Applied Mathematics and Computation 404 (2021) 126254

Contents lists available at ScienceDirect

Applied Mathematics and Computation

journal homepage: www.elsevier.com/locate/amc

Memory-based movement with spatiotemporal distributed delays in diffusion and reaction

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ARTICLE INFO

Article history:
Received 25 December 2020
Revised 2 March 2021
Accepted 28 March 2021

Keywords:
Spatial memory
Spatiotemporal delay
Hopf bifurcation
Steady state bifurcation

ABSTRACT

In this paper, we investigate the spatiotemporal dynamics of a single-species model with spatiotemporal delays characterizing spatial memory and maturation. Through stability and bifurcation analysis, we find that the spatial memory-based diffusion coefficient, the spatiotemporal diffusive delay and spatiotemporal reaction delay have important effects on the dynamics of the model and their combined impact can cause the destabilization of the positive constant steady state and give rise to steady state and Hopf bifurcations. Taking the coefficient of spatial memory diffusion as the bifurcation parameter, the critical values of steady state and Hopf bifurcations are rigorously determined. Furthermore, we apply the theoretical results to a modified diffusive logistic model with predation and obtain spatially inhomogeneous steady states and spatially homogeneous and inhomogeneous periodic solutions via numerical simulations.

1. Introduction

In the past few decades, the reaction-diffusion equations have been used by many investigators to model the movement of animals. In particular, the Fickian diffusion is commonly applied to describe the random walk of mobile animals. As for the directional movement, the advection term is additionally introduced to the typical reaction-diffusion equation to describe the movement in an advective environment like a river or a slope. Different from the physical process, the cognition and memory of animals play a significant role in their movements [1], which implies that the directional movement is common for the highly developed animals. Considering the episodic-like spatial memory of animals, Shi et al. [14] incorporated a delayed diffusion term into the reaction-diffusion model, which has the form

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 \Delta u + d_2 div(u \nabla u(x, t-\tau)) + f(u), & x \in \Omega,\ t > 0, \\ \frac{\partial u}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \end{cases} \tag{1.1}$$

where $d_1 > 0$ and $d_2 \in \mathbb{R}$ denote the diffusion rates corresponding to random movement and memory-based movement, respectively; τ is the averaged memory period (also known as the memory delay); $f(u)$ stands for the chemical reaction such as birth/death of a species; Ω is a connected open region in $\mathbb{R}^N (N \geq 1)$ with a smooth boundary $\partial\Omega$ and ν is the outward

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https://doi.org/10.1016/j.amc.2021.126254
0096-3003/

unit normal vector of the boundary $\partial\Omega$. The homogeneous Neumann boundary condition describes the circumstance when there is no animals cross the boundary. Comparing with the classical reaction-diffusion equation, there is a directed movement toward the negative or positive gradient of the density distribution function at past time in model (1.1). As for the biological meaning, $d_2 > 0$ indicates that animals leave away from high density to low density, which is converse for $d_2 < 0$, while $d_2 = 0$ means that there is no spatial memory diffusion. In addition, it was revealed that the stability of the positive constant steady state completely relies on the property of the reaction term f and the relation between the diffusion rates d_1 and d_2 but is independent of the time delay τ [14].

In [13], Shi et al. considered that the reaction term does not occur instantaneously and introduced the time delay, say σ (also known as the maturation delay), into the reaction term f of model (1.1) and proposed the following model:

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 \Delta u + d_2 div(u \nabla u(x, t-\tau)) + f(u, u(x, t-\sigma)), & x \in \Omega,\ t > 0, \\ \frac{\partial u}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0. \end{cases} \tag{1.2}$$

In [13], the influence of the memory delay and the maturation delay on the constant steady state was investigated, and it was shown that the boundaries of the stable region in the two-delay parameter plane consist of Hopf bifurcation curves.

In model (1.2), the spatial memory diffusion and the reaction term are based on the memory (or history) of a particular past time density distribution. As a matter of fact, the information on the space and the previous time is also essential in the population of a species. Since the animals are moving, they may be anywhere in the past time. Based on the assumption that the population at any previous time makes a contribution to the current growth rate, the spatiotemporal delay was firstly introduced by Britton [3] for the unbounded domain and by Gourley and So [8] for the bounded domain. Moreover, the influence of the spatiotemporal delay on the population dynamics has recently been a hot topic of research in the field of applied mathematics. The periodic solutions and travelling waves induced by the spatiotemporal delay were studied in [2,6,7,18] for the case of the unbounded domain, and Hopf bifurcation induced by the spatiotemporal delay were discussed in [4,9,10,17,21] for the case of the bounded domain. All the above spatiotemporal delays were incorporated in the reaction term only. For the spatial memory delay, it is more realistic to use spatiotemporal delay because the gain and loss of the knowledge are accumulated over time, and the cognition depends on the distance due to the range of vision if there exists no knowledge transfer among animals.

