Bifurcation analysis in a diffusion mussel-algae interaction system with delays considering the half-saturation constant

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Abstract In this paper, the kinetics of a class of delayed reaction-diffusion mussel-algae system under Neumann boundary conditions with the half-saturation constant is studied. The global existence and priori bounds as well as the existence conditions of positive equilibrium are obtained. The half-saturation constant affects the stability of the system and may result in Turing instability. When the half-saturation constant exceeds a certain critical value, the boundary equilibrium is globally asymptotically stable which means that the larger half-saturation constant forces the mussel population toward extinction. By analyzing the distribution of the roots of the characteristic equation with two delays, the stability conditions of the positive equilibrium in the parameter space are obtained. The stability of the positive equilibrium can be changed by steady-state bifurcation, Hopf bifurcation, Hopf-Hopf bifurcation or Hopf-steady state bifurcation, which can be verified by some numerical simulations. Among the parameters, the half-saturation constant and two delays drive the complexity of system dynamics.

Keywords Mussel-algae system · Half-saturation constant · Delay · Stability · Bifurcation

Mathematics Subject Classification 34C23 · 92D25 · 34D20

1 Introduction

There has been great interest in dynamical characteristics (including stable, unstable, bifurcation and oscillatory behavior) of population models since Vito Volterra and James Lotka proposed the seminal models of predator-prey models in the mid-1920s. The mussel-algal interaction model is one of them. Mussel beds are a typical system for studying pattern formation, in which patterns develop at two different scales, namely large scale banded patterns and small scale reticulated patterns. Recently, the emergence of nonlinear traveling waves in such systems has led to some researchers to propose this mechanism to better understand the periodic patterns observed in young beds of mussels feeding on algae. Many ecologists and mathematicians had used the mussel-algal model to study the development of mussel beds. Particularly, van de Koppel et al. [1] reported that these river beds occurred on the soft substrates of tidal pools at the edge of the Wadden Sea. Their model included a positive feedback to describe these promoting effects at higher mussel densities. From these observations, van de Koppel et al. [2] and Liu et al. [3] devised a field experiment containing
a young mussel homogeneous substrate covered by a relatively stationary seawater layer including algae as a food source and observed various clumps or gapped type patterns. These laboratory experiments, consisting of young mussel beds, were initially distributed evenly over a homogeneous substrate covered with a static ocean layer containing algae, replicating patterns observed in the field. Van de Kopp et al. [1] proposed a coupled partial differential equation with two components containing the diffusion effect of mussel and advection effect of algae, but ignored the lateral diffusion effect of latter, which provided an explanation for the pattern formation of mussel. Based on the nonlinear numerical methods, Wang et al. [4] performed stability analyses for linear systems, compared numerical results for nonlinear systems, and focused on the sensitivity of model parameters to evaluate their effects on the velocity, amplitude, and wavelength of banded migration modes. Liu et al. [5] extended the simulation to two dimensions. Cangelosi et al. [6] modified the unidirectional advection formula of algal concentration into random Brownian dispersion, and obtained a Turing patterns similar to that of the original algal model. The system is given as follows:

\[
\begin{align*}
\frac{\partial A(x,t)}{\partial t} &= D_A \Delta A(x,t) + \rho (A_u - A(x,t)) \\
&\quad - V \frac{\partial A(x,t)}{\partial x} - \frac{k}{\rho} M(x,t) A(x,t), \\
\frac{\partial M(x,t)}{\partial t} &= D_M \Delta M(x,t) + ecM(x,t)A(x,t) \\
&\quad - d_M \frac{k_M}{k_M + M(x,t)} M(x,t),
\end{align*}
\]

where \( A(x,t) \) and \( M(x,t) \) are the algae concentrations in the lower water layer overlying the mussel bed and the mussel biomass density on the sediment at time \( t \) and space \( x \in \Omega \). \( \Omega \subseteq \mathbb{R}^d \) is a bounded domain with a smooth boundary \( \partial \Omega \). \( \Delta \) is Laplace operator and \( \rho \) is the exchange rate between the upper and lower water layers. \( A_u \) describes the uniform concentration of algae in the upper water body. The velocity \( V \) of the tidal current is assumed to be acting in the positive direction of \( x \). \( c \) is the consumption constant and \( H \) is the height of the lower water layer. \( e \) is the biomass conversion constant for mussel to ingesting algae. The maximal mussel mortality rate per capita \( d_M \) represents mussel loss due to predation or dislodgement. \( k_M \) is the value of \( M(x,t) \) at which mortality is half maximal. \( D_M \) is a measure of mussel motility caused by their pedal locomotion mechanism and its concomitant byssal thread deployment [4]. The diffusion of algae consists of two parts: an active lateral diffusion \( D_A \) because their mechanism of locomotion is flagella and a passive vertical diffusion \( \rho \) on account of the photo-gyro-gravitactic driven exchange between the upper and lower benthic water layers [7] (see Fig. 1).

Note that although on the large scale, the algae was considered advection and tidal flows, on the small scale they actually dispersed in the liquid as Brownian particles. The experiments had shown that mussels could move actively within and between clusters, meaning that advection and tidal currents in small scales had little effect on mussel beds. Although advection and diffusion were two different ecological processes, in real mussel bed ecosystems, the two processes were usually coexisting and had the same activation-inhibition mechanism [8].

The advection and diffusion are equivalent for the emergence of spatial self-organizing patterns. Song et al. [9] and Jiang [10] studied Turing-Hopf bifurcations of system (1) under \( V = 0 \) and Neumann boundary conditions based on the normal form method, and obtained explicit dynamic classification at the critical point. Based on system (1), Shen and Wei [11, 12] considered the effects of delay. Shen and Wei [13] considered that the mortality involves a positive feedback term resulting from the reduction of dislodgment and predation and a negative feedback term resulting from the intraspecific competition for mussel. Their results suggested that the regular patterning in mussel beds were caused by the high mobility of algae or the low diffusion of mussels. Zhong et al. [14] investigated the spatiotemporal dynamics for a diffusive mussel-algae model near a Hopf bifurcation point. They found that the strip patterns were mainly induced by Turing instability in equilibrium and spot patterns were mainly induced by Turing instability in limit cycles by numerical simulations. In this paper, we use the suggestion in [15] to introduce saturated growth in the mussel population and revise system (1) as

\[
\begin{align*}
\frac{\partial A(x,t)}{\partial t} &= D_A \Delta A(x,t) + \rho (A_u - A(x,t)) \\
&\quad - \frac{H}{\beta + A(x,t)} A(x,t), \\
\frac{\partial M(x,t)}{\partial t} &= D_M \Delta M(x,t) + ec \frac{A(x,t)}{\beta + A(x,t)} M(x,t) \\
&\quad - d_M \frac{k_M}{k_M + M(x,t)} M(x,t),
\end{align*}
\]

where \( \beta \) is the half-saturation constant.
By introducing the dimensionless variables:
\[
\tilde{x} = x \sqrt{w/DA}, \quad w = ck_M/H, \quad \tilde{t} = d_M t,
\]
\[
m = M/k_M, \quad a = A/A_u, \quad \alpha = \rho/w, \quad r = d_M/w, \quad \gamma = ec/d_M.
\]
\[
\mu = D_M/D_A \gamma, \quad b = \beta/A_u
\]
and removing the “−”, system (2) becomes
\[
\begin{align*}
\frac{\partial a(x,t)}{\partial \tilde{t}} &= \Delta a(x,t) + \alpha \left(1 - a(x,t)\right) - \frac{a(x,t)m(x,t)}{b + a(x,t)}, \\
\frac{\partial m(x,t)}{\partial \tilde{t}} &= \mu \Delta m(x,t) + \frac{\gamma a(x,t)m(x,t)}{b + a(x,t)} - \frac{m(x,t)}{1 + m(x,t),}
\end{align*}
\]

In 1986, Stepan carried out the first Hopf analysis in the presence of a single delay and the possibility of Hopf-Hopf bifurcation appeared \[16\]. It is well known that the delay may lead to periodic oscillations and the diffusion may cause Turing instability \[17–19\]. Inspired by the work of \[10–12,15\], we establish a delayed mussel-algae system with the Neumann boundary conditions in one-dimensional space as follows:

\[
\begin{align*}
\frac{\partial a(x,t)}{\partial \tilde{t}} &= \Delta a(x,t) + \alpha \left(1 - a(x,t)\right) - \frac{a(x,t)m(x,t)}{b + a(x,t)}, \\
\frac{\partial m(x,t)}{\partial \tilde{t}} &= \mu \Delta m(x,t) + \frac{\gamma a(x,t)m(x,t)}{b + a(x,t)} - \frac{m(x,t)}{1 + m(x,t),} \\
\frac{\partial a(x,t)}{\partial x} &= \frac{a(x,t)}{1 + \tau_2}, \\
a(x, t) &= \varphi(x, t) \geq 0, \quad m(x, t) = \psi(x, t) \geq 0, \\
a(x, 0) &= \nu_1(x) \geq 0, \quad m(x, 0) := \nu_2(x) \geq 0,
\end{align*}
\]
where \( \tau = \max\{\tau_1, \tau_2\} \). \( \tau_1 \) represents the period of digestion of mussel, i.e. the consumption of algae in earlier times can make the mussel population in a later time in order to be more practical. \( \tau_2 \) represents the mortality of mussel depending on the state whether they have been eaten in the past. A system with two time delays can produce complex dynamics \[20,21\]. This paper will try to explore the complex bifurcation phenomena of system (4).

Compared with the work in \[10–12,15\], this article has two innovations: firstly, the half-saturation term is introduced into the mussel population growth function and the effect to the dynamics of system is investigated; secondly, two different delays are introduced and the bifurcation problem caused by delays is discussed.

Define the Sobolev space with real-value
\[
X = \left\{ (u_1, u_2) \in H^2(0, l\pi) \times H^2(0, l\pi) \middle| \frac{\partial u_1}{\partial x} = \frac{\partial u_2}{\partial x} = 0, \quad x = 0, \quad l\pi \right\}
\]
and its complexification \( \mathbb{X} = X \oplus iX = \{ \alpha + \beta \mid \alpha, \beta \in X \} \) with \( L^2 \) inner product defined as

\[
\begin{align*}
\int_{-l\pi}^{l\pi} (u_1, u_2) \cdot (v_1, v_2) &= \int_{-l\pi}^{l\pi} (u_1 \cdot v_1 + u_2 \cdot v_2), \\
x \in (0, l\pi), \quad t > 0, \\
x \in (0, l\pi), \quad t \geq 0, \\
x = 0, \quad l\pi, \quad t > 0, \\
x \in [0, l\pi], \quad t \in [-\pi, 0], \\
x \in [0, l\pi],
\end{align*}
\]
where \( W_1 = (w_{11}, w_{12})^T \in \mathbb{R} \) and \( W_2 = (w_{21}, w_{22})^T \in \mathbb{R} \).

The structure of this paper is as follows. In next section, the existence conditions of the positive equilibrium are given. When the two delays do not exist, we get the global existence and a priori bound of solutions, at the same time, the conditions of Turing instability are obtained. When the two delays do not exist, we get the global existence and a priori bound of solutions, at the same time, the conditions of Turing instability are given in Sect. \ref{sec:Turing}. Furthermore, for the delayed system, when the half-saturation constant exceeds some critical value, the mussel population will die out. By analyzing the distribution of eigenvalues, we obtain the stability conditions for the positive equilibrium in the parameter space. The positive equilibrium can lose the stability by the steady-state bifurcation, Hopf bifurcation, Hopf-steady state bifurcation or Hopf-Hopf bifurcation or Hopf-steady state bifurcation. These results are shown in Sect. \ref{sec:Hysteresis}. At last, some numerical simulations verify that the dynamic behaviors of the system caused by the half-saturation constant are consistent with the theoretical findings and some new findings are foreseen.

