## Research Article

# Stability and Hopf Bifurcation in a Diffusive Predator-Prey System with Beddington-DeAngelis Functional Response and Time Delay 

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This paper is concerned with a diffusive predator-prey system with Beddington-DeAngelis functional response and delay effect. By analyzing the distribution of the eigenvalues, the stability of the positive equilibrium and the existence of spatially homogeneous and spatially inhomogeneous periodic solutions are investigated. Also, it is shown that the small diffusion can affect the Hopf bifurcations. Finally, the direction and stability of Hopf bifurcations are determined by normal form theory and center manifold reduction for partial functional differential equations.

## 1. Introduction

In this paper, we will study the stability and Hopf bifurcations of a diffusive predator-prey system with Beddington-DeAngelis functional response and delay effect as follows:

$$
\begin{gather*}
u_{t}=d_{1} \Delta u(t, x)+u(t, x)(1-u(t-\tau, x))-s P(u, v), \quad t>0, x \in \Omega, \\
v_{t}=d_{2} \Delta v(t, x)+r P(u, v)-d v(t, x), \quad t>0, x \in \Omega  \tag{1.1}\\
\partial_{v} u=\partial_{v} v=0, \quad t>0, x \in \partial \Omega, \\
u(0, x)=u_{0}(x) \geq 0, \quad v(0, x)=v_{0}(x) \geq 0, \quad x \in \Omega,
\end{gather*}
$$

where $u$ and $v$ denote the population densities of prey and predator species at time $t$ and space $x$, respectively; the positive constants $d_{1}$ and $d_{2}$ represent the diffusion coefficients of prey and predator species, respectively; $s>0$ ( $s$ is called the capturing rate) and $r>0$ ( $r$ is
called the conversion rate) represent the strength of the relative effect of the interaction on the two species; $d$ denotes the death rate of predator species; $P(u, v)=u v /(m+u+n v)$ is the Beddington-DeAngelis functional response function with $m$ and $n$ are positive numbers; $\tau \geq 0$ denotes the generation time of the prey species; $\Omega$ is a bounded domain in $R^{N}$ ( $N$ is any positive integer) with a smooth boundary $\partial \Omega ; \Delta$ is the Laplacian operator on $\Omega ; v$ is the outward normal to $\partial \Omega$; homogeneous Neumann boundary conditions reflect the situation where the population cannot move across the boundary of the domain.

System (1.1) includes the models which have been discussed by many researchers; for examples, when $\tau=0$, the models were considered in [1, 2]; if $d_{1}=d_{2}=0$ and $\tau=0$, it was discussed in [3]; if $P(u, v)=1$, it was discussed in [4]. Moreover, when $\tau=0$ and $P(u, v)=u^{2} v /\left(1+u^{2}\right)$, system (1.1) can be transformed into Narcisa Apreutesei's model (see [5]).

There has been an increasing interest in the study of diffusive predator-prey system (see $[1,2,4,6-14]$ and references therein) with functional response. As is known to all, the Beddington-DeAngelis functional response, proposed by Beddington [6] and DeAngelis et al. [8], is more general than those the above authors considered, and it has been studied extensively in the literature [1-3, 7, 14-16]. However, to the authors' best knowledge, few researches have been done on the diffusive predator-prey system with BeddingtonDeAngelis functional response and time delay.

The aim of this paper is to extend and develop the work in [1, 2]; that is, we will study the stability and Hopf bifurcation of a diffusive predator-prey system with BeddingtonDeAngelis functional response and delay. The system we consider here is more general than the system in $[1,2]$.

The rest of the paper is organized as follows. In Section 2, we analyze the distribution of the roots of the characteristic equation and give various conditions on the stability of a positive constant steady state and the existence of Hopf bifurcation. In Section 3, we discuss the effect of diffusion on the Hopf bifurcation. In Section 4, by applying the normal form theory and the center manifold reduction of partial functional differential equations by Wu [17], an explicit algorithm for determining the direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions is given.

## 2. Analysis of the Characteristic Equations

In this section, by choosing the delay $\tau$ as the bifurcation parameter and analyzing the associated characteristic equation of (1.1) at the positive constant steady state, we investigate the stability of the positive constant steady state of (1.1) and obtain the conditions under which (1.1) undergoes Hopf bifurcation.

It can be seen that homogeneous Neumann boundary conditions imposed on (1.1) lead to $E_{1}(0,0)$ and $E_{2}(1,0)$, always being two boundary equilibria for any feasible parameters, and (1.1) always having a unique positive constant steady state $E\left(u^{*}, v^{*}\right)$ provided that the condition
(A1) $0<d<\left(r u^{*} /\left(u^{*}+m\right)\right)$, hold, where

$$
\begin{equation*}
u^{*}=\frac{-(s r-n r-s d)+\sqrt{(s r-n r-s d)^{2}+4 s m n d r}}{2 r n}, \quad v^{*}=\frac{(r-d) u^{*}-d m}{d n} . \tag{2.1}
\end{equation*}
$$

Under (A1), let $\bar{u}=u-u^{*}, \bar{v}=v-v^{*}$ and drop the bars for simplicity of notations, then (1.1) can be transformed into the following equivalent system:

$$
\begin{gather*}
u_{t}=d_{1} \Delta u(t, x)+\left(u+u^{*}\right)\left(1-\left(u(t-\tau, x)+u^{*}\right)\right)-\frac{s\left(u+u^{*}\right)\left(v+v^{*}\right)}{m+\left(u+u^{*}\right)+n\left(v+v^{*}\right)} \\
v_{t}=d_{2} \Delta v(t, x)+\frac{r\left(u+u^{*}\right)\left(v+v^{*}\right)}{m+\left(u+u^{*}\right)+n\left(v+v^{*}\right)}-d\left(v+v^{*}\right) \tag{2.2}
\end{gather*}
$$

Let $P(u, v)=u v /(m+u+n v)$. By $u^{*}\left(1-u^{*}\right)-\left(s u^{*} v^{*} /\left(m+u^{*}+n v^{*}\right)\right)=0$ and $-d v^{*}+$ $\left(r u^{*} v^{*} /\left(m+u^{*}+n v^{*}\right)\right)=0$ (2.2) becomes

$$
\begin{gather*}
u_{t}=d_{1} \Delta u(t, x)+\left(1-u^{*}-a_{1}\right) u(t)-u^{*} u(t-\tau, x)-a_{2} v-u u(t-\tau, x)-f(u, v), \\
v_{t}=d_{2} \Delta v(t, x)+b_{1} u(t)+\left(b_{2}-d\right) v(t)+g(u, v) \tag{2.3}
\end{gather*}
$$

where $a_{1}=s P_{10}\left(u^{*}, v^{*}\right), a_{2}=s P_{01}\left(u^{*}, v^{*}\right), b_{1}=r P_{10}\left(u^{*}, v^{*}\right), b_{2}=r P_{01}\left(u^{*}, v^{*}\right)$, and

$$
\begin{equation*}
f(u, v)=s \sum_{i+j=2}^{3} \frac{P_{i j}}{i!j!} u^{i} v^{j}+\text { h.o.t., } \quad g(u, v)=r \sum_{i+j=2}^{3} \frac{P_{i j}}{i!j!} u^{i} v^{j}+\text { h.o.t., } \tag{2.4}
\end{equation*}
$$

where $\partial^{i+j} P(u, v) /\left.\partial u^{i} \partial v^{j}\right|_{(u, v)=\left(u^{*}, v^{*}\right)}$ denoted by $P_{i j}$ and h.o.t. for shorthand of "higher order terms."

Denote $u_{1}(t)=u(t, \cdot), u_{2}(t)=v(t, \cdot)$, and $U=\left(u_{1}, u_{2}\right)^{T}$. Then (2.3) can be transformed into an abstract differential equation in the phase space $\ell=C([-\tau, 0], X)$,

$$
\begin{equation*}
\dot{U}(t)=D \Delta U(t)+L\left(U_{t}\right)+F\left(U_{t}\right) \tag{2.5}
\end{equation*}
$$

with

$$
\begin{align*}
D & =\left(\begin{array}{cc}
d_{1} & 0 \\
0 & d_{2}
\end{array}\right), \quad L(\phi)=\left(\begin{array}{cc}
1-u^{*}-a_{1} & -a_{2} \\
b_{1} & b_{2}-d
\end{array}\right)\binom{\phi_{1}(0)}{\phi_{2}(0)}+\left(\begin{array}{cc}
-u^{*} & 0 \\
0 & 0
\end{array}\right)\binom{\phi_{1}(-\tau)}{\phi_{2}(-\tau)}, \\
F(\phi) & =\binom{-\phi_{1}(0) \phi_{1}(-\tau)-s \sum_{i+j=2}^{3} \frac{P_{i j}}{i!j!} \phi_{1}^{i}(0) \phi_{2}^{j}(0)}{r \sum_{i+j=2}^{3} \frac{P_{i j}}{i!j!} \phi_{1}^{i}(0) \phi_{2}^{j}(0)}, \tag{2.6}
\end{align*}
$$

where $\phi=\left(\phi_{1}, \phi_{2}\right)^{T} \in \ell$.
The linearization of (2.5) is given by

$$
\begin{equation*}
\dot{U}(t)=D \Delta U(t)+L\left(U_{t}\right) \tag{2.7}
\end{equation*}
$$

