Bifurcation Analysis in a Diffusion Mussel-Algae Interaction System with Delays Considering the Half-Saturation Constant

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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 affect 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 parameters, the half-saturation constant and two delays drive the complexity of system dynamics.

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

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1 Introduction

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

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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. Especially, 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 Koppel 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:

$$\begin{cases} \frac{\partial \mathbf{A}(x,t)}{\partial t} = \mathbf{D}_\mathbf{A} \Delta \mathbf{A}(x,t) + \rho (\mathbf{A}_u - \mathbf{A}(x,t)) - \frac{V \partial \mathbf{A}(x,t)}{\partial x} - \frac{c}{H} \mathbf{M}(x,t) \mathbf{A}(x,t), \\ \frac{\partial \mathbf{M}(x,t)}{\partial t} = \mathbf{D}_\mathbf{M} \Delta \mathbf{M}(x,t) + e c \mathbf{M}(x,t) \mathbf{A}(x,t) - d_\mathbf{M} \frac{k_\mathbf{M}}{k_\mathbf{M} + \mathbf{M}(x,t)} \mathbf{M}(x,t), \end{cases} \quad (1)$$

where $\mathbf{A}(x,t)$ and $\mathbf{M}(x,t)$ 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 $x \in \Omega$. $\Omega \subseteq \mathbb{R}^n$ is a bounded domain with a smooth boundary $\partial\Omega$. Δ is Laplace operator. ρ is the exchange rate between the upper and lower water layers. $\mathbf{A}_u$ 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 $d_\mathbf{M}$ represents mussel loss due to predation or dislodgement. $k_\mathbf{M}$ is the value of $\mathbf{M}(x,t)$ at which mortality is half maximal. $\mathbf{D}_\mathbf{M}$ 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 $\mathbf{D}_\mathbf{A}$ because their mechanism of locomotion is flagella and a passive vertical diffusion ρ 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

Fig. 1 Schematic for the mussel-algae interaction-diffusion system [6]. Concentration of algae in the upper water layer is taken to be constant (A_u). Algae passively diffuse into the benthic layer at a rate ρ and become available to the mussel for consumption at rate c .

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

$$\begin{cases} \frac{\partial A(x,t)}{\partial t} = D_A \Delta A(x,t) + \rho (A_u - A(x,t)) - \frac{c}{H} \frac{A(x,t)}{\beta + A(x,t)} M(x,t), \\ \frac{\partial M(x,t)}{\partial t} = D_M \Delta M(x,t) + ec \frac{A(x,t)}{\beta + A(x,t)} M(x,t) - d_M \frac{k_M}{k_M + M(x,t)} M(x,t), \end{cases} \quad (2)$$

where β is the half-saturation constant.

By introducing the dimensionless variables:

$$\begin{aligned} \bar{x} &= x \sqrt{w/D_A}, \quad w = ck_M/H, \quad \bar{t} = d_M t, \quad \mathbf{m} = \mathbf{M}/k_M, \quad \mathbf{a} = \mathbf{A}/A_u, \\ \alpha &= \rho/w, \quad r = d_M/w, \quad \gamma = ec/d_M, \quad \mu = D_M/D_A \gamma, \quad b = \beta/A_u \end{aligned}$$

and removing the "–", system (2) becomes

$$\begin{cases} r \frac{\partial \mathbf{a}(x,t)}{\partial t} = \Delta \mathbf{a}(x,t) + \alpha \left(1 - \mathbf{a}(x,t) \right) - \frac{\mathbf{a}(x,t) \mathbf{m}(x,t)}{b + \mathbf{a}(x,t)}, \\ \frac{\partial \mathbf{m}(x,t)}{\partial t} = \mu \Delta \mathbf{m}(x,t) + \frac{\gamma \mathbf{a}(x,t) \mathbf{m}(x,t)}{b + \mathbf{a}(x,t)} - \frac{\mathbf{m}(x,t)}{1 + \mathbf{m}(x,t)}. \end{cases} \quad (3)$$

It is well known that the delay may lead to periodic oscillations and the diffusion may cause Turing patterns. Inspired by the work of [11, 12, 15], we establish a delayed mussel-algae system with the Neumann boundary conditions in one dimensional space x as follows:

$$\begin{cases} r \frac{\partial \mathbf{a}(x,t)}{\partial t} = \Delta \mathbf{a}(x,t) + \alpha \left(1 - \mathbf{a}(x,t) \right) - \frac{\mathbf{a}(x,t) \mathbf{m}(x,t)}{b + \mathbf{a}(x,t)}, & x \in (0, l\pi), t > 0, \\ \frac{\partial \mathbf{m}(x,t)}{\partial t} = \mu \Delta \mathbf{m}(x,t) + \frac{\gamma \mathbf{a}(x,t - \tau_1) \mathbf{m}(x,t)}{b + \mathbf{a}(x,t - \tau_1)} - \frac{\mathbf{m}(x,t)}{1 + \mathbf{m}(x,t - \tau_2)}, & x \in (0, l\pi), t \geq 0, \\ \frac{\partial \mathbf{m}(x,t)}{\partial x} = \frac{\partial \mathbf{a}(x,t)}{\partial x} = 0, & x = 0, l\pi, t > 0, \\ \mathbf{a}(x,t) = \varphi(x,t) \geq 0, \mathbf{m}(x,t) = \psi(x,t) \geq 0, & x \in [0, l\pi], t \in [-\tau, 0], \\ \mathbf{a}(x,0) := v_1(x) \geq 0, \mathbf{m}(x,0) := v_2(x) \geq 0, & x \in [0, l\pi], \end{cases} \quad (4)$$

where $\tau = \max\{\tau_1, \tau_2\}$, τ_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. τ_2 represents the mortality of mussel depending on the state whether they have been eaten in the past.

Compared with the work in [10, 11, 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

$$\mathbf{X} = \left\{ (u_1, u_2) \in \mathbf{H}^2(0, l\pi) \times \mathbf{H}^2(0, l\pi) \mid \frac{\partial u_1}{\partial x} = \frac{\partial u_2}{\partial x} = 0, x = 0, l\pi \right\}$$

and its complexification $\mathbb{X} = \mathbf{X} \oplus i\mathbf{X} = \{\alpha + i\beta \mid \alpha, \beta \in \mathbf{X}\}$ with $\mathbf{L}^2$ inner product defined as

$$\langle W_1, W_2 \rangle = \int_0^{l\pi} (\overline{w_{11}} w_{21} + \overline{w_{12}} w_{22}) dx,$$

where $W_1 = (w_{11}, w_{12})^T \in \mathbb{X}$ and $W_2 = (w_{21}, w_{22})^T \in \mathbb{X}$.

The arrangement of this article is as follows. In next section, the existence conditions of the positive equilibrium are given. When the 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 Section 3. 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 via the steady state bifurcation, Hopf bifurcation, Hopf-Hopf bifurcation or Hopf-steady state bifurcation. These results are shown in Section 4. At last, some numerical simulations can verify that the dynamic behaviors of system caused by half-saturation constant are consistent with the theoretical findings and some new findings are predicted.

2 Equilibrium

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

$$\begin{cases} \frac{\mathbf{a}\mathbf{m}}{b+\mathbf{a}} = \alpha(1-\mathbf{a}), \\ \frac{\gamma\mathbf{a}\mathbf{m}}{b+\mathbf{a}} = \frac{\mathbf{m}}{1+\mathbf{m}}. \end{cases} \quad (5)$$

The boundary equilibrium $\mathbf{E}_0(1, 0)$ always exists. The existence of positive equilibrium $\mathbf{E}^*(\mathbf{a}^*, \mathbf{m}^*)$ needs some analyses described as follows.

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

$$F(\mathbf{a}) := \mathbf{a}^2 + L_1\mathbf{a} + L_2 = 0, \quad (6)$$

where

$$L_1 = b - \frac{1}{\alpha} + \frac{1}{\gamma\alpha} - 1 \text{ and } L_2 = \left(\frac{1}{\gamma\alpha} - 1\right)b.$$

If (6) has a root $\mathbf{a}^*$ satisfying $0 < \mathbf{a}^* < 1$, then (5) exists a positive equilibrium $\mathbf{E}^*(\mathbf{a}^*, \mathbf{m}^*)$, where

$$\mathbf{m}^* = \frac{\alpha(b+\mathbf{a}^*)(1-\mathbf{a}^*)}{\mathbf{a}^*}. \quad (7)$$

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

(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 (6) exists a uniquely positive root

$$0 < \mathbf{a}_+^* = \frac{-L_1 + \sqrt{\delta}}{2} < 1 \quad (8)$$

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

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

$$(A2) \quad L_1 < 0, L_2 > 0, \delta > 0, F(1) < 0,$$

holds, then (6) exists a uniquely positive solution

$$0 < \mathbf{a}_-^* = \frac{-L_1 - \sqrt{\delta}}{2} < 1 \quad (9)$$

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

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

$$(A21) \quad \alpha(b-1) < 1, \max\left\{\frac{1}{\alpha+(1-\sqrt{b\alpha})^2}, b+1\right\} < \gamma < \frac{1}{\alpha}$$

or

$$(A22) \quad \alpha(b-1) < 1, \max\left\{\frac{1}{\alpha+1-b\alpha}, b+1\right\} < \gamma < \frac{1}{\alpha+(1+\sqrt{b\alpha})^2}.$$

(3) If the following condition holds,

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

i.e.,

$$(A31) \quad 1 - \alpha \leq b\alpha < 1 + \alpha, \frac{1}{\alpha + (1 - \sqrt{b\alpha})^2} < \gamma < \frac{1}{\alpha}$$

or

$$(A32) \quad (b+1)\alpha < 1, \frac{1}{\alpha + (1 - \sqrt{b\alpha})^2} < \gamma < \min \left\{ b+1, \frac{1}{1 - \alpha(b+1)} \right\},$$

then (5) exists two positive roots

$$0 < \mathbf{a}_{\pm}^* = \frac{-L_1 \pm \sqrt{\delta}}{2} < 1. \quad (10)$$

Hence system (4) exists two positive equilibrium $E_{\pm}^*(\mathbf{a}_{\pm}^*, \mathbf{m}_{\pm}^*)$ and $\mathbf{m}_{\pm}^*$ satisfies (7).