In this paper, we restrict model (1.2) to one dimensional domain $\Omega = (0, \ell\pi)$ and incorporate the spatiotemporal delays into the spatial memory diffusion and the reaction term by replacing $u(x, t-\tau)$ and $u(x, t-\sigma)$, respectively, with

$$g_1 ** u(x,t) = \int_{-\infty}^{t} \int_0^{\ell\pi} G(x, y, t-s) h_1(t-s, \tau) u(y, s) dy ds, \tag{1.3}$$

and

$$g_2 ** u(x,t) = \int_{-\infty}^{t} \int_0^{\ell\pi} G(x, y, t-s) h_2(t-s, \sigma) u(y, s) dy ds, \tag{1.4}$$

and then obtain the following equation:

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 u_{xx} + d_2 (u v_x)_x + f(u, w), & x \in (0, \ell\pi),\ t > 0, \\ u_x(0,t) = u_x(\ell\pi, t) = 0, & t > 0, \end{cases} \tag{1.5}$$

where $v = g_1 ** u(x,t)$ and $w = g_2 ** u(x,t)$. According to [8], the spatial kernel $G(x, y, t)$ in (1.3) (or (1.4)) can be chosen as the fundamental solution of the heat equation $G_t = d_1 G_{yy}$ with the homogeneous Neumann boundary condition and the initial condition $G(x, y, 0) = \delta(x-y)$, i.e.

$$G(x, y, t) = \frac{1}{\ell\pi} + \frac{2}{\ell\pi} \sum_{n=1}^{\infty} e^{-\frac{d_1 n^2}{\ell^2} t} \cos\frac{n}{\ell}x \cos\frac{n}{\ell}y, \tag{1.6}$$

while the temporal kernel $h_1(t, \tau)$ in (1.3) measures the effect of the memory before the present time on the spatial diffusion and the temporal kernel $h_2(t, \sigma)$ in (1.4) often reflects the effect of the past population density on the present birth and/or death rate. In the literature, the temporal kernels are often chosen as the “weak” or “strong” delay kernel, i.e., $h_1(t, \tau) = \frac{t^m}{\tau^{(m+1)} m!} e^{-\frac{t}{\tau}}$ and $h_2(t, \sigma) = \frac{t^m}{\sigma^{(m+1)} m!} e^{-\frac{t}{\sigma}}$, $m = 0, 1$, where τ and σ are identified as the average delay, respectively, since $\int_0^{+\infty} t h_1(t, \tau) dt = (m+1)\tau$ and $\int_0^{+\infty} t h_2(t, \sigma) dt = (m+1)\sigma$. Actually, the temporal kernels $h_1(t, \tau)$ and $h_2(t, \sigma)$ have different underlying mechanisms. The first temporal kernel represents the gain and loss of the knowledge: the ”weak” kernel $h_1(t, \tau) = \frac{1}{\tau} e^{-\frac{t}{\tau}}$ only describes loss due to memory waning, while the strong kernel $h_1(t, \tau) = \frac{t}{\tau^2} e^{-\frac{t}{\tau}}$ describes both gain due to learning and loss due to memory waning. The second temporal kernel represents maturation process. In this paper, for the two temporal kernels, we consider the following four cases:

(I) weak/weak; (II) strong/weak; (III) weak/strong; (IV) strong/strong.

In addition, we are interested in the effects of the spatial memory-based diffusion coefficient and the average delays on the stability of the positive constant steady state and the spatiotemporal dynamics induced by steady state and Hopf bifurcations.

There has recently been an increasing activity and interest on the study of the spatial movement with memory. In [11], Shi et al. investigated a modified version of model (1.1) that contains a memory-based spatiotemporal delay, and they found that steady state and Hopf bifurcations can occur under certain assumptions. Moreover, the effect of the nonlocal reaction on the dynamics of model (1.1) was studied in [16], where the existence of Turing-Hopf bifurcation was proved.

The rest of this paper is organized as follows. In Section 2, the stability and bifurcation analysis of the positive constant steady state of model (1.5) are discussed. In Section 3, a modified logistic model with predation and Neumann boundary condition is investigated to illustrate our theoretical results. Finally, we conclude and discuss our results in Section 4. Throughout this paper, $\mathbb{N}_0$ represents the set of the nonnegative integers, while $\mathbb{N}$ denotes the set of the positive integers.

2. Stability and bifurcation analysis

As for model (1.5), we suppose there exists a positive constant u_* such that $f(u_*, u_*) = 0$. Then linearization of model (1.5) about u_* is given by

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 u_{xx} + d_2 u_* v_{xx} + Au + Bw, & x \in (0, \ell\pi),\ t > 0, \\ u_x(0,t) = u_x(\ell\pi, t) = 0, & t > 0, \end{cases} \tag{2.1}$$

where $A = f_u(u_*, u_*)$, and $B = f_w(u_*, u_*)$. When $A + B < 0$, the positive constant steady state of $u'(t) = f(u(t), u(t))$ is asymptotically stable.

For $x \in (0, \ell\pi)$ and $\Delta = \frac{\partial^2}{\partial x^2}$, $\cos\frac{nx}{\ell}$ is the eigenfunction corresponding to the eigenvalue $-\frac{n^2}{\ell^2}$. Then, by setting $u = e^{\lambda t}\cos\frac{nx}{\ell}$, we obtain the characteristic equations associated with (2.1)

$$\lambda + d_1\frac{n^2}{\ell^2} + d_2 u_* \frac{n^2}{\ell^2}\bar{g}_1(\tau, m, \lambda) - A - B\bar{g}_2(\sigma, m, \lambda) = 0,\ n \in \mathbb{N}_0, \tag{2.2}$$

where

$$\bar{g}_1(\tau, m, \lambda) = \frac{1}{\left(1 + \tau d_1\frac{n^2}{\ell^2} + \tau\lambda\right)^{(m+1)}},\ m = 0, 1, \tag{2.3}$$

and

$$\bar{g}_2(\sigma, m, \lambda) = \frac{1}{\left(1 + \sigma d_1\frac{n^2}{\ell^2} + \sigma\lambda\right)^{(m+1)}},\ m = 0, 1, \tag{2.4}$$

with $m = 0, 1$ corresponding to the "weak" or "strong" temporal kernels, respectively. For $n = 0$, Eq. (2.2) becomes

$$\begin{cases} \lambda - A - \frac{B}{1+\sigma\lambda} = 0, & \text{for Cases (I) or (II)}, \\ \lambda - A - \frac{B}{(1+\sigma\lambda)^2} = 0, & \text{for Cases (III) or (IV)}. \end{cases} \tag{2.5}$$