and its characteristic equation is

$$
\begin{equation*}
\lambda y-D \Delta y-L\left(e^{\lambda} y\right)=0 \tag{2.8}
\end{equation*}
$$

where $y \in \operatorname{dom}(\Delta)$ and $y \neq 0, \operatorname{dom}(\Delta) \subset X$.
From the properties of the Laplacian operator defined on the bounded domain, the operator $\Delta$ on $X$ has the eigenvalues $-k^{2}$ with the relative eigenfunctions

$$
\begin{equation*}
\beta_{k}^{1}=\binom{\gamma_{k}}{0}, \quad \beta_{k}^{2}=\binom{0}{\gamma_{k}} \tag{2.9}
\end{equation*}
$$

where $\gamma_{k}=\cos k x, k \in N_{0}=\{0,1,2, \ldots\}$. Clearly, $\left(\beta_{k^{\prime}}^{1} \beta_{k}^{2}\right)_{k=0}^{\infty}$ construct a basis of the phase space $X$ and therefore any element $y$ in $X$ can be expanded as Fourier series in the following form:

$$
\begin{equation*}
y=\sum_{k=0}^{\infty}\left(\left\langle y, \beta_{k}^{1}\right\rangle \beta_{k}^{1}+\left\langle y, \beta_{k}^{2}\right\rangle \beta_{k}^{2}\right)=\sum_{k=0}^{\infty}\left(\beta_{k}^{1}, \beta_{k}^{2}\right)\binom{\left\langle y, \beta_{k}^{1}\right\rangle}{\left\langle y, \beta_{k}^{2}\right\rangle} \tag{2.10}
\end{equation*}
$$

Some simple computations show that

$$
\begin{equation*}
L\left(\phi^{T}\binom{\beta_{k}^{1}}{\beta_{k}^{2}}\right)=L(\phi)^{T}\binom{\beta_{k}^{1}}{\beta_{k}^{2}}, \quad k \in N_{0} . \tag{2.11}
\end{equation*}
$$

From (2.10)-(2.11), (2.8) is equivalent to

$$
\sum_{k=0}^{\infty}\left(\left\langle y, \beta_{k}^{1}\right\rangle,\left\langle y, \beta_{k}^{2}\right\rangle\right)\left[\left(\lambda I_{2}+D k^{2}\right)-\left(\begin{array}{cc}
-u^{*} e^{-\lambda \tau}+1-u^{*}-a_{1} & -a_{2}  \tag{2.12}\\
b_{1} & b_{2}-d
\end{array}\right)\right]\binom{\beta_{k}^{1}}{\beta_{k}^{2}}=0
$$

Assume that
(A2) $1-u^{*}-a_{1}<0, b_{2}-d<0$.
Let $-a_{3}=1-u^{*}-a_{1},-b_{3}=b_{2}-d, p=a_{3}+b_{3}, r=a_{3} b_{3}+a_{2} b_{1}, s=u^{*}, q=b_{3} u^{*}$, then we conclude that the characteristic equation (2.8) is equivalent to the sequence of the characteristic equations:

$$
\begin{equation*}
\lambda^{2}+\left(d_{1} k^{2}+d_{2} k^{2}+p\right) \lambda+d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r+\left(s \lambda+d_{2} s k^{2}+q\right) e^{-\lambda \tau}=0 \tag{2.13}
\end{equation*}
$$

Obviously, for all $k \in N_{0}, \lambda=0$ is not a root of (2.13).
Equation (2.13) with $\tau=0$ is equivalent to the following quadratic equations:

$$
\begin{equation*}
\lambda^{2}+\left(d_{1} k^{2}+d_{2} k^{2}+p+s\right) \lambda+d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r+d_{2} s k^{2}+q=0 \tag{2.14}
\end{equation*}
$$

Let $\lambda_{1}$ and $\lambda_{2}$ be the two roots of (2.14). Then, for all $k \in N_{0}$,

$$
\begin{gather*}
\lambda_{1}+\lambda_{2}=-\left(d_{1} k^{2}+d_{2} k^{2}+p+s\right)<0  \tag{2.15}\\
\lambda_{1} \lambda_{2}=d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r+d_{2} s k^{2}+q>0
\end{gather*}
$$

Therefore, we have the following Lemma.
Lemma 2.1. Assume that (A1) and (A2) hold. Then the equilibrium $E\left(u^{*}, v^{*}\right)$ of (1.1) with $\tau=0$ is asymptotically stable.

Assume that

$$
(A 3) s^{2}-p^{2}+2 r<0, r>q \text {; }
$$

(A4) $b_{3} d_{1}+a_{3} d_{2}-d_{2} s \geq 0$, or $\left(b_{3} d_{1}+a_{3} d_{2}-d_{2} s\right)^{2}<4 d_{1} d_{2}(r-q)$, if $b_{3} d_{1}+a_{3} d_{2}-d_{2} s<0$.
Theorem 2.2. If (A1)-(A4) hold, then all roots of (2.13) have negative real parts for all $\tau \geq 0$. Furthermore, the equilibrium $E\left(u^{*}, v^{*}\right)$ of the system (1.1) is asymptotically stable for all $\tau \geq 0$.

Proof. Let $\lambda=i \omega(\omega>0)$ be a root of the characteristic equation (2.13). Then $\omega$ satisfies the following equation for some $k \in N_{0}$ :

$$
\begin{align*}
& -\omega^{2}+\left(d_{1} k^{2}+d_{2} k^{2}+p\right) i \omega+d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2} \\
& \quad+a_{3} d_{2} k^{2}+r+\left(s \omega i+d_{2} s k^{2}+q\right)(\cos \omega \tau-i \sin \omega \tau)=0 \tag{2.16}
\end{align*}
$$

Separating the real and imaginary parts of (2.16) leads to

$$
\begin{gather*}
-\omega^{2}+d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r+s \omega \sin \omega \tau+\left(d_{2} s k^{2}+q\right) \cos \omega \tau=0  \tag{2.17}\\
\left(d_{1} k^{2}+d_{2} k^{2}+p\right) \omega+s \omega \cos \omega \tau-\left(d_{2} s k^{2}+q\right) \sin \omega \tau=0
\end{gather*}
$$

which implies that

$$
\begin{align*}
\omega^{4}+ & {\left[\left(d_{1}^{2}+d_{2}^{2}\right) k^{4}+2 a_{3} d_{1} k^{2}+2 b_{3} d_{2} k^{2}-\left(s^{2}-p^{2}+2 r\right)\right] \omega^{2} } \\
& +\left[\left(d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r\right)^{2}-\left(d_{2} s k^{2}+q\right)^{2}\right]=0 \tag{2.18}
\end{align*}
$$

Let $z=\omega^{2}$, then (2.18) can be rewritten into the following form:

$$
\begin{align*}
z^{2}+ & {\left[\left(d_{1}^{2}+d_{2}^{2}\right) k^{4}+2 a_{3} d_{1} k^{2}+2 b_{3} d_{2} k^{2}-\left(s^{2}-p^{2}+2 r\right)\right] z } \\
& +\left[\left(d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r\right)^{2}-\left(d_{2} s k^{2}+q\right)^{2}\right]=0 \tag{2.19}
\end{align*}
$$

By (A3) and (A4), for all $k \in N_{0}$, we have

$$
\begin{gather*}
-\left(d_{1}^{2}+d_{2}^{2}\right) k^{4}-2 a_{3} d_{1} k^{2}-2 b_{3} d_{2} k^{2}+\left(s^{2}-p^{2}+2 r\right)<0,  \tag{2.20}\\
d_{1} d_{2} k^{4}+\left(b_{3} d_{1}+a_{3} d_{2}-d_{2} s\right) k^{2}+r-q>0,
\end{gather*}
$$

which imply that (2.19) has no positive roots. Hence, the characteristic equation (2.13) has no purely imaginary roots. By Lemma 2.1 and the theorem proved by Ruan and Wei [18], all roots of (2.13) have negative real parts.

Notice that (2.13) with $k=0$ is the characteristic equation of the linearization of (1.1) corresponding system without diffusion (ordinary differential equations, ODEs) at the positive equilibrium. And it has been considered under the condition:
(B1) $r<q$.
It is easy to get that when

$$
\begin{equation*}
\tau=\tau_{j}^{0}=\frac{1}{\omega_{+}^{0}} \arccos \left\{\frac{\left(q\left(\left(\omega_{+}^{0}\right)^{2}-r\right)-p s\left(\omega_{+}^{0}\right)^{2}\right)}{s^{2}\left(\omega_{+}^{0}\right)^{2}+q^{2}}+2 j \pi\right\}, \quad(j=0,1,2, \ldots), \tag{2.21}
\end{equation*}
$$

Equation (2.13) with $k=0$ has simple imaginary roots $\pm i \omega_{+}^{0}$, and $\operatorname{Re}(d \lambda / d \tau)_{\tau=\tau_{j}^{0}}>0$, where $\lambda(\tau)$ is the root of (2.13) with $k=0$ satisfying $\lambda\left(\tau_{j}^{0}\right)=i \omega_{+}^{0}$ and

$$
\begin{equation*}
\omega_{+}^{0}=\frac{\sqrt{2}}{2}\left[s^{2}-p^{2}+2 r+\sqrt{\left(s^{2}-p^{2}+2 r\right)^{2}-4\left(r^{2}-q^{2}\right)}\right]^{1 / 2}, \tag{2.22}
\end{equation*}
$$

and $\tau_{0}^{0}=\min \left\{\tau_{j}^{0}, j \in\{0,1,2, \ldots\}\right\}$. Assume that
(B2) $d_{1}^{2}+d_{2}^{2}+2 a_{3} d_{1}+2 b_{3} d_{2}>s^{2}-p^{2}+2 r, d_{1} d_{2}+b_{3} d_{1}+a_{3} d_{2}-d_{2} s+r-q>0$.
We have the following result.
Theorem 2.3. Assume that (A1), (A2), (B1), and (B2) are satisfied. Then for $\tau=\tau_{j}^{0}(j=0,1,2, \ldots)$, (2.13) has a pair of simple imaginary roots $\pm i \omega_{+}^{0}$, and all roots of (2.13), except $\pm i \omega_{+}^{0}$, have no zero real parts. Moreover, all the roots of (2.13) with $\tau=\tau_{j}^{0}$, except $\pm i \omega_{+}^{0}$, have negative real parts.