\section{Equilibrium}

The equilibrium \( E(\mathbf{a}, m) \) of system \((4)\) satisfies the following equations:

\[
\begin{align*}
\frac{am}{b+a} &= \alpha(1-a), \\
\frac{m}{b+a} &= \frac{m}{m+1}.
\end{align*}
\]

The boundary equilibrium \( E_0(1, 0) \) always exists. The existence of positive equilibrium \( E^*(\mathbf{a}^*, m^*) \) needs some analyses described as follows.

From Eq. \((5)\), it obtains that \( \mathbf{a} \) must satisfy the following equation:

\[
F(\mathbf{a}) := \mathbf{a}^2 + L_1 \mathbf{a} + L_2 = 0,
\]

where

\[
L_1 = b - \frac{1}{\alpha} + \frac{1}{\gamma_a} - 1 \quad \text{and} \quad L_2 = \left(\frac{1}{\gamma_a} - 1\right)b.
\]

If Eq. \((6)\) has a root \( \mathbf{a}^* \) satisfying \( 0 < \mathbf{a}^* < 1 \), then system \((4)\) exists a positive equilibrium \( E^*(\mathbf{a}^*, m^*) \), where

\[
m^* = \frac{\alpha(b+a^*)(1-a^*)}{a^*}.
\]

The existence of positive root of Eq. \((6)\) is given as follows.

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(1) If \( L_2 < 0 \) and \( F(1) > 0 \), then there exists a unique \( \mathbf{a}^* \) such that \( 0 < \mathbf{a}^* < 1 \). Furthermore, \( L_2 < 0 \) is equivalent to \( \gamma > \frac{1}{\alpha} \) and \( F(1) > 0 \) is equivalent to \( b + 1 > \gamma \). Hence, if

\[
A1 \quad \frac{1}{\alpha} < \gamma < b + 1
\]

holds, then Eq. \((6)\) exists a uniquely positive root

\[
0 < \mathbf{a}^*_+ = -\frac{-L_1+\sqrt{L_2}}{2} < 1
\]

and system \((4)\) exists a uniquely positive equilibrium \( E^*_+(\mathbf{a}^*_+, m^*_+) \) and \( m^*_+ \) satisfies the equality \((7)\).

(2) If \( L_2 > 0 \), then Eq. \((6)\) may exist positive root only if \( L_1 < 0 \). However, \( L_1 < 0 \) is equivalent to \( \alpha + 1 > b\alpha \) and \( \gamma > \frac{1}{\gamma_a-b\alpha} \). Let \( \delta = L_1^2 - 4L_2 = \left(\frac{1}{\gamma_a} - 1\right)^2 - 2(b + 1\frac{1}{\alpha})(\frac{1}{\gamma_a} - 1) + (b - \frac{1}{\alpha})^2 \). Hence if

\[
A2 \quad L_1 < 0, \; L_2 > 0, \; \delta > 0, \; F(1) < 0
\]

holds, then Eq. \((6)\) exists a uniquely positive solution

\[
0 < \mathbf{a}^*_- = -\frac{-L_1-\sqrt{L_2}}{2} < 1
\]

and at the same time, system \((4)\) exists a uniquely positive equilibrium \( E^*_-(\mathbf{a}^*_-, m^*_-) \) and \( m^*_- \) satisfies Eq. \((7)\).

The condition \((A2)\) is equivalent to one of the following

\[
\begin{align*}
& \text{or} \\
& \text{or}
\end{align*}
\]

(3) If the following condition holds,

\[
A3 \quad -2 < L_1 < 0, \; L_2 > 0, \; \delta > 0, \; F(1) > 0,
\]

i.e.,

\[
A31 \quad 0 < \mathbf{a}^* < 1 + \alpha, \quad \frac{1}{\alpha + (1 - \sqrt{b\alpha})^2} < \gamma < \frac{1}{\alpha}
\]

or
(A32) \( (b + 1) \alpha < 1, \)
\[
\frac{1}{\alpha + (1 - \sqrt{b \alpha})^2} < \gamma < \min \left\{ b + 1, \frac{1}{1 - \alpha (b + 1)} \right\},
\]
then Eq. (5) exist two positive roots
\[
0 < a^*_1 = \frac{-b + \sqrt{b}}{2} < 1.
\]
Hence system (4) exists two positive equilibrium \( E^*_\pm (a^*_\pm, m^*_\pm) \) and \( m^*_\pm \) satisfy the equality (7).

Denote
\[
\mathcal{T} = \{(b, \alpha_1, \gamma) : (A1) \text{ or } (A2) \text{ or } (A3) \text{ hold.}\}
\]
If \( (b, \alpha_1, \gamma) \in \mathcal{T} \), then system (4) exists at least one positive equilibrium, otherwise, the positive equilibrium does not exist.

3 Dynamics of system (3)

In this section, we focus on system (3) to investigate the property of solutions and Turing instability.

3.1 Existence and priori bound of solutions

In this part, the sufficient conditions for the existence of a positive solution of system (3) are given and a priori bound of solutions is derived.

Theorem 1 (i) If \( v_i(x) \geq 0 \) and \( v_i(x) \neq 0 \) \( (i = 1, 2) \), then system (3) exists a unique solution
\[
(a(x, t), m(x, t))\]
satisfying
\[
0 < a(x, t) \leq a^*(t), \quad 0 < m(x, t) \leq m^*(t) \quad \text{for } t > 0 \quad \text{and } x \in [0, l\pi],
\]
where \( (a^*(t), m^*(t)) \) is the unique solution of
\[
\begin{align*}
\frac{da(t)}{dt} &= \alpha \left( 1 - a(t) \right), \\
\frac{dm(t)}{dt} &= \frac{\gamma a(t)m(t)}{b+a(t)} - \frac{m(t)}{1+m(t)}, \\
a(0) &= v_1^*, \quad m(0) = v_2^* = \sup_{x \in [0, l\pi]} v_2(x).
\end{align*}
\]
(ii) If \( b + 1 > \gamma \), then all solutions \( (a(x, t), m(x, t)) \) of system (3) satisfy the following estimates
\[
\lim_{t \to \infty} \sup_{x \in [0, l\pi]} a(t, x) \leq 1 \quad \text{and}
\]
\[
\lim_{t \to \infty} \sup_{x \in [0, l\pi]} m(x, t) \leq \frac{b + 1 - \gamma}{\gamma} := m^*.
\]

Proof Define
\[
\begin{align*}
g_1(a, m) &= \alpha \left( 1 - a \right) - \frac{am}{b+a} \quad \text{and} \quad g_2(a, m) = \frac{am}{b+a} - \frac{m}{1+m},
\end{align*}
\]
which has \( \frac{\partial g_1}{\partial m} \leq 0 \) and \( \frac{\partial g_2}{\partial a} \geq 0 \) for \( (a, m) \in \mathbb{R}^2_+ \). Then system (3) is a mixed quasi-monotone system [22, 23].

Denote
\[
(P_1(t, x), Z_1(t, x)) = (0, 0) \quad \text{and} \quad (P_2(t, x), Z_2(t, x)) = (a^*(t), m^*(t)).
\]
Since \( 0 \leq v_i(x) \leq v_i^* \) \( (i = 1, 2) \),
\[
r \frac{\partial P_2}{\partial t} - \Delta P_2 - g_1(P_2, Z_1)
\]
\[
= 0 \geq -\alpha
\]
\[
= r \frac{\partial P_1}{\partial t} - \Delta P_1 - g_1(P_1, Z_2),
\]
\[
\frac{\partial Z_2}{\partial t} - \mu \Delta Z_2 - g_2(P_2, Z_2)
\]
\[
= 0 \geq 0
\]
\[
= \frac{\partial Z_1}{\partial t} - \mu \Delta Z_1 - g_2(P_1, Z_1),
\]
hence \( (P_1(t, x), Z_1(t, x)) \) and \( (P_2(t, x), Z_2(t, x)) \) are the lower-solution and upper-solution of system (3), respectively. From [24, 25], it can know that system (3) exists a uniquely global solution \( (a(x, t), m(x, t)) \) satisfying
\[
0 \leq a(x, t) \leq a^*(t) \quad \text{and} \quad 0 \leq m(x, t) \leq m^*(t) \quad \text{for } t \geq 0.
\]
The strong maximum principle implies that \( a(x, t) > 0 \) and \( m(x, t) > 0 \) when \( t > 0 \) for all \( x \in [0, l\pi] \). This completes the proof of (i).

It has known that \( a(x, t) \leq a^*(t) \) for \( t > 0 \), and \( a^*(t) \) is the unique solution of
\[
\begin{align*}
r \frac{da(t)}{dt} &= \alpha \left( 1 - a \right), \\
a(0) &= v_1^* > 0,
\end{align*}
\]
which yields to \( \lim_{t \to \infty} a^*(t) = 1 \). Thus for any \( \varepsilon > 0 \), there exists \( T_0 > 0 \) such that
\[
a(x, t) < 1 + \varepsilon \quad \text{for } t > T_0 \quad \text{and} \quad x \in [0, l\pi]
\]
which implies that \( \lim_{t \to \infty} \sup_{x \in [0, l\pi]} a(x, t) \leq 1 \).

From \( m(x, t) \leq m^*(t) \) for \( t > 0 \), and \( m^*(t) \) is the unique solution of
\[
\begin{align*}
\frac{dm(t)}{dt} &= \frac{\gamma a(t)m(t)}{b+a(t)} - \frac{m(t)}{1+m(t)}, \\
m(0) &= v_2^* > 0,
\end{align*}
\]

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to prove the boundedness of \( m(x, t) \), it only needs to prove that \( m^*(t) \) is bounded since \( m^*(t) \) is a upper-solution of \( m(x, t) \). According to \( a(x, t) \leq 1 + e \), it has \( \frac{dm(t)}{dr} \leq \frac{y(1+e)}{b+1+e} - \frac{1}{1+m(t)} \) which yields to
\[
\lim_{t \to \infty} \sup m(t) \leq \frac{b+1+e(1+e)}{y(1+e)} \text{.}
\]
Since the randomicity of \( e \), \( \lim_{t \to \infty} \sup m^*(t) \leq \frac{b+1+e}{y} \) if \( b+1 > \gamma \). This means \( \lim_{t \to \infty} \sup m(x, t) \leq \frac{b+1+e}{y} \). This completes the proof of (ii).

\( \Box \)

### 3.2 Stability of the nonspatial system

In this subsection, we discuss the dynamics of the following nonspatial system:

\[
\begin{align*}
\frac{da}{dt} &= \alpha(1-a) - \frac{am}{b+a}, \\
\frac{dm}{dt} &= \frac{yma}{b+m} - \frac{m}{1+m}.
\end{align*}
\]

(The linearization of system (11) is)

\[
\begin{align*}
\frac{da}{dt} &= b_{11}a + b_{12}m, \\
\frac{dm}{dt} &= b_{21}a + b_{22}m,
\end{align*}
\]

whose characteristic equation is expressed as

\[ \lambda^2 + T_0 \lambda + J_0 = 0, \]

where

\[ T_0 = -(b_{11} + b_{22}) \text{ and } J_0 = b_{11}b_{22} - b_{12}b_{21}. \]

For the equilibrium \( E_0 \), it has \( b_{11} = -\frac{y}{r} \), \( b_{12} = -\frac{1}{r(b+1)} \), \( b_{21} = 0 \), \( b_{22} = \frac{y}{b+1} - 1 \), \( T_0 = \frac{1}{r} \alpha + \frac{r(b+1-\gamma)}{b+1} \) and \( J_0 = \alpha^2(b+1-\gamma)/r(b+1) \), which means that \( E_0 \) is locally asymptotically stable for \( b+1 > \gamma \) and unstable for \( b+1 < \gamma \).