If $B = 0$, then $\lambda = A < 0$. Moreover, if $B \neq 0$, then assuming that λ is a root of Eq. (2.5) with nonnegative real part, we have $1 + \sigma\lambda \neq 0$. Thus, when $B \neq 0$, the distribution of roots with nonnegative real parts of Eq. (2.5) is the same as that of the following equation

$$\begin{cases} \sigma\lambda^2 + (1 - \sigma A)\lambda - (A + B) = 0, & \text{for Cases (I) or (II)}, \\ \sigma^2\lambda^3 + \sigma(2 - \sigma A)\lambda^2 + (1 - 2\sigma A)\lambda - (A + B) = 0, & \text{for Cases (III) or (IV)}. \end{cases} \tag{2.6}$$

Notice that the corresponding ordinary differential system of system (1.5) is

$$u'(t) = f\left(u(t), \int_{-\infty}^{t} h_2(t - s, \sigma)u(s)ds\right), \tag{2.7}$$

and the characteristic equation of the linearized system of (2.7) at u_* is also Eq. (2.5), which has been studied by Zuo and Song [20]. We first introduce the following results from [20] with a minor revision.

Lemma 2.1. *Assume that $A + B < 0$.*

(I) *For the weak temporal kernel $h_2(t, \sigma) = \frac{1}{\sigma}e^{-\frac{t}{\sigma}}$, we have*

- (i) *if either $B \geq 0$, or $B < 0$ and $\sigma \leq -\frac{1}{B}$, then all roots of Eq. (2.6) have negative real parts;*
- (ii) *if $B < 0$ and $\sigma > -\frac{1}{B}$, then all roots of Eq. (2.6) have negative real parts for $\sigma A < 1$, and Eq. (2.6) has at least one root with positive real part for $\sigma A > 1$ and a pair of purely imaginary roots for $\sigma A = 1$.*

(II) *For the strong temporal kernel $h_2(t, \sigma) = \frac{t}{\sigma^2}e^{-\frac{t}{\sigma}}$, we have*

- (i) *if either $B \geq 0$, or $B < 0$ and $\sigma \leq -\frac{1}{2B}$, then all roots of Eq. (2.6) have negative real parts;*

(*ii*) *if* $B<0$ *and* $\sigma>-\frac{1}{2B}$, *then all roots of Eq. (2.6) have negative real parts for* $A<\frac{1}{\sigma}-\sqrt{-\frac{B}{2\sigma}}$, *and Eq. (2.6) has at least one root with positive real part for* $A>\frac{1}{\sigma}-\sqrt{-\frac{B}{2\sigma}}$ *and a pair of purely imaginary roots for* $A=\frac{1}{\sigma}-\sqrt{-\frac{B}{2\sigma}}$.

Lemma 2.2.

(*I*) *When* $A+B<0$ *and* $h_2(t,\sigma)=\frac{1}{\sigma}e^{-\frac{t}{\sigma}}$, *we have*

(*i*) *if either* $B\geq 0$, *or* $B<0$ *and* $\sigma\leq-\frac{1}{B}$, *then the positive steady state* u_* *of system (2.7) is asymptotically stable;*

(*ii*) *if* $B<0$ *and* $\sigma>-\frac{1}{B}$, *then the positive steady state* u_* *of system (2.7) is asymptotically stable for* $\sigma A<1$ *and unstable for* $\sigma A>1$, *and system (2.7) undergoes Hopf bifurcation at* $\sigma=\frac{1}{A}$.

(*II*) *When* $A+B<0$ *and* $h_2(t,\sigma)=\frac{t}{\sigma^2}e^{-\frac{t}{\sigma}}$, *we have*

(*i*) *if either* $B\geq 0$, *or* $B<0$ *and* $\sigma\leq-\frac{1}{2B}$, *then the positive steady state* u_* *of system (2.7) is asymptotically stable;*

(*ii*) *if* $B<0$ *and* $\sigma>-\frac{1}{2B}$, *then the positive steady state* u_* *of system (2.7) is asymptotically stable for* $A<\frac{1}{\sigma}-\sqrt{-\frac{B}{2\sigma}}$ *and unstable for* $A>\frac{1}{\sigma}-\sqrt{-\frac{B}{2\sigma}}$, *and system (2.7) undergoes Hopf bifurcation at* $\sigma=\sigma_H^0$, *where* σ_H^0 *is the positive root of the equation* $A=\frac{1}{\sigma}-\sqrt{-\frac{B}{2\sigma}}$.

Remark 2.1. From Lemma 2.2, we know that for $B\geq 0$, the stability of the positive steady state u_* of system (2.7) is independent of the type of the kernel function, i.e., the stability region in the $A-\sigma$ plane is the same no matter what the kernel function is considered. But, for $B<0$, the type of the kernel functions can affect the stability of u_* and the stability region for the weak kernel is less than that for the strong kernel in the $A-\sigma$ plane.

Notice the fact that the periodic solution of system (2.7) is also the spatially homogeneous periodic solution of system (1.5). Thus, by Lemma 2.2, we obtain the following theorem for system (1.5).

Theorem 2.1. *Assume that* $A+B<0$.

