Bifurcation analysis in a diffusive mussel-algae model with delay

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July 26, 2018

Abstract

The dynamics of a reaction diffusion mussel-algae system with a delay subject to Neumann boundary conditions is considered. The existence of positive solutions and global stability of the boundary equilibrium are obtained when delay is zero. The stability of the positive constant steady state and existence of Hopf bifurcation are established by analyzing the distribution of eigenvalues when the delay is not zero. Furthermore, by using the theory of normal form and center manifold reduction for partial functional differential equations, an algorithm for determining the direction of Hopf bifurcation and stability of bifurcating periodic solutions is derived. Finally, some numerical simulations are presented to illustrate the analytical results obtained.

Keywords: mussel-algae system; reaction diffusion; global stability; Hopf bifurcation; delay.

1 Introduction

Two-component interactions coupled by dispersion and advection have been formulated for explaining pattern formation \[1, 9, 16\]. The researchers’ interests are the processes that generate spatial complexity in ecosystems. In particular, van de Koppel \textit{et al.} \cite{23} studied the regular spatial patterns in young mussel beds on soft sediments in the Wadden Sea by means of a spatially explicit model describing changes in local population biomass of algae.

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and mussels. The model considered the dispersal effect of the mussel and the advection effect by tidal current for the algae but neglecting the dispersal effect for the latter. The simulations has shown that the coupling between dispersion and advection can lead to spatial pattern. A successful model deserves a further study, such as the implications of advection caused by tidal flow [20], kinetic behavior of the patterned solutions [25], interactions between different forms of self-organization [11, 12, 24].

In 2015, based on the field experiment consisting of a young mussel bed on a homogeneous substrate covered by a relatively quiescent layer of marine water in which advection was minimized as much as possible (for more details about the experiment, see [11, 24]), Cangelosi et al. extended the dispersion-advection system in the case of replacing the advection term for the algae by a lateral diffusive one instead of the form [4]:

\[
\begin{align*}
\frac{\partial M}{\partial t} &= D_M \Delta M + ecMA - d_M \frac{k_M}{k_M + M} M, \\
\frac{\partial A}{\partial t} &= D_A \Delta A + (A_{up} - A)f - \frac{c}{H}MA.
\end{align*}
\] (1.1)

where \( M = M(x,t) \) is the mussel biomass density on the sediment, \( A = A(x,t) \) is the algae concentration in the lower water layer overlying the mussel bed, \( x \in \Omega \) is spatial variable, and \( \Omega \) is a bounded domain in \( \mathbb{R}^n \) with a smooth boundary \( \partial \Omega \). Here, \( e \) is a conversion constant relating ingested algae to mussel biomass production, \( c \) is the consumption constant, \( d_M \) is the maximal per capita mussel mortality rate, \( k_M \) is the value of \( M \) at which mortality is half maximal, \( A_{up} \) describes the uniform concentration of algae in the upper reservoir water layer, \( f \) is the rate of exchange between the lower and upper water layers, \( H \) is the height of the lower water layer, and \( D_M \) and \( D_A \) are the diffusion coefficients of the mussel and algae, respectively.

For the sake of simplicity, we shall introduce the following dimensionless change of variables:

\[
\begin{align*}
m &= \frac{M}{k_M}, \quad a &= \frac{A}{A_{up}}, \quad \omega = \frac{ck_M}{H}, \quad \hat{t} = d_M t, \quad \alpha = \frac{f}{\omega}, \\
r &= \frac{ecA_{up}}{d_M}, \quad \gamma = \frac{d_M}{\omega}, \quad d = \frac{D_M}{\gamma D_A}, \quad \hat{x} = x \sqrt{\frac{\omega}{D_A}}.
\end{align*}
\]

and after removing the hat, we have

\[
\begin{align*}
\frac{\partial m}{\partial \hat{t}} &= d \Delta m + rma - \frac{m}{1 + m}, \\
\gamma \frac{\partial a}{\partial \hat{t}} &= \Delta a + \alpha(1 - a) - ma.
\end{align*}
\] (1.2a)
We point out that most studies of system (1.2a) concentrate on the patterns and numerical bifurcation, see for examples [10, 19, 24, 25]. We shall investigate the periodic solutions bifurcated from the constant coexistence equilibrium solution. The dynamics near the bifurcation point can well explain the periodic change of population in predator-prey systems. For further mathematical analysis, we supplement system (1.2a) with the following initial-boundary value conditions:

\[
\begin{align*}
\partial_\nu m &= \partial_\nu a = 0, \quad x \in \partial \Omega, \quad t > 0, \\
m(x, 0) &= m_0(x) \geq 0, \quad a(x, 0) = a_0(x) \geq 0, \quad x \in \Omega. 
\end{align*}
\]

(1.2b)

Since time delay has been commonly used in modeling biological systems and can significantly change the dynamics of these systems [18, 28, 29]. In this article, we consider the following delayed mussel-algae system:

\[
\begin{align*}
\frac{\partial m(x, t)}{\partial t} &= d \Delta m(x, t) + m(x, t) \left( ra(x, t - \tau) - \frac{1}{1 + m(x, t - \tau)} \right), \quad x \in \Omega, \quad t > 0, \\
\gamma \frac{\partial a(x, t)}{\partial t} &= \Delta a(x, t) + \alpha (1 - a(x, t)) - m(x, t) a(x, t), \quad x \in \Omega, \quad t > 0, \\
\partial_\nu m &= \partial_\nu a = 0, \quad x \in \partial \Omega, \quad t > 0, \\
m(x, t) &= m_0(x, t) \geq 0, \quad a(x, t) = a_0(x, t) \geq 0, \quad x \in \Omega, \quad -\tau \leq t \leq 0.
\end{align*}
\]

(1.3)

where \( \tau \) is the digestion period of mussel and the mortality of mussels depends on the state whether they have eaten in the past. The homogeneous Neumann boundary condition implies that there is no population movement across the boundary \( \partial \Omega \).

Define the real-value Sobolev space

\[ X := \left\{(u, v) \in H^2(\Omega) \times H^2(\Omega) | \partial_\nu u = \partial_\nu v = 0, x \in \partial \Omega \right\} \]

and its complexification, \( X_C := X \oplus iX = \{x_1 + ix_2 | x_1, x_2 \in X\} \) with a complex-valued \( L^2 \) inner product \( < \cdot, \cdot > \) which defined as

\[ < U_1, U_2 > = \int_{\Omega} (\bar{u}_1 u_2 + \bar{v}_1 v_2) dx \]

with \( U_i = (u_i, v_i)^T \in X_C, i = 1, 2. \)

The system (1.3) always has a non-negative constant solution: \( E_0(0, 1) \), which is a boundary equilibrium corresponding to bare sediment where no mussels exist, biologically, we would like to see the coexistence state corresponding to a positive equilibrium. In order for this to happen, we make the following assumption:

\[ (H1) \quad 0 < \alpha < 1 < r < \alpha^{-1}. \]
The assumption (H1) guarantees the system has a positive equilibrium \( E_*(m^*, a^*) \) with

\[ m^* = \frac{\alpha(r - 1)}{1 - \alpha r}, \quad a^* = \frac{1 - \alpha r}{r(1 - \alpha)}. \]

The highlights of this article is the proof of global existence and boundedness of solutions and a detailed bifurcation analysis about the positive equilibrium. In our stability analyses to follow we first employ \( r \) as a bifurcation parameter, and consider the Hopf bifurcation of system (1.2) at the positive equilibrium. Then for functional differential system (1.3), we show the existence of Hopf bifurcation caused by delay \( \tau \), moreover, we give the direction and stability of bifurcating periodic solutions.

The organization of the remaining part of this paper is as follows. In Section 2, for system (1.2), the global existence and boundedness result of the solutions are given in Section 2.1, and the global asymptotically stability of boundary equilibrium is proved under some additional conditions in Section 2.2. The linear stability and Hopf bifurcation are investigated in Section 2.3 with the spatial domain \( \Omega = (0, l\pi), \ l \in \mathbb{R}^+ \). In Section 3, for system (1.3), the stability of the positive constant steady state is considered, and the existence of the related Hopf bifurcation at the critical points is investigated with delay as the bifurcation parameter. In Section 4, the direction of Hopf bifurcation near the positive equilibrium and stability of the bifurcating periodic solutions are shown by applying the normal form theory and center manifold reduction for partial functional differential equations. Some numerical simulations are presented in Section 5.