For any positive steady state \( E^*(a^*, m^*) \) with \( (b, \alpha, \gamma) \in \mathbb{T} \), it has

\[
\begin{align*}
b_{11} &= -\frac{1}{r}[\alpha + \frac{bm^*}{(b+a)^2}] < 0, \\
b_{12} &= -\frac{a^*m^*}{(b+a)^2} < 0, \\
b_{21} &= \frac{ym^*}{(b+m)^2} > 0, \\
b_{22} &= \frac{m^*}{(1+m)^2} > 0, \\
T_0 &= \frac{1}{r} \left[ \alpha + \frac{bm^*}{(b+a)^2} \right] - \frac{m^*}{(1+m)^2}, \\
J_0 &= \frac{m^*}{r(1+m)^2(b+a)^2} \left[ -\alpha(a^*)^2 - 2aaba^* + b - ab^2 \right].
\end{align*}
\]

Since \( 0 < a^* < 1 \), it has \( J_0 < 0 \) if \( 1 - ab < 0 \). If \( 1 - ab > 0 \) and \( a^* \geq 1 \), then \( J_0 > 0 \). If \( 1 - ab > 0 \) and \( a^* < 1 \), then \( J_0 > 0 \) for \( 0 < a^* < a^* \) and \( J_0 < 0 \) for \( a^* > a^* \), where \( a^* = \sqrt{\frac{b}{a}} - b \). It has the following results.

**Theorem 2** For \((b, \alpha, \gamma) \in \mathbb{T}, \) if \( b > \frac{1}{\alpha} \), then \( E^* \) is unstable. If \( b < \frac{1}{\alpha} \) and \( a^* \geq 1 \), then \( E^* \) is locally asymptotically stable. If \( b < \frac{1}{\alpha} \) and \( a^* < 1 \), then \( E^* \) is locally asymptotically stable for \( 0 < a^* < a^* \) and unstable for \( a^* > a^* \).

**Remark 1** 2, the parameter \( b \) has directly effect to the stability of \( E^* \).

Taking \( r = 0.5, \mu = 0.6, \alpha = 0.01 \), we can draw the \((b, \gamma)\) plane plot in where the stability regions of \( E^* \) are given (see Fig. 2A). In the region II, Hopf bifurcation line is given in Fig. 2B. We can choose \( \gamma = 10 \) and obtain \( b = 2.727 \) and 6.7151, the system exists stable periodic solutions and the phase plots are shown in Fig. 2C, D.

Obviously, \( r \) does not affect the existence of \( E^* \), but it does affect its stability. Solving \( T_0 = 0 \) for \( r \), it has

\[ r \leq r(\alpha, \gamma, b) = \frac{m^* + a^*}{\alpha(b+a)^2 + bm^*(1+m)^2} \]

We have the following results on the stability and Hopf bifurcation of system (11) at \( E^* \).

**Theorem 3** If \( J_0 > 0 \) and \( r(\alpha, \gamma, b) \) is defined as (13), then \( E^* \) is locally asymptotically stable for \( r < r(\alpha, \gamma, b) \) and unstable for \( r > r(\alpha, \gamma, b) \).

### 3.3 Turing instability

In this subsection, we take the effect of diffusion into account on the dynamical behavior of system (3) and investigate the diffusion-driven instability for \( E^* \) under the condition \( (b, \alpha, \gamma) \in \mathbb{T}, J_0 > 0 \) and \( r < r(\alpha, \gamma, b) \).

The linearization of system (3) at \( E^* \) is

\[
\begin{pmatrix}
\frac{da}{dt} \\
\frac{dm}{dt}
\end{pmatrix} = D \Delta \begin{pmatrix}
a \\
m
\end{pmatrix} + \tilde{D} \begin{pmatrix}
a \\
m
\end{pmatrix},
\]

where

\[ D = \begin{pmatrix}
\frac{1}{r} & 0 \\
0 & \mu
\end{pmatrix} \quad \text{and} \quad \tilde{D} = \begin{pmatrix}
b_{11} & b_{12} \\
b_{21} & b_{22}
\end{pmatrix},
\]

where \( b_{ij} \) (i, j = 1, 2) are given as (12).

The characteristic equation of system (14) constrained by Neumann boundary conditions is

\[ \Delta_k = \lambda^2 + T_k \lambda + J_k = 0 \quad \text{for } k \in \mathbb{N}, \]

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where $k$ is the wave number,

$$T_k = \left( \mu + \frac{1}{r} \right) \frac{k^2}{l^2} + T_0$$

and

$$J_k = \frac{\mu k^4}{l^4} - \left( \mu b_{11} + \frac{b_{22}}{r} \right) \frac{k^2}{l^2} + J_0.$$

Hence $T_k > 0$ must hold for any $k \in \mathbb{N}$ if $J_0 > 0$ and $r < r(\alpha, \gamma, b)$.

If $E^*$ is stable in the absence of diffusion, but becomes unstable in the opposite case, we call this as Turing instability. Therefore, Turing instability only occurs when there is at least one positive integer $k$ such that $J_k < 0$. We get the following result.

**Theorem 4** If the conditions $(b, \alpha, \gamma) \in \mathbb{T}$, $J_0 > 0$ and $r < r(\alpha, \gamma, b)$ hold, then there is no diffusion-driven Turing instability when $\mu \geq \mu^*$, where $\mu^* = \frac{b_{22}}{rb_{11}}$.

Define

$$p(k^2) = \frac{\mu}{l^4} k^4 - \left( \frac{\mu b_{11}}{l^2} + \frac{b_{22}}{r l^2} \right) k^2 + J_0.$$

Let $k_{\min}^2$ be the minimum value of $p(k^2)$. Thus if $\mu < \mu^*$, then

$$k_{\min}^2 = \frac{r l^2}{2 \mu} \left( \mu b_{11} + \frac{b_{22}}{r} \right).$$
If \( p(k_{\text{min}}^2) < 0 \), the sufficient condition for the system to be unstable reduces to
\[
4b_{12}b_{21}\mu + r\left(\mu b_{11} - \frac{b_{21}}{r}\right)^2 > 0.
\]

**Theorem 5** Turing instability occurs for system (3) under the following conditions:
\[
(b, \alpha, \gamma) \in \mathbb{T}, \quad J_0 > 0, \quad r < r(\alpha, \gamma, b, \mu b_{11}) > 0 \quad \text{(TI)}
\]
\[
b_{21} > 0 \quad \text{and} \quad 4b_{12}b_{21}\mu + r(\mu b_{11} - \frac{b_{21}}{r})^2 > 0.
\]

At the same time, let the two roots of \( p(k^2) \) be \( k_-^2 \) and \( k_+^2 \), then \( k^2 \in (k_-^2, k_+^2) \) limits the range of Turing instability for a locally stable steady state.

Choosing \( l = 1, r = 0.1, \mu = 0.02, \alpha = 0.2, \gamma = 2 \) and let \( b = 0.2, 0.3, 0.5 \), respectively, we can find that the range of Turing instability becomes larger as \( b \) increasing (see Fig. 3).

### 4 Spatiotemporal dynamics of system (4)

Let \( \overline{E}(\overline{a}, \overline{m}) \) be any equilibrium, define \( u = a - \overline{a} \) and \( v = m - \overline{m} \), then system (4) becomes
\[
\begin{align*}
\frac{\partial u(x, t)}{\partial t} &= \Delta u(x, t) - \left[\alpha + \frac{b\overline{m}}{(b + \overline{a})^2}\right]u(x, t) - \frac{\overline{a}}{b + \overline{a}}v(x, t) + \ldots, \\
\frac{\partial v(x, t)}{\partial t} &= \mu \Delta v(x, t) + \frac{b\overline{m}}{(b + \overline{a})^2}u(x, t - \tau_1) + \frac{\overline{m}}{(1 + \overline{m})^2}v(x, t - \tau_2) + \frac{\gamma \overline{m}}{b + \overline{a}} - \frac{\overline{a}}{1 + \overline{m}}v(x, t) + \ldots
\end{align*}
\] (15)

whose characteristic equation is
\[
D_k(\lambda, \tau_1, \tau_2) = \lambda^2 + \left[\frac{\mu k^2}{l^2} - \frac{\rho}{r_{22}} + \frac{k^2}{r_{11}} + I + \left[\frac{\mu k^2}{l^2} - \frac{\rho}{r_{22}}\right]e^{-\lambda \tau_1} - \frac{k^2}{r_{22}}e^{-\lambda \tau_2} + \lambda + \frac{k^2}{r_{11}}\right] = 0,
\]
where
\[
\begin{align*}
l_{11} &= \frac{\alpha}{r} + \frac{\rho}{r_{22}} > 0, \quad l_{12} = \frac{\overline{a}}{r}\overline{m} > 0, \\
l_{21} &= \frac{\overline{m}}{(b + \overline{a})^2} > 0, \quad l_{22} = \frac{\overline{m}}{(1 + \overline{m})^2} > 0 \quad \text{and} \quad l_0^2 = \frac{\gamma \overline{m}}{b + \overline{a}} - \frac{\overline{a}}{1 + \overline{m}}.
\end{align*}
\]

#### 4.1 Stability of boundary equilibrium \( E_0(1, 0) \)

For equilibrium \( E_0(1, 0) \) it has \( l_{21} = 0, l_{22} = 0 \) and let
\[
C_k := \frac{\mu k^2}{l^2} - \frac{\gamma}{b + \overline{a}} + 1 + \frac{k^2}{r_{11}} + \frac{\rho}{r}
\]
and
\[
S_k := \left[\frac{\mu k^2}{l^2} - \frac{\gamma}{b + \overline{a}} + 1\right] \left[\frac{k^2}{r_{22}} + \frac{\rho}{r}\right] > 0.
\]

Hence, if \( b + 1 > \gamma \), then \( C_k > 0, S_k > 0 \) for any \( k \in \mathbb{N} \) and \( E_0 \) is locally asymptotically stable, otherwise, if \( b + 1 < \gamma \), it has \( S_0 = \frac{\rho}{r} [1 - \frac{\gamma}{b + \overline{a}}] < 0 \), then \( E_0(1, 0) \) is unstable.

In the following, we prove the globally asymptotically stability of \( E_0(1, 0) \) for system (4).

**Theorem 6** Let \( (a(x, t), m(x, t)) \) be a solution of system (4) and \( v_i(x) \neq 0 \ (i = 1, 2) \). If \( b + 1 > \gamma \), then \( E_0(1, 0) \) is globally asymptotically stable for \( x \in [0, l\pi] \).

**Proof** Define
\[
f_1(u, v) = \alpha(1 - u) - \frac{\mu u}{b + \overline{a}} \quad \text{and} \quad f_2(u, v) = \frac{\gamma \mu v}{b + \overline{a}} - \frac{\overline{a}}{1 + \overline{m}}v
\]
where \( u = (u_1, u_2)^T \) and \( v = (v_1, v_2)^T \). It is obvious that \( f = (f_1, f_2) \) is mixed quasi-monotone in \( \mathbb{R}^2_+ \times \mathbb{R}^2_+ \). Let \((\bar{a}, \bar{m}) = (M_1, M_2)\) and \((\tilde{a}, \tilde{m}) = (0, 0)\), where \( M_1 \) and \( M_2 \) are any constants satisfying
\[
M_1 > 1 \text{ and } M_2 > 0.
\]

Since
\[
\alpha(1 - \bar{a}) - \frac{\bar{m}a}{b + a} \leq 0, \quad \alpha(1 - \tilde{a}) - \frac{\tilde{m}a}{b + a} \geq 0,
\]
and
\[
\frac{\gamma \bar{a} m}{b + a} - \frac{\bar{m} m}{1 + m} \leq 0, \quad \frac{\gamma \tilde{a} m}{b + a} - \frac{\tilde{m} m}{1 + m} \geq 0,
\]
then \((\bar{a}, \bar{m})\) and \((\tilde{a}, \tilde{m})\) are a coupled upper solution and lower solution of system (4).

When
\[
0 \leq u_1, v_1 \leq M_1 \text{ and } 0 \leq u_2, v_2 \leq M_2,
\]
we denote the Lipschitz constants of \( f_1 \) and \( f_2 \) by \( K_1 \) and \( K_2 \). From Theorem 2.1 of [26], we see that a uniquely global solution \((a, m)\) of system (4) exists and satisfies
\[
(0, 0) \leq (a, m) \leq (M_1, M_2)
\]
whenever
\[
(0, 0) \leq (\varphi(x, t), \psi(x, t)) \leq (M_1, M_2).
\]
The maximum principle implies that \( a(x, t), m(x, t) \geq 0 \) for \( t > 0 \) and \( x \in (0, l\pi) \) when \( \varphi(x, t) \neq 0 \) and \( \psi(x, t) \neq 0 \).