Denote

$$\mathbb{T} = \{(b, \alpha, \gamma) \mid (A1) \text{ or } (A2) \text{ or } (A3) \text{ hold.}\}$$

If $(b, \alpha, \gamma) \in \mathbb{T}$, 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, we give a sufficient condition for the existence of a positive solution of system (3). Meanwhile, we also derive a priori bound of solutions.

Theorem 1 (i) If $v_i(x) \geq 0$ and $v_i(x) \not\equiv 0$ ($i = 1, 2$), then system (3) exists a unique solution $(\mathbf{a}(t, x), \mathbf{m}(t, x))$ satisfying

$$0 < \mathbf{a}(x, t) \leq \mathbf{a}^*(t), 0 < \mathbf{m}(x, t) \leq \mathbf{m}^*(t) \text{ for } t > 0 \text{ and } x \in [0, l\pi],$$

where $(\mathbf{a}^*(t), \mathbf{m}^*(t))$ is the unique solution of

$$\begin{cases} r \frac{d\mathbf{a}(t)}{dt} = \alpha[1 - \mathbf{a}(t)], \\ \frac{d\mathbf{m}(t)}{dt} = \frac{\gamma \mathbf{a}(t) \mathbf{m}(t)}{b + \mathbf{a}(t)} - \frac{\mathbf{m}(t)}{1 + \mathbf{m}(t)}, \\ \mathbf{a}(0) = v_1^* = \sup_{x \in [0, l\pi]} v_1(x), \\ \mathbf{m}(0) = v_2^* = \sup_{x \in [0, l\pi]} v_2(x). \end{cases}$$

(ii) If $b+1 > \gamma$, then all solutions $(\mathbf{a}(x, t), \mathbf{m}(x, t))$ of system (3) satisfy the following estimates

$$\limsup_{t \rightarrow \infty} \mathbf{a}(t, x) \leq 1 \text{ and } \limsup_{t \rightarrow \infty} \mathbf{m}(x, t) \leq \frac{b+1-\gamma}{\gamma} := \mathbf{m}^{\#}.$$

Proof Define

$$g_1(\mathbf{a}, \mathbf{m}) = \alpha \left(1 - \mathbf{a} \right) - \frac{\mathbf{a}\mathbf{m}}{b+\mathbf{a}} \text{ and } g_2(\mathbf{a}, \mathbf{m}) = \frac{\mathbf{a}\mathbf{m}}{b+\mathbf{a}} - \frac{\mathbf{m}}{1+\mathbf{m}},$$

which has $\frac{\partial g_1}{\partial \mathbf{m}} \leq 0$ and $\frac{\partial g_2}{\partial \mathbf{a}} \geq 0$ for $(\mathbf{a}, \mathbf{m}) \in \mathbb{R}_+^2 = \{(\mathbf{a}, \mathbf{m}) : \mathbf{a} \geq 0, \mathbf{m} \geq 0\}$. Then system (3) is a mixed quasi-monotone system [18, 19].

Denote

$$(P_1(t, x), Z_1(t, x)) = (0, 0) \text{ and } (P_2(t, x), Z_2(t, x)) = (\mathbf{a}^*(t), \mathbf{m}^*(t)).$$

Since $0 \leq v_i(x) \leq v_i^*$ ($i = 1, 2$),

$$\begin{aligned} r \frac{\partial P_2}{\partial t} - \Delta P_2 - g_1(P_2, Z_1) &= 0 \geq -\alpha = r \frac{\partial P_1}{\partial t} - \Delta P_1 - g_1(P_1, Z_2), \\ \frac{\partial Z_2}{\partial t} - \mu \Delta Z_2 - g_2(P_2, Z_2) &= 0 \geq 0 = \frac{\partial Z_1}{\partial t} - \mu \Delta Z_1 - g_2(P_1, Z_1), \end{aligned}$$

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 [16, 17], it can know that system (3) has a uniquely global solution $(\mathbf{a}(x, t), \mathbf{m}(x, t))$ satisfying

$$0 \leq \mathbf{a}(x, t) \leq \mathbf{a}^*(t) \text{ and } 0 \leq \mathbf{m}(x, t) \leq \mathbf{m}^*(t) \text{ for } t \geq 0.$$

The strong maximum principle implies that $\mathbf{a}(x, t) > 0$ and $\mathbf{m}(x, t) > 0$ when $t > 0$ for all $x \in [0, l\pi]$. This completes the proof of (i).

It has known that $\mathbf{a}(x, t) \leq \mathbf{a}^*(t)$ for $t > 0$, and $\mathbf{a}^*(t)$ is the unique solution of

$$\begin{cases} r \frac{d\mathbf{a}}{dt} = \alpha (1 - \mathbf{a}), \\ \mathbf{a}(0) = v_1^* > 0, \end{cases}$$

which yields to $\lim_{t \rightarrow \infty} \mathbf{a}^*(t) = 1$. Thus for any $\varepsilon > 0$, there exists $T_0 > 0$ such that

$$\mathbf{a}(x, t) \leq 1 + \varepsilon \text{ for } t > T_0 \text{ and } x \in [0, l\pi]$$

which implies that $\limsup_{t \rightarrow \infty} \mathbf{a}(x, t) \leq 1$.

From $\mathbf{m}(x, t) \leq \mathbf{m}^*(t)$ for $t > 0$, and $\mathbf{m}^*(t)$ is the unique solution of

$$\begin{cases} \frac{d\mathbf{m}(t)}{dt} = \frac{\gamma \mathbf{a}(t) \mathbf{m}(t)}{b + \mathbf{a}(t)} - \frac{\mathbf{m}(t)}{1 + \mathbf{m}(t)}, \\ \mathbf{m}(0) = v_2^* > 0. \end{cases}$$

To prove the boundedness of $\mathbf{m}(x, t)$, we only need to prove that $\mathbf{m}^*(t)$ is bounded since $\mathbf{m}^*(t)$ is a upper-solution of $\mathbf{m}(x, t)$. According to $\mathbf{a}(x, t) \leq 1 + \varepsilon$, it has $\frac{d\mathbf{m}(t)}{dt} \leq \left[\frac{\gamma(1+\varepsilon)}{b+1+\varepsilon} - \frac{1}{1+\mathbf{m}(t)} \right] \mathbf{m}(t)$ which yields to $\limsup_{t \rightarrow \infty} \mathbf{m}(t) \leq \frac{b+1-\gamma+(1-\gamma)\varepsilon}{\gamma(1+\varepsilon)}$. Since the randomness of ε , $\limsup_{t \rightarrow \infty} \mathbf{m}^*(t) \leq \frac{b+1-\gamma}{\gamma}$ if $b+1 > \gamma$. This means $\limsup_{t \rightarrow \infty} \mathbf{m}(x, t) \leq \frac{b+1-\gamma}{\gamma}$. This completes the proof of (ii). $\square$

3.2 Stability of the nonspatial system

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

$$\begin{cases} r \frac{da}{dt} = \alpha(1-a) - \frac{am}{b+a}, \\ \frac{dm}{dt} = \frac{\gamma am}{b+a} - \frac{m}{1+m}. \end{cases} \quad (11)$$

The linearization of system (11) is

$$\begin{cases} \frac{da}{dt} = b_{11}a + b_{12}m, \\ \frac{dm}{dt} = b_{21}a + b_{22}m, \end{cases}$$

whose characteristic equation is

$$\lambda^2 + T_0\lambda + J_0 = 0,$$

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

$$b_{11} = -\frac{\alpha}{r}, \quad b_{12} = -\frac{1}{r(b+1)}, \quad b_{21} = 0, \quad b_{22} = \frac{\gamma}{b+1} - 1$$

and

$$T_0 = \frac{1}{r} \left[\alpha + \frac{r(b+1-\gamma)}{b+1} \right], \quad J_0 = \alpha \frac{r(b+1-\gamma)}{r(b+1)},$$

which means that E_0 is locally asymptotically stable for $b+1 > \gamma$ and unstable for $b+1 < \gamma$.

