&\quad - \frac{h(u(x,t)+u^*)^2(v(x,t)+v^*)}{(u(x,t)+u^*)^2+(v(x,t)+v^*)^2}, \\
\frac{\partial v(x,t)}{\partial t} &= d_2\Delta v(x,t) - d\big(v(x,t)+v^*\big) \\
&\quad + \frac{s(u(x,t-\tau)+u^*)^2(v(x,t)+v^*)}{(u(x,t-\tau)+u^*)^2+(v(x,t-\tau)+v^*)^2}, \\
u_x(0,t) &= u_x(l\pi,t) = v_x(0,t) = v_x(l\pi,t) = 0, \quad t \geqslant 0,
\end{aligned} \tag{12}$$

and $(0,0)$ is the constant equilibrium point of (12).

Let

$$\begin{aligned}
f^{(1)}(u,v) &= a(u(x,t)+u^*)(1-u(x,t)-u^*) - \frac{h(u(x,t)+u^*)^2(v(x,t)+v^*)}{(u(x,t)+u^*)^2+(v(x,t)+v^*)^2}, \\
f^{(2)}(u,v,w) &= -d(v+v^*) + \frac{s(u+u^*)^2(v+v^*)}{(u+u^*)^2+(w+v^*)^2}.
\end{aligned}$$

Define $f^{(1)}_{ij}$ $(i+j \geqslant 1)$ and $f^{(2)}_{ijl}$ $(i+j+l \geqslant 1)$ by

$$f^{(1)}_{ij} = \frac{\partial^{i+j} f^{(1)}}{\partial u^i \partial v^j}(0,0), \qquad f^{(2)}_{ijl} = \frac{\partial^{i+j+l} f^{(2)}}{\partial u^i \partial v^j \partial w^l}(0,0,0).$$

By virtue of Taylor expansions, (12) can be rewritten as

$$\begin{aligned}
\frac{\partial u(x,t)}{\partial t} &= d_1\Delta u(x,t) + \left(\frac{2hd}{s^2}\sqrt{(s-d)d} - a\right)u(x,t) - \frac{dh}{s^2}(2d-s)v(x,t) \\
&\quad + \sum_{i+j\geqslant 2} \frac{1}{i!j!} f^{(1)}_{ij}(0,0)u^i(x,t)v^j(x,t), \\
\frac{\partial v(x,t)}{\partial t} &= d_2\Delta v(x,t) + 2\frac{s-d}{s}\sqrt{(s-d)d}\,u(x,t-\tau) - \frac{2d}{s}(s-d)v(x,t-\tau) \\
&\quad + \sum_{i+j+l\geqslant 2} \frac{1}{i!j!l!} f^{(2)}_{ijl}(0,0,0)u^i(x,t-\tau)v^j(x,t)v^l(x,t-\tau).
\end{aligned} \tag{13}$$

Denote $U_1(t) = u(\cdot,t), U_2(t) = v(\cdot,t)$ and $U = (U_1,U_2)^{\mathrm{T}}$. Then (13) can be rewritten as an abstract differential equation in the phase space $\mathscr{C} = C([-\tau,0],X)$,

$$\dot{U}(t) = D\Delta U(t) + L(U_t) + F(U_t), \tag{14}$$

where $D = \begin{pmatrix} d_1 & \\ & d_2 \end{pmatrix}$ and $L : \mathscr{C} \to X$, $F : \mathscr{C} \to X$ are defined by

$$L(\phi) = \begin{pmatrix} (\frac{2dh}{s^2}\sqrt{(s-d)d} - a)\phi_1(0) - \frac{dh}{s^2}(2d-s)\phi_2(0) \\ 2\frac{s-d}{s}\sqrt{(s-d)d}\phi_1(-\tau) - \frac{2d}{s}(s-d)\phi_2(-\tau) \end{pmatrix}$$

and

$$F(\phi) = \begin{pmatrix} \sum_{i+j\geqslant 2} \frac{1}{i!j!} f_{ij}^{(1)}(0,0)\phi_1^i(0)\phi_2^j(0) \\ \sum_{i+j+l\geqslant 2} \frac{1}{i!j!l!} f_{ijl}^{(2)}(0,0,0)\phi_1^i(-\tau)\phi_2^j(0)\phi_2^l(-\tau) \end{pmatrix},$$

respectively, for $\phi = (\phi_1, \phi_2)^{\mathrm{T}} \in \mathscr{C}$.

Some computations show that the characteristic equation of the linearization of (14) is equivalent to the sequence of the transcendental equations

$$\lambda^2 + \left((d_1+d_2)\frac{n^2}{l^2} - p\right)\lambda + \frac{d_1 d_2 n^4}{l^4} - \frac{d_2 n^2}{l^2}p + \mathrm{e}^{-\lambda\tau}\left(k\lambda + kd_1\frac{n^2}{l^2} + r\right) = 0, \quad (15)$$

where $p = 2hd/s^2\sqrt{(s-d)d} - a$, $k = 2d/s(s-d)$, $r = 2d(s-d)/s^2(as - h\sqrt{(s-d)d})$. By (H2), we obtain $k > 0$ and $r > 0$.

If $d_1 = d_2 = 0$, then (15) is reduced to

$$\lambda^2 - p\lambda + \mathrm{e}^{-\lambda\tau}(k\lambda + r) = 0. \quad (16)$$

Obviously, $\lambda = 0$ is not the root of (16) since $r > 0$, and Bogdanov–Takens singularity does not occur at the positive equilibrium E at the absence of diffusion.

Next we consider the system with diffusion. Equation (15) with $\tau = 0$ is the following sequence of quadratic equations:

$$\lambda^2 - T_n\lambda + D_n = 0, \quad n = 0, 1, 2, \ldots, \quad (17)$$

where

$$T_n = -(d_1+d_2)\frac{n^2}{l^2} + p - k, \qquad D_n = d_1 d_2\frac{n^4}{l^4} - (d_2 p - d_1 k)\frac{n^2}{l^2} + r.$$

If $h \in (0, (as^2 + 2ds(s-d))/(2d\sqrt{(s-d)d}))$, then $p - k < 0$. And hence, from $d_2 < d_1$, it follows that $d_2 p - d_1 k < (d_2 - d_1)k \leqslant 0$. This and $r > 0$ imply that

$$T_n \leqslant p - k < 0, \quad D_n \geqslant 0 \quad \forall n \in N_0 = \{0, 1, 2, \ldots\}.$$

Thus, the roots of Eq. (17) have real parts for $h \in (0, (as^2 + 2ds(s-d))/(2d\sqrt{(s-d)d}))$.