Proof. Let $\lambda=i \omega_{1}\left(\omega_{1}>0\right)$ be a root of (2.13) with $k \geq 1$. By the same way in Theorem 2.2, we can obtain

$$
\begin{align*}
\omega_{1}^{4}+ & {\left[\left(d_{1}^{2}+d_{2}^{2}\right) k^{4}+2 a_{3} d_{1} k^{2}+2 b_{3} d_{2} k^{2}-\left(s^{2}-p^{2}+2 r\right)\right] \omega_{1}^{2} } \\
& +\left[\left(d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r\right)^{2}-\left(d_{2} s k^{2}+q\right)^{2}\right]=0, \tag{2.23}
\end{align*}
$$

for all $k \geq 1$.

Set $z=\omega_{1}^{2}$, then

$$
\begin{align*}
z^{2} & +\left[\left(d_{1}^{2}+d_{2}^{2}\right) k^{4}+2 a_{3} d_{1} k^{2}+2 b_{3} d_{2} k^{2}-\left(s^{2}-p^{2}+2 r\right)\right] z \\
& +\left[\left(d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r\right)^{2}-\left(d_{2} s k^{2}+q\right)^{2}\right]=0 \tag{2.24}
\end{align*}
$$

Let $z_{1}$ and $z_{2}$ be the roots of (2.24) with $k \geq 1$. We know that if $z_{1}+z_{2}<0$ and $z_{1} z_{2}>0$, then (2.13) with $k \geq 1$ has no purely imaginary roots.

By (B2), it follows that, for $\forall k \geq 1$,

$$
\begin{align*}
& -\left(d_{1}^{2}+d_{2}^{2}\right) k^{4}-2 a_{3} d_{1} k^{2}-2 b_{3} d_{2} k^{2}+\left(s^{2}-p^{2}+2 r\right) \\
& \quad \leq-\left(d_{1}^{2}+d_{2}^{2}+2 a_{3} d_{1}+2 b_{3} d_{2}\right)+\left(s^{2}-p^{2}+2 r\right)<0  \tag{2.25}\\
& d_{1} d_{2} k^{4}+\left(b_{3} d_{1}+a_{3} d_{2}-d_{2} s\right) k^{2}+r-q \geq d_{1} d_{2}+b_{3} d_{1}+a_{3} d_{2}-d_{2} s+r-q>0
\end{align*}
$$

Therefore, (2.13) with $k \geq 1$ have no purely imaginary roots.
Summarizing the above results and combining Theorem 2.3, we have the following theorem on the stability of the positive equilibrium $E\left(u^{*}, v^{*}\right)$ of system (1.1) and the existence of Hopf bifurcation at $E\left(u^{*}, v^{*}\right)$.

Theorem 2.4. Assume that (A1), (A2), (B1), and (B2) hold. For system (1.1), the following statements are true:
(I) If $\tau \in\left[0, \tau_{0}^{0}\right)$, then the equilibrium point $E\left(u^{*}, v^{*}\right)$ is asymptotically stable;
(II) If $\tau>\tau_{0}^{0}$, then the equilibrium point $E\left(u^{*}, v^{*}\right)$ is unstable;
(III) $\tau=\tau_{j}^{0}(j=0,1,2, \ldots)$ are Hopf bifurcation values of system (1.1), and these Hopf bifurcations are all spatially homogeneous.

By the same way in Theorem 2.2, let $\lambda=i \omega(\omega>0)$ be a root of the characteristic equation (2.13), then $\omega$ satisfies the following equation:

$$
\begin{align*}
& \omega^{4}+\left[\left(d_{1}^{2}+d_{2}^{2}\right) k^{4}+2 a_{3} d_{1} k^{2}+2 b_{3} d_{2} k^{2}-\left(s^{2}-p^{2}+2 r\right)\right] \omega^{2} \\
& \quad+\left[\left(d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r\right)^{2}-\left(d_{2} s k^{2}+q\right)^{2}\right]=0 \tag{2.26}
\end{align*}
$$

for $k \in N_{0}$.
Now, we make the following assumptions. For a certain $k_{0}=\{1,2, \ldots\}$,
(C1) $d_{1} d_{2}+b_{3} d_{1}+a_{3} d_{2}-d_{2} s+r-q>0$;
(C2) $\left(\left(s^{2}-p^{2}+2 r\right) / k_{0}^{2}\right)<d_{1}^{2}+d_{2}^{2}+2 a_{3} d_{1}+2 b_{3} d_{2}<s^{2}-p^{2}+2 r$;
(C3) $\left[\left(d_{1}^{2}+d_{2}^{2}\right) k^{4}+2 a_{3} d_{1} k^{2}+2 b_{3} d_{2} k^{2}-\left(s^{2}-p^{2}+2 r\right)\right]^{2},-4\left[\left(d_{1} d_{2}^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r\right)^{2}-\right.$ $\left.\left(d_{2} s^{2}+q\right)^{2}\right] \geq 0, k \in N_{0} \backslash\left\{k_{0}\right\}$.

Under the assumptions (C1) and (C2), (2.26) with $k=k_{0}$ has only a positive solution $\omega_{+}^{k_{0}}$,

$$
\begin{equation*}
\omega_{+}^{k_{0}}=\frac{\sqrt{2}}{2} \sqrt{B+\sqrt{B^{2}-4\left[\left(d_{1} d_{2} k_{0}^{4}+a_{3} d_{2} k_{0}^{2}+b_{3} d_{1} k_{0}^{2}+r\right)^{2}-\left(d_{2} k_{0}^{2} s+q\right)^{2}\right]}} \tag{2.27}
\end{equation*}
$$

where $B=s^{2}-p^{2}+2 r-\left(d_{1}^{2}+d_{2}^{2}\right) k_{0}^{4}-2 a_{3} d_{1} k_{0}^{2}-2 b_{3} d_{2} k_{0}^{2}<0$.
Set $z=\omega^{2}$, then (2.26) can be transformed into the following equation:

$$
\begin{align*}
z^{2}+ & {\left[\left(d_{1}^{2}+d_{2}^{2}\right) k^{4}+2 a_{3} d_{1} k^{2}+2 b_{3} d_{2} k^{2}-\left(s^{2}-p^{2}+2 r\right)\right] z } \\
& +\left[\left(d_{1} d_{2} k^{4}+b_{3} d_{1} k^{2}+a_{3} d_{2} k^{2}+r\right)^{2}-\left(d_{2} s k^{2}+q\right)^{2}\right]=0 \tag{2.28}
\end{align*}
$$

Let $z_{1}$ and $z_{2}$ be the roots of (2.28). If the assumptions (C1)-(C3) hold, we have

$$
\begin{gather*}
z_{1}+z_{2}=-\left(d_{1}^{2}+d_{2}^{2}\right) k^{4}-2 a_{3} d_{1} k^{2}-2 b_{3} d_{2} k^{2}+\left(s^{2}-p^{2}+2 r\right) \leq s^{2}-p^{2}+2 r<0  \tag{2.29}\\
z_{1} z_{2}=\left(d_{1} d_{2} k^{4}+a_{3} d_{2} k^{2}+b_{3} d_{1} k^{2}+r\right)^{2}-\left(d_{2} k^{2} s+q\right)^{2}>0
\end{gather*}
$$

for $k \in N_{0} \backslash\left\{k_{0}\right\}$.
Therefore, (2.13) with $k \in N_{0} \backslash\left\{k_{0}\right\}$ has no solutions with zero real parts. In addition, similar to the proof of Theorem 2.2, we have

$$
\begin{gather*}
-\left(\omega_{+}^{k_{0}}\right)^{2}+d_{1} d_{2} k_{0}^{4}+b_{3} d_{1} k_{0}^{2}+a_{3} d_{2} k_{0}^{2}+r+s \omega_{+}^{k_{0}} \sin \omega_{+}^{k_{0}} \tau+\left(d_{2} s k_{0}^{2}+q\right) \cos \omega_{+}^{k_{0}} \tau=0  \tag{2.30}\\
\left(d_{1} k_{0}^{2}+d_{2} k_{0}^{2}+p\right) \omega_{+}^{k_{0}}+s \omega_{+}^{k_{0}} \cos \omega_{+}^{k_{0}} \tau-\left(d_{2} s k_{0}^{2}+q\right) \sin \omega_{+}^{k_{0}} \tau=0
\end{gather*}
$$