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

$$\begin{cases} b_{11} = -\frac{1}{r} \left[\alpha + \frac{bm^*}{(b+a^*)^2} \right] < 0, \\ b_{12} = -\frac{a^*}{r(b+a^*)} < 0, \\ b_{21} = \frac{\gamma bm^*}{(b+a^*)^2} > 0, \\ b_{22} = \frac{m^*}{(1+m^*)^2} > 0, \\ T_0 = \frac{1}{r} \left[\alpha + \frac{bm^*}{(b+a^*)^2} \right] - \frac{m^*}{(1+m^*)^2}, \\ J_0 = \frac{m^*}{r(1+m^*)^2(b+a^*)^2} \left[-\alpha(a^*)^2 - 2\alpha ba^* + b - \alpha b^2 \right]. \end{cases} \quad (12)$$

Since $0 < \mathbf{a}^* < 1$, it has $J_0 < 0$ if $1 - \alpha b < 0$. If $1 - \alpha b > 0$ and $\mathbf{a}^\diamond \geq 1$, then $J_0 > 0$. If $1 - \alpha b > 0$ and $\mathbf{a}^\diamond < 1$, then $J_0 > 0$ for $0 < \mathbf{a}^* < \mathbf{a}^\diamond$ and $J_0 < 0$ for $\mathbf{a}^* > \mathbf{a}^\diamond$, where $\mathbf{a}^\diamond = \sqrt{\frac{b}{\alpha}} - b$. 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 $\mathbf{a}^\diamond \geq 1$, then E^* is locally asymptotically stable. If $b < \frac{1}{\alpha}$ and $\mathbf{a}^\diamond < 1$, then E^* is locally asymptotically stable for $0 < \mathbf{a}^* < \mathbf{a}^\diamond$ and unstable for $\mathbf{a}^* > \mathbf{a}^\diamond$.

Remark 1 From Theorem 2, the parameter b has directly effect to the stability of E^* .

Fig. 2 (A) In the region I, E^* is stable and unstable in the region II and Hopf bifurcation may occur. In the regions III and IV, E^* does not exist and E_0 is stable. (B) Hopf bifurcation lines in the region II. (C) The phase plot for $b=2.727$. (D) The phase plot for $b=6.7151$.

Taking $r = 0.5$, $\mu = 0.6$, $\alpha = 0.01$, we can draw the (b, γ) plane plot in where the stability regions of E^* are given (see Figure 2 (A)). In the region II, Hopf bifurcation line is given in Figure 2 (B). 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. 2 (C)-(D).

Obviously, r does not affect the existence of E^* , but it does affect its stability. Next, we investigate the effect of r on the stability of E^* . Solving $T_0 = 0$ for r , it has

$$r \doteq r(\alpha, \gamma, b) = \frac{\mathbf{m}^*(b + \mathbf{a}^*)^2}{\alpha(1 + \mathbf{m}^*)^2(b + \mathbf{a}^*)^2 + b\mathbf{m}^*(1 + \mathbf{m}^*)^2}. \quad (13)$$

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

$$\begin{pmatrix} \frac{\partial \mathbf{a}}{\partial t} \\ \frac{\partial \mathbf{m}}{\partial t} \end{pmatrix} = D\Delta \begin{pmatrix} \mathbf{a} \\ \mathbf{m} \end{pmatrix} + \tilde{D} \begin{pmatrix} \mathbf{a} \\ \mathbf{m} \end{pmatrix}, \quad (14)$$

where

$$D\Delta = \begin{pmatrix} \frac{1}{r} \frac{\partial^2}{\partial x^2} & 0 \\ 0 & \mu \frac{\partial^2}{\partial x^2} \end{pmatrix} \text{ and } \tilde{D} = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix},$$

where b_{ij} ($i, j = 1, 2$) are the same as (12).

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

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

where k is the wave number,

$$T_k = \left(\mu + \frac{1}{r} \right) \frac{k^2}{l^2} + T_0 \text{ and } J_k = \frac{\mu k^4}{r l^4} - \left(\mu b_{11} + \frac{b_{22}}{r} \right) \frac{k^2}{l^2} + J_0.$$

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 $\mu^* = -\frac{b_{22}}{r b_{11}}$.*

Define

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

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 $p(k_{min}^2) < 0$, the sufficient condition for the system to be unstable reduces to

$$4b_{12}b_{21}\mu + r \left(\mu b_{11} - \frac{b_{22}}{r} \right)^2 > 0.$$

Theorem 5 *Turing instability occurs for system (3) under the following conditions:*

$$(TI) \quad \begin{aligned} & (b, \alpha, \gamma) \in \mathbb{T}, J_0 > 0, r < r(\alpha, \gamma, b), \mu b_{11} + \frac{b_{22}}{r} > 0 \\ & \text{and } 4b_{12}b_{21}\mu + r \left(\mu b_{11} - \frac{b_{22}}{r} \right)^2 > 0. \end{aligned}$$

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).

Fig. 3 The graph of the function $p(k^2)$ for the different b .

4 Spatiotemporal dynamics of system (4)

Let $\bar{E}(\bar{\mathbf{a}}, \bar{\mathbf{m}})$ be any equilibrium, define $u = \mathbf{a} - \bar{\mathbf{a}}$ and $v = \mathbf{m} - \bar{\mathbf{m}}$, then system (4) becomes

$$\begin{cases} r \frac{\partial u(x,t)}{\partial t} = \Delta u(x,t) - \left[\alpha + \frac{b\bar{\mathbf{m}}}{(b+\bar{\mathbf{a}})^2} \right] u(x,t) - \frac{\bar{\mathbf{a}}}{b+\bar{\mathbf{a}}} v(x,t) + \dots, \\ \frac{\partial v(x,t)}{\partial t} = \mu \Delta v(x,t) + \frac{b\gamma\bar{\mathbf{m}}}{(b+\bar{\mathbf{a}})^2} u(x,t - \tau_1) + \frac{\bar{\mathbf{m}}}{(1+\bar{\mathbf{m}})^2} v(x,t - \tau_2) \\ \quad + \left[\frac{\gamma\bar{\mathbf{a}}}{b+\bar{\mathbf{a}}} - \frac{1}{1+\bar{\mathbf{m}}} \right] v(x,t) + \dots, \end{cases} \quad (15)$$

whose characteristic equation is

$$\begin{aligned} \mathbf{D}_k(\lambda, \tau_1, \tau_2) = & \lambda^2 + \left[\frac{\mu k^2}{l^2} - l_{22}^0 + \frac{k^2}{rl^2} + l_{11} \right] \lambda + \left[\frac{\mu k^2}{l^2} - l_{22}^0 \right] \left[\frac{k^2}{rl^2} + l_{11} \right] \\ & + \gamma l_{12} l_{21} e^{-\lambda \tau_1} - l_{22} e^{-\lambda \tau_2} \left[\lambda + \frac{k^2}{rl^2} + l_{11} \right] = 0, \end{aligned} \quad (16)$$

where

$$\begin{aligned} l_{11} = \frac{\alpha}{r} + \frac{l_{21}}{r} &> 0, \quad l_{12} = \frac{\bar{\mathbf{a}}}{r(b+\bar{\mathbf{a}})} > 0, \quad l_{21} = \frac{b\bar{\mathbf{m}}}{(b+\bar{\mathbf{a}})^2} \geq 0, \\ l_{22} = \frac{\bar{\mathbf{m}}}{(1+\bar{\mathbf{m}})^2} &\geq 0 \text{ and } l_{22}^0 = \frac{\gamma\bar{\mathbf{a}}}{b+\bar{\mathbf{a}}} - \frac{1}{1+\bar{\mathbf{m}}}. \end{aligned}$$

4.1 Stability of boundary equilibrium $E_0(1, 0)$

For the equilibrium E_0 , it has $l_{21} = 0$, $l_{22} = 0$ and let

$$\mathbf{C}_k := \frac{\mu k^2}{l^2} - \frac{\gamma}{b+1} + 1 + \frac{k^2}{rl^2} + \frac{\alpha}{r}$$

and

$$S_k := \left[\frac{\mu k^2}{l^2} - \frac{\gamma}{b+1} + 1 \right] \left[\frac{k^2}{rl^2} + \frac{\alpha}{r} \right].$$

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 $S_0 = \frac{\alpha}{r} \left[1 - \frac{\gamma}{b+1} \right] < 0$, 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 $(\mathbf{a}(x, t), \mathbf{m}(x, t))$ 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

$$f_1(u, v) = \alpha(1 - u) - \frac{uv}{b+u} \text{ and } f_2(u, v) = \frac{\gamma uv}{b+u} - \frac{v}{1+v},$$

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 $\mathbf{R}_+^2 \times \mathbf{R}_+^2$. Let $(\tilde{\mathbf{a}}, \tilde{\mathbf{m}}) = (M_1, M_2)$ and $(\hat{\mathbf{a}}, \hat{\mathbf{m}}) = (0, 0)$, where M_1 and M_2 are any constants satisfying

$$M_1 > 1 \text{ and } M_2 > 0.$$

Since

$$\alpha(1 - \tilde{\mathbf{a}}) - \frac{\tilde{\mathbf{m}}\tilde{\mathbf{a}}}{b+\tilde{\mathbf{a}}} = 0 \leq 0, \quad \alpha(1 - \hat{\mathbf{a}}) - \frac{\hat{\mathbf{m}}\hat{\mathbf{a}}}{b+\hat{\mathbf{a}}} \geq 0,$$

and

$$\frac{\gamma\tilde{\mathbf{a}}\tilde{\mathbf{m}}}{b+\tilde{\mathbf{a}}} - \frac{\tilde{\mathbf{m}}}{1+\tilde{\mathbf{m}}} \leq 0, \quad \frac{\gamma\hat{\mathbf{a}}\hat{\mathbf{m}}}{b+\hat{\mathbf{a}}} - \frac{\hat{\mathbf{m}}}{1+\hat{\mathbf{m}}} = 0 \geq 0,$$

then $(\tilde{\mathbf{a}}, \tilde{\mathbf{m}})$ and $(\hat{\mathbf{a}}, \hat{\mathbf{m}})$ 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 the Theorem 2.1 of [20], we see that a uniquely global solution $(\mathbf{a}, \mathbf{m})$ of system (4) exists and satisfies

$$(0, 0) \leq (\mathbf{a}, \mathbf{m}) \leq (M_1, M_2)$$

whenever

$$(0, 0) \leq (\varphi(x, t), \psi(x, t)) \leq (M_1, M_2).$$

The maximum principle implies that $\mathbf{a}(x, t), \mathbf{m}(x, t) > 0$ for $t > 0$ and $x \in (0, l\pi)$ when $\varphi(x, t) \neq 0$ and $\psi(x, t) \neq 0$.