If $h \in ((as^2 + 2ds(s-d))/(2d\sqrt{(s-d)d}), +\infty)$, then $p - k > 0$. Hence $T_0 = p - k > 0$. This implies that Eq. (17) has at least a root with positive real part.

And if $h = (as^2 + 2ds(s-d))/(2d\sqrt{(s-d)d})$, then $p - k = 0$. Hence we have

$$T_0 = 0, \quad T_n < 0 \quad \forall n \in N = \{1, 2, \ldots\},$$
$$D_n = d_1 d_2\frac{n^4}{l^4} + (d_1 - d_2)k\frac{n^2}{l^2} + r \geqslant r > 0 \quad \forall n \in N_0.$$

Thus Eq. (17) has a pair of simple purely imaginary roots, and other roots have negative real parts. Meanwhile, by $\mathrm{d}T_0(p)/(\mathrm{d}p)|_{p=k} = 1 > 0$, the transversality condition holds.

Summarizing the discussion above, we have the following conclusions.

Lemma 2. *Suppose that* (H1) *and* (H2) *are satisfied. Then the positive equilibrium* $E(u^*, v^*)$*, of system* (5) *with* $\tau = 0$ *is asymptotically stable when* $h \in (0, (as^2 + 2ds(s-d))/(2d\sqrt{(s-d)d}))$*, and unstable when* $h \in ((as^2+2ds(s-d))/(2d\sqrt{(s-d)d}), +\infty)$*. And* $h = (as^2 + 2ds(s-d))/(2d\sqrt{(s-d)d})$ *is a Hopf bifurcation value of system* (5) *with* $\tau = 0$ *and the bifurcating periodic solutions are all spatially homogeneous.*

Now we consider the effects of delay τ on the stability of the equilibrium $E(u^*, v^*)$ of system (5). We confine $h \in (0, (as^2+2ds(s-d))/(2d\sqrt{(s-d)d}))$, that is, $E(u^*, v^*)$ is stable when $\tau = 0$. It is well known that $\mathrm{i}\omega$ ($\omega > 0$) is a root of Eq. (15) if and only if ω satisfies the following equation for some $n \in N_0$:

$$-\omega^2+\left((d_1+d_2)\frac{n^2}{l^2}-p\right)\mathrm{i}\omega+d_1d_2\frac{n^4}{l^4}-\frac{d_2n^2}{l^2}p+\mathrm{e}^{-\mathrm{i}\omega\tau}\left(k\omega\mathrm{i}+d_1\frac{n^2}{l^2}k+r\right) = 0. \quad (18)$$

Separating the real and imaginary parts of Eq. (18) leads to

$$\begin{aligned} &-\omega^2 + d_1d_2\frac{n^4}{l^4} - d_2p\frac{n^2}{l^2} + \left(d_1k\frac{n^2}{l^2} + r\right)\cos\omega\tau + k\omega\sin\omega\tau = 0, \\ &\left((d_1+d_2)\frac{n^2}{l^2} - p\right)\omega + k\omega\cos\omega\tau - \left(d_1k\frac{n^2}{l^2} + r\right)\sin\omega\tau = 0, \end{aligned} \quad (19)$$

which implies that

$$\omega^4 - P_n\omega^2 + Q_n = 0, \quad n = 0, 1, 2, \ldots, \quad (20)$$

where

$$\begin{aligned} P_n &= -\left(d_1^2 + d_2^2\right)\frac{n^4}{l^4} + 2d_1p\frac{n^2}{l^2} + k^2 - p^2, \\ Q_n &= D_n\left(d_1d_2\frac{n^4}{l^4} - (d_2p + d_1k)\frac{n^2}{l^2} - r\right). \end{aligned}$$

By $Q_0 = -r^2 < 0$ and $D_n > 0$, there exists $n_0 \in \{1, 2, \ldots\}$ such that

$$Q_n < 0, \quad n \in \{0, 1, 2, \ldots, n_0 - 1\}, \quad \text{and} \quad Q_n \geqslant 0, \quad n \in \{n_0, n_0 + 1, \ldots\}.$$

If $p \in (-\infty, -k]$, then $P_n \leqslant k^2 - p^2 \leqslant 0$ for all $n \in N_0$.

If $p \in (-k, k)$, we assume further,

(H3) $-(d_1^2 + d_2^2)(n_0^4/l^4) + 2d_1p(n_0^2/l^2) + k^2 - p^2 < 0$.

By (H3), it follows that

$$P_n \leqslant -\left(d_1^2 + d_2^2\right)\frac{n_0^4}{l^4} + 2d_1p\frac{n_0^2}{l^2} + k^2 - p^2 < 0 \quad \forall n \geqslant n_0.$$

Thus Eq. (15) with $n \geqslant n_0$ have no purely imaginary roots.

And $Q_n < 0$ for all $n \in \{0, 1, 2, \dots, n_0 - 1\}$. Thus Eq. (20) has only a positive root

$$\omega_+^n = \frac{\sqrt{2}}{2}\sqrt{P_n + \sqrt{P_n^2 - 4\left[\left(d_1 d_2 \frac{n^4}{l^4} - d_2 p \frac{n^2}{l^2}\right)^2 - \left(d_1 k \frac{n^2}{l^2} + r\right)^2\right]}},$$

where $P_n = -(d_1^2 + d_2^2)(n^4/l^4) + 2d_1 p(n^2/l^2) + k^2 - p^2$.

In addition, by Eq. (19), we have

$$\sin \omega_+^n \tau = \frac{k\omega(\omega^2 - d_1 d_2 \frac{n^4}{l^4} + d_2 p \frac{n^2}{l^2}) + ((d_1 + d_2)\frac{n^2}{l^2} - p)(d_1 k \frac{n^2}{l^2} + r)\omega}{k^2\omega^2 + (d_1 k \frac{n^2}{l^2} + r)^2} \triangleq F(\omega_+^n),$$

$$\cos \omega_+^n \tau = \frac{(\omega^2 - d_1 d_2 \frac{n^4}{l^4} + d_2 p \frac{n^2}{l^2})(d_1 k \frac{n^2}{l^2} + r) - ((d_1 + d_2)\frac{n^2}{l^2} - p)k\omega^2}{k^2\omega^2 + (d_1 k \frac{n^2}{l^2} + r)^2} \triangleq E(\omega_+^n).$$

Define

$$\tau_j^n = \begin{cases} \frac{1}{\omega_+^n}(\arccos E(\omega_+^n) + 2j\pi) & \text{if } F(\omega_+^n) \geqslant 0, \\ \frac{1}{\omega_+^n}(2\pi - \arccos E(\omega_+^n) + 2j\pi) & \text{if } F(\omega_+^n) < 0. \end{cases}$$

Obviously, $\tau_0^n = \min_{j \in N_0}\{\tau_j^n\}$.