2 Existence and linear stability analysis for model without delay

2.1 Existence and boundedness

In this subsection, we first state the global existence result of the solutions of the initial value problem (1.2), for more details of abstract theory, refer to [2, 3, 27].

**Theorem 2.1.** Assume that \( \alpha, \gamma, r \) and \( d \) are all positive, the initial data \((m_0(x), a_0(x))\) satisfies \( m_0(x) \geq 0, a_0(x) \geq 0, \) and \( m_0(x) \neq 0, a_0(x) \neq 0 \) for \( x \in \Omega \). Then

1. The system (1.2) has a unique nonnegative solution \((m(x,t), a(x,t))\) satisfying

\[ 0 < m(x,t), \quad 0 < a(x,t) \leq \max\{\|a_0\|_\infty, 1\}, \quad x \in \Omega, t > 0. \]

where \( \|\phi\|_\infty = \sup_{x \in \Omega} \phi(x) \).
2. Moreover, if $0 < r < 1$ and $0 < \alpha r < \frac{1}{2}$, then the first component $m(x, t)$ of the solutions of system (1.2) satisfies the following estimate

$$
\limsup_{t \to \infty} m(x, t) \leq 1, \quad x \in \bar{\Omega}.
$$

Proof. Let $(m(t), a(t))$ be the unique solution of the following ODE system

$$
\begin{align*}
\frac{dm}{dt} &= rma - \frac{m}{1 + m}, \\
\gamma \frac{da}{dt} &= \alpha(1 - a) - ma, \\
\end{align*}
$$

(2.1)

with

$$
\begin{align*}
m_0(x) &= \sup_{x \in \Omega} m_0(x), \\
a_0(x) &= \sup_{x \in \Omega} a_0(x); \\
\end{align*}
$$

Define

$$
\begin{align*}
f(m, a) &= rma - \frac{m}{1 + m}, \\
h(m, a) &= \frac{1}{\gamma} \left( \alpha(1 - a) - ma \right).
\end{align*}
$$

Then for any $(m, a) \in \mathbb{R}^2_+ = \{(m, a)|m \geq 0, a \geq 0\}$, we have $D_a f = rm \geq 0$, $D_m h = -\gamma^{-1}a \leq 0$, thus system (1.2) is a mixed quasi-monotone system. Moreover $(0, 0)$ and $(m(t), a(t))$ are the lower-solution and upper-solution of system (1.2), respectively. From Theorem 3.3 (Chapter 8, page 400) in [14], we know that system (1.2) has a unique solution $(m(x, t), a(x, t))$ which satisfies

$$
0 \leq m(x, t) \leq m(t), \quad 0 \leq a(x, t) \leq a(t), \quad t \geq 0.
$$

Note that $m_0(x) \geq 0(\neq 0)$, $a_0(x) \geq 0(\neq 0)$, hence from the strong maximum principle for parabolic equations, we obtain that $m(x, t) > 0$, $a(x, t) > 0$. Again from (1.2), we have

$$
\begin{align*}
\gamma \frac{\partial a}{\partial t} - \Delta a &= \alpha(1 - a) - ma \leq \alpha(1 - a), \quad x \in \Omega, \quad t > 0, \\
\partial_n a &= 0, \quad x \in \partial\Omega, \quad t > 0, \\
a(x, 0) &= a_0(x) \geq 0(\neq 0), \quad x \in \Omega.
\end{align*}
$$

(2.2)

Applying the comparison principle, we have $a(x, t) \leq \max\{\|a_0\|_\infty, 1\}$. This complete the first part of Theorem 2.1.

We now discuss the boundedness of $m(x, t)$ under the condition $0 < r < 1$ and $0 < \alpha r < \frac{1}{2}$.
From (2.2), we obtain that for any $a_0 > 0$, and $\varepsilon_0 > 0$, there exists a $t_0 > 0$, such that $a(t) \leq 1 + \varepsilon_0$ for $t \geq t_0$. Rewrite the nullclines of $m$ and $a$ in the first quadrant then we have

$$a_f = \frac{1}{r(1 + m)} := f^1(m), \quad a_h = \frac{\alpha}{\alpha + m} := f^2(m).$$

and

$$a_f - a_h = \frac{1}{r(1 + m)} - \frac{\alpha}{\alpha + m} = \frac{1}{r(1 + m)(\alpha + m)}(\alpha + m - \alpha r(1 + m))$$

$$> 0$$

That is, the $a-$isocline $h(m, a) = 0$ is below the $m-$isocline $f(m, a) = 0$ in the first quadrant.

Since $m(t)$ is a upper-solution of $m(x, t)$, next we shall discuss the boundedness of $m(t)$, to show this, we first justify two claims.

Claim 1: There exists a $t_1 > t_0$ such that $m(t_1) < 1$.

If not, we assume that $m(t) \geq 1$ holds for all $t > t_0$. Let $w(t) = \frac{1}{\gamma}m(t) + ra(t)$, then we have

$$\frac{dw}{dt} = \frac{1}{\gamma}(r\alpha - ra - \frac{m}{1 + m}) \leq \frac{1}{\gamma}(r\alpha - ra - \frac{1}{2})$$

$$\leq \frac{1}{\gamma}(r\alpha - \frac{1}{2})$$

$$= \mu < 0$$

which indicates $w(t) \to -\infty$ as $t \to \infty$ and this contradicts the definition of $w(t)$.

Claim 2: There exists a $t_2 > t_1$, such that $m(t) \leq 1$ for all $t > t_2$.

In fact, if $t^* \text{satisfies} a(t^*) = f^1(m(t^*))$ in the first quadrant, then we have

$$\gamma \frac{da}{dt} \big|_{t=t^*} = \alpha(1 - a(t^*)) - m(t^*)a(t^*) = \alpha - \frac{\alpha + m(t^*)}{r(1 + m(t^*))}$$

$$\leq \alpha - \frac{\alpha}{r} = \frac{\alpha}{r}(r - 1)$$

$$< 0$$

which indicates that the vector field $(f(m, a), h(m, a))$ points towards left when $(m, a) = (m, f^1(m))$.

Let $\phi_t(m_0, a_0)$ be the trajectory of Eq.(2.1) with the initial value $(m_0, a_0)$ at $t = 0$, and denote

$$\Omega_1 = \{(m, a) : 0 < m < 1, \ 0 < a < \min\{1 + \varepsilon_0, f^1(m)\}\},$$

$$\Omega_2 = \{(m, a) : 1 < m, \ 0 < a < \min\{1 + \varepsilon_0, f^1(m)\}\},$$

$$\Omega_3 = \{(m, a) : 0 < m, \ f^1(m) < a\}.$$
If the initial value \((m_0, a_0) \in \Omega_1 \cup \Omega_2\), then \(m(t)\) will monotone decrease. According to Claim 1, there exists a \(t_1\), such that \(m(t_1) < 1\) and \(a(t_1) < 1 + \varepsilon\). Moreover, from (2.3), \(\Omega_1\) is an invariant region for Eq. (2.4). Therefore, \(\phi_t(m_0, a_0) \in \Omega_1\) for any \(t > t_1\).

On the other hand, for any \((m, a) \in \Omega_3\), we have
\[
\frac{dm}{dt} > 0 \text{ and } \frac{da}{dt} < 0.
\] (2.4)

If the initial value \((m_0, a_0) \in \Omega_3\), then from (2.4) and Claim 1, we obtain that there exists a \(t'_2\), such that the trajectory \(\phi_t(m_0, a_0)\) with \((m_0, a_0) \in \Omega_3\) meets the \(m\)-nullcline at \(t = t'_2\) and then enter the region \(\Omega_1 \cup \Omega_2\) (otherwise, \(m(t) \to \infty\) as \(t \to \infty\) which contradicts Claim 1), and eventually reach the invariant region \(\Omega_1\), see Fig.1.

By Claim 1 and Claim 2, we have
\[
\limsup_{t \to \infty} m(x, t) \leq 1, \quad x \in \bar{\Omega}.
\]
This completes the proof. \(\Box\)

### 2.2 Global stability of boundary equilibrium

In this subsection, we shall prove the global stability of the boundary equilibrium \(E_0(0, 1)\) for the system (1.2) under some additional assumptions.