(*I*) *When* $h_2(t,\sigma)=\frac{1}{\sigma}e^{-\frac{t}{\sigma}}$, $B<0$ *and* $\sigma>-\frac{1}{B}$, *the positive constant steady state* u_* *is unstable provided that* $\sigma A>1$, *and system (1.5) undergoes spatially homogeneous Hopf bifurcation at* $\sigma=\frac{1}{A}$.

(*II*) *When* $h_2(t,\sigma)=\frac{t}{\sigma^2}e^{-\frac{t}{\sigma}}$, $B<0$ *and* $\sigma>-\frac{1}{2B}$, *the positive constant steady state* u_* *is unstable provided that* $A>\frac{1}{\sigma}-\sqrt{-\frac{B}{2\sigma}}$, *and system (1.5) undergoes spatially homogeneous Hopf bifurcation at* $\sigma=\sigma_H^0$, *where* σ_H^0 *is the positive root of the equation* $A=\frac{1}{\sigma}-\sqrt{-\frac{B}{2\sigma}}$.

In the following, we consider the distribution of roots of Eq. (2.2) for $n\in\mathbb{N}$ and discuss the conditions under which Eq. (2.2) has roots with zero real parts or has no roots with positive real parts. Notice that if λ is a root of Eq. (2.2) with $\mathrm{Re}\lambda\geq 0$, then

$$1+\tau d_1\frac{n^2}{\ell^2}+\tau\lambda\neq 0, \tag{2.8}$$

and

$$1+\sigma d_1\frac{n^2}{\ell^2}+\sigma\lambda\neq 0, \tag{2.9}$$

which will be useful later on.

2.1. Two weak temporal kernels: $h_1(t,\tau)=\frac{1}{\tau}e^{-\frac{t}{\tau}}, h_2(t,\sigma)=\frac{1}{\sigma}e^{-\frac{t}{\sigma}}$

It follows from Lemma 2.1 that for $n=0$, all roots of Eq. (2.2) have negative real parts if one of the following two conditions is satisfied:

$(H1)$ $B\geq 0, A<-B$;

$(H2)$ $B<0$ and $(\sigma,A)\in\left\{(\sigma,A)\Big|\ 0<\sigma\leq-\frac{1}{B}, A<-B\right\}\cup\left\{(\sigma,A)\Big|\ \sigma>-\frac{1}{B},\ A<\frac{1}{\sigma}\right\}$.

In this subsection, we suppose $(H1)$ or $(H2)$ holds. For $d_2=0$ and $B=0$, we have

$$\lambda+d_1\frac{n^2}{\ell^2}-A=0,\ \ n\in\mathbb{N}. \tag{2.10}$$

Moreover, using (2.8) and (2.9), we find that for $d_2\neq 0$ and $B=0$, Eq. (2.2) becomes

$$\left(\lambda+d_1\frac{n^2}{\ell^2}-A\right)\left(1+\tau d_1\frac{n^2}{\ell^2}+\tau\lambda\right)+d_2u_*\frac{n^2}{\ell^2}=0,\ \ n\in\mathbb{N}; \tag{2.11}$$

for $d_2=0$ and $B\neq 0$, Eq. (2.2) reads as

$$\left(\lambda+d_1\frac{n^2}{\ell^2}-A\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}+\sigma\lambda\right)-B=0,\ \ n\in\mathbb{N}; \tag{2.12}$$

and for $d_2\neq 0$ and $B\neq 0$, Eq. (2.2) can be written as

$$\sigma\tau\lambda^3+P_n\lambda^2+Q_n\lambda+R_n=0,\ \ n\in\mathbb{N}, \tag{2.13}$$

where

$$P_n=3\sigma\tau d_1\frac{n^2}{\ell^2}+\sigma+\tau-\tau\sigma A>0, \tag{2.14}$$

$$Q_n=3\sigma\tau\left(d_1\frac{n^2}{\ell^2}\right)^2+2(\sigma+\tau-\tau\sigma A)d_1\frac{n^2}{\ell^2}+1-\sigma A-(A+B)\tau+d_2\sigma u_*\frac{n^2}{\ell^2}, \tag{2.15}$$

and

$$\begin{aligned} R_n &= \sigma\tau\left(d_1\tfrac{n^2}{\ell^2}\right)^3+(\sigma+\tau-\tau\sigma A)\left(d_1\tfrac{n^2}{\ell^2}\right)^2 \\ &\quad +(1-\sigma A-\tau A-\tau B)d_1\tfrac{n^2}{\ell^2}-(A+B)+d_2u_*\tfrac{n^2}{\ell^2}\left(\sigma d_1\tfrac{n^2}{\ell^2}+1\right). \end{aligned} \tag{2.16}$$

Since $(H1)$ or $(H2)$ holds, it is easy to see that $P_n>0$. In addition, it follows from Eq. (2.13) that

$$\begin{aligned} &\sigma\tau\lambda^3+P_n\lambda^2+Q_n\lambda+R_n \\ = &\begin{cases} \left(\lambda+d_1\frac{n^2}{\ell^2}-A\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}+\sigma\lambda\right)\left(1+\tau d_1\frac{n^2}{\ell^2}+\tau\lambda\right), & d_2=0, B=0,\\ \left(\left(\lambda+d_1\frac{n^2}{\ell^2}-A\right)\left(1+\tau d_1\frac{n^2}{\ell^2}+\tau\lambda\right)+d_2u_*\frac{n^2}{\ell^2}\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}+\sigma\lambda\right), & d_2\neq 0, B=0,\\ \left(\left(\lambda+d_1\frac{n^2}{\ell^2}-A\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}+\sigma\lambda\right)-B\right)\left(1+\tau d_1\frac{n^2}{\ell^2}+\tau\lambda\right), & d_2=0, B\neq 0. \end{cases} \end{aligned}$$