Let \((\bar{a}, \bar{m}) = (1 + \varepsilon, M_2)\) and \((\tilde{a}, \tilde{m}) = (\varepsilon, 0)\), where \( \varepsilon \) and \( M_2 \) are positive constants. It is easy to verify that \((1 + \varepsilon, M_2)\) and \((\varepsilon, 0)\) are a coupled upper solution and lower solution of system (4) when \( \varepsilon \) is sufficiently small. We define two sequences \( \{a^{(n)}, m^{(n)}\} \) and \( \{\bar{a}^{(n)}, \bar{m}^{(n)}\} \) as follows:
\[
\begin{align*}
\bar{a}^{(n)} &= \bar{a}^{(n-1)} + \frac{1}{K_1} \left[ \alpha(1 - \bar{a}^{(n-1)}) - \frac{\bar{m}^{(n-1)} }{b + \bar{a}^{(n-1)}} \right], \\
\tilde{a}^{(n)} &= \tilde{a}^{(n-1)} + \frac{1}{K_1} \left[ \alpha(1 - \tilde{a}^{(n-1)}) - \frac{\tilde{m}^{(n-1)} }{b + \tilde{a}^{(n-1)}} \right], \\
\bar{m}^{(n)} &= \bar{m}^{(n-1)} + \frac{1}{K_2} \left[ \gamma \bar{a}^{(n-1)} \bar{m}^{(n-1)} - \frac{\bar{m}^{(n-1)} }{1 + \bar{m}^{(n-1)}} \right], \\
\tilde{m}^{(n)} &= \tilde{m}^{(n-1)} + \frac{1}{K_2} \left[ \gamma \tilde{a}^{(n-1)} \tilde{m}^{(n-1)} - \frac{\tilde{m}^{(n-1)} }{1 + \tilde{m}^{(n-1)}} \right],
\end{align*}
\]
for \( n = 1, 2, \ldots \), where \( \{a^{(0)}, m^{(0)}\} = (1 + \varepsilon, M_2) \), \( \{\bar{a}^{(0)}, \bar{m}^{(0)}\} = (\varepsilon, 0) \) and \( K_i \ (i = 1, 2) \) are the Lipschitz constants.

From Lemma 2.1 of [26], it knows that
\[
(a^{(n)}, \bar{m}^{(n)}) \rightarrow (\bar{a}, \bar{m}) \text{ as } n \rightarrow \infty
\]
and
\[
(a^{(n)}, \tilde{m}^{(n)}) \rightarrow (\tilde{a}, \tilde{m}) \text{ as } n \rightarrow \infty
\]
with
\[
\varepsilon \leq a \leq \bar{a} \leq 1 + \varepsilon \text{ and } 0 \leq \tilde{m} \leq \bar{m} \leq M_2.
\]
Since \( m^{(0)} = 0 \), it has \( m^{(n)} = 0 \) for \( n = 1, 2, \ldots \), which implies \( m = 0 \). From (17), we obtain that \( \bar{a}, \bar{m} \) and \( a \) satisfy
\[
\begin{align*}
\alpha(1 - \bar{a}) &= 0, \\
\alpha(1 - a) - \frac{ma}{b + a} &= 0, \\
\frac{\gamma \bar{a} m}{b + a} - \frac{m m}{1 + m} &= 0.
\end{align*}
\]
From the first equation of Eq. (18), it has \( \bar{a} = 1 \). In combination with Theorem 1, it has
\[
\frac{\gamma}{b + 1} - \frac{1}{1 + m} < 0 \text{ if } b + 1 > \gamma,
\]
then \( \bar{m} = 0 \) and \( a = 1 \). From Theorem 2.2 of [26] and the arbitrary largeness of \( M_2 \), the solution \((a, m)\) of system (4) satisfies that \( (a, m) \rightarrow (1, 0) \) as \( t \rightarrow \infty \) when \( \varepsilon < \varphi \leq 1 + \varepsilon \) and \( \psi \geq 0 \) in \([0, l\pi] \times [-\tau, 0]\). The comparison theorem for parabolic boundary-value problems implies that \( a(x, t) \leq \eta(x, t) \) in \([0, l\pi] \times [0, \infty)\), where \( \eta(x, t) \) is the positive solution of
\[
\begin{align*}
\frac{\partial \eta}{\partial t} &= \Delta \eta + \alpha(1 - \eta), \quad x \in (0, l\pi), \ t > 0, \\
\frac{\partial \eta}{\partial x} &= 0, \quad x = 0, \ t > 0, \\
\eta(x, 0) &= v_1(x) > 0, \quad x \in (0, l\pi).
\end{align*}
\]
Then \( \eta(x, t) \rightarrow 1 \) as \( t \rightarrow \infty \). So there exists \( t_0 > 0 \) such that \( a(x, t) \leq 1 + \varepsilon \) in \([0, l\pi] \times [t_0, \infty)\). Since \( \varepsilon \) sufficiently small and Corollary 2.1 of [26], we can obtain the conclusion. This completes the proof. \( \Box \)

4.2 Stability of the positive equilibrium and bifurcation

From Theorem 6, it knows that \( E_0(1, 0) \) is globally asymptotically stable when \( b + 1 > \gamma \). Hence, \( E^* \) is unstable when \( b + 1 > \gamma \), which is contained in the conditions (A1) and (A3). Hence, we only need to investigate the stability of the positive equilibrium under the condition (A2). In this section, it uses \( E^*(a^*, m^*) \) instead of \( E_*(a^*, m^*) \) as the positive equilibrium of system (4) and the parameters \( b, \alpha, \gamma \) satisfy (A2).

At \( E^* \), system (15) becomes

\[ \Box \text{ Springer} \]
\[
\begin{align*}
\frac{\partial u(x,t)}{\partial t} &= \Delta u(x,t) - \left[ \alpha + \frac{b m^*}{(b + a^*)^2} \right] u(x,t) - \frac{a^*}{b + a^*} v(x,t) + \ldots, \\
\frac{\partial v(x,t)}{\partial t} &= \mu \Delta v(x,t) + \frac{b m^*}{(b + a^*)^2} \left[ u(x,t - \tau_1) + \frac{m^*}{(1+m^*)^2} v(x,t - \tau_2) + \ldots, \right]
\end{align*}
\]

(19)

whose characteristic equation is

\[
D_k(\lambda, \tau_1, \tau_2) = \lambda^2 + \left[ l_{11} + \left( \frac{1}{r} + \mu \right) \frac{k^2}{r^2} \right] \lambda + \frac{\mu k^2}{r^2}
\]

\[
\left[ \frac{k^2}{r^2} + l_{11} \right] \gamma l_{12} l_{21} e^{-\lambda \tau_1} - l_{22} \gamma l_{12} l_{21}
\]

\[
\lambda + \frac{k^2}{r^2} + l_{11} \gamma l_{21} e^{-\lambda \tau_2} = 0, \quad (20)
\]

where

\[ l_{11} = \frac{1}{r} [\alpha + l_{21}] > 0, \quad l_{12} = \frac{a^*}{r (b + a^*)} > 0, \]

\[ l_{21} = \frac{b m^*}{(b + a^*)^2} > 0 \quad \text{and} \quad l_{22} = \frac{m^*}{(1+m^*)^2} > 0. \]

The stability/instability of \( E^* \) can be determined by the root distribution of the characteristic equation (20) for \( k \in \mathbb{N} \).

Define

\[ J_{1k} = \frac{k^2}{r^2} + l_{11} > 0, \quad J_{2k} = \frac{\mu k^2}{r^2} - l_{22}, \]

\[ q_k = \frac{J_{1k} J_{2k}}{Q} \quad \text{and} \quad Q = \gamma l_{12} l_{21}. \]

From Eq. (20),

\[ D_k(0, \tau_1, \tau_2) = J_{1k} J_{2k} + Q \quad \text{and} \quad D(+\infty, \tau_1, \tau_2) = +\infty. \]

If there exists some \( k \) satisfying \( q_k < -1 \), then \( D_k(0, \tau_1, \tau_2) < 0 \). Hence, \( E^* \) is unstable. In the following, we assume \( q_k \geq -1 \) to investigate the stability of \( E^* \). In addition, under the condition (H1), \( \lambda = 0 \) is not the root of Eq. (20).

In the absence of delay, we firstly seek for the conditions at which \( E^* \) is stable for \( \tau_1 = \tau_2 = 0 \). Taking \( \tau_1 = \tau_2 = 0 \), Eq. (20) becomes

\[ D_k(\lambda, 0, 0) = \lambda^2 + [J_{1k} + J_{2k}] \lambda + J_{1k} J_{2k} + Q = 0, \]

(21)

and if \( k_0 \) is just right an integer, then \( J_{2k} = 0 \) for \( k = k_0 \), otherwise,

\[ J_{2k} = \begin{cases} > 0, & k \geq k_0 + 1, \\ < 0, & k < k_0, \end{cases} \]

where \( \lfloor \sqrt{\frac{k_2}{\mu}} \rfloor \) and \([ \cdot ]\) is the integral function.

On the basis of Routh-Hurwitz criterion, if \( (H1) \)

\[ l_{11} > l_{22}, \quad l_{11} l_{22} < Q \]

holds, then \( J_{1k} + J_{2k} > 0 \) and \( q_k > -1 \) and all roots of Eq. (21) have negative real parts for any \( k \in \mathbb{N} \).

Particularly, if \( \frac{b}{(b+1)^2} \geq \alpha \) holds, then all roots of Eq. (21) have negative real parts for any \( k \in \mathbb{N} \) and any \( \gamma > 0 \).

The following Lemma is from [27].

\[ \boxed{\text{Lemma 1}} \]

When \( r, \mu, \gamma, \alpha, b, \tau_1 \) and \( \tau_2 \) change in the parameter space, the number (counting multiplicities) of eigenvalues of \( \text{Re}(\lambda) > 0 \) changes only when an eigenvalue passes through the imaginary axis in the complex plane.

From Lemma 1, if all roots of the characteristic equation (20) have negative real parts, then the trivial solution of system (19) will be asymptotically stable. The trivial solution of system (19) can only be unstable as the root of the characteristic equation changes through the imaginary axis. Therefore, the stability changes in parameter space at points where Eq. (20) has a root with zero real part.

Firstly, we consider the zero root of Eq. (20), \( \lambda = 0 \), which will occur when \( q_k = -1 \) for some \( k < k_0 \) and \( \lambda = 0 \) is not the root for any \( k \geq k_0 \).

Furthermore,

\[ D_k(\lambda, \tau_1, \tau_2) \]

\[ \begin{align*}
\left. \frac{D_k(\lambda, \tau_1, \tau_2)}{\partial \lambda} \right|_{\lambda = 0} &= 2 \lambda + [l_{11} + \left( \frac{1}{r} + \mu \right) \frac{k^2}{r^2}] - \tau_1 Q e^{-\lambda \tau_1} \\
+ &\tau_2 l_{22} [\lambda + J_{1k}] e^{-\lambda \tau_2} - l_{22} e^{-\lambda \tau_2} \\
\end{align*}
\]

and

\[ \left. \frac{D_k(\lambda, \tau_1, \tau_2)}{\partial \lambda} \right|_{\lambda = 0}'' = 2 + \tau_1^2 Q e^{-\lambda \tau_1} + \tau_2 l_{22} e^{-\lambda \tau_2} - \tau_2^2 l_{22} [\lambda + J_{1k}] e^{-\lambda \tau_2} + \tau_2 l_{22} e^{-\lambda \tau_2}. \]

Hence

\[ D_k(0, \tau_1, \tau_2) \]

\[ \begin{align*}
\left. \frac{D_k(0, \tau_1, \tau_2)}{\partial \lambda} \right|_{\lambda = 0} &= J_{1k} + J_{2k} - \tau_1 Q + \tau_2 l_{22} J_{1k} \\
&= J_{1k} + J_{2k} + \tau_1 J_{1k} J_{2k} + \tau_2 l_{22} J_{1k} \\
&= (1 + \tau_2 l_{22}) J_{1k} + (1 + \tau_1 J_{1k}) J_{2k}. \\
\end{align*}
\]

Thus for some \( k < k_0 \), the root \( \lambda = 0 \) is simple and passes through the zero with nonzero speed everywhere on the line \( q_k = -1 \) except for one possibly isolated point given by

\[ \tau_1 = -\frac{(J_{1k} + J_{2k}) + \tau_2 l_{22} J_{1k}}{J_{1k} J_{2k}} := \tau_{1k}^* \]

Hence, for \( q_k = -1 \), Eq. (20) has a simple zero root when \( J_{1k} + J_{2k} > 0 \), \( k < k_0 \) and \( \tau_1 \neq \tau_{1k}^* \).