**Theorem 2.2.** Assume that \(\alpha, \gamma, r\) and \(d\) are all positive and the initial data \((m_0(x), a_0(x))\) satisfies the hypotheses of Theorem 2.1. Then

1. If \(r\) satisfies \(0 < r < 1\), then \(E_0(0, 1)\) is locally asymptotically stable.

2. If \(r\) satisfies \(r > 1\), then \(E_0(0, 1)\) is unstable.

3. If \(\alpha, r\) satisfy \(0 < r < \frac{1}{2}\) and \(0 < \alpha r < \frac{1}{2}\), then \(E_0(0, 1)\) is globally asymptotically stable.

**Proof.** The proof of Part 1 and Part 2 for local properties can be seen in the beginning of Section 2.3 in which spatial domain \(\Omega\) can work for arbitrary higher dimension. Next, we use Lyapunov functional to prove the global attractivity.

Define
\[
V(m, a) = \gamma r \int_{\Omega} \int_{1}^{a} \frac{\xi - 1}{\xi} d\xi dx + \int_{\Omega} m dx
\]
Figure 1: Basic phase portrait of (2.1) with $0 < r < 1$ and $0 < \alpha r < \frac{1}{2}$. The dashed-dotted curve is the $m$-nullcline $a_j = f^1(m)$, the dashed line is the $a$-nullcline $a_h = f^2(m)$, the horizontal dot curve is $m = 1$. The parameters used are given by $r = 0.8$, $\alpha = 0.5$, $\gamma = 8$.

Then

$$
\dot{V}(m, a) = \gamma r \int_\Omega \frac{a - 1}{a} a_t \, dx + \int_\Omega m_t \, dx
$$

$$
= -r \int_\Omega \frac{1}{a^2} |\nabla a|^2 \, dx - \alpha r \int_\Omega \frac{(1 - a)^2}{a} \, dx + \int_\Omega \left(r - \frac{1}{1 + m}\right) m \, dx
$$

Since $0 < r < \frac{1}{2}$ and $0 < \alpha r < \frac{1}{2}$ from Theorem 2.1 we have that $m(x, t) \leq 1$ when $t \geq t_2$, then $r - \frac{1}{1 + m} \leq r - \frac{1}{2} < 0$. Hence $\dot{V}(m, a) \leq 0$. Moreover, $\dot{V}(m, a) = 0$ implies that $a = 1$, 

8
and \( m = 0 \) or \( m = \frac{1}{r} - 1 \). So from the LaSalle invariance principle, we have that

\[
\omega\left((m_0(x), a_0(x))\right) \subset \left\{ (0, 1), \left( \frac{1}{r} - 1, 1 \right) \right\}.
\]

where \( \omega(x) \) is the \( \omega \)-limit set of \( x \). Note that \( \lim_{t \to \infty} m(x, t) \leq 1 \), then \( \left( \frac{1}{r} - 1, 1 \right) \notin \omega\left((m_0(x), v_0(x))\right) \). Hence, we have

\[
\omega\left((m_0(x), a_0(x))\right) = \{(0, 1)\},
\]

which is the desired result.

2.3 Linear stability and Hopf bifurcation

In this subsection, we shall investigate the linear stability and Hopf bifurcation of system (1.2), and restrict the spatial domain \( \Omega = (0, l\pi) \) of which the structure of the eigenvalues is clear.

Denote \( U = (m, a)^T \), then the linearization of system (1.2) is

\[
\Gamma U = D\Delta U + L_e U,
\]

where \( \Gamma, D, L_e \) are defined as

\[
\Gamma = \begin{pmatrix} 1 & 0 \\ 0 & \gamma \end{pmatrix}, \quad D = \begin{pmatrix} d & 0 \\ 0 & 1 \end{pmatrix}, \quad L_e = \begin{pmatrix} ra - 1/(1 + m)^2 & rm \\ a & -(\alpha + m) \end{pmatrix}.
\]

Then the characteristic equation of (2.5) at the equilibrium points \( E_0(0, 1) \) and \( E_*(m^*, a^*) \) with Neumann boundary conditions can be obtained, and we first show the characteristic equation corresponding to \( E_0(0, 1) \), namely:

\[
(\lambda + 1 - r + d\frac{n^2}{l^2})(\gamma\lambda + \alpha + \frac{n^2}{l^2}) = 0
\]

where \( n \in \mathbb{N}_0 := \mathbb{N} \cup \{0\} \). By straightforward calculation, we have the following stability information: \( E_0 \) is locally asymptotically stable when \( 0 < r < 1 \), and unstable when \( r > 1 \). Our main concern is the dynamics of positive equilibrium \( E_*(m^*, a^*) \), the characteristic equation at \( E_*(m^*, a^*) \) can be written as

\[
\gamma\lambda^2 + \widetilde{T}_n\lambda + \widetilde{D}_n = 0
\]

(2.7)
where
\[
\tilde{T}_n = (1 + \gamma d) \frac{n^2}{l^2} + \frac{\alpha}{a^*} - \gamma r a^* m^* + \alpha (r - 1) a^*.
\]

\[
\tilde{D}_n = d \frac{n^4}{l^4} + \left( \frac{d a^*}{a^*} - r^2 a^* m^* \right) \frac{n^2}{l^2} + \alpha r \left( r - 1 \right) a^*.
\]

and the eigenvalues \( \lambda_n \) are given by
\[
\lambda_n = \frac{-\tilde{T}_n \pm \sqrt{\tilde{T}_n^2 - 4\gamma \tilde{D}_n}}{2\gamma}, \tag{2.8}
\]

In the remaining part of this section, we choose \( r \) as our bifurcation parameter and present some necessary conditions under which the branch is occurred.

It is well known that, when the system (1.2) undergoes a Hopf bifurcation at the critical value \( r_H \), there exist a neighborhood \( N(r_H) \) of \( r_H \) such that for any \( r \in N(r_H) \), the characteristic equation (2.7) has a pair of simple, conjugate complex roots \( \lambda(r) = \beta(r) \pm i\omega(r) \) which continuously differentiable in \( r \) and satisfy \( \beta(r_H) = 0, \omega(r_H) > 0, \beta'(r_H) \neq 0, \) and all other roots have non-zero real parts. We shall identify the above conditions through the following form:
\[
\tilde{T}_n(r_H) = 0, \quad \tilde{D}_n(r_H) > 0, \quad \beta'(r_H) \neq 0, \quad \tilde{T}_j(r_H) \neq 0, \quad \tilde{D}_j(r_H) \neq 0, \quad j \neq n. \tag{2.9}
\]

Note that if (H1) holds, then \( \tilde{D}_0 = \alpha r (r - 1) a^* > 0 \). According to the recent work of [21], we just state the following lemma without proof.

**Lemma 2.3.** Suppose that (H1) holds. Let \( r^* = \frac{1}{4} \alpha^{-1} \left( \alpha + \sqrt{\alpha^2 + 8\alpha} \right) \). Then

1. If \( 1 < r_H < r^* \), then \( \beta'(r_H) > 0 \);
2. If \( r^* < r_H < \alpha^{-1} \), then \( \beta'(r_H) < 0 \);

The Lemma 2.3 indicates that the transversality condition can always be satisfied as long as \( r_H \neq r^* \), and the changes in the real part of the eigenvalues can be clearly demonstrated. If \( 1 < r_H < r^* \), the real part of one pair of complex roots of characteristic equation (2.7) becomes positive when \( r \) increases across the threshold \( r^* \); and if \( r^* < r_H < \alpha^{-1} \), the real part of one pair of complex roots of characteristic equation (2.7) becomes negative when \( r \) increases across \( r^* \). Namely, if \( 1 < r_H < r^* \), the positive constant steady state loses its stability when \( r \) increases across \( r^* \), while if \( r^* < r_H < \alpha^{-1} \), the positive constant steady state regains its stability when \( r \) increases across \( r^* \).
Denote $H_0(r) = \frac{1-\alpha r}{1-\alpha}$, $P_0(r) = \frac{r(1-\alpha)}{\gamma(r-1)}$. From discussions above, the determination of Hopf bifurcation points reduces to describing the set

$$S := \{ r \in (1, \alpha^{-1}) \setminus \{r^*\} : \text{for some } n \in \mathbb{N}_0, (2.9) \text{ is satisfied}\}$$

when the other parameters $\alpha, \gamma, d$ are given appropriately. The above analysis permits us to give the following stability results for system (1.2) without diffusion, the graphical results can be seen in Fig.2.