Thus, when $d_2=0$ and $B\neq 0$, the roots of Eq. (2.13) except $\lambda=-\frac{1+\tau d_1\frac{n^2}{\ell^2}}{\tau}<0$ are the same as those of Eq. (2.12). Similarly, for $d_2=0$ and $B=0$, the roots of Eq. (2.13) except $\lambda=-\frac{1+\tau d_1\frac{n^2}{\ell^2}}{\tau}<0$ and $\lambda=-\frac{1+\sigma d_1\frac{n^2}{\ell^2}}{\sigma}<0$ are the same as those of Eq. (2.10), while for $d_2\neq 0$ and $B=0$, the roots of Eq. (2.13) except $\lambda=-\frac{1+\sigma d_1\frac{n^2}{\ell^2}}{\sigma}<0$ are the same as those of Eq. (2.11). Then, we can analyze the distribution of roots of Eq. (2.13) for all cases.

Applying the Routh-Hurwitz criterion, we have the following result on the distribution of roots of Eq. (2.13).

Lemma 2.3. *Assume that* $(H1)$ *or* $(H2)$ *holds.*

(I) All roots of Eq. (2.13) have negative real parts if and only if $R_n>0$ *and* $P_nQ_n-\sigma\tau R_n>0$.
(II) If $R_n=0$ *and* $Q_n=0$, *then Eq. (2.13) has a zero root of multiplicity 2 and a negative real root.*
(III)If $R_n=0$ *and* $Q_n>0$, *then Eq. (2.13) has a simple zero root and two roots with negative real parts.*
(IV) If $R_n=0$ *and* $Q_n<0$, *then Eq. (2.13) has a simple zero root, a positive real root and a negative real root.*
(V) Eq. (2.13) has a pair of purely imaginary roots $\pm i\sqrt{\frac{Q_n}{\sigma\tau}}$ *and a negative real root if and only if* $Q_n>0$ *and* $P_nQ_n-\sigma\tau R_n=0$.

In what follows, we take d_2 as a parameter. When either $(H1)$ or $(H2)$ holds, we have $1-\sigma A>0$ and $A+B<0$. Then, a direct computation yields the following lemma for R_n.

Lemma 2.4. *Assume that* $(H1)$ *or* $(H2)$ *holds. For* R_n, *we have*

(I) if $d_2\geq 0$, *then* $R_n>0$ *for any* $n\in\mathbb{N}$;
(II) if $d_2<0$, *then*

$$R_n\begin{cases} >0, & d_2>d_{2,1}^T(\sigma,n^2),\\ =0, & d_2=d_{2,1}^T(\sigma,n^2),\\ <0, & d_2<d_{2,1}^T(\sigma,n^2), \end{cases} \tag{2.17}$$

where

$$\begin{aligned} &d_{2,1}^T(\sigma,n^2) \\ = &-\frac{\sigma\tau\left(d_1\frac{n^2}{\ell^2}\right)^3+(\sigma+\tau-\tau\sigma A)\left(d_1\frac{n^2}{\ell^2}\right)^2+(1-\sigma A-\tau A-\tau B)d_1\frac{n^2}{\ell^2}-(A+B)}{u_*\frac{n^2}{\ell^2}\left(\sigma d_1\frac{n^2}{\ell^2}+1\right)}<0,\ \ n\in\mathbb{N}. \end{aligned} \tag{2.18}$$

According to Lemma 2.4, we have the following result on zero roots of Eq. (2.13).

Lemma 2.5. *Assume that* $(H1)$ *or* $(H2)$ *holds, and* $d^T_{2,1}(\sigma, n^2)$ *is defined by (2.18). Denote*

$$N_T = \begin{cases} 1, & \text{if } z^* \le 1, \\ \left[\sqrt{z^*}\right], & \text{if } z^* > 1 \text{ and } d^T_{2,1}\left(\sigma, \left(\left[\sqrt{z^*}\right]\right)^2\right) \ge d^T_{2,1}\left(\sigma, \left(\left[\sqrt{z^*}\right]+1\right)^2\right), \\ \left[\sqrt{z^*}\right]+1, & \text{if } z^* > 1 \text{ and } d^T_{2,1}\left(\sigma, \left(\left[\sqrt{z^*}\right]\right)^2\right) < d^T_{2,1}\left(\sigma, \left(\left[\sqrt{z^*}\right]+1\right)^2\right), \end{cases} \tag{2.19}$$

where $z^* > 0$ *is the root of the equation* $\dfrac{\partial d^T_{2,1}(\sigma, z)}{\partial z} = 0$*. Then we have the following statements.*

(I) If $d_2 \ge 0$*, then Eq. (2.13) has no zero roots for any* $n \in \mathbb{N}$*.*
(II) If $d_2 < 0$*, then*

(i) if $d_2 > d^T_{2,1}(\sigma, N_T^2)$*, then Eq. (2.13) has no zero roots for any* $n \in \mathbb{N}$*;*
(ii) if $d_2 < d^T_{2,1}(\sigma, N_T^2)$*, then Eq. (2.13) has at least one root with positive real part for* $n = N_T$*.*

Proof. It is clear that $\lambda = 0$ is a root of Eq. (2.13) if and only if $R_n = 0$. Thus, the conclusion of (I) follows directly from (I) of Lemma 2.4.

Next, we restrict our attention to $d_2 < 0$. It follows from (II) of Lemma 2.4 that for any $n \in \mathbb{N}$, Eq. (2.13) has a zero root provided that $d_2 = d^T_{2,1}(\sigma, n^2) < 0$.