Let $(\tilde{\mathbf{a}}, \tilde{\mathbf{m}}) = (1 + \varepsilon, M_2)$ and $(\hat{\mathbf{a}}, \hat{\mathbf{m}}) = (\varepsilon, 0)$, where ε 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 ε is sufficiently small. We define two sequences $\{\bar{\mathbf{a}}^{(n)}, \bar{\mathbf{m}}^{(n)}\}$ and $\{\underline{\mathbf{a}}^{(n)}, \underline{\mathbf{m}}^{(n)}\}$ as follows:

$$\begin{cases} \bar{\mathbf{a}}^{(n)} = \bar{\mathbf{a}}^{(n-1)} + \frac{1}{K_1} \left[\alpha(1 - \bar{\mathbf{a}}^{(n-1)}) - \frac{\bar{\mathbf{m}}^{(n-1)}\bar{\mathbf{a}}^{(n-1)}}{b+\bar{\mathbf{a}}^{(n-1)}} \right], \\ \underline{\mathbf{a}}^{(n)} = \underline{\mathbf{a}}^{(n-1)} + \frac{1}{K_1} \left[\alpha(1 - \underline{\mathbf{a}}^{(n-1)}) - \frac{\bar{\mathbf{m}}^{(n-1)}\underline{\mathbf{a}}^{(n-1)}}{b+\underline{\mathbf{a}}^{(n-1)}} \right], \\ \bar{\mathbf{m}}^{(n)} = \bar{\mathbf{m}}^{(n-1)} + \frac{1}{K_2} \left[\frac{\gamma\underline{\mathbf{a}}^{(n-1)}\bar{\mathbf{m}}^{(n-1)}}{b+\underline{\mathbf{a}}^{(n-1)}} - \frac{\bar{\mathbf{m}}^{(n-1)}}{1+\bar{\mathbf{m}}^{(n-1)}} \right], \\ \underline{\mathbf{m}}^{(n)} = \underline{\mathbf{m}}^{(n-1)} + \frac{1}{K_2} \left[\frac{\gamma\bar{\mathbf{a}}^{(n-1)}\underline{\mathbf{m}}^{(n-1)}}{b+\bar{\mathbf{a}}^{(n-1)}} - \frac{\underline{\mathbf{m}}^{(n-1)}}{1+\underline{\mathbf{m}}^{(n-1)}} \right], \end{cases} \quad (17)$$

for $n = 1, 2, \dots$, where $(\bar{\mathbf{a}}^{(0)}, \bar{\mathbf{m}}^{(0)}) = (1 + \varepsilon, M_2)$, $(\underline{\mathbf{a}}^{(0)}, \underline{\mathbf{m}}^{(0)}) = (\varepsilon, 0)$ and K_i ($i = 1, 2$) are the Lipschitz constants.

From Lemma 2.1 of [20], it knows that

$$(\bar{\mathbf{a}}^{(n)}, \bar{\mathbf{m}}^{(n)}) \rightarrow (\bar{\mathbf{a}}, \bar{\mathbf{m}}) \text{ as } n \rightarrow \infty$$

and

$$(\underline{\mathbf{a}}^{(n)}, \underline{\mathbf{m}}^{(n)}) \rightarrow (\underline{\mathbf{a}}, \underline{\mathbf{m}}) \text{ as } n \rightarrow \infty$$

with

$$\varepsilon \leq \underline{\mathbf{a}} \leq \bar{\mathbf{a}} \leq 1 + \varepsilon \text{ and } 0 \leq \underline{\mathbf{m}} \leq \bar{\mathbf{m}} \leq M_2.$$

Since $\underline{\mathbf{m}}^{(0)} = 0$, it has $\underline{\mathbf{m}}^{(n)} = 0$ for $n = 1, 2, \dots$, which implies $\underline{\mathbf{m}} = 0$. From (17), we obtain that $\bar{\mathbf{a}}, \bar{\mathbf{m}}$ and $\underline{\mathbf{a}}$ satisfy

$$\begin{cases} \alpha(1 - \bar{\mathbf{a}}) = 0, \\ \alpha(1 - \underline{\mathbf{a}}) - \frac{\bar{\mathbf{m}}\underline{\mathbf{a}}}{b + \underline{\mathbf{a}}} = 0, \\ \frac{\gamma\underline{\mathbf{a}}\bar{\mathbf{m}}}{b + \underline{\mathbf{a}}} - \frac{\bar{\mathbf{m}}}{1 + \bar{\mathbf{m}}} = 0. \end{cases} \quad (18)$$

From the first equation of (18), it has $\bar{\mathbf{a}} = 1$. In combination with Theorem 3.1, it has

$$\frac{\gamma}{b+1} - \frac{1}{1+\bar{\mathbf{m}}} < 0 \text{ if } b+1 > \gamma,$$

then $\bar{\mathbf{m}} = 0$ and $\underline{\mathbf{a}} = 1$. From Theorem 2.2 of [20] and the arbitrary largeness of M_2 , the solution $(\mathbf{a}, \mathbf{m})$ of (4) satisfies that $(\mathbf{a}, \mathbf{m}) \rightarrow (1, 0)$ 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 $\mathbf{a}(x, t) \leq \eta(x, t)$ in $[0, l\pi] \times [0, \infty)$, where $\eta(x, t)$ is the positive solution of

$$\begin{cases} r \frac{\partial \eta}{\partial t} = \Delta \eta + \alpha(1 - \eta), & x \in (0, l\pi), t > 0, \\ \frac{\partial \eta}{\partial x} = 0, & x = 0, l\pi, t > 0, \\ \eta(x, 0) = v_1(x) > 0, & x \in (0, l\pi). \end{cases}$$

Then $\eta(x, t) \rightarrow 1$ as $t \rightarrow \infty$. So there exists $t_0 > 0$ such that $\mathbf{a}(x, t) \leq 1 + \varepsilon$ in $[0, l\pi] \times [t_0, \infty)$. Since ε is sufficiently small and Corollary 2.1 of [20], we can obtain the conclusion. This completes the proof. $\square$

4.2 Stability of the positive equilibrium and bifurcation

From Theorem 4.1, 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 $E^*(\mathbf{a}^*, \mathbf{m}^*)$ instead of $E_-^*(\mathbf{a}^*, \mathbf{m}^*)$ as the positive equilibrium of system (4) and the parameters b, α, γ satisfy (A2). At E^* , (15) becomes

$$\begin{cases} r \frac{\partial u(x, t)}{\partial t} = \Delta u(x, t) - \left[\alpha + \frac{b\mathbf{m}^*}{(b + \mathbf{a}^*)^2} \right] u(x, t) - \frac{\mathbf{a}^*}{b + \mathbf{a}^*} v(x, t) + \dots, \\ \frac{\partial v(x, t)}{\partial t} = \mu \Delta v(x, t) + \frac{b\gamma\mathbf{m}^*}{(b + \mathbf{a}^*)^2} u(x, t - \tau_1) + \frac{\mathbf{m}^*}{(1 + \mathbf{m}^*)^2} v(x, t - \tau_2) + \dots, \end{cases} \quad (19)$$

whose characteristic equation is

$$\begin{aligned} D_k(\lambda, \tau_1, \tau_2) = & \lambda^2 + \left[l_{11} + \left(\frac{1}{r} + \mu \right) \frac{k^2}{l^2} \right] \lambda + \frac{\mu k^2}{l^2} \left[\frac{k^2}{r l^2} + l_{11} \right] \\ & + \gamma l_{12} l_{21} e^{-\lambda \tau_1} - l_{22} \left[\lambda + \frac{k^2}{r l^2} + l_{11} \right] e^{-\lambda \tau_2} = 0, \end{aligned} \quad (20)$$

where

$$l_{11} = \frac{1}{r} [\alpha + l_{21}] > 0, \quad l_{12} = \frac{a^*}{r(b+a^*)} > 0, \quad l_{21} = \frac{b m^*}{(b+a^*)^2} > 0 \text{ and } l_{22} = \frac{m^*}{(1+m^*)^2} > 0.$$

The stability/instability of E^* can be determined by the root distribution of the characteristic equation (20) for $k \in \mathbb{N} = \{0, 1, 2, \dots\}$. Define

$$J_{1k} = \frac{k^2}{r l^2} + l_{11} > 0, \quad J_{2k} = \frac{\mu k^2}{l^2} - l_{22}, \quad q_k = \frac{J_{1k} J_{2k}}{Q} \text{ and } Q = \gamma l_{12} l_{21}.$$

From (20),

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

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 (20).