**Theorem 2.4.** Assume that (H1) is satisfied. For system (1.2) without diffusion,

1. If $H_0^2(r) < P_0(r)$, the positive equilibrium $E_*(m^*, a^*)$ of system (1.2) is locally asymptotically stable;
2. If $H_0^2(r) > P_0(r)$, the positive equilibrium $E_*(m^*, a^*)$ of system (1.2) is unstable;
3. If $r_H \in S$ satisfies the equation $H_0^2(r) = P_0(r)$, the system (1.2) undergoes a Hopf bifurcation at $r = r_H$ which corresponds to spatially homogeneous periodic solution; the critical curve of Hopf bifurcation is defined by $H_0^2(r) = P_0(r)$.

Figure 2: (a) The critical curve of Hopf bifurcation on $\alpha - r$ plane. The vertical dotted curve is $\alpha = 0.45$ and intersects with the Hopf bifurcation curve at two critical points with $r_1 = 1.0865, r_2 = 1.7286$ respectively. (b) The limit cycle bifurcated from the positive equilibrium when $r = 1.2 \in (r_1, r_2)$. The other parameters are chosen as: $\gamma = 8, d = 0.1$.  

11
Remark 2.5. When $\tau > 0$, the characteristic equation corresponding to $E_0(0,1)$ for system (1.3) has the same expression with Eq. (2.6). Therefore, $E_0(0,1)$ is locally asymptotically stable for any $\tau > 0$ when $0 < r < 1$ (see Fig. 7).

Remark 2.6. For system (1.2), the work of global existence of periodic solutions induced by Hopf bifurcation is still a spot worth to study. We can verify numerically there exists at least one periodic orbit when $r \in (r_1, r_2)$. Actually, we have performed some numerical simulations (see Fig. 3), the results show that periodic solutions are globally existent. The Hopf branch connects two critical points $H_1$ at $r_1$ and $H_2$ at $r_2$.

![Figure 3](https://via.placeholder.com/150)

Figure 3: Simulations of global existence of periodic solutions for system (1.2). Solid lines mark stable portions of the branch. Black lines represent the homogeneous equilibrium, red lines and blue lines represent maximum and minimum amplitude, respectively. (a) The amplitude of mussel biomass $m$. (b) The amplitude of algae concentration $a$. The parameters are chosen as: $\gamma = 8, \alpha = 0.45, d = 0.1$.

### 2.4 Turing instability

In this subsection we shall consider the Turing instability driven by diffusion. The non-equilibrium phase transition corresponding to the Turing bifurcation is the transformation from uniform steady state to spatial periodic oscillating state. Moreover, the system should be stable to uniform homogeneous perturbations, and unstable to nonhomogeneous cases. To ensure our stability analysis valid, we make the following assumption:

(H2) \[ H_0^2(r) - P_0(r) < 0. \]
According to the analysis above, we have

**Lemma 2.7.** Let \( g(r) = m^* (d^* \rho_0 - H^0_0) \), \( \Lambda = g^2(r) - 4d \tilde{D}_0 \). Suppose that (H1) and (H2) holds. Then the positive equilibrium \( E_*(m^*, a^*) \) of system (1.2) is locally asymptotically stable if either of the \( I_1 \) or \( I_2 \) holds; the positive equilibrium \( E_*(m^*, a^*) \) of system (1.2) is unstable if \( I_3 \) holds, where \( I_1, I_2, I_3 \) are given respectively by

\[
(I_1) \quad g(r) > 0, \\
(I_2) \quad g(r) < 0 \text{ and } \Lambda < 0, \\
(I_3) \quad g(r) < 0 \text{ and } \Lambda > 0.
\]

**Proof.** The sign of \( \tilde{D}_n \) will be determined by an argument of \( g(r) \) and \( \Lambda \) in the following three cases:

(a): If \( g(r) \geq 0 \), then
\[
\tilde{D}_n \geq \tilde{D}_0 > 0 \text{ for all } n \in \mathbb{N}_0;
\]
(b): If \( g(r) < 0 \), but \( \Lambda < 0 \), then
\[
\tilde{D}_n \geq \tilde{D}_0 > 0 \text{ for all } n \in \mathbb{N}_0;
\]
(c): If \( g(r) < 0 \), but \( \Lambda \geq 0 \), then there exists \( N_1, N_2 \) with \( N_1 \leq N_2 \) such that:
\[
\tilde{D}_n > 0, \quad \text{for } 0 \leq n < N_1 \text{ or } n > N_2.
\]

and
\[
\tilde{D}_n \leq 0, \quad \text{for } N_1 \leq n \leq N_2.
\]

Combined with the first case of Lemma 2.4, the Lemma 2.7 follows immediately. \( \Box \)

Lemma 2.7 indicates there is no diffusion-driven Turing instability under \( (I_1) \) or \( (I_2) \), in this case, diffusion does not change the stability of the positive equilibrium. Recall that \( \tilde{T}_n > \tilde{T}_0 > 0 \) for \( n \in \mathbb{N} \), the positive equilibrium in the nonhomogeneous case changes its stability only when \( \tilde{D}_n \) changes sign from positive to negative. Then a requirement for the occurrence of a Turing instability is the satisfaction of the condition \( \tilde{D}_{n_c} = 0 \), and the critical wave number \( k_c \) can be obtained from

\[
k_c^2 := \frac{n_c^2}{l^2} = \frac{1}{2d} \left( \frac{m^*}{(1 + m^*)^2} - \frac{d\alpha}{a^*} \right),
\]

and the necessary condition of Turing instability can be derived by:

\[
\alpha d^2 r^2 R_0 + \alpha (r - 1)^2 R_0^{-1} - 2d(r - 1)(2 - \alpha r) = 0.
\]
where \( R_0 = \frac{(1 - \alpha)^3}{(1 - \alpha r)^2} \) and (2.11) is independent of the wave number. The critical curves of Turing bifurcation defined by formula (2.11) can be seen in Fig.4.

![Figure 4: The critical curve of Turing bifurcation in \( \alpha - r \) plane with values of parameters are chosen as follows: \( d = 0.01 \).](image)

The critical bifurcation curves divide the \( \alpha - r \) plane into four regions under the condition (H1) in Fig.4. When \( d = 0.01 \), \( T_b \) is the only region where Turing instability occurs since \( g(r) > 0 \) in region \( T_d \), and \( g^2(r) - 4d\widetilde{D}_0 < 0 \) in \( T_a \) and \( T_c \). In region \( T_a \), all the eigenvalues of characteristic equation (2.7) have negative real part, that is, the constant steady state \( E_*(m^*, a^*) \) is locally asymptotically stable; When the parameters vary across the curve \( l_1 \) into the region \( T_b \), there is a eigenvalue that moves from the left half complex plane to the right through the origin, and a spatial periodic oscillating state appears from the constant steady state due to the Turing bifurcation; Similarly, when the parameters pass through \( l_2 \) into region \( T_c \) or even \( T_d \), the only positive eigenvalue move back to the left half complex plane, the spatial periodic oscillating state disappears, and \( E_*(m^*, a^*) \) regain its stability.

**Remark 2.8.** According to the research presented by [22], the formation mechanism of Turing pattern is a nonlinear reaction kinetics process coupled with a special type of diffusion process,
and the special diffusion process requires that the diffusion velocity of activator must be far less than that of the inhibitor in the system. Generally, the interaction-diffusion predator-prey model also follows such mechanism. By calculating the Jacobian matrix at the equilibrium, we can identify the role of predator and prey in activator-inhibitor systems: in most cases, the prey serves as the “activator”, while predator serves as the “inhibitor”. However, under (H2), according to lemma 2.7, if Turing instability occurs in model (1.2), then \( d\gamma < 1 \) must hold, that is, the diffusion velocity of predator must be far less than that of the prey; on the other hand, from the Jacobian matrix \( J = (J_{ij}) \) at the \( E^\ast(m^\ast,a^\ast) \), we know that \( J_{11} > 0, J_{22} < 0 \), all those indicate that in our model the mussels (predator) play the role “activator”, while algae, the “inhibitor”.

3 The existence of Hopf bifurcation induced by delay

In this section, we shall study the stability of the positive constant steady state \( E^\ast(m^\ast,a^\ast) \) and the existence of Hopf bifurcation for (1.3) with \( \tau \geq 0 \). In order to concentrate on the investigation of Hopf bifurcation, in the remaining part of this section, we always assume that (H1) and (H2) are satisfied.