which implies that

$$
\begin{aligned}
\sin \left(\omega_{+}^{k_{0}} \tau\right)= & \frac{\left[\left(\omega_{+}^{k_{0}}\right)^{2}-d_{1} d_{2} k_{0}^{4}-b_{3} d_{1} k_{0}^{2}-a_{3} d_{2} k_{0}^{2}-r\right] s \omega_{+}^{k_{0}}}{\left(d_{2} s k_{0}^{2}+q\right)^{2}+s^{2}\left(\omega_{+}^{k_{0}}\right)^{2}} \\
& +\frac{\left(d_{1} k_{0}^{2}+d_{2} k_{0}^{2}+p\right)\left(d_{2} s k_{0}^{2}+q\right) \omega_{+}^{k_{0}}}{\left(d_{2} s k_{0}^{2}+q\right)^{2}+s^{2}\left(\omega_{+}^{k_{0}}\right)^{2}} \triangleq F\left(\omega_{+}^{k_{0}}\right)
\end{aligned}
$$

$$
\begin{align*}
\cos \left(\omega_{+}^{k_{0}} \tau\right)= & \frac{\left[\left(\omega_{+}^{k_{0}}\right)^{2}-d_{1} d_{2} k_{0}^{4}-b_{3} d_{1} k_{0}^{2}-a_{3} d_{2} k_{0}^{2}-r\right]\left(d_{2} s k_{0}^{2}+q\right)}{\left(d_{2} s k_{0}^{2}+q\right)^{2}+s^{2}\left(\omega_{+}^{k_{0}}\right)^{2}} \\
& -\frac{\left(d_{1} k_{0}^{2}+d_{2} k_{0}^{2}+p\right) s\left(\omega_{+}^{k_{0}}\right)^{2}}{\left(d_{2} s k_{0}^{2}+q\right)^{2}+s^{2}\left(\omega_{+}^{k_{0}}\right)^{2}} \triangleq E\left(\omega_{+}^{k_{0}}\right) . \tag{2.31}
\end{align*}
$$

Define

$$
\tau_{j}^{k_{0}}=\left\{\begin{array}{ll}
\frac{1}{\omega_{+}^{k_{0}}}\left(\arccos \left(E\left(\omega_{+}^{k_{0}}\right)\right)+2 j \pi\right) & \text { if } F\left(\omega_{+}^{k_{0}}\right) \geq 0,  \tag{2.32}\\
\frac{1}{\omega_{+}^{k_{0}}}\left(2 \pi-\arccos \left(E\left(\omega_{+}^{k_{0}}\right)\right)+2 j \pi\right) & \text { if } F\left(\omega_{+}^{k_{0}}\right)<0,
\end{array} \text { for } j \in\{0,1,2, \ldots\}\right.
$$

From the above analysis, we have the following Theorem.
Theorem 2.5. Assume that (A1), (A2), and (C1)-(C3) hold. Then for $\tau=\tau_{j}^{k_{0}}(j=0,1,2, \cdots)$, (2.13) has a pair of simple imaginary roots $\pm i \omega_{+}^{k_{0}}$, and all roots of (2.13), except $\pm i \omega_{+}^{k_{0}}$, have no zero real parts. Moreover, all the roots of (2.13) with $\tau=\tau_{j}^{k_{0}}$, except $\pm i \omega_{+}^{k_{0}}$, have negative real parts.

Let $\lambda(\tau)=\alpha(\tau)+i \beta(\tau)$ be the root of (2.13) near $\tau=\tau_{j}^{k_{0}}$ satisfying

$$
\begin{equation*}
\alpha\left(\tau_{j}^{k_{0}}\right)=0, \quad \beta\left(\tau_{j}^{k_{0}}\right)=\omega_{+}^{k_{0}}, \quad j=0,1,2, \ldots, \tag{2.33}
\end{equation*}
$$

where $\omega_{+}^{k_{0}}$ and $\tau_{j}^{k_{0}}$ are given by (2.27) and (2.32), respectively. Then we have the following transversality condition.

Lemma 2.6. Assume that (A1), (A2), and (C1)-(C3) hold. Then

$$
\begin{equation*}
\left\{\operatorname{Re}\left(\frac{d \lambda}{d \tau}\right)\right\}_{\tau=\tau_{j}^{k_{0}}}>0 \tag{2.34}
\end{equation*}
$$

Proof. Differentiating the two sides of (2.13) with respect to $\tau$ yields

$$
\begin{equation*}
\left(\frac{d \lambda}{d \tau}\right)^{-1}=\frac{\left(2 \lambda+d_{1} k_{0}^{2}+d_{2} k_{0}^{2}+p\right) e^{\lambda \tau}+s}{s \lambda^{2}+s \lambda d_{2} k_{0}^{2}+\lambda q}-\frac{\tau}{\lambda} . \tag{2.35}
\end{equation*}
$$

From (2.30), we have

$$
\begin{align*}
\operatorname{Re}\left(\frac{d \lambda}{d \tau}\right)_{\tau=\tau_{j}^{k_{0}}}^{-1} & =\operatorname{Re}\left[\frac{\left(2 \lambda+d_{1} k_{0}^{2}+d_{2} k_{0}^{2}+p\right) e^{\lambda \tau}+s}{s \lambda^{2}+s \lambda d_{2} k_{0}^{2}+\lambda q}-\frac{\tau}{\lambda}\right]_{\tau=\tau_{j}^{k_{0}}} \\
& =\frac{2\left(\omega_{+}^{k_{0}}\right)^{2}-s^{2}+p^{2}-2 r+\left(d_{1}^{2}+d_{2}^{2}\right) k_{0}^{4}+2 a_{3} d_{1} k_{0}^{2}+2 b_{3} d_{2} k_{0}^{2}}{s^{2}\left(\omega_{+}^{k_{0}}\right)^{2}+\left(s d_{2} k_{0}^{2}+q\right)^{2}}  \tag{2.36}\\
& =\frac{2\left(\omega_{+}^{k_{0}}\right)^{2}-B}{s^{2}\left(\omega_{+}^{k_{0}}\right)^{2}+\left(s d_{2} k_{0}^{2}+q\right)^{2}}
\end{align*}
$$

according to (2.27), and then

$$
\begin{equation*}
\left\{\operatorname{Re}\left(\frac{d \lambda}{d \tau}\right)\right\}_{\tau=\tau_{j}^{k_{0}}}=\left\{\operatorname{Re}\left(\frac{d \lambda}{d \tau}\right)^{-1}\right\}_{\tau=\tau_{j}^{k_{0}}}>0 \tag{2.37}
\end{equation*}
$$

Applying Lemma 2.6 and Theorem 2.5, we draw the following conclusions.
Theorem 2.7. Assume that (A1), (A2), and (C1)-(C3) hold. For system (1.1), the following statements are true:
(I) If $\tau \in\left[0, \tau_{0}^{k_{0}}\right)$, then the equilibrium point $E\left(u^{*}, v^{*}\right)$ is asymptotically stable;
(II) If $\tau>\tau_{0}^{k_{0}}$, then the equilibrium point $E\left(u^{*}, v^{*}\right)$ is unstable;
(III) $\tau=\tau_{j}^{k_{0}}(j=0,1,2, \ldots)$ are Hopf bifurcation values of system (1.1), and these Hopf bifurcations are all spatially inhomogeneous.

## 3. The Effect of Diffusion on Hopf Bifurcations

In the previous section, we have studied the Hopf bifurcations from the positive constant steady-state $E\left(u^{*}, v^{*}\right)$ of (1.1) when $\tau$ crosses through the critical value $\tau_{j}^{k}\left(k=0, k_{0} ; j=\right.$ $1,2,3, \ldots)$ and have the following conclusions.
(I) If (B2) holds, then system (1.1) and the corresponding system without diffusion (ODEs) have the same Hopf bifurcations, containing the existence and properties of Hopf bifurcations. In this case, the diffusion has no effect on the Hopf bifurcations of ODEs.
(II) If (B2) does not hold, then system (1.1) and ODEs have the different Hopf bifurcations. In this case, the diffusion has the effect on the Hopf bifurcations of ODEs.

According to Theorems 2.4 and 2.7, system (1.1) undergoes Hopf bifurcations under the different conditions. Comparing the conditions of Theorems 2.4 and 2.7, we have the following conclusions.
(I) When system (1.1) undergoes spatially homogeneous Hopf bifurcation, diffusion coefficients satisfy the condition:

$$
\begin{equation*}
d_{1}^{2}+d_{2}^{2}+2 a_{3} d_{1}+2 b_{3} d_{2}>s^{2}-p^{2}+2 r \tag{3.1}
\end{equation*}
$$

and in this case, system (1.1) and ODEs have the same properties of Hopf bifurcation.
(II) When system (1.1) undergoes spatially inhomogeneous Hopf bifurcation, diffusion coefficients satisfy the condition

$$
\begin{equation*}
d_{1}^{2}+d_{2}^{2}+2 a_{3} d_{1}+2 b_{3} d_{2}<s^{2}-p^{2}+2 r \tag{3.2}
\end{equation*}
$$

and in this case, system (1.1) and ODEs have the different properties of Hopf bifurcation.
Summarizing the above results, we can obtain the conclusion. The big diffusion has no effect on the Hopf bifurcation of system (1.1), the small diffusion can make system (1.1) undergo the spatially inhomogeneous Hopf bifurcation.