Denote

$$\tilde{\tau} = \min_{n \in \{0,1,\dots,n_0-1\}} \{\tau_0^n\}. \tag{21}$$

Let $\lambda(\tau) = \alpha(\tau) + \mathrm{i}\beta(\tau)$ be the roots of Eq. (15) near $\tau = \tau_j^n$, $n \in \{0, 1, 2, \dots, n_0 - 1\}$, satisfying $\alpha(\tau_j^n) = 0$, $\beta(\tau_j^n) = \omega_+^n$, $j = 0, 1, 2, \dots$.

Lemma 3. *The transversality condition holds, i.e.* $\mathrm{Re}(\mathrm{d}\lambda/\mathrm{d}\tau|_{\tau=\tau_j^n}) > 0$.

Proof. Differentiating the two sides of Eq. (15) with respect to τ, we obtain

$$\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1} = \frac{(2\lambda + (d_1 + d_2)\frac{n^2}{l^2} - p)\mathrm{e}^{\lambda\tau} + k}{\lambda(k\lambda + d_1 k \frac{n^2}{l^2} + r)} - \frac{\tau}{\lambda}.$$

By (19), we have

$$\begin{aligned} &\mathrm{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\bigg|_{\tau=\tau_j^n}\right)^{-1} \\ &\quad= \mathrm{Re}\,\frac{(2\mathrm{i}\omega_+^n + (d_1 + d_2)\frac{n^2}{l^2} - p)\mathrm{e}^{\mathrm{i}\omega_+^n\tau_j^n} + k - \tau_j^n(k\omega_+^n \mathrm{i} + d_1 k \frac{n^2}{l^2} + r)}{\mathrm{i}\omega_+^n(k\omega_+^n \mathrm{i} + d_1 k \frac{n^2}{l^2} + r)} \\ &\quad= \frac{-((d_1 + d_2)\frac{n^2}{l^2} - p)(k\omega_+^n \cos\omega_+^n\tau_j^n - (d_1 k \frac{n^2}{l^2} + r)\sin\omega_+^n\tau_j^n)}{(k^2(\omega_+^n)^2 + (d_1 k \frac{n^2}{l^2} + r)^2)\omega_+^n} \\ &\qquad+ \frac{2\omega_+^n(k\omega_+^n \sin\omega_+^n\tau_j^n + (d_1 k \frac{n^2}{l^2} + r)\cos\omega_+^n\tau_j^n) - k^2\omega_+^n}{(k^2(\omega_+^n)^2 + (d_1 k \frac{n^2}{l^2} + r)^2)\omega_+^n} \end{aligned}$$

$$= \frac{((d_1+d_2)\frac{n^2}{l^2}-p)^2\omega_+^n + 2\omega_+^n((\omega_+^n)^2 - d_1d_2\frac{n^4}{l^4} + d_2p\frac{n^2}{l^2}) - k^2\omega_+^n}{(k^2(\omega_+^n)^2 + (d_1k\frac{n^2}{l^2}+r)^2)\omega_+^n}$$
$$= \frac{\sqrt{\Delta}}{k^2(\omega_+^n)^2 + (d_1k\frac{n^2}{l^2}+r)^2} > 0,$$

where $\Delta = P_n^2 - 4[(d_1d_2(n^4/l^4) - d_2p(n^2/l^2))^2 - (d_1k(n^2/l^2)+r)^2]$. □

These points τ_j^n, $j = 0,1,2,\dots$, $n = 0,1,2,\dots,n_0-1$, are potential Hopf bifurcation values. But it is possible that $\tau_i^{n_1} = \tau_j^{n_2}$ for some i, j, n_1, n_2. In this case, $\pm \mathrm{i}\omega_j^n$ are not a pair of simple eigenvalues of Eq. (15) and the dimension of center manifold at the equilibrium can be at least as high as two, and we shall not consider Hopf bifurcations at such points.

Assume $\tau_i^{n_1} \neq \tau_j^{n_2}$ for all $i, j \in \{0,1,2,\dots\}$, $n_1, n_2 \in \{0,1,2,\dots,n_0-1\}$. Applying the theorem proved by Ruan and Wei [24], and combining Lemmas 2 and 3, we arrive at the following stability results.

Theorem 5. *Suppose the conditions* (H1) *and* (H2) *hold for* $p \in (-\infty, -k]$ *and* (H1)–(H3) *hold for* $p \in (-k, k)$. *And* $\tilde{\tau}$ *is given by* (21). *Then the following results are true when* $h \in (0, (as^2 + 2ds(s-d))/(2d\sqrt{(s-d)d}))$:

(i) *The positive equilibrium* $E(u^*, v^*)$ *of system* (5) *is asymptotically stable for* $\tau \in [0, \tilde{\tau})$ *and unstable for* $\tau \in (\tilde{\tau}, +\infty)$.

(ii) $\tau = \tau_j^n$, $j = 0,1,2,\dots$, $n = 0,1,2,\dots,n_0-1$, *are Hopf bifurcation values of system* (5). *Furthermore, if* $n = 0$, *these bifurcating periodic solutions are all spatially homogeneous, otherwise, these bifurcating periodic solutions are all spatially inhomogeneous.*

Remark. The characteristic equations (15) have two pairs of purely imaginary roots and the transversality condition holds for $\tau = \tau_i^{k_1} = \tau_j^{k_2}$ for some $i, j \in N_0$, $k_1, k_2 \in \{0,1,2,\dots,n_0-1\}$. Thus a double-Hopf bifurcation occurs at $E(u^*, v^*)$ when $\tau = \tau_i^{k_1} = \tau_j^{k_2}$.