Here let the phase space \( \mathcal{C} := C([-\tau,0],X_{\mathcal{C}}) \) with the sup norm. The linearization of system (1.3) at \( E^\ast(m^\ast,a^\ast) \) is given by

\[
\Gamma \dot{U}(t) = D\Delta U(t) + L_\ast(U_t),
\]

where \( L_\ast: \mathcal{C} \rightarrow X_{\mathcal{C}} \) is defined as

\[
L_\ast(\phi) = L_1\phi(0) + L_2\phi(-\tau),
\]

with

\[
L_1 = \begin{pmatrix}
0 & 0 \\
-a^\ast & -(\alpha + m^\ast)
\end{pmatrix},
L_2 = \begin{pmatrix}
m^\ast & rm^\ast \\
(1+m^\ast)^2 & 0 \\
0 & 0
\end{pmatrix},
\]

\[
\phi(t) = (\phi_1(t), \phi_2(t))^T, \quad \phi_1(t) = \begin{pmatrix}
\phi_1(t), & \phi_2(t) + \cdot
\end{pmatrix}^T, \quad \phi_2(t) = \begin{pmatrix}
\phi_1(t+\cdot), & \phi_2(t+\cdot)
\end{pmatrix}^T.
\]

The corresponding characteristic equation satisfies

\[
\lambda \Gamma \xi - D\Delta \xi - L_\ast(e^{\lambda \cdot} \xi) = 0,
\]

where \( \xi \in \text{dom}(\Delta) \setminus \{0\} \). Namely, we have

\[
\det \left( \lambda \Gamma + D\frac{n^2}{l^2} - L_1 - L_2 e^{-\lambda \tau} \right) = 0, \quad n \in \mathbb{N}_0.
\]
That is, each characteristic value \( \lambda \) is a root of the equation
\[
\gamma \lambda^2 + T_n \lambda + (B \lambda + M_n)e^{-\lambda \tau} + D_n = 0, \quad n \in \mathbb{N}_0,
\] (3.3)
where
\[
T_n = \alpha + m^* + (1 + \gamma d) \frac{n^2}{l^2}, \quad M_n = ra^*m^*(1 - \alpha r - ra^* \frac{n^2}{l^2});
\]
\[
D_n = d(\alpha + m^* + \frac{n^2}{l^2} \frac{n^2}{l^2}), \quad B = -\gamma r^2a^*m^*.
\] (3.4)
Next, we will show another assumption to ensure that \( \lambda = 0 \) is not the root of Eq.(3.3). Recall that \( g(r) = m^*(d\gamma P_0 - H_0) \), according to Lemma 2.7, we make the following assumption:

\[
(H3) \begin{cases}
    d\gamma P_0 - H_0^2 > 0, \\
    \text{or} \\
    d\gamma P_0 - H_0^2 < 0, \text{ and } (d\gamma P_0 - H_0^2)^2 - \frac{4d\tilde{D}_0}{m^*} < 0.
\end{cases}
\]

From the result in [17], as parameter \( \tau \) varies, the sum of the orders of the zeros of Eq.(3.3) in the open right half plane can change only if a pair of conjugate complex roots appear on or cross the imaginary axis. Now we would like to seek critical values of \( \tau \) such that there exists a pair of simple purely imaginary eigenvalues. Let \( \pm i\omega (\omega > 0) \) be solutions of the \((n + 1)\)th equation of Eq.(3.3). Then we have
\[
-\gamma \omega^2 + iT_n \omega + (i\omega B + M_n)e^{-i\omega \tau} + D_n = 0.
\]
Separating the real and imaginary parts, it follows that
\[
\begin{aligned}
M_n \cos \omega \tau + \omega B \sin \omega \tau &= \gamma \omega^2 - D_n, \\
M_n \sin \omega \tau - \omega B \cos \omega \tau &= T_n \omega.
\end{aligned}
\] (3.5)
Then we have
\[
\gamma^2 \omega^4 + (T_n^2 - 2\gamma D_n - B^2)\omega^2 + D_n^2 - M_n^2 = 0.
\] (3.6)
Denote \( z = \omega^2 \). Then (3.6) can be rewritten as
\[
\gamma^2 z^2 + T_n z + D_n^2 - M_n^2 = 0.
\] (3.7)
where
\[
\mathcal{T}_n = T_n^2 - 2\gamma D_n - B^2 = (1 + \gamma^2 d^2) \frac{n^4}{l^4} + \frac{2\alpha n^2}{a^* l^2} + \left(\frac{\alpha}{a^*} + \gamma r^2a^*m^*\right)\left(\frac{\alpha}{a^*} - \gamma r^2a^*m^*\right).
\]
Note that $\frac{\alpha}{a*} - \gamma r^2 a^{*2} m^* > 0$ is automatically satisfied due to the assumption (H2). Hence $\mathcal{J}_n > 0$ for all $n \in \mathbb{N}_0$.

Now we show the sufficient condition when Eq.(3.7) has positive roots. If $D_n^2 - M_n^2 < 0$, Eq.(3.7) has a unique positive root given by

$$z_n = \frac{-\mathcal{J}_n + \sqrt{\mathcal{J}_n^2 - 4\gamma^2(D_n^2 - M_n^2)}}{2\gamma^2},$$

where

$$D_n - M_n = \frac{d n^4}{l^4} + (d a* + r^2 a^{*2} m*) \frac{n^2}{l^2} - ar(r-1)a* \to \infty, \text{ as } n \to \infty,$$

with

$$D_0 - M_0 = -ar(r-1)a* < 0,$$

then we can find a constant $N_3 \in \mathbb{N}$ such that

$$D_n - M_n < 0, \text{ for } 0 \leq n < N_3,$$

and

$$D_n - M_n \geq 0, \text{ for } n \geq N_3.$$

Here we denote the set

$$\mathcal{S}_0 = \{n \in \mathbb{N}_0 | \text{Eq.(3.7) has positive roots under (H1)} \sim (H3)\}.$$

By the analysis above, we know that if $n \in \mathcal{S}_0$, then Eq.(3.3) has purely imaginary roots as long as $\tau$ takes the critical values which can be determined by Eq.(3.5), given by

$$\tau_{n,j} = \begin{cases} \frac{1}{\omega_n} \left( \arccos \left( \frac{\gamma M_n - BT_n}{\omega_n^2 - D_n M_n} \right) + j 2\pi \right), & \text{sin } \omega \tau > 0 \\ \frac{1}{\omega_n} \left( - \arccos \left( \frac{\gamma M_n - BT_n}{\omega_n^2 - M_n D_n} \right) + 2(j + 1)\pi \right), & \text{sin } \omega \tau < 0 \end{cases}, \quad j \in \mathbb{N}_0. \quad (3.9)$$

where $\omega_n = \sqrt{z_n}$.

Following the work of [6], we have

**Lemma 3.1.** Suppose that (H1)$\sim$(H3) are satisfied. Then

$$\beta'(\tau_{n,j}) > 0, \text{ for } j \in \mathbb{N}_0, \ n \in \mathcal{S}_0,$$

where

$$\beta(\tau) = \text{Re} \lambda(\tau).$$
Proof. Substituting $\lambda(\tau)$ into Eq.(3.3) and taking the derivative with respect to $\tau$ on both side, we obtain that

$$
\left(2\gamma\lambda + T_n + B e^{-\lambda\tau} - \tau(B\lambda + M_n)e^{-\lambda\tau}\right)\frac{d\lambda}{d\tau} - \lambda(B\lambda + M_n)e^{-\lambda\tau} = 0.
$$

Thus

$$
\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{2\gamma\lambda + T_n + B e^{-\lambda\tau} - \tau(B\lambda + M_n)e^{-\lambda\tau}}{\lambda(B\lambda + M_n)e^{-\lambda\tau}}.
$$

By Eq.(3.3) and Eq.(3.5), we have

$$
\text{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}_{\tau = \tau_{n,j}} = \text{Re}\left[\frac{(2\gamma\lambda + T_n)e^{\lambda\tau}}{\lambda(B\lambda + M_n)} + \frac{B}{\lambda(B\lambda + M_n)}\right]_{\tau = \tau_{n,j}}
= \text{Re}\left[\frac{(2\gamma\lambda + T_n)e^{\lambda\tau}}{\lambda(B\lambda + M_n)} - B^2 - 2\gamma^2\omega_n^2 - 2\gamma D_n + T_n^2\right]
= \frac{(\gamma\omega_n^2 - D_n)^2 + \omega_n^2 T_n^2}{B^2\omega_n^2 + M_n^2}
= \frac{\sqrt{(T_n^2 - 2\gamma D_n - B^2)^2 - 4\gamma^2(D_n^2 - M_n^2)}}{B^2\omega_n^2 + M_n^2}.
$$

Since the sign of $\text{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}$ is same as that of $\text{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}$, the lemma follows immediately. \qed

From (3.9), for a fixed $n \in S_0$, we have that

$$
\tau_{n,j} \leq \tau_{n,j+1}, \quad j \in \mathbb{N}_0.
$$

Let $\tau^* = \min_{n \in S_0}\{\tau_{n,0}\}$ be the smallest critical value such that the stability of $E_*$ will change. Summarizing the above analysis, we have the following lemma.