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

$$D_k(\lambda, 0, 0) = \lambda^2 + [J_{1k} + J_{2k}] \lambda + J_{1k} J_{2k} + Q = 0, \quad (21)$$

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 $k_0 = \left\lceil l \sqrt{\frac{l_{22}}{\mu}} \right\rceil$ and $\lceil \cdot \rceil$ is the integral function.

On the basis of Routh-Hurwitz criterion, if

$$(H1) \quad l_{11} > l_{22}, \quad l_{11} l_{22} < Q,$$

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

The following Lemma is from [21].

Lemma 1 *When $r, \mu, \gamma, \alpha, b, \tau_1$ and τ_2 change in the parameter space, the number (counting multiplicities) of eigenvalues of $\mathbf{Re}(\lambda) > 0$ 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 (19) will be asymptotically stable. The trivial solution of (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 (20) has roots with zero real parts.

Firstly, consider the zero root of (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,

$$\begin{aligned} \left[D_k(\lambda, \tau_1, \tau_2) \right]_{\lambda}' &= 2\lambda + [l_{11} + (\frac{1}{r} + \mu)\frac{k^2}{l^2}] - \tau_1 Q e^{-\lambda \tau_1} \\ &\quad + \tau_2 l_{22} [\lambda + J_{1k}] e^{-\lambda \tau_2} - l_{22} e^{-\lambda \tau_2} \end{aligned}$$

and

$$\begin{aligned} \left[D_k(\lambda, \tau_1, \tau_2) \right]_{\lambda}'' &= 2 + \tau_1^2 Q e^{-\lambda \tau_1} + \tau_2 l_{22} e^{-\lambda \tau_2} \\ &\quad - \tau_2^2 l_{22} [\lambda + J_{1k}] e^{-\lambda \tau_2} + \tau_2 l_{22} e^{-\lambda \tau_2}. \end{aligned}$$

Hence

$$\begin{aligned} \left[D_k(0, \tau_1, \tau_2) \right]_{\lambda}' &= J_{1k} + J_{2k} - \tau_1 Q + \tau_2 l_{22} J_{1k} \\ &= J_{1k} + J_{2k} + \tau_1 J_{1k} J_{2k} + \tau_2 l_{22} J_{1k} \\ &= (1 + \tau_2 l_{22}) J_{1k} + (1 + \tau_1 J_{1k}) J_{2k}. \end{aligned}$$

Thus for some $k < k_0$, the root $\lambda = 0$ is simple and passes through the zero with non zero 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 $q_k = -1$, (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 $\tau_1 = \tau_{1k}^*$,

$$\begin{aligned} \left[D_k(0, \tau_{1k}^*, \tau_2) \right]_{\lambda}'' &= 2 + \tau_{1k}^{*2} Q + 2\tau_2 l_{22} - \tau_2^2 l_{22} J_{1k} \\ &= 2 + \frac{[(J_{1k} + J_{2k}) + \tau_2 l_{22} J_{1k}]^2}{Q} + 2\tau_2 l_{22} - \tau_2^2 l_{22} J_{1k} \\ &= \frac{1}{Q} \left[J_{1k}^2 + J_{2k}^2 + 2\tau_2 l_{22} J_{1k}^2 + \frac{\mu k^2 \tau_2^2 l_{22} J_{1k}^2}{l^2} \right] > 0, \end{aligned}$$

which means $\lambda = 0$ is the double zero root of (20).

We summarize as follows.

Theorem 7 (i) When $q_0 < -1$, (20) has at least one positive root;
(ii) For some $k < k_0$, when $q_k = -1$, $J_{1k} + J_{2k} > 0$, if $\tau_1 \neq \tau_{1k}^*$, $\lambda = 0$ is a simple zero root of (20); if $\tau_1 = \tau_{1k}^*$, then $\lambda = 0$ is the double zero root of (20).

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

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

We investigate the existence of a pure imaginary root for (22). The analysis of (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 8 Assume that $\tau_2 = 0$ and (H1) holds.

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

(b) If $k \in \mathbb{S}_1 := \{k \in \mathbb{N} \mid -1 < q_k < 1\}$ holds, then there exists one series of critical delays τ_{1k}^n such that (22) has a pair of purely imaginary roots $\pm i w_+^k$ at τ_{1k}^n . All the roots of (22) have negative real parts when $\tau_1 \in [0, \tau_{1k}^0)$ and for $\tau_1 > \tau_{1k}^0$, there exists at least one root with positive real parts, where $\tau_{1k}^0 = \min_{k \in \mathbb{S}_1} \{\tau_{1k}^0\}$. When it crosses a τ_{1k}^n , the number of positive real parts root increase by 2 as the increase of n for fixed Q in (Q, τ_1) plane, where τ_{1k}^n is shown in (24) and

$$w_+^k = \sqrt{\frac{-(J_{1k}^2 + J_{2k}^2) + \sqrt{(J_{1k}^2 - J_{2k}^2)^2 + 4Q^2}}{2}}.$$

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

$$\begin{cases} -w^2 + J_{1k}J_{2k} = -Q \cos w\tau_1, \\ w(J_{1k} + J_{2k}) = Q \sin w\tau_1, \end{cases} \quad (23)$$

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

$$\tau_{1k}^n = \frac{1}{w} \left[\arccos \left(\frac{w^2 - J_{1k}J_{2k}}{Q} \right) + 2n\pi \right] := \tau_{1k}^n(w), \quad n \in \mathbb{N}. \quad (24)$$

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

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

which yields to

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

From (25), if $q_0 \geq 1$, then $q_k \geq 1$ and (25) has no any positive root for any k . On the contrary, if $-1 < q_k < 1$, (25) has a uniquely positive root w_+^k . Thus, if $k \in \mathbb{S}_1$, then (22) exists purely imaginary roots as long as τ_1 takes the critical values determined by (24).

Furthermore, for $k \in \mathbb{S}_1$, differentiating equation (22) with respect to τ_1 , it gets

$$\frac{d\lambda}{d\tau_1} = \frac{-\lambda^3 - (J_{1k} + J_{2k})\lambda^2 - J_{1k}J_{2k}\lambda}{2\lambda + J_{1k} + J_{2k} + \tau_1[\lambda^2 + (J_{1k} + J_{2k})\lambda + J_{1k}J_{2k}]}.$$

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

$$\left. \frac{d\operatorname{Re}\lambda}{d\tau_1} \right|_{\lambda=iw_+, \tau_1=\tau_{1k}^n} = \frac{w_+^2(J_{1k}^2 + J_{2k}^2 + w_+^2)}{\Delta} > 0,$$

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

Next, we fix (Q, τ_1) in the stable regions and regard τ_2 as a parameter to investigate the distributions of the roots to (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) $k \in \mathbb{S}_1$ and $\tau_1 \in [0, \tau_1^0]$.

The results of Theorem 8 show that if (C1) or (C2) is satisfied, E^* is stable when $\tau_2 = 0$. As τ_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 (20), separating its real and imaginary parts, it obtains the following equations:

$$\begin{cases} Q \cos \omega \tau_1 = \omega^2 - (J_{2k} + l_{22})J_{1k} + l_{22} [J_{1k} \cos \omega \tau_2 + \omega \sin \omega \tau_2] := Q_k^c, \\ Q \sin \omega \tau_1 = \omega [J_{1k} + J_{2k} + l_{22}] - l_{22} [\omega \cos \omega \tau_2 - J_{1k} \sin \omega \tau_2] := Q_k^s. \end{cases} \quad (27)$$

Eliminating τ_2 from (27) gives

$$\begin{aligned} F_k(\omega) := & \left[Q \cos \omega \tau_1 - \omega^2 + (J_{2k} + l_{22})J_{1k} \right]^2 \\ & + \left[\omega (J_{1k} + J_{2k} + l_{22}) - Q \sin \omega \tau_1 \right]^2 - l_{22}^2 [J_{1k}^2 + \omega^2] = 0. \end{aligned} \quad (28)$$

Theorem 9 For fixed $l, r, \gamma, \alpha, b, \mu$ and τ_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 (C1) or (C2).