3 Direction and stability of the Hopf bifurcations

In this section, we consider the stability, the direction and the period of bifurcating periodic solutions by using the normal formal theory and the center manifold theorem of partial functional differential equation presented in [25, 26] and [27]. Without loss of generality, denote any one of the these critical values τ_j^n, $j \in \{0,1,2,\dots\}$, $n \in \{0,1,2,\dots,n_0-1\}$, by τ^* at which Eq. (15) has a pair of simply purely imaginary roots $\pm \mathrm{i}\omega_+^n$, denoted by $\pm \mathrm{i}\omega$.

Let $\tau = \tau^* + \alpha$, $\alpha \in R$, $\tilde{u}(\cdot,t) = u(\cdot,\tau t)$, $\tilde{v}(\cdot,t) = v(\cdot,\tau t)$, $\tilde{U}(t) = (\tilde{u}(\cdot,t), \tilde{v}(\cdot,t))$, and drop the tildes for simplicity. Then system (14) can be written as

$$\frac{\mathrm{d}U(t)}{\mathrm{d}t} = \tau D\Delta U(t) + L(\alpha)(U_t) + f(U_t, \alpha), \tag{22}$$

in the space $\mathscr{C} = C([-1,0], X)$, where, for $\phi = (\phi_1, \phi_2) \in \mathscr{C}$,

$$
\begin{aligned}
L(\alpha)(\phi) &= (\tau^* + \alpha)\begin{pmatrix} (\frac{2dh}{s^2}\sqrt{(s-d)d} - a)\phi_1(0) - \frac{dh}{s^2}(2d-s)\phi_2(0) \\ 2\frac{s-d}{s}\sqrt{(s-d)d}\phi_1(-1) - \frac{2d}{s}(s-d)\phi_2(-1) \end{pmatrix}, \\
f(\phi,\alpha) &= (\tau^* + \alpha)\begin{pmatrix} \sum_{i+j\geqslant 2} \frac{1}{i!j!} f_{ij}^{(1)}(0,0)\phi_1^i(0)\phi_2^j(0) \\ \sum_{i+j+l\geqslant 2} \frac{1}{i!j!l!} f_{ijl}^{(2)}(0,0,0)\phi_1^i(-1)\phi_2^j(0)\phi_2^l(-1) \end{pmatrix}.
\end{aligned} \tag{23}
$$

Note that $\alpha = \tau - \tau^*$, then $\alpha = 0$ is a Hopf bifurcation value of (22).

By the Riesz representation theorem, there exists a 2×2 matrix function $\eta(\theta, \alpha)$ $(-1 \leqslant \theta \leqslant 0)$ such that

$$
-\tau D \frac{n^2}{l^2}\phi(0) + L(\alpha)(\phi) = \int_{-1}^{0} \mathrm{d}[\eta(\theta,\alpha)]\phi(\theta)
$$

for $\phi \in C([-1,0], R^2)$. In fact, we can choose

$$
\eta(\theta,\alpha) = \begin{cases} (\tau^*{+}\alpha)\begin{pmatrix} -d_1\frac{n^2}{l^2} + \frac{2dh}{s^2}\sqrt{(s{-}d)d} - a & -\frac{dh}{s^2}(2d{-}s) \\ 0 & -d_2\frac{n^2}{l^2} \end{pmatrix}, & \theta = 0, \\ 0, & \theta \in (-1,0), \\ (\tau^*{+}\alpha)\begin{pmatrix} 0 & 0 \\ -2\frac{s-d}{s}\sqrt{(s{-}d)d} & \frac{2d}{s}(s{-}d) \end{pmatrix}, & \theta = -1. \end{cases}
$$

For $\phi \in C^1([-1,0], R^2),\ \psi \in C([0,1], R^2)$, define A_1 and A_1^* as

$$
A_1\bigl(\phi(\theta)\bigr) = \begin{cases} \frac{d\phi(\theta)}{d\theta}, & \theta \in [-1,0), \\ \int_{-1}^{0} d\eta(\theta,0)\phi(\theta), & \theta = 0, \end{cases}
$$

$$
A_1^*\bigl(\psi(s)\bigr) = \begin{cases} -\frac{d\psi(s)}{ds}, & s \in (0,1], \\ \int_{-1}^{0} d\eta(\theta,0)\psi(-\theta), & s = 0. \end{cases}
$$

Then A_1^* is the formal adjoint of A_1 [27, 28] under the bilinear pairing

$$
(\psi,\phi)_0 = \overline{\psi}(0)\phi(0) + \tau^* \int_{-1}^{0} \overline{\psi}(\xi+1)\begin{pmatrix} 0 & 0 \\ 2\frac{s-d}{s}\sqrt{(s{-}d)d} & -\frac{2d}{s}(s{-}d) \end{pmatrix}\phi(\xi)\,\mathrm{d}\xi. \tag{24}
$$

It can be verified that $q(\theta) = (1,\xi)^{\mathrm{T}}\mathrm{e}^{\mathrm{i}\omega\tau^*\theta}$, $\theta \in [-1,0]$ is an eigenvector of A_1 corresponding to $\mathrm{i}\omega\tau^*$, and $q^*(s) = r(1,\eta)\mathrm{e}^{\mathrm{i}\omega\tau^* s}$, $s \in [0,1]$, is an eigenvector of A_1^*

corresponding to $-\mathrm{i}\omega\tau^*$, where

$$\xi = \frac{s^2}{dh(s-2d)}\left(\frac{d_1 n^2}{l^2} - \frac{2dh}{s^2}\sqrt{(s-d)d} + a + \mathrm{i}\omega\right),$$
$$\eta = \frac{s\mathrm{e}^{-\mathrm{i}\omega\tau^*}}{2(s-d)\sqrt{(s-d)d}}\left(\frac{d_1 n^2}{l^2} - \frac{2dh}{s^2}\sqrt{(s-d)d} + a - \mathrm{i}\omega\right),$$
$$\bar{r} = \left\{1 + \xi\bar{\eta} + \tau^*\left(\frac{2(s-d)}{s}\sqrt{(s-d)d} - \frac{2d}{s}(s-d)\xi\right)\bar{\eta}\mathrm{e}^{-\mathrm{i}\omega\tau^*}\right\}^{-1}.$$

Then $P = \operatorname{span}\{q(\theta), \bar{q}(\theta)\}$ and $P^* = \operatorname{span}\{q^*(s), \overline{q^*}(s)\}$ are the center subspace of system, see [25].