Lemma 3.2. Assume that (H1)$\sim$(H3) are satisfied. Then for

$$
\tau = \tau_{n,j}, \quad j \in \mathbb{N}_0, \ n \in S_0.
$$

the $(n+1)$th equation of (3.3) has a pair of simple pure imaginary roots $\pm i\omega_n$, and all the other roots have non-zero real parts. Moreover, all the roots of Eq.(3.3) have negative real parts for $\tau \in [0, \tau^*)$, and for $\tau > \tau^*$, Eq.(3.3) has at least one pair of conjugate complex roots with positive real parts.

Lemma 3.1 and Lemma 3.2 lead to the following theorem.

Theorem 3.3. Assume that (H1)$\sim$(H3) are satisfied. Then system (1.3) undergoes a Hopf bifurcation at the equilibrium $E_*(u^*, v^*)$ when $\tau = \tau_{n,j}$, for $j \in \mathbb{N}_0, \ n \in S_0$. Furthermore, the positive equilibrium $E_*(u^*, v^*)$ of system (1.3) is asymptotically stable for $\tau \in [0, \tau^*)$, and unstable for $\tau > \tau^*$. 

18
4 Direction of Hopf bifurcation and stability of bifurcating periodic solution

In this section, we shall study the direction of Hopf bifurcation near the positive equilibrium and stability of the bifurcating periodic solutions. By using the normal form theory and center manifold reduction due to [7, 8, 26], we shall show more detailed information of Hopf bifurcation caused by delay.

Rescaling the time $t \mapsto t/\tau$, let $\tilde{m}(x,t) = m(x,t) - m^*$, $\tilde{a}(x,t) = a(x,t) - a^*$, and drop the tilde for convenience of notation, then we have

$$
\begin{cases}
\frac{\partial m}{\partial t} = \tau \big[ d \Delta m + r^2 a^2 m^* m_t(-1) + r m^* a_t(-1) + f_1(m_t, a_t) \big], \quad x \in \Omega, \ t > 0, \\
\frac{\partial a}{\partial t} = \tau \big[ \Delta a - a^* a + f_2(m_t, a_t) \big], \quad x \in \Omega, \ t > 0, \\
\frac{\partial m}{\partial \nu} = 0, \quad \frac{\partial a}{\partial \nu} = 0, \quad x \in \partial \Omega, \ t > 0, \\
m(x,t) = m_0(x,t) - m^*, \ a(x,t) = a_0(x,t) - a^*, \quad x \in \Omega, -1 \leq t \leq 0,
\end{cases}
$$

(4.1)

where

$$
m_t(\theta) = m(x, t + \theta), \ a_t(\theta) = a(x, t + \theta), \ \theta \in [-1, 0],
$$

and for $\phi_1, \phi_2 \in \mathcal{C} := C([-1, 0], X_{\mathcal{C}})$

$$
f_1(\phi_1, \phi_2) = r \phi_1(0) \phi_2(-1) - \frac{m^*}{(1 + m^*)^2} \phi_1^2(-1) + \frac{1}{(1 + m^*)^3} \phi_1(0) \phi_1(-1)
$$

$$
+ \frac{m^*}{(1 + m^*)^4} \phi_1^3(-1) - \frac{1}{(1 + m^*)^5} \phi_1(0) \phi_1^2(-1) + \mathcal{O}(4),
$$

(4.2)

$$
f_2(\phi_1, \phi_2) = -\phi_1(0) \phi_2(0).
$$

Let $\tau = \tau^* + \epsilon$, as we discussed in Section 3 that the system (4.1) undergoes a Hopf bifurcation at the equilibrium $(0,0)$ when $\epsilon = 0$. Then we can rewrite system (4.1) in an abstract form in the space $\mathcal{C}$ as

$$
\dot{U}(t) = \tilde{D} \Delta U(t) + L_\epsilon(U_t) + F(\epsilon, U_t),
$$

(4.3)

where

$$
\tilde{D} = (\tau^* + \epsilon) \Gamma^{-1} D \quad \text{and} \quad L_\epsilon : \mathcal{C} \to X_{\mathcal{C}}, \ F : \mathcal{C} \to X_{\mathcal{C}}
$$

are defined, respectively, by

$$
L_\epsilon(\phi) = (\tau^* + \epsilon) \Gamma^{-1} L_1 \phi(0) + (\tau^* + \epsilon) \Gamma^{-1} L_2 \phi(-1),
$$

19
\[
F(\epsilon, \phi) = \Gamma^{-1}(F_1(\epsilon, \phi), F_2(\epsilon, \phi))^T,
\]
with
\[
(F_1(\epsilon, \phi), F_2(\epsilon, \phi)) = (\tau^* + \epsilon)(f_1(\phi_1, \phi_2), f_2(\phi_1, \phi_2)),
\]
where \(f_1\) and \(f_2\) are defined by (4.2).

The linearized equation at the origin \((0, 0)\) has the form
\[
\dot{U}(t) = \tilde{D}\Delta U(t) + L_\epsilon(U_t).
\]
According to the theory of semigroup of linear operator [15], we know that the solution operator of (4.4) is a \(C_0\)-semigroup, and the infinitesimal generator \(A_\epsilon\) is given by
\[
A_\epsilon \phi = \begin{cases} 
\dot{\phi}(\theta), & \theta \in [-1, 0), \\
\tilde{D}\Delta \phi(0) + L_\epsilon(\phi), & \theta = 0,
\end{cases}
\]
with
\[
dom(A_\epsilon) := \{ \phi \in C : \dot{\phi} \in C, \phi(0) \in \text{dom}(\Delta), \dot{\phi}(0) = \tilde{D}\Delta \phi(0) + L_\epsilon(\phi) \}.
\]
In order to study the dynamics near the Hopf bifurcation, we need to extend the domain of solution operator to a space of some discontinuous. Let
\[
\mathcal{BC} := \left\{ \phi : [-1, 0] \to X_C \mid \text{\phi is continuous on } [-1, 0), \lim_{\theta \to 0^-} \phi(\theta) \in X_C \text{ exists} \right\}
\]
Hence, equation (4.1) can be rewritten as the abstract ODE in \(\mathcal{BC}\):
\[
\dot{U}_t = A_\epsilon U_t + X_0 F(\epsilon, U_t),
\]
where
\[
X_0(\theta) = \begin{cases} 
0, & \theta \in [-1, 0), \\
I, & \theta = 0.
\end{cases}
\]
We denote
\[
b_n = \frac{\cos(nx/l)}{\| \cos(nx/l) \|}, \quad \beta_n = \{\beta_n^1, \beta_n^2\} = \{(b_n, 0)^T, (0, b_n)^T\},
\]
where
\[
\| \cos(nx/l) \| = \left( \int_0^{l\pi} \cos^2(nx/l) dx \right)^{\frac{1}{2}}.
\]
For \(\phi = (\phi^{(1)}, \phi^{(2)})^T \in C\), denote
\[
\phi_n = \langle \phi, \beta_n \rangle = \langle (\phi^{(1)}, \phi^{(2)}) \rangle^T.
\]
Define \( A_{\epsilon,n} \) as
\[
A_{\epsilon,n}(\phi_n(\theta)\beta_n) = \begin{cases} 
\dot{\phi}_n(\theta)\beta_n, & \theta \in [-1,0), \\
\int_{-1}^{0} d\eta_n(\epsilon,\theta)\phi_n(\theta)\beta_n, & \theta = 0,
\end{cases} \tag{4.7}
\]
and
\[
L_{\epsilon,n}(\phi_n) = (\tau^* + \epsilon)\Gamma^{-1}L_1\phi_n(0) + (\tau^* + \epsilon)\Gamma^{-1}L_2\phi_n(-1),
\]
\[
\int_{-1}^{0} d\eta_n(\epsilon,\theta)\phi_n(\theta) = -\frac{n^2}{l^2}\tilde{D}\phi_n(0) + L_{\epsilon,n}(\phi_n),
\]
where
\[
\eta_n(\epsilon,\theta) = \begin{cases} 
-(\tau^* + \epsilon)\Gamma^{-1}L_2, & \theta = -1, \\
0, & \theta \in (-1,0), \\
(\tau^* + \epsilon)\Gamma^{-1}L_1 - \frac{n^2}{l^2}\tilde{D}, & \theta = 0.
\end{cases}
\]
Denote \( A^* \) as the adjoint operator of \( A_0 \) on \( C^*: = C([0,1], X_C) \).
\[
A^*\psi(s) = \begin{cases} 
-\dot{\psi}(s), & s \in (0,1], \\
\sum_{n=0}^{\infty} \int_{-1}^{0} d\eta_n^T(0,\theta)\psi_n(-\theta)\beta_n, & s = 0.
\end{cases}
\]
Now, we introduce the bilinear formal \((\cdot, \cdot)\) on \( C^* \times C \)
\[
(\psi, \phi) = \sum_{k,j=0}^{\infty} (\psi_k, \phi_j)_c \int_{\Omega} b_kb_j dx,
\]
where
\[
\psi = \sum_{n=0}^{\infty} \psi_n\beta_n \in C^*, \quad \phi = \sum_{n=0}^{\infty} \phi_n\beta_n \in C,
\]
and
\[
\phi_n \in C := C([-1,0], \mathbb{R}^2), \quad \psi_n \in C^* := C([0,1], \mathbb{R}^2).
\]
Notice that
\[
\int_{\Omega} b_kb_j dx = 0 \text{ for } k \neq j,
\]
we have
\[
(\psi, \phi) = \sum_{n=0}^{\infty} (\psi_n, \phi_n)_c |b_n|^2;
\]
where $(\cdot, \cdot)_c$ is the bilinear form defined on $C^* \times C$