Letting $z = n^2$, we have

$$\frac{\partial d^T_{2,1}(\sigma, z)}{\partial z} = \frac{\zeta(\sigma, z)}{\frac{u_*}{\ell^2}\left(\sigma \frac{d_1}{\ell^2} z^2 + z\right)^2}, \tag{2.20}$$

where

$$\zeta(\sigma, z) = -\sigma^2\tau\left(\frac{d_1}{\ell^2}z\right)^4 - 2\sigma\tau\left(\frac{d_1}{\ell^2}z\right)^3 - (\sigma^2 A + \sigma\tau B + \tau)\left(\frac{d_1}{\ell^2}z\right)^2 - 2\sigma(A+B)\frac{d_1}{\ell^2}z - (A+B).$$

Then, it is easy to verify that

$$\frac{\partial \zeta(\sigma, z)}{\partial z} = -4\sigma^2\tau\left(\frac{d_1}{\ell^2}\right)^4 z^3 - 6\sigma\tau\left(\frac{d_1}{\ell^2}\right)^3 z^2 - 2(\sigma^2 A + \sigma\tau B + \tau)\left(\frac{d_1}{\ell^2}\right)^2 z - 2\sigma(A+B)\frac{d_1}{\ell^2}, \tag{2.21}$$

and

$$\frac{\partial^2 \zeta(\sigma, z)}{\partial z^2} = -12\sigma^2\tau\left(\frac{d_1}{\ell^2}\right)^4 z^2 - 12\sigma\tau\left(\frac{d_1}{\ell^2}\right)^3 z - 2(\sigma^2 A + \sigma\tau B + \tau)\left(\frac{d_1}{\ell^2}\right)^2. \tag{2.22}$$

Since $-12\sigma^2\tau\left(\frac{d_1}{\ell^2}\right)^4 < 0$ and $-12\sigma\tau\left(\frac{d_1}{\ell^2}\right)^3 < 0$, we see that if $\sigma^2 A + \sigma\tau B + \tau \ge 0$, then $\dfrac{\partial^2\zeta(\sigma, z)}{\partial z^2} < 0$ for $z > 0$, while if $\sigma^2 A + \sigma\tau B + \tau < 0$, then there exists $z_1^* > 0$ such that $\dfrac{\partial^2\zeta(\sigma, z)}{\partial z^2} > 0$ for $0 < z < z_1^*$ and $\dfrac{\partial^2\zeta(\sigma, z)}{\partial z^2} < 0$ for $z > z_1^*$. Hence, using (2.21) and $\dfrac{\partial\zeta(\sigma, 0)}{\partial z} = -2\sigma(A+B)\frac{d_1}{\ell^2} > 0$, we find that there exists $z_2^* > 0$ such that

$$\frac{\partial\zeta(\sigma, z)}{\partial z} \begin{cases} > 0, & 0 < z < z_2^*, \\ = 0, & z = z_2^*, \\ < 0, & z > z_2^*, \end{cases}$$

which, together with $\zeta(\sigma, 0) = -(A+B) > 0$ and (2.20), implies that there exists $z^* > 0$ such that

$$\frac{\partial d^T_{2,1}(\sigma, z)}{\partial z} \begin{cases} > 0, & 0 < z < z^*, \\ = 0, & z = z^*, \\ < 0, & z > z^*. \end{cases}$$

This, along with (2.17), proves (II). This completes the proof. □

Under the hypotheses of the above lemma, it follows from (2.17) that 0 is a root of Eq. (2.13) if and only if $d_2 = d^T_{2,1}(\sigma, n^2)$. Then, assuming that 0 is a simple root of Eq. (2.13) and taking d_2 as a bifurcation parameter, we have

$$\left.\frac{d\lambda(d_2)}{dd_2}\right|_{d_2 = d^T_{2,1}(\sigma, n^2)} = -\frac{u_* n^2(\sigma d_1 n^2 + \ell^2)}{\ell^4 Q_n} \neq 0. \tag{2.23}$$

We next investigate the existence of the purely imaginary roots of Eq. (2.13), which is determined by the signs of Q_n and $P_nQ_n - \sigma\tau R_n$, where Q_n is defined by (2.15) and

$$\begin{aligned} P_nQ_n - \sigma\tau R_n = & 8\sigma^2\tau^2\Big(d_1\tfrac{n^2}{\ell^2}\Big)^3 + 8\sigma\tau(\sigma+\tau-\tau\sigma A)\Big(d_1\tfrac{n^2}{\ell^2}\Big)^2 \\ & +2\sigma\tau(1-\sigma A - A\tau - B\tau)d_1\tfrac{n^2}{\ell^2} \\ & +2(\sigma+\tau-\tau\sigma A)^2 d_1\tfrac{n^2}{\ell^2} + (1-\sigma A)\big(\sigma+\tau-\tau\sigma A-(A+B)\tau^2\big) \\ & +d_2u_*\sigma^2\tfrac{n^2}{\ell^2}\Big(2\tau d_1\tfrac{n^2}{\ell^2}+1-\tau A\Big). \end{aligned} \tag{2.24}$$

Recall that when either $(H1)$ or $(H2)$ holds, we see that $1-\sigma A>0$ and $A+B<0$. Then, we obtain the following results that will be useful later on.