## 4. Direction of Hopf Bifurcation and Stability of the Bifurcating Periodic Orbits

In this section, we will study the directions, stability, and the period of bifurcating periodic solutions by using normal formal theory and center manifold theorem of partial functional differential equations presented in [17]. For fixed $j \in\{0,1,2, \ldots\}$, we denote $\tau_{j}^{k}$ by $\tilde{\tau}$. Let

$$
\begin{align*}
\tilde{u}(t, x) & =u(\tau t, x), \quad \tilde{v}(t, x)=v(\tau t, x), \quad \tau=\mu+\tau_{k}, \\
u_{1}(t) & =u(t, \cdot), \quad u_{2}(t)=v(t, \cdot), \quad U=\left(u_{1}, u_{2}\right)^{T}, \tag{4.1}
\end{align*}
$$

and drop the tilde for the sake of simplicity. Then system (1.1) can be written as

$$
\begin{equation*}
\dot{U}(t)=\tilde{\tau} D \Delta U(t)+L(\tilde{\tau})\left(U_{t}\right)+f\left(U_{t}, \mu\right) \tag{4.2}
\end{equation*}
$$

where $D=\left(\begin{array}{cc}d_{1} & 0 \\ 0 & d_{2}\end{array}\right), L(\mu)(\cdot): \ell \rightarrow X$, and $f: \ell \times R \rightarrow X$ are given, respectively, by

$$
\begin{gather*}
L(\mu)(\phi)=(\mu+\tilde{\tau})\left(\left(\begin{array}{cc}
1-u^{*}-a_{1} & -a_{2} \\
b_{1} & b_{2}-d
\end{array}\right)\binom{\phi_{1}(0)}{\phi_{2}(0)}+\left(\begin{array}{cc}
-u^{*} & 0 \\
0 & 0
\end{array}\right)\binom{\phi_{1}(-1)}{\phi_{2}(-1)}\right)  \tag{4.3}\\
f(\phi, \mu)=(\mu+\tilde{\tau})\binom{-\phi_{1}(0) \phi_{1}(-1)-s \sum_{i+j=2}^{3} \frac{P_{i j}}{i!j!} \phi_{1}^{i}(0) \phi_{2}^{j}(0)}{r \sum_{i+j=2}^{3} \frac{P_{i j}}{i!j!} \phi_{1}^{i}(0) \phi_{2}^{j}(0)}+\text { h.o.t., } \tag{4.4}
\end{gather*}
$$

for $\phi=\left(\phi_{1}, \phi_{2}\right)^{T} \in \ell$, where h.o.t. denotes high order terms.

Consider the linear equation

$$
\begin{equation*}
\dot{U}(t)=\tilde{\tau} D \Delta U(t)+L(\tilde{\tau})\left(U_{t}\right) \tag{4.5}
\end{equation*}
$$

From the discussion of Theorems 2.3 and 2.5 in Section 2, we know that the origin $(0,0)$ is an equilibrium of (4.2), and for $\tau=\tilde{\tau}$, the characteristic equation of (4.5) has a pair of simple purely imaginary eigenvalues $\bigwedge_{0}=\left\{i \omega_{+}^{k} \tilde{\tau},-i \omega_{+}^{k} \tilde{\tau}\right\},\left(k=0, k_{0}\right)$.

Consider the ordinary functional differential equation

$$
\begin{equation*}
\dot{X}(t)=-\tilde{\tau} D k^{2} X(t)+L(\tilde{\tau})\left(X_{t}\right) \tag{4.6}
\end{equation*}
$$

By the Riesz representation theorem, there exists a $2 \times 2$ matrix function $\eta(\theta, \tilde{\tau})(-1 \leq \theta \leq 0)$, whose entry is of bounded variation such that

$$
\begin{equation*}
-\widetilde{\tau} D k^{2} \phi(0)+L(\widetilde{\tau})(\phi)=\int_{-1}^{0} d[\eta(\theta, \widetilde{\tau})] \phi(\theta) \tag{4.7}
\end{equation*}
$$

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

$$
\eta(\theta, \tilde{\tau})= \begin{cases}\tilde{\tau}\left(\begin{array}{cc}
-d_{1} k^{2}+1-u^{*}-a_{1} & -a_{2} \\
b_{1} & -d_{2} k^{2}+b_{2}-d
\end{array}\right), & \theta=0  \tag{4.8}\\
0, & \theta \in(-1,0) \\
\tilde{\tau}\left(\begin{array}{cc}
-u^{*} & 0 \\
0 & 0
\end{array}\right), & \theta=-1\end{cases}
$$

Let $A(\tilde{\tau})$ denote the infinitesimal generators of the semigroup induced by the solutions of (4.6) and $A^{*}$ be the formal adjoint of $A(\tilde{\tau})$ under the bilinear pairing

$$
\begin{equation*}
(\psi, \phi)=\psi(0) \phi(0)-\int_{-1}^{0} \int_{\xi=0}^{\theta} \psi(\xi-\theta) d[\eta(\theta, \tilde{\tau})] \phi(\xi) d \xi \tag{4.9}
\end{equation*}
$$

for $\phi \in C\left([-1,0], R^{2}\right), \psi \in\left(C[0,1], R^{2}\right)$. Then $A(\widetilde{\tau})$ and $A^{*}$ are a pair of adjoint operators. From the discussion in Section 2, we know that $A(\widetilde{\tau})$ has a pair of simple purely imaginary eigenvalues $\pm i \omega_{+}^{k} \tilde{\tau}$, and they are also eigenvalues of $A^{*}$. Let $P$ and $Q$ be the center subspaces, that is, the generalized eigenspace of $A(\widetilde{\tau})$ and $A^{*}$ associated with $\Lambda_{0}$, respectively. Then $Q$ is the adjoint space of $P$ and $\operatorname{dim} P=\operatorname{dim} Q=2$, see [17].

Direct computations give the following results.

Lemma 4.1. Let

$$
\begin{equation*}
C=-\frac{i \omega_{+}^{k}+d_{1} k^{2}-1+u^{*}+a_{1}+u^{*} e^{-i \omega_{+}^{k} \tilde{\tau}}}{a_{2}}, \quad D=\frac{-i \omega_{+}^{k}+d_{1} k^{2}-1+u^{*}+a_{1}+u^{*} e^{-i \omega_{+}^{k} \tilde{\tau}}}{b_{1}} \tag{4.10}
\end{equation*}
$$

Then,

$$
\begin{equation*}
p_{1}(\theta)=e^{i \omega_{+}^{k} \tilde{\tau}}(1, C)^{T}, \quad p_{2}(\theta)=\overline{p_{1}(\theta)}, \quad-1 \leq \theta \leq 0 \tag{4.11}
\end{equation*}
$$

is a basis of $P$ with $\bigwedge_{0}$, and

$$
\begin{equation*}
q_{1}(s)=(1, D) e^{-i \omega_{+}^{k} \tilde{\tau}}, \quad q_{2}(s)=\overline{q_{1}(s)}, \quad 0 \leq s \leq 1 \tag{4.12}
\end{equation*}
$$

is a basis of $Q$ with $\wedge_{0}$.
Let $\Phi=\left(\Phi_{1}, \Phi_{2}\right)$ and $\Psi^{*}=\left(\Psi_{1}^{*}, \Psi_{2}^{*}\right)^{T}$ with

$$
\begin{align*}
& \Phi_{1}(\theta)=\frac{p_{1}(\theta)+p_{2}(\theta)}{2}=\binom{\operatorname{Re}\left\{e^{i \omega_{+}^{k} \tilde{\tau}} \theta\right\}}{\operatorname{Re}\left\{C e^{i \omega_{+}^{k} \tilde{\tau}} \theta\right\}} \\
& \Phi_{2}(\theta)=\frac{p_{1}(\theta)-p_{2}(\theta)}{2 i}=\binom{\operatorname{Im}\left\{e^{i \omega_{+}^{k} \tilde{\tau}} \theta\right\}}{\operatorname{Im}\left\{C e^{i \omega_{+}^{k} \tilde{\tau}} \theta\right\}}, \tag{4.13}
\end{align*}
$$

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

$$
\begin{align*}
& \Psi_{1}^{*}(s)=\frac{q_{1}(s)+q_{2}(s)}{2}=\binom{\operatorname{Re}\left\{e^{-i \omega_{+}^{k} \tau_{k}} \theta\right\}}{\operatorname{Re}\left\{D e^{-i \omega_{+}^{k} \tilde{\tau}} \theta\right\}},  \tag{4.14}\\
& \Psi_{2}^{*}(s)=\frac{q_{1}(s)-q_{2}(s)}{2 i}=\binom{\operatorname{Im}\left\{e^{-i \omega_{+}^{k} \tilde{\tau}} \theta\right\}}{\operatorname{Im}\left\{D e^{-i \omega_{+}^{k} \tilde{\tau}} \theta\right\}},
\end{align*}
$$

for $s \in[0,1]$.
Define

$$
\Psi=\left(\Psi_{1}, \Psi_{2}\right)^{T}=\left(\begin{array}{ll}
\left(\Psi_{1}^{*}, \Phi_{1}\right) & \left(\Psi_{1}^{*}, \Phi_{2}\right)  \tag{4.15}\\
\left(\Psi_{2}^{*}, \Phi_{1}\right) & \left(\Psi_{2}^{*}, \Phi_{2}\right)
\end{array}\right)^{-1} \Psi^{*}
$$

then $\Psi$ construct a new basis for $Q$ and $(\Psi, \Phi)=I_{2}$, see [17]. In addition, $f_{k} \triangleq\left(\beta_{k^{\prime}}^{1} \beta_{k}^{2}\right)$, where

$$
\begin{equation*}
\beta_{k}^{1}=\binom{\cos k x}{0}, \quad \beta_{k}^{1}=\binom{0}{\cos k x} \tag{4.16}
\end{equation*}
$$