In addition, $f_n \triangleq (\beta_n^1, \beta_n^2)$, where $\beta_n^1 = \binom{\cos\frac{nx}{l}}{0}$, $\beta_n^2 = \binom{0}{\cos\frac{nx}{l}}$. Let $c \cdot f_n = c_1\beta_n^1 + c_2\beta_n^2$ for $c = (c_1, c_2)^{\mathrm{T}} \in C([-1,0], X)$.

Let $\langle\cdot,\cdot\rangle$ be the complex-valued L^2 inner product on Hilbert space X_C, defined as

$$\langle U_1, U_2\rangle = \frac{1}{l\pi}\int_0^{l\pi} u_1\bar{v_1}\,\mathrm{d}x + \frac{1}{l\pi}\int_0^{l\pi} u_2\bar{v_2}\,\mathrm{d}x \tag{25}$$

for $U_1 = (u_1, u_2)^{\mathrm{T}}$, $U_2 = (v_1, v_2)^{\mathrm{T}} \in X_C$. And $\langle\beta_0^1, \beta_0^1\rangle = 1$, $\langle\beta_n^1, \beta_n^1\rangle = 1/2$, $n = 1, 2, \dots,$

$$\langle\phi, f_n\rangle = \left(\langle\phi, \beta_n^1\rangle, \langle\phi, \beta_n^2\rangle\right)^{\mathrm{T}}, \quad \text{where } \phi \in C\left([-1,0], X\right). \tag{26}$$

Then the center subspace of linear equation of (22) with $\alpha = 0$ is given by $P_{CN}\mathscr{C}$, where

$$P_{CN}\mathscr{C}(\phi) = \Phi\left(\Psi, \langle\phi, f_n\rangle\right)\cdot f_n, \qquad P_{CN}\mathscr{C} = \left\{\left(q(\theta)z + \bar{q}(\theta)\bar{z}\right)\cdot f_n,\ z \in C\right\}. \tag{27}$$

Following the algorithms in Hassard [27], the solutions of (22) at $\alpha = 0$ are as follows:

$$U_t = \left(q(\theta)z(t) + \bar{q}(\theta)\bar{z}(t)\right)\cdot f_n + W\left(z(t), \bar{z}(t), \theta\right), \tag{28}$$

where

$$W(z, \bar{z}) \triangleq W\left(z(t), \bar{z}(t), \theta\right) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots. \tag{29}$$

Moreover, at $\tau = \tau^*$, $\dot{z} = \mathrm{i}\omega\tau^* z + g(z, \bar{z})$, where

$$g(z, \bar{z}) = \overline{q^*}(0)\left\langle f(U_t, 0), f_n\right\rangle = g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + \cdots. \tag{30}$$

Notice that $\int_0^{l\pi}\cos^3(nx/l)\,\mathrm{d}x = 0$, $1/(l\pi)\int_0^{l\pi}\cos^4(nx/l)\,\mathrm{d}x = 3/8$, $n = 1, 2, \dots,$ and combine $\overline{q^*}(0) = \bar r(1, \bar\eta)$ and (23), (25), (26), (28) and (30), we have

$$g_{20} = \begin{cases} 0, & n = 1, 2, \dots, \\ \tau^* \bar r \{ f_{20}^{(1)} + f_{02}^{(1)} \xi^2 + 2 f_{11}^{(1)} \xi + \bar\eta [(f_{200}^{(2)} + f_{002}^{(2)} \xi^2) \mathrm{e}^{-2\mathrm{i}\omega\tau^*} \\ \quad + f_{020}^{(2)} \xi^2 + 2(f_{110}^{(2)} \xi + f_{011}^{(2)} \xi^2) \mathrm{e}^{-\mathrm{i}\omega\tau^*} + 2 f_{101}^{(2)} \xi \mathrm{e}^{-2\mathrm{i}\omega\tau^*}] \}, & n = 0, \end{cases}$$

$$g_{11} = \begin{cases} 0, & n = 1, 2, \dots, \\ \tau^* \bar r \{ f_{20}^{(1)} + f_{02}^{(1)} |\xi|^2 + 2 f_{11}^{(1)} \operatorname{Re} \xi + \bar\eta [f_{200}^{(2)} + (f_{020}^{(2)} + f_{002}^{(2)}) |\xi|^2 \\ \quad + 2 f_{110}^{(2)} \operatorname{Re}(\xi \mathrm{e}^{\mathrm{i}\omega\tau^*}) + 2 f_{101}^{(2)} \operatorname{Re} \xi + 2 f_{011}^{(2)} |\xi|^2 \cos \omega\tau^*] \}, & n = 0, \end{cases}$$