However, when \( q_k = -1 \) and \( \tau_1 = \tau_{1k}^* \),

\[ \left. \frac{D_k(0, \tau_{1k}^*, \tau_2)}{\partial \lambda} \right|_{\lambda = 0}'' = 2 + \tau_{1k}^2 Q + 2 \tau_2 l_{22} - \tau_{2k} l_{22} J_{1k} \]

\[ = 2 + \frac{(J_{1k} + J_{2k} + \tau_2 l_{22} J_{1k})^2}{Q} \]
For some $q_k \in \mathbb{N}$, if $q_k = -1$, $J_{1k} + J_{2k} > 0$, if $\tau_1 \neq \tau_{1k}^n$, $\lambda = 0$ is a simple zero root of Eq. (20); if $\tau_1 = \tau_{1k}^n$, then $\lambda = 0$ is the double zero root of Eq. (20).

Locating the pure imaginary roots is slightly more complicated. In the following, it assumes that (H1) hold. Firstly, let $\tau_2 = 0$, then Eq. (20) becomes

$$ D_k(\lambda, \tau_1, 0) = \lambda^2 + [J_{1k} + J_{2k}]\lambda + J_{1k} J_{2k} + Q e^{-\lambda \tau_1} = 0. \tag{22} $$

We investigate the existence of a pure imaginary root for Eq. (22). The analysis of Eq. (22) is based on the conclusion that the number of characteristic roots with positive real parts will change only when the characteristic roots enter the complex plane through the imaginary axis as the change of parameters.

**Theorem 7** Assume that $\tau_2 = 0$ and (H1) are satisfied.

(a) If $q_0 \geq 1$ holds, then all the roots of Eq. (22) have negative real parts for any $k \in \mathbb{N}$ and $\tau_1 \geq 0$.

(b) If $k \in S_1 \equiv \{k \in \mathbb{N} - 1 < q_k < 1\}$ holds, then there exists one series of critical delays $\tau_{1k}^n$ such that Eq. (22) has a pair of purely imaginary roots $\pm iw_{n}^k$ at $\tau_{1k}^n$. All the roots of Eq. (22) have negative real parts when $\tau_1 \in [0, \tau_1^0)$ and for $\tau_1 > \tau_1^0$, there exists at least one root with positive real parts, where $\tau_1^0 = \min \{\tau_{1k}^0\}$.

Next, we fix $(Q, \tau_1)$ in the stable regions and regard $\tau_2$ as the parameter to investigate the distributions of the roots of Eq. (20). For convenience, we make the following assumptions:

(C1) $q_0 \geq 1$ and $\tau_1 \geq 0$ for any $k \in \mathbb{N};$

(C2) $k \in S_1$ and $\tau_1 \in [0, \tau_1^0].$

The results of Theorem 8 show that if (C1) or (C2) is satisfied, $\mathcal{E}^*$ is stable when $\tau_2 = 0$. As $\tau_2$ varies, in order to obtain the boundary of stability, let $\lambda = \pm i\omega$ ($\omega > 0$) be root of the $(k + 1)$th equation of Eq. (20), separating its real and imaginary parts, it obtains the following equations:

$$ G(w) := w^4 + (J_{1k}^2 + J_{2k}^2)w^2 + (J_{1k} J_{2k})^2 - Q^2 = 0, \tag{25} $$

which yields to

$$ Q = \sqrt{w^4 + (J_{1k}^2 + J_{2k}^2)w^2 + (J_{1k} J_{2k})^2} := Q(w). \tag{26} $$

From Eq. (25), if $q_0 \geq 1$, then $q_k \geq 1$ and Eq. (25) has no any positive root for any $k$. On the contrary, if $-1 < q_k < 1$, Eq. (25) has a uniquely positive root $w_{n}^k$. Thus, if $k \in S_1$, then Eq. (22) exists purely imaginary roots as long as $\tau_1$ takes the critical values determined by the equality (24).

Furthermore, for $k \in S_1$, differentiating Eq. (22) with respect to $\tau_1$, it gets

$$ \frac{d\lambda}{d\tau_1} = -\frac{\lambda - (J_{1k}^2 + J_{2k}^2)\lambda^2 - J_{1k} J_{2k}}{2J_{1k} J_{2k} + \tau_1 J_{1k} J_{2k} + J_{1k} J_{2k}}. $$

Substituting $\lambda = iw_{n}^k$ and $\tau_1 = \tau_{1k}^n$ into the above formula leads to the following result

$$ \frac{d\text{Re} \lambda}{d\tau_1}\bigg|_{\lambda = iw_{n}^k, \tau_1 = \tau_{1k}^n} = \frac{w_{n}^k (J_{1k}^2 + J_{2k}^2 + w_{n}^k)^2}{h} > 0, $$

where $h = [J_{1k}^2 + J_{2k}^2 + \tau_{1k}^n (J_{1k} J_{2k} - w_{n}^k)^2 + w_{n}^k J_{1k} J_{2k} + J_{1k} J_{2k})^2].$ This completes the proof.

Proof Without loss of generality, for a fixed $k \in \mathbb{N}$, let $iw$ be the root of the $(k + 1)$th equation of the equation (22) and separate the real and imaginary parts, it has

$$ \begin{align*}
- w^2 + J_{1k} J_{2k} &= -Q \cos w \tau_1, \\
Q (J_{1k} + J_{2k}) &= Q \sin w \tau_1,
\end{align*} \tag{23} $$

and $\sin w \tau_1 > 0$. Furthermore,

$$ \tau_{1k}^n = \frac{1}{w} \left[ \arccos \left( \frac{w^2 - J_{1k} J_{2k}}{Q} \right) + 2n \pi \right] $$

$$ := \tau_{1k}^n(w), \ n \in \mathbb{N}. \tag{24} $$

Squaring and adding the both sides of equations (23), it has

$$ G(w) := w^4 + (J_{1k}^2 + J_{2k}^2)w^2 + (J_{1k} J_{2k})^2 - Q^2 = 0. $$

which yields to

$$ Q = \sqrt{w^4 + (J_{1k}^2 + J_{2k}^2)w^2 + (J_{1k} J_{2k})^2} := Q(w). \tag{26} $$

$$ \frac{d\lambda}{d\tau_1} = -\frac{\lambda - (J_{1k}^2 + J_{2k}^2)\lambda^2 - J_{1k} J_{2k}}{2J_{1k} J_{2k} + \tau_1 J_{1k} J_{2k} + J_{1k} J_{2k}}. $$

Substituting $\lambda = iw_{n}^k$ and $\tau_1 = \tau_{1k}^n$ into the above formula leads to the following result

$$ \frac{d\text{Re} \lambda}{d\tau_1}\bigg|_{\lambda = iw_{n}^k, \tau_1 = \tau_{1k}^n} = \frac{w_{n}^k (J_{1k}^2 + J_{2k}^2 + w_{n}^k)^2}{h} > 0, $$

where $h = [J_{1k}^2 + J_{2k}^2 + \tau_{1k}^n (J_{1k} J_{2k} - w_{n}^k)^2 + w_{n}^k J_{1k} J_{2k} + J_{1k} J_{2k})^2].$ This completes the proof. \[ \square \]
\[ \begin{align*}
Q \cos \omega \tau_1 &= \omega^2 - (J_{2k} + l_{22})J_{1k} + l_{22} \left[ J_{1k} \cos \omega \tau_2 + \omega \sin \omega \tau_2 \right] := Q_k^{*} \\
Q \sin \omega \tau_1 &= \omega \left[ J_{1k} + J_{2k} + l_{22} \right] - l_{22} \left[ \omega \cos \omega \tau_2 - J_{1k} \sin \omega \tau_2 \right] := Q_k^{*}. 
\end{align*} \]

Eliminating \( \tau_2 \) from Eq. (27) gives
\[ F_k(\omega) := \left[ Q \cos \omega \tau_1 - \omega^2 + (J_{2k} + l_{22})J_{1k} \right]^2 \\
+ \left[ \omega (J_{1k} + J_{2k} + l_{22}) - Q \sin \omega \tau_1 \right]^2 \\
- l_{22}^2 [J_{1k}^2 + \omega^2] = 0. \tag{28} \]

**Theorem 9** For fixed \( l, r, \gamma, \alpha, b, \mu \) and \( \tau_1 \), if \( F_k(\omega) = 0 \) has no positive root for any \( k \), then \( E^* \) is locally asymptotically stable for any \( \tau_2 \geq 0 \) under the condition (C1) or (C2).

It can be obtained that \( F_k(0) = [Q + J_{1k} J_{2k} + 2l_{22} J_{1k}] [Q + J_{1k} J_{2k}] > 0 \) and \( F_k(\pm \infty) = + \infty \). Hence, if \( F_k(\omega) = 0 \) has positive roots, then there must be a finite number of roots. It assumes that \( F_k(\omega) = 0 \) has a series of positive and simple roots \( \omega_1 < \omega_2 < \ldots < \omega_N \), Eq. (20) has a series of critical delay \( \tau_2 \) determined by
\[ \tau_{2j} = \frac{\varphi_i + 2\pi j}{\omega} \quad \text{for} \quad j = 1, 2, \ldots, N \text{ and } i \in \mathbb{N}, \tag{29} \]
where \( \varphi \in (0, 2\pi) \) satisfies that
\[ \begin{cases} 
\cos \varphi_j = \frac{Q [J_{1k} \cos \omega \tau_1 \tau_1 - \omega_j \sin \omega_j \tau_1 + (\mu k^2 / \ell^2) J_{1k}^2 + \omega_j^2]}{l_{22} [J_{1k}^2 + \omega_j^2]} \\
\sin \varphi_j = \frac{Q [\omega_j \cos \omega \tau_1 \tau_1 - J_{1k} \sin \omega_j \tau_1 - \omega_j (J_{1k}^2 + \omega_j^2)]}{l_{22} [J_{1k}^2 + \omega_j^2]}
\end{cases} \]

Define
\[ S_2 = \{ k \in \mathbb{N} | F_k(\omega) = 0 \text{ has positive roots under (C1) or (C2)} \}. \]

For \( \tau_2 = 0 \), \( E^* \) is asymptotically stable when \( Q \) and \( \tau_1 \) satisfy (C1) or (C2), it will remain stable until \( \tau_2 \) increases and reaches a value for which Eq. (20) has a root with zero real part. If \( \tau^*_{2j} = \min_{k \in S_2} \{ \tau_{2j}^{0} \} \), then \( \tau^*_{2j} \) is the minimum value of \( \tau_2 \) for which Eq. (20) has purely imaginary roots and the value of \( \tau^* \) will vary in accordance with \( Q \) and \( \tau_1 \).

Therefore, all roots of Eq. (20) have strictly negative real parts when \( \tau_2 \in [0, \tau^*_{2j}(Q, \tau_1)] \), and only a pair of imaginary roots \( \pm i \omega^\delta \) when \( \tau_2 = \tau^*_{2j}(Q, \tau_1). \)

By computing the derivative in Eq. (28) about \( \tau_2 \) with \( i \omega^\delta \) and \( \tau^*_{2j} \) instead of \( \lambda \) and \( \tau_2 \), we can obtain the transversal condition. Applying Hopf bifurcation theorem, we have the following results giving the stability of equilibrium and the existence of Hopf bifurcation for system (19).