Let $c \cdot f_{k}$ be defined by $c \cdot f_{k}=c_{1} \beta_{k}^{1}+c_{2} \beta_{k^{\prime}}^{2} c=\left(c_{1}, c_{2}\right)^{T} \in C([-1,0], X)$.
Then the center subspace of linear equation (4.5) is given by $P_{\mathrm{CN}} \ell$, where

$$
\begin{equation*}
P_{\mathrm{CN}} \ell(\phi)=\Phi\left(\Psi,\left\langle\phi, f_{k}\right\rangle\right) \cdot f_{k}, \quad \phi \in \ell \tag{4.17}
\end{equation*}
$$

and $\ell=P_{\mathrm{CN}} \ell \oplus P_{s} \ell$, and $P_{s} \ell$ denotes the complement subspace of $P_{\mathrm{CN}} \ell$ in $\ell$.
Let $A_{\tilde{\tau}}$ be the infinitesimal generator induced by the solution of (4.5). Then (4.2) can be rewritten as the abstract form

$$
\begin{equation*}
\dot{U}_{t}=A_{\tilde{\tau}} U_{t}+R\left(\mu, U_{t}\right) \tag{4.18}
\end{equation*}
$$

where

$$
R\left(\mu, U_{t}\right)= \begin{cases}0, & \theta \in[-1,0)  \tag{4.19}\\ F\left(U_{t}, \mu\right), & \theta=0\end{cases}
$$

Using the decomposition $\ell=P_{\mathrm{CN}} \ell \oplus P_{s} \ell$ and (4.17), the solution of (4.2) can be written as

$$
\begin{equation*}
U_{t}=\Phi\binom{x_{1}(t)}{x_{2}(t)} \cdot f_{k}+h\left(x_{1}, x_{2}, \mu\right) \tag{4.20}
\end{equation*}
$$

where $\binom{x_{1}(t)}{x_{2}(t)}=\left(\Psi,\left\langle U_{t}, f_{k}\right\rangle\right)$, and $h\left(x_{1}, x_{2}, \mu\right) \in P_{s} \ell, h(0,0,0)=0, D h(0,0,0)=0$. In particular, the solution of (4.2) on the center manifold is given by

$$
\begin{equation*}
U_{t}=\Phi\binom{x_{1}(t)}{x_{2}(t)} \cdot f_{k}+h\left(x_{1}, x_{2}, 0\right) \tag{4.21}
\end{equation*}
$$

Let $z=x_{1}-i x_{2}$ and $\Psi(0)=\left(\Psi_{1}(0), \Psi_{2}(0)\right)^{T}$, and notice that $p_{1}=\Phi_{1}+i \Phi_{2}$, then

$$
\begin{equation*}
\Phi\binom{x_{1}(t)}{x_{2}(t)} \cdot f_{k}=\left(\Phi_{1}, \Phi_{2}\right)\binom{\frac{z+\bar{z}}{2}}{\frac{i(z-\bar{z})}{2}} \cdot f_{k}=\frac{1}{2}\left(p_{1} z+\bar{p}_{1} \bar{z}\right) \cdot f_{k} \tag{4.22}
\end{equation*}
$$

Equation (4.21) can be transformed into

$$
\begin{equation*}
U_{t}=\frac{1}{2}\left(p_{1} z+\bar{p}_{1} \bar{z}\right) \cdot f_{k}+W(z, \bar{z}) \tag{4.23}
\end{equation*}
$$

where $W(z, \bar{z})=h(((z+\bar{z}) / 2),(i(z-\bar{z}) / 2), 0)$. Moreover, by [17], $z$ satisfies

$$
\begin{equation*}
\dot{z}=i \omega_{+}^{k} \tilde{\tau} z+g(z, \bar{z}) \tag{4.24}
\end{equation*}
$$

where

$$
\begin{equation*}
g(z, \bar{z})=\left(\Psi_{1}(0)-i \Psi_{2}(0)\right)\left\langle f\left(U_{t}, 0\right), f_{k}\right\rangle \tag{4.25}
\end{equation*}
$$

Let

$$
\begin{gather*}
W(z, \bar{z})=W_{20} \frac{z^{2}}{2}+W_{11} z \bar{z}+W_{02} \frac{\bar{z}^{2}}{2}+\text { h.o.t., }  \tag{4.26}\\
g(z, \bar{z})=g_{20} \frac{z^{2}}{2}+g_{11} z \bar{z}+g_{02} \frac{\bar{z}^{2}}{2}+g_{21} \frac{z^{2} \bar{z}}{2}+\text { h.o.t. } \tag{4.27}
\end{gather*}
$$

From (4.4) and (4.23), it follows that

$$
\begin{aligned}
& \left\langle f\left(U_{t}, 0\right), f_{k}\right\rangle \\
& =\frac{\tilde{\tau}}{2}\binom{-e^{-i \omega_{+}^{k} \tilde{\tau}}-s P_{11} C-\frac{s P_{20}}{2}-\frac{s P_{02} C^{2}}{2}}{r P_{11} C+\frac{r P_{20}}{2}+\frac{r P_{02} C^{2}}{2}} \frac{1}{\pi} \int_{0}^{\pi} \cos ^{3} k x d x \frac{z^{2}}{2} \\
& \quad+\frac{\tilde{\tau}}{4}\binom{-2 \cos \omega_{+}^{k} \tilde{\tau}-s P_{11}(C+\bar{C})-s P_{20}-s P_{02} C \bar{C}}{r P_{11}(C+\bar{C})+r P_{20}+r P_{02} C \bar{C}} \frac{1}{\pi} \int_{0}^{\pi} \cos ^{3} k x d x z \bar{z} \\
& \\
& +\frac{\tilde{\tau}}{2}\binom{-e^{i \omega_{+}^{k} \tilde{\tau}}-s P_{11} \bar{C}-\frac{s P_{20}}{2}-\frac{s P_{02} \bar{C}^{2}}{2}}{r P_{11} \bar{C}+\frac{r P_{20}}{2}+\frac{r P_{02} \bar{C}^{2}}{2}} \frac{1}{\pi} \int_{0}^{\pi} \cos ^{3} k x d x \frac{\bar{z}^{2}}{2}
\end{aligned}
$$

$$
\begin{align*}
& \times \frac{z^{2} \bar{z}}{2}+\text { h.o.t., } \tag{4.28}
\end{align*}
$$

where $\left\langle W_{i j}^{(n)}(\theta), \cos k x\right\rangle=1 / \pi \int_{0}^{\pi} W_{i j}^{(n)}(\theta)(x) \cos k x d x, i+j=2, n=1,2$.
Notice that $\int_{0}^{\pi} \cos ^{3} k x d x=0$, for all $k \in N=\{1,2, \ldots\}$.
Let $\left(\Psi_{1}, \Psi_{2}\right)=\Psi_{1}(0)-i \Psi_{2}(0)$. Then we can obtain the following quantities:

$$
g_{20}= \begin{cases}0, & k \in N \\ \frac{\tilde{\tau}}{2}\left[\left(-e^{-i \omega_{+}^{k} \tilde{\tau}}-s P_{11} C-\frac{s P_{20}}{2}-\frac{s P_{02} C^{2}}{2}\right) \Psi_{1}\right. & \\ \left.+\left(r P_{11} C+\frac{r P_{20}}{2}+\frac{r P_{02} C^{2}}{2}\right) \Psi_{2}\right], & k=0\end{cases}
$$