$$g_{02} = \overline{g_{20}},$$

$$\begin{aligned}
g_{21} &= \frac{\tau^* \bar r}{l\pi} \Bigg\{ \big(f_{03}^{(1)} \xi^2 \bar\xi + f_{30}^{(1)} + f_{12}^{(1)} \big(\xi^2 + 2|\xi|^2 \big) + f_{21}^{(1)} (2\xi + \bar\xi) \big) \int_0^{l\pi} \cos^4 \frac{nx}{l} \, \mathrm{d}x \\
&+ 2 \int_0^{l\pi} \bigg[f_{20}^{(1)} \bigg(W_{11}^{(1)}(0) + \frac{1}{2} W_{20}^{(1)}(0) \bigg) + f_{02}^{(1)} \bigg(\xi W_{11}^{(2)}(0) + \frac{1}{2} \bar\xi W_{20}^{(2)}(0) \bigg) \bigg] \cos^2 \frac{nx}{l} \, \mathrm{d}x \\
&+ 2 \int_0^{l\pi} \bigg[f_{11}^{(1)} \bigg(W_{11}^{(2)}(0) + \frac{1}{2} W_{20}^{(2)}(0) + \frac{1}{2} \bar\xi W_{20}^{(1)}(0) + \xi W_{11}^{(1)}(0) \bigg) \bigg] \cos^2 \frac{nx}{l} \, \mathrm{d}x \\
&+ \bar\eta \big[\big(f_{300}^{(2)} + f_{003}^{(2)} \xi^2 \bar\xi \big) \mathrm{e}^{-\mathrm{i}\omega\tau^*} + f_{030}^{(2)} \xi^2 \bar\xi + f_{120}^{(2)} \big(2|\xi|^2 \mathrm{e}^{-\mathrm{i}\omega\tau^*} + \xi^2 \mathrm{e}^{\mathrm{i}\omega\tau^*} \big) \\
&+ f_{102}^{(2)} \mathrm{e}^{-\mathrm{i}\omega\tau^*} \big(2|\xi|^2 + \xi^2 \big) + f_{012}^{(2)} \xi^2 \bar\xi \big(2 + \mathrm{e}^{-2\mathrm{i}\omega\tau^*} \big) + f_{021}^{(2)} \xi^2 \bar\xi \big(2\mathrm{e}^{-\mathrm{i}\omega\tau^*} + \mathrm{e}^{\mathrm{i}\omega\tau^*} \big) \\
&+ f_{201}^{(2)} \big(2\xi + \bar\xi \big) \mathrm{e}^{-\mathrm{i}\omega\tau^*} + f_{210}^{(2)} \big(2\xi + \bar\xi \mathrm{e}^{-2\mathrm{i}\omega\tau^*} \big) \\
&+ f_{111}^{(2)} \big(2|\xi|^2 \big(1 + \mathrm{e}^{-2\mathrm{i}\omega\tau^*} \big) + 2\xi^2 \big) \big] \int_0^{l\pi} \cos^4 \frac{nx}{l} \, \mathrm{d}x \\
&+ 2 \int_0^{l\pi} \bigg[f_{110}^{(2)} \bigg(\mathrm{e}^{-\mathrm{i}\omega\tau^*} W_{11}^{(2)}(0) + \frac{1}{2} \mathrm{e}^{\mathrm{i}\omega\tau^*} W_{20}^{(2)}(0) + \frac{1}{2} \bar\xi W_{20}^{(1)}(-1) \bigg) \bigg] \cos^2 \frac{nx}{l} \, \mathrm{d}x \\
&+ 2 \int_0^{l\pi} \bigg[f_{101}^{(2)} \bigg(\frac{1}{2} \mathrm{e}^{\mathrm{i}\omega\tau^*} \big(W_{20}^{(2)}(-1) + \bar\xi W_{20}^{(1)}(-1) \big) + \xi \mathrm{e}^{-\mathrm{i}\omega\tau^*} W_{11}^{(1)}(-1) \bigg) \bigg] \cos^2 \frac{nx}{l} \, \mathrm{d}x \\
&+ 2 \int_0^{l\pi} \bigg[f_{011}^{(2)} \big(\xi W_{11}^{(2)}(-1) + \frac{1}{2} \bar\xi \big(W_{20}^{(2)}(-1) + \mathrm{e}^{\mathrm{i}\omega\tau^*} W_{20}^{(2)}(0) \big) \big) \bigg] \cos^2 \frac{nx}{l} \, \mathrm{d}x \\
&+ 2 \int_0^{l\pi} \bigg[f_{200}^{(2)} \bigg(\mathrm{e}^{-\mathrm{i}\omega\tau^*} W_{11}^{(1)}(-1) + \frac{1}{2} \mathrm{e}^{\mathrm{i}\omega\tau^*} W_{20}^{(1)}(-1) \bigg) \bigg] \cos^2 \frac{nx}{l} \, \mathrm{d}x
\end{aligned}$$

$$+2\int_0^{l\pi} f_{020}^{(2)}\left(\xi W_{11}^{(2)}(0)+\frac{1}{2}\bar{\xi}W_{20}^{(2)}(0)\right)\cos^2\frac{nx}{l}\,\mathrm{d}x$$
$$+2\int_0^{l\pi}\left[f_{110}^{(2)}\xi W_{11}^{(1)}(-1)+f_{101}^{(2)}\mathrm{e}^{-\mathrm{i}\omega\tau^*}W_{11}^{(2)}(-1)+f_{011}^{(2)}\xi\mathrm{e}^{-\mathrm{i}\omega\tau^*}W_{11}^{(2)}(0)\right]\cos^2\frac{nx}{l}\,\mathrm{d}x$$
$$+2\int_0^{l\pi}\left[f_{002}^{(2)}\left(\xi\mathrm{e}^{-\mathrm{i}\omega\tau^*}W_{11}^{(2)}(-1)+\frac{1}{2}\bar{\xi}\mathrm{e}^{\mathrm{i}\omega\tau^*}W_{20}^{(2)}(-1)\right)\right]\cos^2\frac{nx}{l}\,\mathrm{d}x\Bigg\},$$

$n=0,1,2,\ldots.$ Since $W_{20}(\theta)$ and $W_{11}(\theta)$ are in g_{21}, we need to compute them. By Wu [25], $W(z,\bar{z})$ satisfies

$$\dot{W}=A_UW+H(z,\bar{z}), \tag{31}$$

where

$$\begin{aligned}A_UW&=A_UW_{20}(\theta)\frac{z^2}{2}+A_UW_{11}(\theta)z\bar{z}+A_UW_{02}(\theta)\frac{\bar{z}^2}{2}+\cdots,\\ H(z,\bar{z})&=H_{20}\frac{z^2}{2}+H_{11}z\bar{z}+H_{02}\frac{\bar{z}^2}{2}+\cdots\\ &=X_0f(U_t,0)-\Phi\big(\Psi,\langle X_0f(U_t,0),f_n\rangle\big)\cdot f_n.\end{aligned} \tag{32}$$

Thus, from (31), (32), we can obtain that

$$W_{20}=\big(2\mathrm{i}\omega\tau^*-A_U\big)^{-1}H_{20},\qquad W_{11}=-A_U^{-1}H_{11}. \tag{33}$$

From (32) we know that for $-1\leqslant\theta<0$,

$$H(z,\bar{z})=-\big(q(\theta)g_{20}+\bar{q}(\theta)\overline{g_{02}}\big)\cos\frac{nx}{l}\frac{z^2}{2}-\big(q(\theta)g_{11}+\bar{q}(\theta)\overline{g_{11}}\big)\cos\frac{nx}{l}z\bar{z}+\cdots.$$

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

$$H_{20}(\theta)=\begin{cases}0,\\ -g_{20}q(\theta)-\overline{g_{02}}\bar{q}(\theta),\end{cases}\qquad H_{11}(\theta)=\begin{cases}0, & n=1,2,\ldots,\\ -g_{11}q(\theta)-\overline{g_{11}}\bar{q}(\theta), & n=0,\end{cases}$$

and $H(z,\bar{z})(0)=f(U_t,0)-\Phi(\Psi,\langle f(U_t,0),f_n\rangle)\cdot f_n$.