**Theorem 10** If (C1) or (C2) is satisfied and all the roots of Eq. (28) are simple, then there exists exactly a \( \tau_2 \in [0, \tau^*_{2j}(Q, \tau_1)] \) such that the trivial equilibrium of system (19) is asymptotically stable when \( \tau_2 \in [0, \tau^*_{2j}(Q, \tau_1)] \) and \( \tau^*_{2j}(Q, \tau_1) \) is the Hopf bifurcation value.

**Remark 2** In fact, choosing \( \tau_2 \) as bifurcating parameter for a fixed \( \tau_1 \), the stability switches may occur if \( F_k(\omega) = 0 \) has more than a positive root. This fact can be shown in Fig. 14 in Sect. 5.

In general, we can eliminate \( \omega \) from Eq. (27) and get an equation for \( l, k, r, \gamma, a, b, \mu, \tau_1 \) and \( \tau_2 \), which defines a hypersurface in the parameter space. Since this cannot be done in practice, to describe this hypersurface we can represent \( Q \) and \( \tau_1 \) as functions of \( \omega \). Firstly, for fixed \( k \), we find \( Q \) by squaring and adding in both sides of Eq. (27):
\[ Q = Q^k_H(\omega) := \sqrt{(Q_k^c)^2 + (Q_k^c)^2}. \tag{30} \]

Taking the ratio of Eq. (27) and solving for \( \tau_1 \) yields an expression involving the inverse tangent function. Noting that the sign of \( \cos \omega \tau_1 \) may be obtained from Eq. (27), we find that the appropriate expression for \( \tau_1 \) is
\[ \tau_1 = \begin{cases} 1 \omega & \text{artan}(Q_k^c) + 2j\pi, \quad Q_k^c > 0, \\
\frac{1}{\omega} \left[ \text{artan}(Q_k^c) + (2j + 1)\pi \right], \quad Q_k^c < 0, \end{cases} \tag{31} \]
for \( j \in \mathbb{N} \) and \( \text{artan} \) denotes the inverse tangent function which has range \((-\pi/2, \pi/2).\) Clearly, the equality (31) represents an infinite curve family. We take notice of the following limits,
\[ \lim_{l \to +\infty} Q^k_H(\omega) = |J_{1k} J_{2k}| = \begin{cases} -J_{1k} J_{2k}, \quad k < k_0, \\
J_{1k} J_{2k}, \quad k \geq k_0 + 1, \end{cases} \]
\[ \lim_{l \to +\infty} Q^k_H(\omega) = +\infty, \quad \lim_{l \to +\infty} J_{1k}(\omega) = 0 \]
and
\[ \lim_{l \to +\infty} \tau^j_{1k}(\omega) = \begin{cases} -J_{1k} J_{2k} \tau^j_{1k} J_{1k} J_{2k}, \quad \tau^*_{1k}, \quad j = 0, \\
+\infty, \quad \tau^*_{1k}, \quad j = 0, \end{cases} \]
for \( j \in \mathbb{N} \) and \( \text{artan} \) denotes the inverse tangent function which has range \((-\pi/2, \pi/2).\) Clearly, the equality (31) represents an infinite curve family. We take notice of the following limits,
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J_{1k} J_{2k}, \quad k \geq k_0 + 1, \end{cases} \]
\[ \lim_{l \to +\infty} Q^k_H(\omega) = +\infty, \quad \lim_{l \to +\infty} J_{1k}(\omega) = 0 \]
and
\[ \lim_{l \to +\infty} \tau^j_{1k}(\omega) = \begin{cases} -J_{1k} J_{2k} \tau^j_{1k} J_{1k} J_{2k}, \quad \tau^*_{1k}, \quad j = 0, \\
+\infty, \quad \tau^*_{1k}, \quad j = 0, \end{cases} \]
for \( j \in \mathbb{N} \) and \( \text{artan} \) denotes the inverse tangent function which has range \((-\pi/2, \pi/2).\) Clearly, the equality (31) represents an infinite curve family. We take notice of the following limits,
In summary, the line \( q_k = -1 \) represents the set of points in parameter space for which Eq. (20) has a zero eigenvalue. The curves (with multiple branches) defined by the equalities (30) and (31) represent the sets of points in parameter space for which Eq. (20) has a pair of purely imaginary eigenvalues. We refer to the lines \( q_k = -1 \) in the \((Q, \tau_1)\)-plane as the \( = 0 \) line or Turing line, and the curves defined by the equalities (30) and (31) as the \( = i\omega \) curves. Now we give two theorems which describe how the real parts of the roots of Eq. (20) change as the \( \lambda = 0 \) line or \( \lambda = i\omega \) curve is crossed in the \((Q, \tau_1)\)-plane.

**Theorem 11** For some \( k \), consider crossing \( \lambda = 0 \) line, when moving along the line \( \tau_1 = \text{constant} \) and the direction of increasing \( Q \) in the \((Q, \tau_1)\)-plane, the number of roots of the characteristic equation (20) with \( \Re(\lambda) > 0 \) increases by 1, unless \( \tau_1 < \tau_{1k}^* \) in which case it decreases by 1.

**Proof** Differentiating Eq. (20) with respect to \( Q \), it can obtain

\[
\frac{d\lambda}{dQ} = \frac{2\lambda J_{1k} + J_{2k} + l_{22} - \tau_1 Q e^{-\lambda \tau_1} + \tau_2 \left[ \lambda^2 + (J_{1k} + J_{2k} + l_{22}) \lambda + (J_{2k} + l_{22}) J_{1k} + Q e^{-\lambda \tau_1} \right] - l_{22} e^{-\lambda \tau_1}}{B_1^2 + B_2^2}.
\]

If \( \lambda = 0 \) is the root of Eq. (20), then \( q_k = -1 \) and the above derivative becomes

\[
\frac{d\lambda}{dQ} \bigg|_{\lambda=0, q_k=-1} = -\frac{1}{J_{1k} + J_{2k} + \tau_1 J_{2k} + \tau_2 J_{1k} l_{22}} \neq 0.
\]

Hence, \( \frac{d\lambda}{dQ} \bigg|_{\lambda=0, q_k=-1} > 0 \) if and only if

\[
J_{1k} + J_{2k} + \tau_1 J_{1k} J_{2k} + \tau_2 J_{1k} l_{22} < 0 \quad (>) 0,
\]

that is, \( \tau_1 > (<) \tau_{1k}^* \). Here \( \tau_{1k}^* > 0 \) holds because of \( k < 0 \). This completes the proof. \( \Box \)

**Theorem 12** For some \( k \), in the direction of increasing \( Q \), as moving along a line \( \tau_1 = \text{constant} \) in the \((Q, \tau_1)\)-plane, if this line cuts a branch of the \( \lambda = i\omega \) curves along which \( \tau_{1k}^j \) is a decreasing (increasing) function of \( \omega \), then as this branch is crossed, the number of roots of the characteristic equation (20) with \( \Re(\lambda) > 0 \) increases (decreases) by 2.

**Proof** The \( \lambda = i\omega \) curves defined by the equalities (30) and (31) give the points in the \((Q, \tau_1)\)-plane, where the real part of \( \lambda \) is zero. We can now prove our claim by considering the appropriate derivatives. Differentiating the equalities (31) with respect to \( \omega \), we get

\[
\frac{d\tau_{1k}^j}{d\omega} = -\frac{1}{\omega Q_H^j} \left\{ (Q_k^j \omega) \sin \omega \tau_{1k}^j + \tau_{1k}^j Q_H^j \right\}.
\]

Taking the derivative of Eq. (20) with respect to \( Q \) and substituting \( \lambda = i\omega \) leads to the following expression:

\[
\frac{d\Re\lambda}{dQ} \bigg|_{\lambda=i\omega} = \frac{1}{B_1^2 + B_2^2} \left\{ (Q_k^j \omega) \sin \omega \tau_{1k}^j - (Q_k^j \omega) \cos \omega \tau_{1k}^j + \tau_{1k}^j Q_H^j \right\},
\]

where

\[
B_1 = J_{1k} + \frac{\mu k^2}{l^2} - \tau_{1k}^j Q_H^j \cos \omega \tau_{1k}^j + \tau_{2k} [J_{1k} \cos \omega \tau_2 + \omega \sin \omega \tau_2 - l_{22} \cos \omega \tau_2] + l_{22} \sin \omega \tau_2.
\]

By Eq. (32), \( \text{Sign} \left\{ \frac{d\Re\lambda}{dQ} \bigg|_{\lambda=i\omega} \right\} = -\text{Sign} \left\{ \frac{d\tau_{1k}^j}{d\omega} \right\}. \)

Hence, \( \frac{d\tau_{1k}^j}{d\omega} < 0 \) implies that \( \frac{d\Re\lambda}{dQ} > 0 \). Thus, when \( \tau_{1k}^j \) is a decreasing function of \( \omega \), the real part of \( \lambda \) becomes positive and the characteristic equation (20) has a pair of roots with positive real part. Similarly, if \( \frac{d\tau_{1k}^j}{d\omega} > 0 \), then the real part of \( \lambda \) becomes negative, which completes the proof. \( \Box \)

**Remark 3** Lemma 1 indicates that with fixed \( k, \alpha, \beta, \mu, r, \gamma, \tau_1 \) and \( \tau_2 \), a completely stable region can be obtained from these subsets by increasing until the \( \lambda = 0 \) line or \( \lambda = i\omega \) curve is reached. Theorems 11 and 12 describe how the real part of the root of the characteristic equation changes when the boundary of the stable region is crossed.

For fixed \( k, r, \gamma, \alpha, \beta, \mu \) and \( \tau_2 \), the equalities (30) and (31) describe the curves which lie in the right of the
some assertions for the stability of $E^*$. 

**Theorem 13** For fixed $l, k, r, \gamma, \alpha, b, \mu$ and $\tau_2$, if $Q^k_H(\omega)$ as defined by the equality (30) is monotone on $\omega$, then there are no intersection points of the curves defined by the equalities (30) and (31). If $Q^k_H(\omega)$ is increasing on $\omega$ then there are no intersection points of the line $q_k = -1$ with the curves defined by the equalities (30) and (31).

**Proof** Consider first intersections of the curves defined by the equalities (30) and (31). Since these curves are defined according to $\omega$ parameter, the intersection of two different curves occurs when $Q$ and $\tau_1$ have the same values. If $Q^k_H(\omega)$ is monotone on $\omega$ then this is impossible. Now consider the curves defined by the equalities (30) and (31). Consideration of $Q^k_H(\omega)$ in (30) and (31). Consideration of $Q^k_H(\omega)$ in (30) and (31). Consideration of $Q^k_H(\omega)$ in (30) and (31). Consideration of $Q^k_H(\omega)$ in (30) and (31). Consideration of $Q^k_H(\omega)$ in (30) and (31).

Since the complexity of $Q^k_H$ as the function of $\omega$, we only can obtain the following monotonicity.

**Theorem 14** For fixed $l, k, r, \gamma, \alpha, \mu$ and $b$, if

$$\tau_2 < \frac{l^2}{\mu k^2} + \frac{l_2\sqrt{\frac{J_2}{J_2}} + l_2^2\mu k^2}{l_2^2\mu k^2}$$

then $Q^k_H$ is monotone increasing in $\omega$.