$g_{11}= \begin{cases}0, & k \in N, \\ \tilde{\tau} \begin{array}{ll}4 & \left(-2 \cos \omega_{+}^{k} \tilde{\tau}-s P_{11}(C+\bar{C})-s P_{20}-s P_{02} C \bar{C}\right) \Psi_{1} \\ & \\ & \left.\left(r P_{11}(C+\bar{C})+r P_{20}+r P_{02} C \bar{C}\right) \Psi_{2}\right],\end{array} & k=0 .\end{cases}$
$g_{02}=\overline{g_{20}}$,

$$
\begin{align*}
g_{21}=\tilde{\tau}[ & -\left\langle\left(\frac{W_{20}^{(1)}(0)}{2} e^{i \omega_{+}^{k} \tilde{\tau}}+W_{11}^{(1)}(0) e^{-i \omega_{+}^{k} \tilde{\tau}}+\frac{W_{20}^{(1)}(-1)}{2}+W_{11}^{(1)}(-1)\right) \cos k x, \cos k x\right\rangle \\
& -s P_{11}\left\langle\left(\frac{W_{20}^{(1)}(0)}{2} \bar{C}+W_{11}^{(1)}(0) C+W_{20}^{(2)}(0) 2+W_{11}^{(2)}(0)\right) \cos k x, \cos k x\right\rangle \\
& -s\left\langle\left[P_{20}\left(\frac{W_{20}^{(1)}(0)}{2}+W_{11}^{(1)}(0)\right)+P_{02}\left(\frac{W_{20}^{(2)}(0)}{2} \overline{\mathrm{C}}+W_{11}^{(2)}(0) C\right)\right] \cos k x, \cos k x\right\rangle \\
& -s\left\langle\left[P_{21}\left(\frac{\bar{C}}{8}+\frac{C}{4}\right)+P_{12}\left(\frac{C^{2}}{8}+\frac{C \bar{C}}{4}\right)\right] \cos ^{3} k x, \cos k x\right\rangle \\
& \left.-s\left\langle\left(\frac{P_{30}}{8}+\frac{P_{03} C^{2} \bar{C}}{8}\right) \cos ^{3} k x, \cos k x\right\rangle\right] \Psi_{1} \\
+\tau & r P_{11}\left\langle\left(\frac{W_{20}^{(1)}(0)}{2} \bar{C}+W_{11}^{(1)}(0) C+W_{20}^{(2)}(0) 2+W_{11}^{(2)}(0)\right) \cos k x, \cos k x\right\rangle \\
& +r\left\langle\left[P_{20}\left(\frac{W_{20}^{(1)}(0)}{2}+W_{11}^{(1)}(0)\right)+P_{02}\left(\frac{W_{20}^{(2)}(0)}{2} \bar{C}+W_{11}^{(2)}(0) C\right)\right] \cos k x, \cos k x\right\rangle \\
& +r\left\langle\left[P_{21}\left(\frac{\bar{C}}{8}+\frac{C}{4}\right)+P_{12}\left(\frac{C^{2}}{8}+\frac{C \bar{C}}{4}\right)\right] \cos ^{3} k x, \cos k x\right\rangle \\
& \left.+r\left\langle\left(\frac{P_{30}}{8}+\frac{P_{03} C^{2} \bar{C}}{8}\right) \cos ^{3} k x, \cos k x\right\rangle\right] \Psi_{2 .} \tag{4.29}
\end{align*}
$$

Since $W_{20}(\theta)$ and $W_{11}(\theta)$ for $\theta \in[-1,0]$ appear in $g_{21}$, we need to compute them. It follows from (4.26) that

$$
\begin{gather*}
\dot{W}(z, \bar{z})=W_{20} z \dot{z}+W_{11} \dot{z} \bar{z}+W_{11} \bar{z} \dot{\bar{z}}+W_{02} \bar{z} \dot{\bar{z}}+\text { h.o.t., }  \tag{4.30}\\
A_{\tilde{\tau}} W=A_{\tilde{\tau}} W_{20} \frac{z^{2}}{2}+A_{\tilde{\tau}} W_{11} z \bar{z}+A_{\tilde{\tau}} W_{02} \frac{\bar{z}^{2}}{2}+\text { h.o.t. } \tag{4.31}
\end{gather*}
$$

In addition, by [17], $W(z, \bar{z})$ satisfies

$$
\begin{equation*}
\dot{W}=A_{\tilde{\tau}} W+H(z, \bar{z}) \tag{4.32}
\end{equation*}
$$

where

$$
\begin{equation*}
H(z, \bar{z})=H_{20} \frac{z^{2}}{2}+H_{11} z \bar{z}+H_{02} \frac{\bar{z}^{2}}{2}+\text { h.o.t. }=X_{0} f\left(U_{t}, 0\right)-\Phi\left(\Psi,\left\langle X_{0} f\left(U_{t}, 0\right), f_{k}\right\rangle\right) \cdot f_{k} \tag{4.33}
\end{equation*}
$$

Thus, from (4.24), (4.27)-(4.33), we can obtain that

$$
\begin{gather*}
\left(2 i \omega_{+}^{k} \tilde{\tau}-A_{\tilde{\tau}}\right) W_{20}=H_{20} \\
-A_{\tilde{\tau}} W_{11}=H_{11}  \tag{4.34}\\
\left(-2 i \omega_{+}^{k} \tilde{\tau}-A_{\tilde{\tau}}\right) W_{02}=H_{02}
\end{gather*}
$$

Noticing that $A_{\tilde{\tau}}$ has only two eigenvalues $\pm i \omega_{+}^{k} \tilde{\tau}$; therefore, (4.34) has a unique solution $W_{i j}$ in $Q$ given by

$$
\begin{gather*}
W_{20}=\left(2 i \omega_{+}^{k} \tilde{\tau}-A_{\tilde{\tau}}\right)^{-1} H_{20} \\
W_{11}=-A_{\tilde{\tau}}^{-1} H_{11}  \tag{4.35}\\
W_{02}=\left(-2 i \omega_{+}^{k} \tilde{\tau}-A_{\tilde{\tau}}\right)^{-1} H_{02}
\end{gather*}
$$

From (4.33), we know that for $-1 \leq \theta<0$,

$$
\begin{align*}
H(z, \bar{z}) & =-\Phi(\theta) \Psi(0)\left\langle f\left(U_{t}, 0\right), f_{k}\right\rangle \cdot f_{k} \\
& =-\left(\frac{p_{1}(\theta)+p_{2}(\theta)}{2}, \frac{p_{1}(\theta)-p_{2}(\theta)}{2 i}\right)\left(\Psi_{1}(0), \Psi_{2}(0)\right)\left\langle f\left(U_{t}, 0\right), f_{k}\right\rangle \cdot f_{k} \\
& =-\frac{1}{2}\left(p_{1}(\theta)\left(\Psi_{1}(0)-i \Psi_{2}(0)\right)\right)+p_{2}(\theta)\left(\Psi_{1}(0)+i \Psi_{2}(0)\right)\left\langle f\left(U_{t}, 0\right), f_{k}\right\rangle \cdot f_{k}  \tag{4.36}\\
& =-\frac{1}{2}\left(p_{1}(\theta) g_{20}+p_{2}(\theta) \overline{g_{02}}\right) \cdot f_{k} \frac{z^{2}}{2}-\frac{1}{2}\left(p_{1}(\theta) g_{11}+p_{2}(\theta) \overline{g_{11}}\right) \cdot f_{k} z \bar{z}+\text { h.o.t. }
\end{align*}
$$

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

$$
\begin{align*}
& H_{20}(\theta)= \begin{cases}0, & k \in N \\
-\frac{1}{2}\left[p_{1}(\theta) g_{20}+p_{2}(\theta) \overline{g_{02}}\right] \cdot f_{0}, & k=0\end{cases}  \tag{4.37}\\
& H_{11}(\theta)= \begin{cases}0, & k \in N \\
-\frac{1}{2}\left[p_{1}(\theta) g_{11}+p_{2}(\theta) \overline{g_{11}}\right] \cdot f_{0}, & k=0\end{cases} \tag{4.38}
\end{align*}
$$

$$
\begin{align*}
& H(z, \bar{z})(0)= f\left(U_{t}, 0\right)-\Phi\left(\Psi,\left\langle f\left(U_{t}, 0\right), f_{k}\right\rangle\right) \cdot f_{k,} \\
& H_{20}(0)=\left\{\begin{array}{ll}
\frac{\tilde{\tau}}{2}\binom{-e^{-i \omega_{+}^{k} \tilde{\tau}}-s P_{11} C-\frac{s P_{20}}{2}-\frac{s P_{02} C^{2}}{2}}{r P_{11} C+\frac{r P_{20}}{2}+\frac{r P_{02} C^{2}}{2}} \cos ^{2} k x, & k \in N, \\
\tilde{\tau}\binom{-e^{-i \omega_{+}^{k} \tilde{\tau}}-s P_{11} C-\frac{s P_{20}}{2}-\frac{s P_{02} C^{2}}{2}}{r P_{11} C+\frac{r P_{20}}{2}+\frac{r P_{02} C^{2}}{2}} & k=0 . \\
-\frac{1}{2}\left[p_{1}(\theta) g_{20}+p_{2}(\theta) \overline{\left.g_{02}\right]} \cdot f_{0},\right.
\end{array}\right) \\
& H_{11}(0)= \begin{cases} \\
\frac{\tilde{\tau}}{4}\binom{-2 \cos \omega_{+}^{k} \tilde{\tau}-s P_{11}(C+\bar{C})-s P_{20}-s P_{02} C \bar{C}}{r P_{11}(C+\bar{C})+r P_{20}+r P_{02} C \bar{C}} \cos ^{2} k x, & k \in N, \\
\tilde{\tau}\binom{-2 \cos \omega_{+}^{k} \tilde{\tau}-s P_{11}(C+\bar{C})-s P_{20}-s P_{02} C \bar{C}}{r P_{11}(C+\bar{C})+r P_{20}+r P_{02} C \bar{C}} & k=0 . \\
-\frac{1}{2}\left[p_{1}(\theta) g_{11}+p_{2}(\theta) \overline{\left.g_{11}\right]} \cdot f_{0},\right.\end{cases} \tag{4.39}
\end{align*}
$$

By the definition of $A_{\tilde{\tau}}$, we have from (4.34),

$$
\begin{equation*}
\dot{W}_{20}(\theta)=2 i \omega_{+}^{k} \tilde{\tau} W_{20}(\theta)+\frac{1}{2}\left[p_{1}(\theta) g_{20}+p_{2}(\theta) \overline{g_{02}}\right] \cdot f_{k},-1 \leq \theta \leq 0 . \tag{4.40}
\end{equation*}
$$