$$(\psi_n, \phi_n)_c = \psi_n(0) \phi_n(0) - \int_{-1}^0 \int_0^\theta \psi_n(\xi - \theta) d\eta_n(0, \theta) \phi_n(\xi) d\xi.$$ 

Let

$q(\theta)b_{n_0} = q(0)e^{i\omega_0 \tau^* \theta}b_{n_0}, \quad q^*(s)b_{n_0} = q^*(0)e^{-i\omega_0 \tau^* s}b_{n_0}$

be the eigenfunctions of $\mathcal{A}_0$ and $\mathcal{A}^*$ corresponding to the eigenvalues $i\omega_0 \tau^*$. By direct calculations, we have

$q(0) = (1, q_1)^T, \quad q^*(0) = M(q_2, 1), \quad \langle q^*, q \rangle_c = 1,$

where

$q_1 = \frac{-a^*}{i\gamma \omega_0 + \alpha + m^* + n_0^2/l^2}, \quad q_2 = \frac{i\gamma \omega_0 + \alpha + m^* + n_0^2/l^2}{rm^*e^{-i\omega_0 \tau^*}}, \quad M = \frac{(q_1 + q_2)e^{i\omega_0 \tau^*} + \tau^* q_2(r^2 a^* m^* + q_1 m^*)}{(q_1 + q_2)e^{i\omega_0 \tau^*} + \tau^* q_2(r^2 a^* m^* + q_1 m^*)}$.

Then we decompose the space $C$ as follows

$C = P \oplus Q,$

where

$P = \{zq_{n_0} + \bar{z}\bar{q}_{n_0} \mid z \in \mathbb{C}\}, \quad Q = \{\phi \in C \mid \langle q^*_n b_{n_0}, \phi \rangle = 0 \text{ and } (\bar{q}^* b_{n_0}, \phi) = 0\}.$

That is $P$ is the 2-dimensional center subspace spanned by the basis vectors of the linear operator $\mathcal{A}_0$ associated with purely imaginary eigenvalues $\pm i\omega_0 \tau^*$, and $Q$ is the complement space of $P$.

Thus, system \((4.6)\) can be rewritten as

$U_t = z(t)q(\cdot)b_{n_0} + \bar{z}(t)\bar{q}(\cdot)b_{n_0} + W(t, \cdot),$ 

where

$z(t) = (q^* b_{n_0}, U_t), \quad W(t, \cdot) \in Q, \quad (4.8)$

and

$W(t, \theta) = U_t(\theta) - 2\text{Re}\{z(t)q(\theta)b_{n_0}\}. \quad (4.9)$

Then we have

$\dot{z}(t) = i\omega_0 \tau^* z(t) + q^*(0)\langle F(0, U_t), \beta_{n_0}\rangle, \quad (4.10)$

22
where
\[ \langle F, \beta_n \rangle := (\langle F_1, b_n \rangle, \langle F_2, b_n \rangle)^T. \]

It follows from Appendix A of \[8\] (also see \[13\]), there exists a center manifold \( \mathcal{C}_0 \) and we can write \( W \) in the following form on \( \mathcal{C}_0 \) nearby \((0, 0)\):

\[
W(t, \theta) = W(z(t), \bar{z}(t), \theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots, \tag{4.11}
\]

For solution \( U_t \in \mathcal{C}_0 \), we denote
\[
F(0, U_t) \mid_{\mathcal{C}_0} = \tilde{F}(0, z, \bar{z}),
\]
and
\[
\tilde{F}(0, z, \bar{z}) = \tilde{F}_{20}\frac{z^2}{2} + \tilde{F}_{11}z\bar{z} + \tilde{F}_{02}\frac{\bar{z}^2}{2} + \tilde{F}_{21}\frac{z^2\bar{z}}{2} + \cdots.
\]

Therefore the system restricted to the center manifold is given by
\[
\dot{z}(t) = i\omega_0\tau^* z(t) + g(z, \bar{z}),
\]
and denote
\[
g(z, \bar{z}) = g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + \cdots.
\]