$$H_{20}(0)=\begin{cases}\tau^*\begin{pmatrix}f_{20}^{(1)}+f_{02}^{(1)}\xi^2+2f_{11}^{(1)}\xi\\ (f_{200}^{(2)}+f_{002}^{(2)}\xi^2)\mathrm{e}^{-2\mathrm{i}\omega\tau^*}+f_{020}^{(2)}\xi^2\\ \quad+2(f_{110}^{(2)}\xi+f_{011}^{(2)}\xi^2)\mathrm{e}^{-\mathrm{i}\omega\tau^*}+2f_{101}^{(2)}\xi\mathrm{e}^{-2\mathrm{i}\omega\tau^*}\end{pmatrix}\\ \quad-g_{20}q(0)-\overline{g_{02}}\bar{q}(0), & n=0,\\ \tau^*\begin{pmatrix}f_{20}^{(1)}+f_{02}^{(1)}\xi^2+2f_{11}^{(1)}\xi\\ (f_{200}^{(2)}+f_{002}^{(2)}\xi^2)\mathrm{e}^{-2\mathrm{i}\omega\tau^*}+f_{020}^{(2)}\xi^2\\ \quad+2(f_{110}^{(2)}\xi+f_{011}^{(2)}\xi^2)\mathrm{e}^{-\mathrm{i}\omega\tau^*}+2f_{101}^{(2)}\xi\mathrm{e}^{-2\mathrm{i}\omega\tau^*}\end{pmatrix}\cos^2\frac{nx}{l}, & n=1,2,\ldots,\end{cases}$$

$$H_{11}(0) = \begin{cases} \tau^* \begin{pmatrix} f_{20}^{(1)} + f_{02}^{(1)}|\xi|^2 + 2f_{11}^{(1)} \operatorname{Re}\xi \\ f_{200}^{(2)} + (f_{020}^{(2)} + f_{002}^{(2)})|\xi|^2 + 2f_{110}^{(2)} \operatorname{Re}(\xi e^{i\omega\tau^*}) \\ +2f_{101}^{(2)} \operatorname{Re}\xi + 2f_{011}^{(2)}|\xi|^2 \cos\omega\tau^* \end{pmatrix} \\ -g_{11}q(0) - \overline{g_{11}}\bar{q}(0), & n = 0, \\ \tau^* \begin{pmatrix} f_{20}^{(1)} + f_{02}^{(1)}|\xi|^2 + 2f_{11}^{(1)} \operatorname{Re}\xi \\ f_{200}^{(2)} + (f_{020}^{(2)} + f_{002}^{(2)})|\xi|^2 + 2f_{110}^{(2)} \operatorname{Re}(\xi e^{i\omega\tau^*}) \\ +2f_{101}^{(2)} \operatorname{Re}\xi + 2f_{011}^{(2)}|\xi|^2 \cos\omega\tau^* \end{pmatrix} \cos^2 \frac{nx}{l}, & n = 1, 2, \dots. \end{cases}$$

By the definition of A_U and $q(\theta) = q(0)e^{i\omega\tau^*\theta}$, $-1 \leqslant \theta \leqslant 0$, we have

$$\begin{aligned} W_{20}(\theta) &= \left(\frac{ig_{20}}{\omega\tau^*}q(\theta) + \frac{i\overline{g_{02}}}{3\omega\tau^*}\overline{q(\theta)}\right) \cdot f_n + E_1 e^{2i\omega\tau^*\theta}, \\ W_{11}(\theta) &= \left(\frac{-ig_{11}q(\theta)}{\omega\tau^*} + \frac{i\overline{q(\theta)}\overline{g_{11}}}{\omega\tau^*}\right) \cdot f_n + E_2. \end{aligned} \tag{34}$$

By A_U again and combining (33) and (34), it follows that

$$E_1 = E_1' \begin{pmatrix} f_{20}^{(1)} + f_{02}^{(1)}\xi^2 + 2f_{11}^{(1)}\xi \\ (f_{200}^{(2)} + f_{002}^{(2)}\xi^2)e^{-2i\omega\tau^*} + f_{020}^{(2)}\xi^2 \\ +2(f_{110}^{(2)}\xi + f_{011}^{(2)}\xi^2)e^{-i\omega\tau^*} + 2f_{101}^{(2)}\xi e^{-2i\omega\tau^*} \end{pmatrix} \cos^2 \frac{nx}{l},$$

where

$$E_1' = \begin{pmatrix} 2i\omega + \frac{d_1n^2}{l^2} - \frac{2dh}{s^2}\sqrt{(s-d)d} + a & \frac{dh}{s^2}(2d - s) \\ -\frac{2(s-d)}{s}\sqrt{(s-d)d}e^{-2i\omega\tau^*} & 2i\omega + \frac{d_2n^2}{l^2} + \frac{2d}{s}(s-d)e^{-2i\omega\tau^*} \end{pmatrix}^{-1}.$$

Similar to the above, we can obtain that

$$E_2 = E_2' \begin{pmatrix} f_{20}^{(1)} + f_{02}^{(1)}|\xi|^2 + 2f_{11}^{(1)} \operatorname{Re}\xi \\ f_{200}^{(2)} + (f_{020}^{(2)} + f_{002}^{(2)})|\xi|^2 + 2f_{110}^{(2)} \operatorname{Re}(\xi e^{i\omega\tau^*}) \\ +2f_{101}^{(2)} \operatorname{Re}\xi + 2f_{011}^{(2)}|\xi|^2 \cos\omega\tau^* \end{pmatrix} \cos^2 \frac{nx}{l},$$

where

$$E_2' = \begin{pmatrix} \frac{d_1n^2}{l^2} - \frac{2dh}{s^2}\sqrt{(s-d)d} + a & \frac{dh}{s^2}(2d - s) \\ -\frac{2(s-d)}{s}\sqrt{(s-d)d} & \frac{d_2n^2}{l^2} + \frac{2d}{s}(s-d) \end{pmatrix}^{-1}.$$

So far, g_{21} can be expressed by the parameters of system (5). Thus, we can compute the following quantities:

$$c_1(0) = \frac{\mathrm{i}}{2\omega\tau^*}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2\right) + \frac{1}{2}g_{21},$$
$$\mu_2 = -\frac{\operatorname{Re}(c_1(0))}{\operatorname{Re}(\lambda'(\tau^*))}, \qquad \beta_2 = 2\operatorname{Re}(c_1(0)),$$
$$T_2 = -\frac{1}{\omega\tau^*}\bigl(\operatorname{Im}\bigl(c_1(0)\bigr) + \mu_2 \operatorname{Im}\bigl(\lambda'(\tau^*)\bigr)\bigr).$$

Combining Lemma3, we have the following results.