It can obtain $F_k(0) = [Q + J_{1k}J_{2k} + 2l_{22}J_{1k}][Q + J_{1k}J_{2k}] > 0$ and $F_k(+\infty) = +\infty$. Hence, if $F_k(\omega) = 0$ has positive roots, then it must has finite positive roots. It assumes that $F_k(\omega) = 0$ has a series of positive and simple roots $\omega_1 < \omega_2 < \dots < \omega_N$, (20) has a series of critical delay τ_2 determined by

$$\tau_{2kj}^i = \frac{\varphi_j + 2i\pi}{\omega_j} \text{ for } j = 1, 2, \dots, N \text{ and } i \in \mathbb{N}, \quad (29)$$

where $\varphi_j \in [0, 2\pi)$ satisfy that

$$\begin{cases} \cos \varphi_j = \frac{Q[J_{1k} \cos \omega_j \tau_1 - \omega_j \sin \omega_j \tau_1] + (\mu k^2 / l^2)(J_{1k}^2 + \omega_j^2)}{l_{22}[J_{1k}^2 + \omega_j^2]}, \\ \sin \varphi_j = \frac{Q[\omega_j \cos \omega_j \tau_1 + J_{1k} \sin \omega_j \tau_1] - \omega_j(J_{1k}^2 + \omega_j^2)}{l_{22}[J_{1k}^2 + \omega_j^2]}. \end{cases}$$

Define

$$\mathbb{S}_2 = \{k \in \mathbb{N} | F_k(\omega) = 0 \text{ has positive roots under (C1) or (C2) for a fixed } \tau_1\}.$$

For $\tau_2 = 0$, E^* is asymptotically stable when Q and τ_1 satisfy (C1) or (C2), it will remain stable until τ_2 increases and reaches a value for which (20) has a root with zero real part. If $\tau_2^c = \min_{k \in \mathbb{S}_2} \{\tau_{2k1}^0, \tau_{2k2}^0, \dots, \tau_{2kN}^0\}$, then τ_2^c is the minimum value of τ_2 for which (20) has purely imaginary roots and the value of τ_2^c will vary in accordance with Q and τ_1 . Therefore, all roots of (20) have strictly negative real parts when $\tau_2 \in [0, \tau_2^c(Q, \tau_1))$, and (20) has only a pair of imaginary roots $\pm i\omega^c$ when $\tau_2 = \tau_2^c(Q, \tau_1)$.

By computing the derivative in (28) about τ_2 and with $i\omega^c$ and τ_2^c instead of λ and τ_2 , we can obtain the transversal condition. Applying Hopf bifurcation theorem, we have the following results giving the stability of equilibrium and existence of Hopf bifurcation to system (19).

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

Remark 2 In fact, when choosing τ_2 as bifurcating parameter for a fixed τ_1 , the stability switches may occur if $F_k(\omega) = 0$ has more than a positive root. This fact can be shown in Figure 14 in Section 5.

Furthermore, in general, we can eliminate ω from (27) and get an equation for $l, k, r, \alpha, b, \gamma, \mu, \tau_1$ and τ_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 τ_1 as functions of ω . Firstly, for fixed k , we find Q by squaring and adding in both sides of (27):

$$Q = Q_H^k(\omega) := \sqrt{(Q_k^c)^2 + (Q_k^s)^2}. \quad (30)$$

Taking the ratio of (27) and solving for τ_1 yields an expression involving the inverse tangent function. Noting that the sign of $\cos \omega \tau_1$ may be obtained from (27), we find that the appropriate expression for τ_1 is

$$\tau_1 = \tau_{1k}^j(\omega) := \begin{cases} \frac{1}{\omega} \left[\arctan\left(\frac{Q_k^s}{Q_k^c}\right) + 2j\pi \right], & Q_k^c > 0, \\ \frac{1}{\omega} \left[\arctan\left(\frac{Q_k^s}{Q_k^c}\right) + (2j+1)\pi \right], & Q_k^c < 0, \end{cases} \quad (31)$$

for $j \in \mathbb{N}$ and $\arctan$ denotes the inverse tangent function which has range $(-\pi/2, \pi/2)$. Clearly, (31) represents an infinite curve family. We note the following limits,

$$\lim_{\omega \rightarrow 0^+} Q_H^k(\omega) = |J_{1k}J_{2k}| = \begin{cases} -J_{1k}J_{2k}, & k < k_0, \\ J_{1k}J_{2k}, & k \geq k_0 + 1, \end{cases}$$

$$\lim_{\omega \rightarrow +\infty} Q_H^k(\omega) = +\infty, \quad \lim_{\omega \rightarrow +\infty} \tau_{1k}^j(\omega) = 0$$

and

$$\lim_{\omega \rightarrow 0^+} \tau_{1k}^j(\omega) = \begin{cases} -\frac{J_{1k}+J_{2k}+\tau_2 l_{22} J_{1k}}{J_{1k}J_{2k}} = \tau_{1k}^*, & j = 0, \\ +\infty, & \text{else.} \end{cases}$$

This value τ_{1k}^* is feasible only if $k < k_0$.

In summary, the line $q_k = -1$ represents the set of points in parameter space for which (20) has a zero eigenvalue. The curves (with multiple branches) defined by (30) and (31) represent the sets of points in parameter space for which (20) has a pair of purely imaginary eigenvalues. We refer to the lines $q_k = -1$ in the (Q, τ_1) -plane as the $\lambda = 0$ line or Turing line, and the curves defined by (30) and (31) as the $\lambda = i\omega$ curves. Now we give two theorems which describe how the real parts of the roots of (20) change as the $\lambda = 0$ line or $\lambda = i\omega$ curves is crossed in the (Q, τ_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, τ_1) -plane, the number of roots of the characteristic equation (20) with $\text{Re}(\lambda) > 0$ increases by 1, unless $\tau_1 < \tau_{1k}^*$ in which case it decreases by 1.

Proof Differentiating (20) with respect to Q , it can obtain

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

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

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

Hence, $\left. \frac{d\lambda}{dQ} \right|_{\lambda=0, q_k=-1} > 0$ (< 0) if and only if

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

that is, $\tau_1 > (<) \tau_{1k}^*$. Here $\tau_{1k}^* > 0$ holds because of $k < k_0$. This completes the proof. $\square$

Theorem 12 For some k , in the direction of increasing Q , as moving along a line $\tau_1 = \text{constant}$ in the (Q, τ_1) -plane, if this line cuts a branch of the $\lambda = i\omega$ curves along which τ_{1k}^j is a decreasing (increasing) function of ω , then as this branch is crossed, the number of roots of the characteristic equation (20) with $\text{Re}(\lambda) > 0$ increases (decreases) by 2.

Proof The $\lambda = i\omega$ curves defined by (30) and (31) give the points in the (Q, τ_1) -plane, where the real part of λ is zero. We can now prove our claim by considering the appropriate derivatives. Differentiating (31) with respect to ω , we get

$$\frac{d\tau_{1k}^j}{d\omega} = -\frac{1}{\omega Q_H^k} \left\{ (Q_k^c)'_{\omega} \sin \omega \tau_{1k}^j - (Q_k^s)'_{\omega} \cos \omega \tau_{1k}^j + \tau_{1k}^j Q_H^k \right\}. \quad (32)$$

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

$$\left. \frac{d\text{Re}\lambda}{dQ} \right|_{\lambda=i\omega} = \frac{1}{B_1^2 + B_2^2} \left\{ (Q_k^c)'_{\omega} \sin \omega \tau_{1k}^j - (Q_k^s)'_{\omega} \cos \omega \tau_{1k}^j + \tau_{1k}^j Q_H^k \right\}, \quad (33)$$

where

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

and

$$B_2 = 2\omega + \tau_{1k}^j Q_H^k \sin \omega \tau_{1k}^j + \tau_2 l_{22} [\omega \cos \omega \tau_2 - J_{1k} \sin \omega \tau_2] + l_{22} \sin \omega \tau_2.$$

By (32), $\text{Sign} \left\{ \left. \frac{d\text{Re}\lambda}{dQ} \right|_{\lambda=i\omega} \right\} = -\text{Sign} \left\{ \frac{d\tau_{1k}^j}{d\omega} \right\}$. Hence $\frac{d\tau_{1k}^j}{d\omega} < 0$ implies that $\left. \frac{d\text{Re}\lambda}{dQ} > 0 \right.$. Thus, when τ_{1k}^j is a decreasing function of ω , the real part of λ 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 λ becomes negative, which completes the proof. $\square$

Remark 3 Lemma 1 indicates that with fixed $k, \alpha, b, \mu, r, \gamma, \tau_1$ and τ_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. Theorem 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 $k, r, \gamma, \alpha, b, \mu$ and τ_2 , (30) and (31) describe the curves which lie in the right of the (Q, τ_1) plane, and are parameterized by ω . However, Q_k^c and Q_k^s is quite complicated functions of ω and the system parameters. Nevertheless, we can still make some assertions for the stability of E^* .

Theorem 13 For fixed $l, k, r, \gamma, \alpha, b, \mu$ and τ_2 , if $Q_H^k(\omega)$ as defined by (30) is monotone on ω , then there are no intersection points of the curves defined by (30) and (31). If $Q_H^k(\omega)$ is increasing on ω then there are no intersection points of the line $q_k = -1$ with the curves defined by (30) and (31).

Proof Consider first intersections of the curves defined by (30) and (31). Since these curves are defined according to ω parameter, the intersection of two different curves occurs when Q and τ_1 have the same values. If $Q_H^k(\omega)$ is monotone on ω then this is impossible. Now consider the curves defined by (30) and (31). Consideration $\lim_{\omega \rightarrow 0^+} Q_H^k(\omega) = |J_{1k}J_{2k}|$, thus if $Q_H^k(\omega)$ is increasing about ω , then there are no intersection points of the line $q_k = -1$ with these curves. This completes the proof. $\square$

Since the complexity of Q_H^k as the function of ω , we only can obtain the following monotonicity.