By direct calculation, we get
\[
g_{20} = \tau^* M \int_0^{l\pi} b_{n_0}^3 dx \left[ q_2 \left( 2r_1 q_1 e^{i\omega_0 \tau^*} + \frac{2}{(1 + m^*)^2} e^{2i\omega_0 \tau^*} - \frac{2m^*}{(1 + m^*)^2} e^{-i\omega_0 \tau^*} \right) - 2\gamma^{-1} q_1 \right],
\]
\[
g_{11} = \tau^* M \int_0^{l\pi} b_{n_0}^3 dx \left[ q_2 \left( r_1 + \frac{1}{(1 + m^*)^2} e^{-i\omega_0 \tau^*} + (r_1^* + \frac{1}{(1 + m^*)^2} e^{i\omega_0 \tau^*} - \frac{2m^*}{(1 + m^*)^3} e^{2i\omega_0 \tau^*} \right) - \gamma^{-1} (q_1 + \bar{q}_1) \right],
\]
\[
g_{02} = \tau^* M \int_0^{l\pi} b_{n_0}^3 dx \left[ q_2 \left( 2r_1^* q_1 e^{i\omega_0 \tau^*} + \frac{2}{(1 + m^*)^3} e^{2i\omega_0 \tau^*} - \frac{2m^*}{(1 + m^*)^3} e^{-i\omega_0 \tau^*} \right) - 2\gamma^{-1} \bar{q}_1 \right],
\]
\[
g_{21} = \tau^* M \left( Q_1 \int_0^{l\pi} b_{n_0}^4 dx + Q_2 \int_0^{l\pi} b_{n_0}^2 dx \right),
\]
23
Comparing the coefficients of (4.12) with the derived function of (4.11), we obtain
\[ (A_0 - 2i\omega_0\tau^*I)W_{20}(\theta) = -H_{20}(\theta), \quad A_0W_{11}(\theta) = -H_{11}(\theta), \quad \cdots. \]
From (4.13) and (4.14), for \(\theta \in [-1, 0)\), we have
\[
W_{20}(\theta) = -\frac{g_{20}}{i\omega_n \tau^*} \left( \frac{1}{q_1} \right) e^{i\omega_n \tau^* \theta b_{n_0} - \frac{g_{02}}{3i\omega_n \tau^*} \left( \frac{1}{q_1} \right) e^{-i\omega_n \tau^* \theta b_{n_0} + E_1 e^{2i\omega_n \tau^* \theta}},
\]
\[
W_{11}(\theta) = \frac{g_{11}}{i\omega_n \tau^*} \left( \frac{1}{q_1} \right) e^{i\omega_n \tau^* \theta b_{n_0} - \frac{g_{11}}{i\omega_n \tau^*} \left( \frac{1}{q_1} \right) e^{-i\omega_n \tau^* \theta b_{n_0} + E_2},
\]
(4.14)
where \(E_1\) and \(E_2\) can be obtained by setting \(\theta = 0\) in \(H\), that is
\[
(A_0 - 2i\omega_n^\tau \tau^* I) E_1 e^{2i\omega_n^\tau \tau^* \theta} |_{\theta=0} + \tilde{F}_{20} = 0, \quad A_0 E_2 |_{\theta=0} + \tilde{F}_{11} = 0.
\]
(4.15)
The terms \(\tilde{F}_{20}\) and \(\tilde{F}_{11}\) are elements in the space \(\mathcal{C}\), and
\[
\tilde{F}_{20} = \sum_{n=1}^{\infty} \langle \tilde{F}_{20}, \beta_n \rangle b_n, \quad \tilde{F}_{11} = \sum_{n=1}^{\infty} \langle \tilde{F}_{11}, \beta_n \rangle b_n.
\]
Denote
\[
E_1 = \sum_{n=0}^{\infty} E_1^n b_n, \quad E_2 = \sum_{n=0}^{\infty} E_2^n b_n,
\]
then from (4.15) we have
\[
(A_0 - 2i\omega_n^\tau \tau^* I) E_1^n b_n e^{2i\omega_n \tau^* \theta} |_{\theta=0} = -\langle \tilde{F}_{20}, \beta_n \rangle b_n,
\]
\[
A_0 E_2^n b_n |_{\theta=0} = -\langle \tilde{F}_{11}, \beta_n \rangle b_n, \quad n = 0, 1, \cdots.
\]
Thus, \(E_1^n\) and \(E_2^n\) could be calculated by
\[
E_1^n = \left( 2i\omega_n^\tau \tau^* I - \int_{0}^{1} e^{2i\omega_n \tau^* \theta} d\eta_n(0, \theta) \right)^{-1} \langle \tilde{F}_{20}, \beta_n \rangle,
\]
\[
E_2^n = - \left( \int_{0}^{1} d\eta_n(0, \theta) \right)^{-1} \langle \tilde{F}_{11}, \beta_n \rangle, \quad n = 0, 1, \cdots,
\]
where
\[
\langle \tilde{F}_{20}, \beta_n \rangle = \begin{cases} \frac{1}{\sqrt{\pi}}, & \hat{F}_{20}, \quad n_0 \neq 0, \ n = 0, \\ \frac{1}{\sqrt{2\pi}}, & \hat{F}_{20}, \quad n_0 \neq 0, \ n = 2n_0, \\ \frac{1}{\sqrt{\pi}}, & \hat{F}_{20}, \quad n_0 = 0, \ n = 0, \\ 0, & other, \end{cases}
\]
\( \langle \hat{F}_{11}, \beta_n \rangle = \begin{cases} \frac{1}{\sqrt{l \pi}} \hat{F}_{11}, & n_0 \neq 0, \ n = 0, \\ \frac{1}{\sqrt{2l \pi}} \hat{F}_{11}, & n_0 \neq 0, \ n = 2n_0, \\ \frac{1}{\sqrt{l \pi}} \hat{F}_{11}, & n_0 = 0, \ n = 0, \\ 0, & \text{other}, \end{cases} \)

\( \hat{F}_{20} = \begin{bmatrix} 2r q_1 e^{-i \omega_{n_0} \tau^*} + \frac{2}{(1 + m^*)^2} e^{-i \omega_{n_0} \tau^*} - \frac{2m^*}{(1 + m^*)^3} e^{-i 2 \omega_{n_0} \tau^*} \\ -2 \gamma^{-1} q_1 \end{bmatrix} \)

\( \hat{F}_{11} = \begin{bmatrix} r (q_1 e^{-i \omega_{n_0} \tau^*} + \bar{q}_1 e^{i \omega_{n_0} \tau^*}) + \frac{2}{(1 + m^*)^3} \\ -\gamma^{-1} (q_1 + \bar{q}_1) \end{bmatrix} \)

Hence, \( g_{21} \) could be represented explicitly.

Denote

\[
\begin{align*}
c_1(0) &= \frac{i}{2 \omega_{n_0} \tau^*} (g_{20} g_{11} - 2 |g_{11}|^2 - \frac{1}{3} |g_{02}|^2) + \frac{1}{2} g_{21}, \\
\mu_2 &= -\frac{\text{Re}(c_1(0))}{\tau^* \text{Re}(\lambda'(\tau^*))}, \quad \beta_2 = 2 \text{Re}(c_1(0)), \\
T_2 &= -\frac{1}{\omega_{n_0} \tau^*} (\text{Im}(c_1(0)) + \mu_2 (\omega_{n_0} + \tau^* \text{Im}(\lambda'(\tau^*)))).
\end{align*}
\]

By the general result of Hopf bifurcation theory [8], the properties of Hopf bifurcation can be determined by the parameters in (4.16): \( \beta_2 \) determines the stability of the bifurcating periodic solutions: the bifurcating periodic solutions are orbitally asymptotically stable(unstable) if \( \beta_2 < 0(>0) \); \( \mu_2 \) 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 when \( \tau > \tau^* (< \tau^*) \); and \( T_2 \) determines the period of the bifurcating periodic solutions: when \( T_2 > 0(<0) \), the period increases(decreases) as the \( \tau \) varies away from \( \tau^* \).

From Lemma 3.1 in Section 3, we know that \( \text{Re}(\lambda'(\tau^*)) > 0 \). Combining with above discuss, we obtain the following theorem.

**Theorem 4.1.** If \( \text{Re}(c_1(0)) < 0(>0) \), then the bifurcating periodic solutions exists for \( \tau > \tau^* (< \tau^*) \) and are orbitally asymptotically stable(unstable).

## 5 Simulations

In this section, we shall show some simulations to illustrate our theoretical results. Let \( l = 1 \), and choose

\[
\gamma = 0.5, \quad d = 1.0, \quad \alpha = 0.10, \quad r = 2.
\]
Since $0 < \alpha < 1 < r < \alpha^{-1}$, then $E_\star(m_\star, a_\star)$ is the only positive equilibrium with $(m_\star, a_\star) = (0.1250, 0.4444)$. One can easily verify that (H1) \sim (H3) are satisfied. By a simple calculation, we also obtain that Eq.(3.7) has a positive root only for $n = 0$, and

$$\omega \approx 0.3253, \quad \tau^* \approx 2.3545.$$  

Furthermore, we have $c_1(0) \approx -13.1406 - 5.99715i$, which means $\beta < 0$, $\mu > 0$. From Theorem 3.3 and 4.1, the positive equilibrium $E_\star(0.1250, 0.4444)$ is locally asymptotically stable when $\tau \in [0, \tau^*)$ (see Fig.5), moreover, system (1.3) undergoes a Hopf bifurcation at $\tau = \tau^*$, the direction of the Hopf bifurcation is forward and bifurcating periodic solutions are orbitally asymptotically stable (see Fig.6).

**Figure 5:** The positive equilibrium is locally asymptotically stable when $\tau \in [0, \tau^*)$, where $\tau = 2 < \tau^* \approx 2.3545$.  

27
Figure 6: The bifurcating periodic solution is orbitally asymptotically stable, where $\tau = 3.6 > \tau^* \approx 2.3545$. 
If we choose
\[ \gamma = 0.5, \quad d = 1.0, \quad \alpha = 0.10, \quad r = 0.5, \quad \tau = 2. \]
Here \( r = 0.5 \in (0, 1) \), from Remark 2.5, we know that the boundary equilibrium \( E_0(0, 1) \) is locally asymptotically stable (see Fig. 7).

The initial conditions are given by
\[ m_0(x, t) = 0.1250 + 0.1 \cos 2x, \quad a_0(x, t) = 0.4444 - 0.1 \cos 2x, \quad (x, t) \in [0, \pi] \times [-\tau, 0]. \]

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