**Proof** From the equalities (30) and (31), it has

$$(Q^k_H)^2 = (Q^k_L)^2 + (Q^k_M)^2.$$ Taking the derivative of both sides with respect to $\omega$ yields

$$Q^k_H \frac{dQ^k_H}{d\omega} = Q^k_L(Q^k_L)' + Q^k_M(Q^k_M)' = 2\omega^3 + \omega [J^2_k + l_2^2 + (J_2k + l_22)^2]$$

$$+ [3 + \tau_2(J_2k + l_22)]\omega^2$$

$$+ [\tau_2(J_2k + l_22)]J^2_k \sin \omega \tau_2$$

$$+ [l_22\omega \tau_2 (\omega^2 + J^2_k)] \cos \omega \tau_2$$

$$\geq 2\omega^3 + \omega [J^2_k + l_2^2 + (J_2k + l_22)^2]$$

$$- \omega [3 + \tau_2(J_2k + l_22)]\omega^2$$

$$+ (1 + \tau_2(J_2k + l_22)) J^2_k$$

$$- \omega l_22 [\tau_2 (\omega^2 + J^2_k) + 2(J_2k + l_22)]$$

$$:= h(\omega).$$

Furthermore,

$$h(\omega) = \left[2 - \tau_2 l_22 \left(4 + \tau_2 (J_2k + l_22)\right)\right] \omega^2$$

$$+ \left[1 - \tau_2 l_22 \left(2 + \tau_2 (J_2k + l_22)\right)\right] J^2_k + J^2_2k.$$ Hence, if $1 - \tau_2 l_22 (2 + \tau_2 (J_2k + l_22)) > 0$ holds, then $h(\omega) > 0$ for any $\omega > 0$, that is, when $\tau_2 < \tau_2^1$, $Q^k_H$ is monotone increasing in $\omega$. This completes the proof. 

**Remark 4** Theorem 14 only gives a sufficient condition, i.e., if the inequality (34) is not satisfied, then $Q^k_H$ may be monotone or non-monotone in $\omega$. In this non-monotone case, the boundary of the stability region can be quite complicated as it is made up of pieces of the $q_k = -1$ and arcs of the curves defined by the equalities (30) and (31). It would be quite difficult to define this boundary analytically, however, we can state the following theorem about the region where the stability is independent of the delays $\tau_1$ and $\tau_2$.

**Theorem 15** If $k \geq k_1 + 1$, then all the roots of Eq. (20) have negative real parts when $-Q^k_{\text{min}} \leq Q < Q^k_{\text{min}}$ for all $\tau_1 > 0$, $\tau_2 > 0$, where $Q^k_{\text{min}} := \frac{J_1k}{J_2k} J_2k - l_2^2$. If $k < k_0$, then there is no such delay independent region, where $k_1 := \left[\frac{\tau_1}{\sqrt{\frac{J_2k}{\mu}^2}}\right] (> k_0 = \left[\frac{\tau_2}{\sqrt{\frac{J_2k}{\mu}^2}}\right]).$

**Proof** From Eq. (27), it has

$$Q^2 = (Q^k_L)^2 + (Q^k_M)^2$$

$$= \left[\omega^2 - (J_2k + l_22) J_1k + l_22 J_1k \cos \omega \tau_2 + \omega \sin \omega \tau_2\right]^2$$

$$+ \left[\omega \cos \omega \tau_2 - J_1k \sin \omega \tau_2\right]^2$$

$$= \left[\omega^2 - \frac{\mu k^2}{J^2_k} J_1k\right]^2 + l_22^2 \left[\omega^2 + J^2_k\right]$$

$$+ 2l_22 \left[\omega^2 - (J_2k + l_22) J_1k\right].$$
Lemma 2 If $\lambda_c = i\omega_c$ is a purely imaginary root of the characteristic equation (20), then $\lambda_c$ is simple and any root $\lambda$ other than $\lambda_c$ and $\bar{\lambda}_c$ satisfies $\lambda \neq m\lambda_c$ for any integer $m$.

Proof To prove that $\lambda_c = i\omega_c$ is simple, we need to show that $D'_k(\lambda_c, \tau_1, \tau_2) \neq 0$, where

$$D'_k(\lambda_c, \tau_1, \tau_2) = 2\lambda_c + J_{1k} + J_{2k} + l_{22} - \tau_1 Q e^{-\lambda \tau_1} - l_{22} e^{-\lambda \tau_2} + \tau_2 l_{22}(\lambda_c + J_{1k}) e^{-\lambda \tau_2}.$$ (36)

Suppose that $D'_k(\lambda_c, \tau_1, \tau_2) = 0$. Substituting $\lambda_c = i\omega_c$, separating the real and imaginary parts, we get

$$\begin{align*}
\tau_1 Q \cos \omega_c \tau_1 &= -(J_{1k} + J_{2k} + l_{22}) + l_{22} \cos \omega_c \tau_2 - \tau_2 f_{22} [J_{1k} \cos \omega_c \tau_2 + \omega_c \sin \omega_c \tau_2]. \\
\tau_1 Q \sin \omega_c \tau_1 &= -2\omega_c \sin \omega_c \tau_2 - \tau_2 f_{22} [\omega_c \cos \omega_c \tau_2 - J_{1k} \sin \omega_c \tau_2].
\end{align*}$$ (37)

Consider the ratio of two equations in the equations (37),

$$\tan \omega_c \tau_1 = -2\omega_c \sin \omega_c \tau_2 - \tau_2 f_{22} [\omega_c \cos \omega_c \tau_2 - J_{1k} \sin \omega_c \tau_2].$$ (38)

Furthermore, $\omega_c$ must satisfy the ratio of two equations in equations (27) when $Q = Q^k_H$ and $\lambda = i\omega_c$. Furthermore, it can obtain

$$\frac{Q^k_H(\omega_c)}{Q^k_H(\omega_c)} = -\frac{Q^k_H(\omega_c)'}{Q^k_H(\omega_c)''}.$$ (39)

Define $\mathcal{H}_{\omega_c} = (Q^k_H(\omega_c)'Q^k_H - (Q^k_H(\omega_c)')^2$, we notice that $\mathcal{H}_{\omega_c}$ is identical to the numerator of Eq. (35). Hence, by Theorem 9, $\mathcal{H}_{\omega_c} > 0$ for all $\tau_2 < \tau_2^f$. Moreover, zeros of $\mathcal{H}_{\omega_c}$ occur when $dQ^k_H(\omega_c)/d\omega = 0$. Therefore, excluding the values of $\omega_c$ satisfying $dQ^k_H(\omega_c)/d\omega = 0$, $\lambda_c = i\omega_c$ is a simple root of Eq. (20).

Further, if the point $(Q^k_H(\lambda_c), \tau_1)$ in the $(Q, \tau_1)$-plane is not an intersection point of two branches of the $\lambda = i\omega$ curve nor an intersection point of the $\lambda = i\omega$ curve and $\lambda = 0$ line, then there is only a pair of eigenvalues with $\text{Re}(\lambda) = 0$ at this point. Thus, any other roots satisfy $\lambda \neq \pm m\omega_c$ for any $m \in \mathbb{N}$. This completes the proof. □

The following result follows from the proof of Theorem 11,

Lemma 3 If $\frac{d\text{Re} \lambda}{dQ}|_{\lambda_c = i\omega_c} = 0$ if and only if $\omega_c$ satisfies

$$\frac{dQ^k_H}{d\omega} |_{\omega = \omega_c} = 0, Q^k_H(\omega_c) \neq 0 \text{ and } \frac{dQ^k_H}{d\omega} |_{\omega \neq \omega_c} \neq 0.$$
Theorem 16 It assumes that $l, k, \alpha, \mu, b, \tau_2, r, \gamma, \tau_2 \geq 0$ and $\tau_1 = \tau_{1c}$ are fixed and $(Q_H^{kc}, \tau_{1c})$ is a point on the $\lambda = i \omega$ curve that is not an intersection point of the branches of the $\lambda = i \omega$ curve or an intersection point of the $\lambda = i \omega$ curve and $\lambda = 0$ line. Let $i \omega_c$ be the purely imaginary root of Eq. (20) such that $Q_H^{kc} = Q_H^k(\omega_c)$ and $\tau_{1c} = \tau_{1k}^j(\omega_c)$ for some $j$, where $Q_H^k(\omega)$ and $\tau_{1k}^j(\omega)$ are defined by (30) and (31). Assume that $\omega_c$ is neither a zero of $dQ_H^k/d\omega$ nor of $d\tau_{1k}^j/d\omega$, then system (4) undergoes a Hopf bifurcation at $Q = Q_H^{kc}$.

We conclude that if system (4) satisfies the appropriate non-resonance conditions, the curves (30) and (31) define the Hopf bifurcation lines on the $(Q, \tau_1)$ plane, and the vertical line $g_k = -1$ defines the steady-state bifurcation. One way to determine the bifurcation properties of Hopf is to analyze the central manifold of the equation using the method in [28]. To determine the type of steady-state bifurcation in the system, we need to analyze the number and stability of non-trivial equilibrium points. To do this, we need to linearize the system about these equilibria, generate a new characteristic equation, and analyze its roots. This is a big task, so we omitted this process due to space constraints.

Codimension-2 bifurcation occurs when two of these different bifurcations happen simultaneously. Hopf-Hopf bifurcation point exists when the characteristic equation has two pairs of pure imaginary roots $\pm i \omega_1$ and $\pm i \omega_2$. For the considered system, these points can occur for any set of the parameters $l, k, r, \alpha, b, \gamma, \mu, \tau_2$ such that $Q_H^k(\omega_1) = Q_H^k(\omega_2)$ and $\tau_{1k}^j(\omega_1) = \tau_{1k}^j(\omega_2)$, for some $j, jj \in \mathbb{N}$. In general, these points cannot be solved in a closed form. However, they can be computed numerically (see Fig. 11A). Hopf-steady state interactions exist when the characteristic equations have both a zero root and a pure imaginary pair. For system (4), these points may be found by solving $Q(\omega) = -J_{1k}J_{2k}$ for $\omega$ and substituting in $\tau_{1k}^j$ as given by the equality (31) where they appear as intersection points of the Hopf bifurcation curves with the line $Q(\omega) = -J_{1k}J_{2k}$ (see Fig. 12B). From Theorem 9, it is clear that neither type of codimension-2 point can occur in system (4) if $\tau_2 < \tau_{2k}^{(1)}$. Codimension-2 points can be the source of more complicated dynamics such as multistability and quasiperiodicity.

**5 Numerical simulation**

Firstly, it chooses the same parameters as [11] except for $l$ and $b$ for system (4), i.e.,

$r = 0.5, \mu = 1, \alpha = 0.1, \gamma = 2, l = 1, b = 2.5$

satisfying $b + 1 > \gamma$. It can obtain that the boundary equilibrium $E_0(1, 0)$ is globally asymptotically stable for system (4) (see Fig. 4).

Secondly, let $\tau_1 = \tau_2 = \tau$, we choose the parameters in (39). From Fig. 5A, for given $b \in (0, 1)$, it can obtain a unique $0 < a^* < 1$. When choosing $b = 0.3, 0.5, 0.8, 0.95$, respectively, which satisfies the condition (A21), system (4) exists a uniquely positive equilibrium $E^*$ and $m^*$ reduces as $b$ increasing while $a^*$ increases as $b$ becomes bigger (see Fig. 5B).

Authors [11] considered the linear growth in mussel population, when $\tau = 3.6$, they obtain that the positive equilibrium is unstable and there exists a stable periodic solution. Next, we choose $\tau = 3.6$ and $b = 0.5$, it can find that $E^*$ is unstable and a stable periodic solution exists (see Fig. 6). Furthermore, it increases $b$ to 0.8, the numerical simulation shows that $E^*$ becomes stable (see Fig. 7). In addition, in [11], when $\tau = 2$, $E^*$ is stable. Here by numerical simulations, it finds that the stability of $E^*$ can not vary despite the change in $b$ (see Fig. 8). These may explain that $b$ can change the oscillation property to stability. That is, $b$ contributes to stabilize the system.

In the following, it investigates the effect of $b$ for the single delay system under the parameters (39). Let
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**Fig. 5** (a,b) plane plot. (a,m) plane plots for different b

**Fig. 6** $E^*$ is unstable and there exists a stable periodic solution for $r_1 = r_2 = 3.6$ and $b = 0.5$

**Fig. 7** $E^*$ is stable for $b = 0.8$

**Fig. 8** $E^*$ is stable for A $b = 0.3$ and B $b = 0.8$
$\tau_2 = 0$ and $\tau_1 = 3.6$, choosing $b = 0.5$, there exists a stable periodic solution (see Fig. 9A), but $b = 0.8$ can obtain that $E^*$ is stable (see Fig. 9B).