Lemma 2.6. *Assume that $(H1)$ or $(H2)$ holds. For Q_n, we have*

(I) if $d_2 \ge 0$, then $Q_n > 0$ for any $n\in\mathbb{N}$;
(II) if $d_2 < 0$, then

$$Q_n \begin{cases} >0, & d_2 > \beta(\sigma,n^2), \\ =0, & d_2 = \beta(\sigma,n^2), \\ <0, & d_2 < \beta(\sigma,n^2), \end{cases} \tag{2.25}$$

where

$$\beta(\sigma,n^2) = -\frac{3\sigma\tau\Big(d_1\tfrac{n^2}{\ell^2}\Big)^2 + 2(\sigma+\tau-\tau\sigma A)d_1\tfrac{n^2}{\ell^2} + 1-\sigma A-(A+B)\tau}{\sigma u_*\tfrac{n^2}{\ell^2}} < 0,\ \ n\in\mathbb{N}. \tag{2.26}$$

Lemma 2.7. *For $P_nQ_n - \sigma\tau R_n$, we have*

(I) if $(H1)$ holds and $d_2\ge 0$, then $P_nQ_n-\sigma\tau R_n > 0$ for any $n\in\mathbb{N}$;
(II) if $(H2)$ holds, $d_2 \ge 0$ and $\frac{1}{\tau} \ge A - \frac{2d_1}{\ell^2}$, then $P_nQ_n-\sigma\tau R_n>0$ for any $n\in\mathbb{N}$;
(III) if the assumptions of (I) or (II) are not satisfied, then for $n=\ell\sqrt{\frac{\tau A-1}{2\tau d_1}}$, $P_nQ_n-\sigma\tau R_n>0$, while for $n\neq \ell\sqrt{\frac{\tau A-1}{2\tau d_1}}$,

$$P_nQ_n - \sigma\tau R_n = 0 \Longleftrightarrow d_2 = d_2^H(\sigma,n^2), \tag{2.27}$$

where

$$\begin{aligned} & d_2^H(\sigma,n^2) \\ = & -\frac{8\sigma^2\tau^2\Big(d_1\frac{n^2}{\ell^2}\Big)^3+8\sigma\tau(\sigma+\tau-\tau\sigma A)\Big(d_1\frac{n^2}{\ell^2}\Big)^2+2\big(\sigma\tau(1-\sigma A-A\tau-B\tau)+(\sigma+\tau-\tau\sigma A)^2\big)d_1\frac{n^2}{\ell^2}}{u_*\sigma^2\frac{n^2}{\ell^2}\Big(2\tau d_1\frac{n^2}{\ell^2}+1-\tau A\Big)} \\ & -\frac{(1-\sigma A)(\sigma+\tau-\tau\sigma A-(A+B)\tau^2)}{u_*\sigma^2\frac{n^2}{\ell^2}\Big(2\tau d_1\frac{n^2}{\ell^2}+1-\tau A\Big)}. \end{aligned} \tag{2.28}$$

Now, we can derive the conditions under which Eq. (2.13) has purely imaginary roots.

Lemma 2.8. *Assume that $d_2^H(\sigma,n^2)$ is defined by (2.28) and*

$$\begin{aligned} & \kappa(\sigma,n^2) \\ = & -\frac{2\sigma^2\tau^2\Big(d_1\frac{n^2}{\ell^2}\Big)^3+\sigma\tau(\sigma(1-\tau A)+4\tau)\Big(d_1\frac{n^2}{\ell^2}\Big)^2+2\tau(\sigma+\tau-\tau\sigma A)d_1\frac{n^2}{\ell^2}+\tau(\sigma B+1-(A+B)\tau)}{u_*\sigma^2\frac{n^2}{\ell^2}\Big(2\tau d_1\frac{n^2}{\ell^2}+1-\tau A\Big)}. \end{aligned} \tag{2.29}$$

(I) When $d_2\ge 0$, $\pm i\omega_n$ are roots of Eq. (2.13) if and only if $n\neq \ell\sqrt{\frac{\tau A-1}{2\tau d_1}}$, $d_2 = d_2^H(\sigma,n^2)$.

(II) When $d_2<0$, $\pm i\omega_n$ are roots of Eq. (2.13) if and only if $n\neq \ell\sqrt{\frac{\tau A-1}{2\tau d_1}}$, $d_2 = d_2^H(\sigma,n^2)$ and $\kappa(\sigma,n^2)>0$.

Proof. From Lemma 2.6, we have $Q_n>0$ for $d_2\ge 0$. This, together with Lemma 2.3, proves (I).

We next focus on $d_2<0$. Note that $\kappa(\sigma,n^2) = d_2^H(\sigma,n^2)-\beta(\sigma,n^2)$. It therefore follows from (2.25) and (2.27) that $Q_n>0$ and $P_nQ_n-\sigma\tau R_n=0$ if and only if $\kappa(\sigma,n^2)>0$ and $d_2=d_2^H(\sigma,n^2)$. Then, using Lemma 2.3, we complete the proof of (II). □

Lemma 2.9. *When $(H1)$ holds, Eq. 2.13 has no purely imaginary roots for any $n\in\mathbb{N}$.*

Proof. From (I) of Lemma 2.7, we see that when $d_2 \geq 0$ and $(H1)$ holds, Eq. 2.13 has no purely imaginary roots for any $n \in \mathbb{N}$. Next, we focus on $d_2 < 0$. When $(H1)$ holds, we have $A < 0$, which implies $n \neq \ell\sqrt{\frac{\tau A-1}{2\tau d_1}}$ for any $n \in \mathbb{N}$. Since $(H1)$ holds and $A < 0$, it then follows from (2.29) that $\kappa(\sigma, n^2) < 0$ for any $n \in \mathbb{N}$. This, together with Lemma 2.8, completes the proof. □