Theorem 6. (i) μ_2 *determines the direction 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* $\tau > \tau^*$ $(\tau < \tau^*)$;

(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 Numerical simulations

In this section, some numerical simulations for a special case of system (5) are given to support our analytical results obtained in Sections 2 and 3. As an example, we consider system (5) with $d_1 = 1$, $d_2 = 0.5$, $a = 0.5$, $s = 0.4$, $d = 0.3$, $h = 0.8$, $l = 2$, that is,

$$\begin{aligned}
&\frac{\partial u(x,t)}{\partial t} = \Delta u(x,t) + 0.5u(x,t)\bigl(1 - u(x,t)\bigr) - \frac{0.8u^2(x,t)v(x,t)}{v^2(x,t) + u^2(x,t)},\\
&\quad x \in (0, 2\pi),\ t \geqslant 0,\\
&\frac{\partial v(x,t)}{\partial t} = 0.5\Delta v(x,t) - 0.3v(x,t) + \frac{0.4u^2(x,t-\tau)v(x,t)}{v^2(x,t-\tau) + u^2(x,t-\tau)},\\
&\quad x \in (0, 2\pi),\ t \geqslant 0,\\
&u_x(0,t) = u_x(2\pi,t) = v_x(0,t) = v_x(2\pi,t) = 0, \quad t \geqslant 0,\\
&u(x,t) = 0.3 + 0.3\cos x, \quad v(x,t) = 0.2 - 0.2\cos x,\\
&\quad (x,t) \in [0, 2\pi] \times [-\tau, 0].
\end{aligned} \tag{35}$$

Obviously, $s > d$ and $h < \min(as/\sqrt{(s-d)d}, (as^2 + 2ds(s-d))/(2d\sqrt{(s-d)d}))$. Then system (35) has a unique positive constant equilibrium $E(0.3072, 0.1774)$. In addition, $p = 0.0196 \in (-k, k) = (-0.15, 0.15)$. And by the formulas as derived in Section 3, we can obtain that $\tilde{\tau} = \min_{n\in\{0,1,\dots,n_0\}}\{\tau_0^n\} = \tau_0^0 = 4.1405$, $C_1(0) \approx -17.0709 - 9.1476\mathrm{i}$. By Theorem 5, we obtain that the positive equilibrium $E(0.3072, 0.1774)$ is asymptotically stable for $\tau \in [0, 4.1405)$ as illustrated in Fig. 1. When τ crosses through the critical value 4.1405, the equilibrium $E(0.3072, 0.1774)$

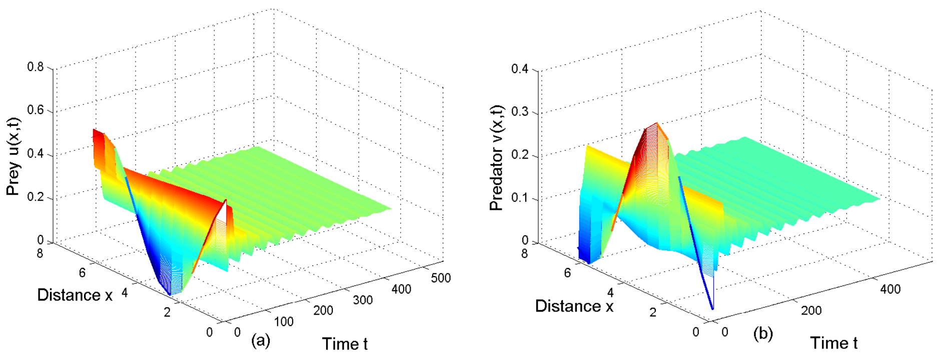

Fig. 1. The positive equilibrium $E(0.3072, 0.1774)$ is asymptotically stable, where $\tau = 3.8 < \tilde{\tau} = 4.1405$.

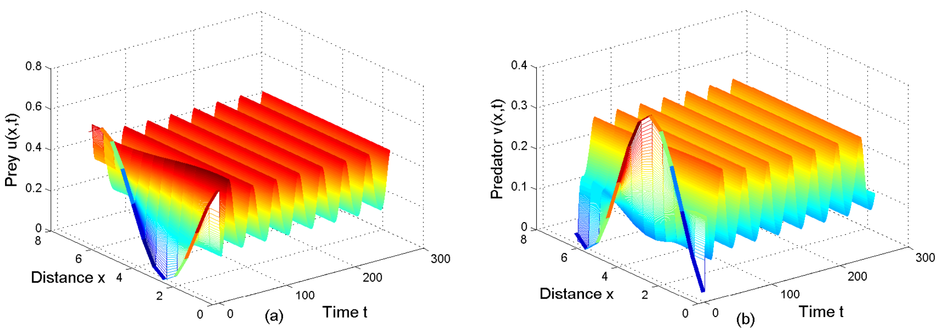

Fig. 2. The periodic solutions bifurcating from the equilibrium are stable, where $\tau = 5 > \tilde{\tau} = 4.1405$.

loses its stability and a family of homogeneous periodic solutions bifurcate from the positive constant steady state. The direction of Hopf bifurcations is forward and the periodic solutions are stable since $\mu_2 = -\mathrm{Re}(C_1(0))/\mathrm{Re}(\lambda'(\tilde{\tau})) \approx 657.967 > 0$, $\beta_2 = 2\,\mathrm{Re}(C_1(0)) \approx -34.1419 < 0$, which are depicted in Fig. 2. And the period increases with the increase of delay since $T_2 \approx 14.6813 > 0$.

5 Conclusion

The dynamics of the diffusive Holling-III ratio-dependent predator-prey system with delay effect are investigated under the Neumann boundary conditions. The global stability and instability of the boundary equilibrium are obtained by the maximum principle and comparison principle of the parabolic equations. It shows that, the diffusion and delay have no effects on the stability of the boundary equilibrium and have effect on the positive coexistence. In particular, the system without delay is dissipative and uniformly persistent. We hope that our work could be instructive to study the population.

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