Furthermore, we choose another parameters $b = 0.5, l = 7$ and the other parameters as (39). When $\tau_2 = 0$, from Theorem 8, it can obtain the $(Q-\tau_1^0)$ plane plots for different $k$ (see Fig. 10A). Under the curve $k = 0$, $E^*$ is stable, otherwise, unstable. Using the above parameters, it has $Q = 0.1531$. Choosing $\tau_1 = 1$ and $\tau_1 = 3$, respectively, it can obtain the stability of $E^*$ (see Figs. 10–11). Furthermore, by choosing the different $k$, the system occurs the Hopf-Hopf bifurcation since there are two pairs of imaginary roots simultaneously (see Fig. 11B). This leads to more complicated dynamical behavior, for example, several cycles may coexist near the intersection point.

Choosing the different $\tau_2$, it can get the different $(Q, \tau_1)$ plane plots where ensures the increasing (decreasing) number of the positive real part roots for the fixed $k = 0$ when the parameters cross these critical boundaries (see Fig. 12). It can choose “+” (increasing) or “-” (decreasing) depending on the transversal condition. From Fig. 12B, at $P_0$ the Turing-Hopf bifurcation occurs.

At last, we investigate the effects of two different delays. Choosing the above parameters, $w_+ = 0.3005$ and $\tau_{10}^0 = 1.8398$.

$\tau_{10}^0$ is the increasing function of $k$ (see Fig. 13A). Hence, we only need compute $\tau_{10}^0$. Under the above parameters, $w_+ = 0.3005$ and $\tau_{10}^0 = 1.8398$. 

Fig. 9 (A) $E^*$ is unstable and there exists a stable periodic solution for $b=0.5$. (B) $E^*$ is stable for $b=0.8$

Fig. 10 $(Q, \tau_{10}^0)$ plots for different $k$ (see A). $E^*$ is stable when $\tau_1 = 1$ (see B)
Fixed τ₁ = 1.7, when τ₂ = 0, E* is stable for any k ∈ N. We can draw the (ω, F₀(ω)) plot shown in Fig. 13B, which can see that there are two roots defined by ω₁ = 0.3129 and ω₂ = 0.3847. However, when k ≥ 1, Fₖ(ω) = 0 has no any positive roots. That is, for τ₁ = 1.7, only two purely imaginary roots are feasible when k = 0, the other situations have no any purely imaginary roots. Furthermore, we get two series of τ₂ as follows τ₂₁ = 19.5542 + 20.0805j and τ₂₂ = 13.0786 + 16.3327j. The transversal condition is negative for τ₂₁ and positive for τ₂₂. Hence, we obtain that E* is stable for τ₂ ∈ [0, τ₂₁) ∪ (τ₂₁, τ₂₂] ∪ (τ₂₂, τ₂₃) and unstable for (τ₂₂, τ₂₁) ∪ (τ₂₁, τ₂₆) ∪ (τ₂₆, τ₂₅) and (τ₂₅, +∞).

Choosing τ₂ = 5, 15, 22, 75, respectively, we can obtain the phase plots as Fig. 14. The stability switch phenomenon occurs. In addition, in [11], if two same delays were considered, the system can not occur the stability switches. This explains the importance of two different delays. These numerical simulations confirm the correctness of the theoretical analyses.

6 Conclusions

In this paper, we analyze in detail a mussel-algae system (4) which improves that in [11] by introducing the half-saturation constant b and two different delays τ₁ and τ₂. The parameters can produce some complicate
effects, such as Turing instability, steady-state bifurcation, Hopf bifurcation, Hopf-Hopf bifurcation or Hopf-steady state bifurcation. Some main results are given as follows:

- Under certain conditions (A1, A2 or A3), there may be one or two positive equilibrium points in system (4). The set of parameters for the existence of positive equilibrium is given.
- For system (3),
  - The existence and uniqueness of solutions are proved by upper and lower solution method, under certain condition \(b + 1 > \gamma\), the optimal bounds of solutions are derived.
  - The stability of the positive equilibrium depends on the half-saturation parameter \(b\) without considering spatial effects. The parameter \(r\) does not affect the existence of the equilibrium, but it will affect the stability of the equilibrium and lead to the occurrence of Hopf bifurcation.
  - Turing instability can occur under certain conditions, the numerical simulations find that the range of Turing instability becomes larger as \(b\) increasing.
  - For system (4),
    - When the \(b + 1 > \gamma\), the boundary equilibrium \(E_0\) is globally asymptotically stable.
    - By analyzing the two-parameter characteristic equation (20), it is found that Eq. (20) may have single or double zero roots under certain conditions. When the parameter \(\tau_2\) is not considered, the condition and critical value of \(\tau_1\) such that the roots of Eq. (20) have strictly negative real parts are obtained.
    - The change of positive real roots in the plane \((Q, \tau_1)\) is obtained. When \((Q, \tau_1)\) is fixed in the stable region, considering the influence of \(\tau_2\), the conditions for \(E^*\) absolute stability and the conditions for Hopf bifurcation occurrence are obtained. Through numerical simulation, it can find that \(\tau_2\) causes the system to produce stable switching phenomenon.
    - The possible intersection of steady-state branch line and Hopf branch line in \((Q, \tau_1)\) plane is discussed, codimension 2 bifurcation may occur.

Our results suggest that the positive equilibrium will lose its stability when \(\tau_1\) or \(\tau_2\) pass through some critical values, and there will be periodic oscillations in populations of species. Compared to the system in [11], by numerical simulations, it can be found that a large half-saturation constant \(b\) can contribute to stabilize the system whether the system is single time delayed or multiple time delayed. Under certain conditions, the double delayed system can occur the stability switches phenomena, which is impossible when \(\tau_1 = \tau_2\). This shows that two single delays can make system more complicated. Beyond that, by numerical simulations, the system may occur more complicated dynamic behavior, such as codimension-2, it still needs furthermore to confirm from the theory. In addition, in this paper, it has investigated the effects of two different delays, but it does not give the stability changes of equilibrium in \((\tau_1, \tau_2)\) parameter plane, which needs the further consideration.
Fig. 14  $E^*$ is stable when $\tau_2 = 5 \in [0, \tau_{22}^0)$ and $\tau_2 = 22 \in (\tau_{21}^0, \tau_{22}^1)$ (see A and C). $E^*$ is unstable and there exists a stable periodic solution when $\tau_2 = 15 \in (\tau_{22}^0, \tau_{21}^0)$ and $\tau_2 = 75 > \tau_{22}^3$ (see B and D).

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Data availability  All data generated or analyzed during this study are included in this published article.

Declarations

Conflicts of interest  The authors declare that they have no conflict of interest.

References

1. van de Koppel, J., Rietkerk, M., Dankers, N., Herman, P.: Self-dependent feedback and regular spatial patterns in young mussel beds. Am. Nat. 165, 66–77 (2005)
2. van de Koppel, J., Gascoigne, J., Theraulaz, G., Rietkerk, M., Mooij, W., Herman, P.: Experimental evidence for spatial self-organization in mussel bed ecosystems. Science 322, 739–742 (2008)
3. Liu, Q., Doelman, A., Rottschafer, V., de Jager, M., Herman, P., Rietkerk, M., van de Koppel, J.: Phase separation explains a new class of self-organized spatial patterns in ecological systems. Proc. Natl. Acad. Sci. 110, 11905–11910 (2013)
4. Wang, R., Liu, Q., Sun, G., Zhen, J., van de Koppel, J.: Nonlinear dynamic and pattern bifurcation in a model for spatial patterns in young mussel beds. J. R. Soc. Interface 6, 705–718 (2008)
5. Liu, Q., Weerman, E., Herman, P., Olff, H., van de Koppel, J.: Alternative mechanisms alter the emergent properties of self-organization in mussel beds. Proc. R. Soc. B Biol. Sci. 279, 2744–2753 (2012)

6. Cangelosi, R., Wollkind, D., Kealy-Dichone, B., Choiya, I.: Nonlinear stability analyses of Turing patterns for a mussel-algae model. J. Math. Biol. 70, 1249–1294 (2015)

7. Williams, C., Bees, M.: A tale of three taxes: photo-gyrovitactict bioconvection. J. Exp. Biol. 214, 2398–2408 (2011)

8. Liu, Q., Rietkerk, M., Herman, P., Piersma, T., Fryxell, J., van de Koppel, J.: Phase separation driven by density-dependent movement: a novel mechanism for ecological patterns. Phys. Life Rev. 19, 107–121 (2016)

9. Song, Y., Jiang, H., Liu, Q., Yuan, Y.: Spatiotemporal dynamics of the diffusive mussel-algae model near Turing-Hopf bifurcation. SIAM J. Appl. Dyn. Syst. 16, 2030–2062 (2017)

10. Jiang, H.: Delay-included Turing-Hopf bifurcation in the diffusive mussel-algae model. Math. Methods Appl. Sci. 44, 12349–12364 (2021)

11. Shen, Z., Wei, J.: Bifurcation analysis in a diffusive mussel-algae model with delay. Int. J. Bifurc. Chaos 29, 1950144 (2019)

12. Shen, Z., Wei, J.: Spatiotemporal patterns in a delayed reaction-diffusion mussel-algae model. Int. J. Bifurc. Chaos 29, 1950164 (2019)

13. Shen, Z., Wei, J.: Stationary pattern of a reaction-diffusion mussel-algae model. Bull. Math. Biol. 82, 1–31 (2020)

14. Zhong, S., Cheng, X., Liu, B.: Spatiotemporal dynamics for a diffusive mussel-algae model near a Hopf bifurcation point. Adv. Diff. Equ. 182, 20 (2021)

15. van de Koppel, J., Rietkerk, M., Dankers, N., Herman, M.: Scale-dependent feedback and regular spatial patterns in young mussel beds. Am. Naturalist 165, 66–77 (2005)

16. Stepan, G.: Great delay in a predator-prey model. Nonlinear Anal. Theory, Methods & Application 9, 913–929 (1986)

17. Zhu, H., Duan, K.: Global stability and periodic orbits for a two-patch diffusion predator-prey model with time delays. Nonlinear Anal. 41, 1083–1096 (2000)

18. Jiang, Z., Wang, L.: Global Hopf bifurcation for a predator-prey system with three delays. Int. J. Bifurc. Chaos 27, 1750108 (2017)

19. Jiang, Z., Guo, Y.: Hopf bifurcation and stability crossing curve in a planktonic resource-consumer system with double delays. Int. J. Bifurc. Chaos 30, 2050190 (2020)

20. Sipahi, R., Olgaç, N.: A unique methodology for the stability robustness of multiple time delay systems. Syst. & Control Lett. 55, 819–825 (2006)

21. Zhang, L., Stepan, G.: Exact stability chart of an elastic beam subjected to delayed feedback. J. Sound & Vib. 367, 219–232 (2016)

22. Gambino, G., Lombardo, M., Sammartino, M.: Pattern formation driven by cross-diffusion in a 2D domain. Nonlinear Anal. Real World Appl. 14, 1755–1779 (2012)

23. Hale, J., Lunel, S.: Introduction to Functional Differential Equations. Springer-Verlag, New York (1993)

24. Pao, C.: Nonlinear Parabolic and Elliptic Equations. Plenum Press, New York (1992)

25. Ye, Q., Li, Z.: Introduction to Reaction-Diffusion Equations. Science Press, Beijing (1994)

26. Pao, C.: Convergence of solutions of reaction-diffusion systems with time delays. Nonlinear Anal. Theory Methods Appl. 48, 349–362 (2002)

27. Ruan, S., Wei, J.: On the zeros of transcendental functions with applications to stability of delay differential equations with two delays. Dyn. Contin. Discret. Impulsive Syst. Ser. A Math. Anal. 10, 863–874 (2003)

28. Wù, J.: Theory and Applications of Partial Functional-Differential Equations. Springer, New York (1996)