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

$$\tau_2 < -\frac{l^2}{\mu k^2} + \frac{l\sqrt{l_{22}^2 l^2 + l_{22}\mu k^2}}{l_{22}\mu k^2} := \tau_{2k}^{(1)}, \quad (34)$$

then Q_H^k is monotone increasing in ω .

Proof From (30) and (31), it has

$$(Q_H^k)^2 = (Q_k^c)^2 + (Q_k^s)^2.$$

Taking the derivative with respect to ω yields

$$\begin{aligned} Q_H^k \frac{dQ_H^k}{d\omega} &= Q_k^c (Q_k^c)'_{\omega} + Q_k^s (Q_k^s)'_{\omega} \\ &= 2\omega^3 + \omega[J_{1k}^2 + l_{22}^2 + (J_{2k} + l_{22})^2] + l_{22}[(3 + \tau_2(J_{2k} + l_{22}))\omega^2 \\ &\quad + (1 + \tau_2(J_{2k} + l_{22}))J_{1k}^2] \sin \omega \tau_2 + l_{22}\omega[\tau_2(\omega^2 + J_{1k}^2) \\ &\quad - 2(J_{2k} + l_{22})] \cos \omega \tau_2 \\ &\geq 2\omega^3 + \omega[J_{1k}^2 + l_{22}^2 + (J_{2k} + l_{22})^2] - \omega \tau_2 l_{22}[(3 + \tau_2(J_{2k} + l_{22}))\omega^2 \\ &\quad + (1 + \tau_2(J_{2k} + l_{22}))J_{1k}^2] - \omega l_{22}[\tau_2(\omega^2 + J_{1k}^2) + 2(J_{2k} + l_{22})] \\ &:= h(\omega), \end{aligned} \quad (35)$$

where

$$h(\omega) = [2 - \tau_2 l_{22}(4 + \tau_2(J_{2k} + l_{22}))]\omega^2 + [1 - \tau_2 l_{22}(2 + \tau_2(J_{2k} + l_{22}))]J_{1k}^2 + J_{2k}^2.$$

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 $\tau_2 < \tau_{2k}^{(1)}$, Q_H^k is monotone increasing in ω . This completes the proof. $\square$

Remark 4 Theorem 14 only gives a sufficient condition, i.e., if (34) is not satisfied, then Q_H^k may be monotone or non-monotone in ω . 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 (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 τ_1 and τ_2 .

Theorem 15 *If some $k \geq k_1 + 1$, then all the roots of (20) have negative real parts for $-Q_{min}^k < Q < Q_{min}^k$ for all $\tau_1 > 0, \tau_2 > 0$, where $Q_{min}^k := J_{1k} \sqrt{J_{2k}^2 - l_{22}^2}$. If $k < k_0$, then there is no such delay independent region, where $k_1 = \left\lceil l \sqrt{\frac{2l_{22}}{\mu}} \right\rceil$ ($> k_0 = \left\lceil l \sqrt{\frac{l_{22}}{\mu}} \right\rceil$).*

Proof From (27), it has

$$\begin{aligned}
 Q^2 &= (Q_k^e)^2 + (Q_k^s)^2 \\
 &= \left\{ \omega^2 - (J_{2k} + l_{22})J_{1k} + l_{22} \left[J_{1k} \cos \omega \tau_2 + \omega \sin \omega \tau_2 \right] \right\}^2 \\
 &\quad + \left\{ \omega \left[J_{1k} + J_{2k} + l_{22} \right] - l_{22} \left[\omega \cos \omega \tau_2 - J_{1k} \sin \omega \tau_2 \right] \right\}^2 \\
 &= \left[\omega^2 - \frac{\mu k^2}{l^2} J_{1k} \right]^2 + l_{22}^2 \left[\omega^2 + J_{1k}^2 \right] + \omega^2 \left[J_{1k} + J_{2k} + l_{22} \right]^2 \\
 &\quad + 2l_{22} \left[\omega^2 - (J_{2k} + l_{22})J_{1k} \right] \left[J_{1k} \cos \omega \tau_2 + \omega \sin \omega \tau_2 \right] \\
 &\quad - 2l_{22} \left[\omega^2 \cos \omega \tau_2 - J_{1k} \omega \sin \omega \tau_2 \right] \left[J_{1k} + J_{2k} + l_{22} \right] \\
 &= \omega^4 + \omega^2 J_{1k}^2 + l_{22}^2 \left[\omega^2 + J_{1k}^2 \right] + \omega^2 (J_{2k} + l_{22})^2 + ((J_{2k} + l_{22})J_{1k})^2 \\
 &\quad + 2l_{22} \left[\omega \sin \omega \tau_2 - (J_{2k} + l_{22}) \cos \omega \tau_2 \right] (J_{1k}^2 + \omega^2) \\
 &= \left\{ \omega^2 (\omega^2 + J_{1k}^2) + l_{22}^2 \left[\omega^2 + J_{1k}^2 \right] + (J_{2k} + l_{22})^2 (\omega^2 + J_{1k}^2) \right. \\
 &\quad \left. + 2l_{22} \left[\omega \sin \omega \tau_2 - (J_{2k} + l_{22}) \cos \omega \tau_2 \right] \right\} (J_{1k}^2 + \omega^2) \\
 &= \left\{ \omega^2 + l_{22}^2 + (J_{2k} + l_{22})^2 + 2l_{22} \left[\omega \sin \omega \tau_2 - (J_{2k} + l_{22}) \cos \omega \tau_2 \right] \right\} (J_{1k}^2 + \omega^2) \\
 &\geq \left\{ \omega^2 - 2l_{22}\omega + l_{22}^2 + (J_{2k} + l_{22})^2 - 2l_{22}(J_{2k} + l_{22}) \right\} J_{1k}^2 \\
 &= \left\{ \omega^2 - 2l_{22}\omega + J_{2k}^2 \right\} J_{1k}^2 \\
 &\geq (J_{2k}^2 - l_{22}^2) J_{1k}^2.
 \end{aligned}$$

Then $Q^2 \geq (J_{2k}^2 - l_{22}^2) J_{1k}^2$ must hold. Hence, if $J_{2k} > l_{22}$, i.e., $k \geq k_1 + 1$, then all the roots of (20) have negative real parts for $-Q_{min}^k < Q < Q_{min}^k$ for all $\tau_1 > 0$ and $\tau_2 > 0$.

However, if $k < k_0$, then $(Q_H^k)^2 = 0$ when $\omega = \sqrt{l_{22}^2 - (J_{2k} + l_{22})^2}$ and

$$\tau_2 = \frac{1}{\sqrt{l_{22}^2 - (J_{2k} + l_{22})^2}} \left[-\arccos\left(\frac{\mu k^2}{l^2 l_{22}}\right) + 2(\ell + 1)\pi \right].$$

Hence there is no region for which all the roots of (20) have negative real parts for all positive values of τ_1 and τ_2 . This completes the proof. $\square$

In the following, we consider the behavior of system (4) near the $\lambda = \mathbf{i}\omega$ curve. We have proved that the characteristic equation has a pair of complex conjugate imaginary roots on this curve, so we can expect (4) to exhibit a Hopf bifurcation on this curve. We firstly establish the usual nonresonant conditions.

Lemma 2 *If $\lambda_c = \mathbf{i}\omega_c$ is a purely imaginary root of the characteristic equation (20), then λ_c is simple and all roots λ other than λ_c and $\bar{\lambda}_c$ satisfy $\lambda \neq m\lambda_c$ for any integer m .*

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

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

Suppose that $D'_k(\lambda_c, \tau_1, \tau_2) = 0$. Substituting $\lambda_c = \mathbf{i}\omega_c$, separating (36) into real and imaginary parts, we get

$$\begin{cases} \tau_1 Q \cos \omega_c \tau_1 = -(J_{1k} + J_{2k} + l_{22}) + l_{22} \cos \omega_c \tau_2 \\ \quad - \tau_2 l_{22} [J_{1k} \cos \omega_c \tau_2 + \omega_c \sin \omega_c \tau_2], \\ \tau_1 Q \sin \omega_c \tau_1 = -2\omega_c - l_{22} \sin \omega_c \tau_2 \\ \quad - \tau_2 l_{22} [\omega_c \cos \omega_c \tau_2 - J_{1k} \sin \omega_c \tau_2]. \end{cases} \quad (37)$$

Consider the ratio of two equations in (37),

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

Furthermore, ω_c must satisfy the ratio of two equations in (27) when $Q = Q_H^k$ and $\lambda = \mathbf{i}\omega_c$. Furthermore, it can obtain

$$\frac{(Q_k^c)'_{\omega_c}}{(Q_k^s)'_{\omega_c}} = -\frac{Q_k^s}{Q_k^c}.$$

Define $\mathcal{H}_{\omega_c} = (Q_k^c)'_{\omega_c} Q_k^c + (Q_k^s)'_{\omega_c} Q_k^s$, we note that $\mathcal{H}_{\omega_c}$ is identical to the numerator of (35). Hence, by Theorem 9, $\mathcal{H}_{\omega_c} > 0$ for all $\tau_2 < \tau_{2k}^{(1)}$. Moreover, zeros of $\mathcal{H}_{\omega_c}$ occur when $dQ_H^k(\omega_c)/d\omega = 0$. Therefore, excluding the values of ω_c satisfying $dQ_H^k(\omega_c)/d\omega = 0$, $\lambda_c = \mathbf{i}\omega_c$ is a simple root of (20).