Note that $p_{1}(\theta)=p_{1}(0) e^{i \omega_{\uparrow}^{k} \tau \theta},-1 \leq \theta \leq 0$. Hence,

$$
\begin{gather*}
W_{20}(\theta)=\frac{1}{2}\left[\frac{i g_{20} p_{1}(\theta)}{\omega_{+}^{k} \tilde{\tau}}+\frac{i \overline{g_{02}} p_{2}(\theta)}{3 \omega_{+}^{k} \tilde{\tau}}\right] \cdot f_{k}+E_{1} e^{2 \omega_{+}^{k} \tilde{\tau} \theta,}  \tag{4.41}\\
E_{1}= \begin{cases}W_{20}, & k \in N, \\
W_{20}(0)-\frac{1}{2}\left[\frac{i g_{20} p_{1}(0)}{\omega_{+}^{0} \tilde{\tau}}+\frac{i \overline{g_{02}} p_{2}(0)}{3 \omega_{+}^{0} \tilde{\tau}}\right] \cdot f_{0}, & k=0 .\end{cases} \tag{4.42}
\end{gather*}
$$

Using the definition of $A_{\tilde{\tau}}$, and combining (4.34) and (4.41), we have

$$
\begin{gather*}
2 i \omega_{+}^{0} \tilde{\tau}\left[-\frac{1}{2}\left(\frac{i g_{20} p_{1}(0)}{\omega_{+}^{0} \tilde{\tau}}+\frac{i \overline{g_{02}} p_{2}(0)}{3 \omega_{+}^{0} \tilde{\tau}} \cdot f_{0}\right)+E_{1}\right]-\tilde{\tau} D \Delta\left[-\frac{1}{2}\left(\frac{i g_{20} p_{1}(0)}{\omega_{+}^{0} \tilde{\tau}}+\frac{i \overline{g_{02}} p_{2}(0)}{3 \omega_{+}^{0} \tilde{\tau}} \cdot f_{0}\right)+E_{1}\right] \\
-L(\widetilde{\tau})\left[-\frac{1}{2}\left(\frac{i g_{20} p_{1}(\theta)}{\omega_{+}^{0} \tilde{\tau}}+\frac{i \overline{g_{02}} p_{2}(\theta)}{3 \omega_{+}^{0} \tilde{\tau}} \cdot f_{0}\right)+E_{1} e^{2 i \omega_{+}^{0} \tilde{\tau} \theta}\right] \\
=\frac{\tilde{\tau}}{2}\binom{-e^{-i \omega_{+}^{k} \tilde{\tau}}-s P_{11} C-\frac{s P_{20}}{2}-\frac{s P_{02} C^{2}}{2}}{r P_{11} C+\frac{r P_{20}}{2}+\frac{r P_{02} C^{2}}{2}}-\frac{1}{2}\left[p_{1}(\theta) g_{20}+p_{2}(\theta) \overline{g_{02}}\right] \cdot f_{0} \tag{4.43}
\end{gather*}
$$

Notice that

$$
\begin{gather*}
\tilde{\tau} D \Delta\left[p_{1}(0) \cdot f_{0}\right]+L(\tilde{\tau})\left[p_{1}(\theta) \cdot f_{0}\right]=i \omega_{+}^{0} \tilde{\tau} p_{1}(0) \cdot f_{0} \\
\tilde{\tau} D \Delta\left[p_{2}(0) \cdot f_{0}\right]+L(\widetilde{\tau})\left[p_{2}(\theta) \cdot f_{0}\right]=-i \omega_{+}^{0} \tilde{\tau} p_{2}(0) \cdot f_{0} \tag{4.44}
\end{gather*}
$$

Then, for $k \in N_{0}$,

$$
\begin{equation*}
2 i \omega_{+}^{0} \tilde{\tau} E_{1}-\tilde{\tau} D \Delta E_{1}-L(\tilde{\tau})\left(E_{1}\right) e^{2 i \omega_{+}^{0} \tilde{\tau} \theta}=\frac{\tilde{\tau}}{2}\binom{-e^{-i \omega_{+}^{k} \tilde{\tau}}-s P_{11} C-\frac{s P_{20}}{2}-\frac{s P_{02} C^{2}}{2}}{r P_{11} C+\frac{r P_{20}}{2}+\frac{r P_{02} C^{2}}{2}} \cos ^{2} k x \tag{4.45}
\end{equation*}
$$

From the above expression, we obtain that

$$
\begin{equation*}
E_{1}=\frac{1}{2} E\binom{-e^{-i \omega_{+}^{k} \tilde{\tau}}-s P_{11} C-\frac{s P_{20}}{2}-\frac{s P_{02} C^{2}}{2}}{r P_{11} C+\frac{r P_{20}}{2}+\frac{r P_{02} C^{2}}{2}} \cos ^{2} k x \tag{4.46}
\end{equation*}
$$

where

$$
E=\left(\begin{array}{cc}
2 i \omega_{+}^{k}+d_{1} k^{2}-1+u^{*}+a_{1}+u^{*} e^{-2 i \omega_{+}^{k} \tilde{\tau}} & a_{2}  \tag{4.47}\\
-b_{1} & 2 i \omega_{+}^{k}+d_{2} k^{2}-b_{2}+d
\end{array}\right)^{-1}
$$

By the same way, we have

$$
\begin{gather*}
-\dot{W}_{11}(\theta)=-\frac{1}{2}\left[p_{1}(\theta) g_{11}+p_{2}(\theta) \overline{g_{11}}\right] \cdot f_{k}, \quad-1 \leq \theta<0 \\
W_{11}(\theta)=\frac{1}{2}\left[\frac{-i g_{11} p_{1}(\theta)}{\omega_{+}^{k} \tilde{\tau}}+\frac{i \overline{g_{11}} p_{2}(\theta)}{\omega_{+}^{k} \tilde{\tau}}\right]+E_{2} \tag{4.48}
\end{gather*}
$$

Similar to the above, we can obtain that

$$
\begin{equation*}
E_{2}=\frac{1}{4} E_{0}\binom{-2 \cos \omega_{+}^{k} \tilde{\tau}-s P_{11}(C+\bar{C})-s P_{20}-s P_{02} C \bar{C}}{r P_{11}(C+\bar{C})+r P_{20}+r P_{02} C \bar{C}} \cos ^{2} k x \tag{4.49}
\end{equation*}
$$

where

$$
E_{0}=\left(\begin{array}{cc}
d_{1} k^{2}-1+2 u^{*}+a_{1} & a_{2}  \tag{4.50}\\
-b_{1} & d_{2} k^{2}-b_{2}+d
\end{array}\right)^{-1}
$$

So far, $W_{20}(\theta)$ and $W_{11}(\theta)$ have been expressed by the parameters of the system (1.1). And, hence, $g_{21}$ can be expressed also. Thus, we can compute the following values:

$$
\begin{gather*}
c_{1}(0)=\frac{i}{2 \omega_{+}^{k} \tilde{\tau}}\left(g_{20} g_{11}-2\left|g_{11}\right|^{2}-\frac{1}{3}\left|g_{02}\right|^{2}\right)+\frac{g_{21}}{2}, \\
\mu_{2}=-\frac{\operatorname{Re}\left\{c_{1}(0)\right\}}{\operatorname{Re}\left\{\lambda^{\prime}\left(\tau_{j}^{k}\right)\right\}}  \tag{4.51}\\
\beta_{2}=2 \operatorname{Re}\left\{c_{1}(0)\right\} \\
T_{2}=-\frac{\operatorname{Im}\left\{c_{1}(0)\right\}+\mu_{2} \operatorname{Im}\left\{\lambda^{\prime}\left(\tau_{j}^{k}\right)\right\}}{\omega_{+}^{k} \tilde{\tau}}
\end{gather*}
$$

where $\mu_{2}$ determines the direction of Hopf bifurcation, $\beta_{2}$ determines the stability of bifurcating periodic solution, and $T_{2}$ determines the period of the bifurcating periodic solution. Hence, we have the following result.

Theorem 4.2. The signs of $\mu_{2}, \beta_{2}, T_{2}$ determine the properties of Hopf bifurcation described in Theorems 2.4 and 2.7. If $\mu_{2}>0\left(\mu_{2}<0\right)$, then the Hopf bifurcation is supercritical (subcritical), and the bifurcating periodic solutions exist (nonexist) for $\tau>\tau_{k}\left(\tau<\tau_{k}\right)$. If $\beta_{2}<0\left(\beta_{2}>0\right)$, then the bifurcating periodic solutions are stable (unstable). If $T_{2}>0\left(T_{2}<0\right)$, then the period of the bifurcating periodic solutions of system (1.1) increases (decreases).

Remark 4.3. From the previous computable results, the expressions of $E_{1}$ and $E_{2}$ contain the diffusion coefficient. According to the definition of $g_{21}$, the values of $g_{21}$ have related on $E_{1}$ and $E_{2}$. Therefore, the signs of $\beta_{2}$ and $\mu_{2}$ which determine the stability and direction of spatially inhomogeneous periodic solutions strictly depend on the diffusion coefficient of $d_{1}$ and $d_{2}$.

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