Further, if the point (Q_H^k, τ_1) in the (Q, τ_1) -plane is not an intersection point of two branches of the $\lambda = \mathbf{i}\omega$ curve nor an intersection point of the $\lambda = \mathbf{i}\omega$ curve and a $\lambda = 0$ line, then there is only a pair of eigenvalues with $\mathbf{Re}(\lambda) = 0$ at this point. Thus, any other roots satisfy $\lambda \neq \pm m\mathbf{i}\omega_c$ for any $m \in \mathbb{N}$. This completes the proof. $\square$

The following result follows from the proof of Theorem 11,

Lemma 3 $\left. \frac{d\mathbf{Re}\lambda}{dQ} \right|_{\lambda_c = \mathbf{i}\omega_c} = 0$ if and only if ω_c satisfies $\left. \frac{d\tau_{1k}^j}{d\omega} \right|_{\omega = \omega_c} = 0$, $Q_H^k(\omega_c) \neq 0$ and $\left. \frac{dQ}{d\omega} \right|_{\omega = \omega_c} \neq 0$.

Furthermore, it can obtain the following result.

Theorem 16 *It assumes that $l, k, \alpha, \mu, b, \tau_2, r, \gamma, \tau_2 \geq 0$ and $\tau_1 = \tau_{1k}^c$ are fixed and (Q_H^{kc}, τ_{1k}^c) 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 a $\lambda = 0$ line. Let $i\omega_c$ be the purely imaginary root of (20) such that $Q_H^{kc} = Q_H^k(\omega_c)$ and $\tau_{1k}^c = \tau_{1k}^j(\omega_c)$ for some j , where $Q_H^k(\omega)$ and $\tau_{1k}^j(\omega)$ are defined by (30) and (31). Assume that ω_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, τ_1) plane, and the vertical line $q_k = -1$ 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 [22]. 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 points occur when two of these different bifurcations happen simultaneously. Points of Hopf-Hopf interaction exist when the characteristic equation has two pairs of pure imaginary roots $\pm i\omega_1$ and $\pm i\omega_2$. For the system we are considering these points can occur for any set of values 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 $\tau_{1k}^j(\omega_1) = \tau_{1k}^{jj}(\omega_2)$, 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 Figure 11(A)). Hopf-steady state interactions exist when the characteristic equations has both a zero root and a pure imaginary pair. For our system these points may be found by solving $Q(\omega) = -J_{1k}J_{2k}$ for ω and substituting in τ_{1k}^j as given by (31) where they appear as intersection points of the Hopf bifurcation curves with the line $Q(\omega) = -J_{1k}J_{2k}$ (see Figure 12(B)). From Theorem 9 it is clear that neither type of codimension-2 point can occur in our system 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

In this section, we will carry out some numerical simulations to confirm the above theoretical analyses and show some new findings. Firstly, we choose $l = 1, b = 2.5$ and the other parameters as [11]:

$$r = 0.5, \mu = 1, \alpha = 0.1, \gamma = 2 \quad (39)$$

satisfying $b + 1 > \gamma$, it knows 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. 5 (A), for given $b \in (0, 1)$, it can obtain a unique $0 < a^* < 1$. When choosing $b = 0.3, 0.5, 0.8, 0.95$,

Fig. 4 $E_0(1,0)$ is stable where $\tau = 1$ and $\tau_1 = 0.5$.

respectively, which satisfies the condition (A21), system (4) exists a uniquely positive equilibrium E^* and $\mathbf{m}^*$ reduces as b increasing while $\mathbf{a}^*$ increases as b becomes bigger (see Fig. 5 (B)).

Fig. 5 (A) (a,b) plane plot. (B) (a,m) plane plot.

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 simulations show 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 system stability.

In the following, it investigates the effect of b to the single delay system under the parameters (39). Let $\tau_2 = 0$ and $\tau_1 = 3.6$, choosing $b = 0.5$, there exists a stable periodic solution (see Fig. 9 (A)), but $b = 0.8$ can obtain that E^* is stable (see Fig. 9 (B)).

Fig. 6 E^* is unstable and there exists a stable periodic solution.

Furthermore, we choose another parameters $b = 0.5, l = 7$ and the other parameters as (39). When $\tau_2 = 0$, from Theorem 4.2, it can obtain the $(Q-\tau_1^0)$ plane plot for different k (see Fig. 10 (A)). Under the curve $k = 0$, E^* is stable and, in the opposite direction, 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. 11 (D)). This leads to more complicated dynamical behavior, for example, several cycles coexist near the intersection point.

Furthermore, choosing the different τ_2 , it can get the different (Q, τ_1) plane plot where ensures the increasing (decreasing) number of the positive real part roots for the fixed $k = 0$ when parameters cross these critical boundaries (see Fig. 12). It can choose "+" (increasing) or "-" (decreasing) depending on the transversal condition. From Fig. 12 (B), at P_0 the Turing-Hopf bifurcation occurs.

At last, we investigate the effects of two different delays. Choosing

$$r = 0.5, \mu = 1.0, \alpha = 0.10, \gamma = 2, b = 0.5, l = 7. \quad (40)$$

It can obtain that τ_{1k}^0 is the increasing function of k (see Fig. 13 (A)). Hence, we only need compute τ_{10}^0 . Under the above parameters, $w_+ = 0.3005$ and $\tau_{10}^0 = 1.8398$. Fixed

Fig. 7 E^* is stable.

Fig. 8 E^* is stable.

$\tau_1 = 1.7$, when $\tau_2 = 0$, E^* is stable for any $k \in \mathbb{N}$. We can draw the $(\omega, F_0(\omega))$ plot shown in Fig. 13 (B), which can see that there are two roots defined by $\omega_1 = 0.3129$ and $\omega_2 = 0.3847$. However, when $k \geq 1$, $F_k(\omega) = 0$ has no any positive roots. That is, for $\tau_1 = 1.7$, 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 τ_2 as follows $\tau_{201}^j = 19.5542 + 20.0805j$ and $\tau_{202}^j = 13.0786 + 16.3327j$. The transver-

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, τ_{1k}^0) plots (see (A)). E^* is stable when $\tau_1 = 1$ (see (B-D)).

sal condition is negative for τ_{201}^j and positive for τ_{202}^j . Hence, we obtain that E^* is stable for $\tau_2 \in [0, \tau_{202}^0) \cup (\tau_{201}^0, \tau_{202}^1) \cup (\tau_{201}^1, \tau_{202}^2) \cup (\tau_{201}^2, \tau_{202}^3)$ and unstable for $(\tau_{202}^0, \tau_{201}^0) \cup (\tau_{202}^1, \tau_{201}^1) \cup (\tau_{202}^2, \tau_{201}^2) \cup (\tau_{202}^3, +\infty)$. Choosing $\tau_2 = 5, 15, 22, 75$, respectively, we can obtain the phase plots as Fig. 14. The stability switch phenomenon exists. In addition, in [11], if two same delays were considered, the system can not oc-

Fig. 11 E^* is unstable and there exists a stable periodic solution when $\tau_1 = 3$ (see (A-C)). (Q, τ_{1k}^n) plot for different k and n (see (D)).

Fig. 12 When $\tau_2 = 2$, the cure τ_1 is monotonous (see (A)) and non-monotonous for $\tau_2 = 50$ (see (B)).

cur the stability switches. This explains the importance of two different delays. These simulations confirm the correctness of the theoretical analyses.

Fig. 13 (A) (k, τ_{lk}^0) plot. (B) $(\omega, F_0(\omega))$ plot.

Fig. 14 (A) E^* is stable when $\tau_2 = 5 \in [0, \tau_{22}^0]$. (B) E^* is unstable and there exists a stable periodic solution when $\tau_2 = 15 \in (\tau_{22}^0, \tau_{21}^0)$. (C) E^* is stable when $\tau_2 = 22 \in (\tau_{21}^0, \tau_{22}^1)$. (d) E^* is unstable and there exists a stable periodic solution when $\tau_2 = 75 > \tau_{22}^3$.

6 Conclusions

We analyze in detail a mussel-algae system with half-saturation constant and two delays. The system (4) improves that in [11] by introducing the half-saturation constant and two different delays. The half-saturation constant b can produce some complicated effects, such as the stability of the positive equilibrium, Turing instability, steady state bifurcation, Hopf bifurcation, Hopf-Hopf bifurcation or Hopf-steady state bifurcation. Our results suggest that the positive equilibrium will lose its stability when τ_1 or τ_2 pass through some critical values, and there will be periodic oscillations in populations of species. Compare with the system in [11], by numerical simulations, it can find that the big half-saturation constant b can contribute to system stability whether the system is single time delay or multi-time delay. Under certain conditions, the double delayed system can occur the stability switches phenomena, which is impossible if $\tau_1 = \tau_2$. 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 investigate the effects of two different delays, but it does not give the stability changes of equilibrium in (τ_1, τ_2) parameter plane, which needs the further consideration.

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Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

Data availability statement

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

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