Lemma 2.10. *Assume that $(H2)$ holds and $d_2 \geq 0$.*

(I) If $\frac{1}{\tau} \geq A - \frac{2d_1}{\ell^2}$, then Eq. (2.13) has no purely imaginary roots for any $n \in \mathbb{N}$.
(II) If $\frac{1}{\tau} < A - \frac{2d_1}{\ell^2}$, then Eq. (2.13) has a pair of purely imaginary roots at $d_2 = d_2^H(\sigma, n^2)$ for $1 \leq n \leq N_H - 1$ and no purely imaginary roots for $n \geq N_H$, where $d_2^H(\sigma, n^2)$ is defined by (2.28) and

$$N_H = \begin{cases} \ell\sqrt{\frac{\tau A-1}{2\tau d_1}}, & \text{if } \ell\sqrt{\frac{\tau A-1}{2\tau d_1}} \text{ is an integer,} \\ \left[\ \ell\sqrt{\frac{\tau A-1}{2\tau d_1}}\ \right]+1, & \text{if } \ell\sqrt{\frac{\tau A-1}{2\tau d_1}} \text{ is not an integer.} \end{cases} \tag{2.30}$$

Proof. (I) follows directly from (II) of Lemma 2.7. Next, we turn our attention to the proof of (II). It is easy to show that

$$2\tau d_1\frac{n^2}{\ell^2}+1-\tau A\begin{cases} < 0, & 1 \leq n \leq N_H - 1, \\ \geq 0, & n \geq N_H, \end{cases} \tag{2.31}$$

where N_H is defined by (2.30) and $N_H \geq 2$ since $\frac{1}{\tau} < A - \frac{2d_1}{\ell^2}$. Noting that $(H2)$ holds and $d_2 \geq 0$ and using (2.24), (2.27) and (2.31), we conclude that $P_nQ_n - \sigma\tau R_n > 0$ for $n \geq N_H$, while for $1 \leq n \leq N_H - 1$,

$$P_nQ_n - \sigma\tau R_n\begin{cases} > 0, & 0 \leq d_2 < d_2^H(\sigma, n^2), \\ = 0, & d_2 = d_2^H(\sigma, n^2), \\ < 0, & d_2 > d_2^H(\sigma, n^2), \end{cases}$$

where $d_2^H(\sigma, n^2)$ is defined by (2.28). Then, by Lemma 2.8, we proves (II). This completes the proof. □

Lemma 2.11. *Assume that $(H2)$ holds and $d_2 < 0$.*

(I) If $\frac{1}{\tau} \leq A$, then Eq. (2.13) has no purely imaginary roots for any $n \in \mathbb{N}$.
(II) If $\frac{1}{\tau} > A$,

$$\sigma_* = \frac{(A+B)\tau - 1}{B} > 0, \tag{2.32}$$

and

$$\xi\left(\sigma, n^2\right) = 2d_1\frac{n^2}{\ell^2} + \frac{1}{\tau} + \frac{B(\sigma-\tau)}{\tau\left(\sigma d_1\frac{n^2}{\ell^2}+1\right)^2},\ n \in \mathbb{N}, \tag{2.33}$$

then we have:

(i) if either $0 < \sigma \leq \sigma_*$, or $\sigma > \sigma_*$ and $A \leq \xi(\sigma, 1)$, then Eq. (2.13) has no purely imaginary roots for any $n \in \mathbb{N}$;
(ii) if $\sigma > \sigma_*$ and $\xi(\sigma, N_*^2) < A \leq \xi(\sigma, (N_*+1)^2)$ for some $N_* \in \mathbb{N}$, then for $n \geq N_* + 1$, Eq. (2.13) has no purely imaginary roots, while for $1 \leq n \leq N_*$, Eq. (2.13) has a pair of purely imaginary roots if and only if $d_2 = d_2^H(\sigma, n^2)$, where $d_2^H(\sigma, n^2)$ is defined by (2.28).

Proof. We first consider $\frac{1}{\tau} \leq A$. When $(H2)$ holds, we see that $\frac{1}{\sigma} > A$ and $A + B < 0$, which implies that

$$\sigma + \tau - \tau\sigma A > 0, \tag{2.34}$$

and

$$\sigma(1-\tau A) + 4\tau = \sigma + \tau(1-\sigma A) + 3\tau > 0. \tag{2.35}$$

Moreover, using $\frac{1}{\tau} \leq A$ and $\frac{1}{\sigma} > A$, we have $\tau > \sigma$ and thus obtain

$$\sigma B + 1 - (A+B)\tau > \sigma B + \sigma A - (A+B)\tau = (\sigma-\tau)(B+A) > 0. \tag{2.36}$$

If $A - \frac{2d_1}{\ell^2} < \frac{1}{\tau} \leq A$, then we find that for any $n \in \mathbb{N}$,

$$2\tau d_1\frac{n^2}{\ell^2} + 1 - \tau A > 0 \text{ and } n \neq \ell\sqrt{\frac{\tau A-1}{2\tau d_1}}, \tag{2.37}$$

which, together with (2.29) and (2.34)–(2.36), indicate $\kappa(\sigma, n^2) < 0$ for any $n \in \mathbb{N}$.

Similarly, if $\frac{1}{\tau} \le A - \frac{2d_1}{\ell^2}$, then we also have $\kappa(\sigma, n^2) < 0$ for $n > \ell\sqrt{\frac{\tau A-1}{2\tau d_1}}$. Moreover, it follows from (2.24), $(H2)$ and $d_2 < 0$ that $P_nQ_n - \sigma\tau R_n > 0$ for $n \le \ell\sqrt{\frac{\tau A-1}{2\tau d_1}}$. In terms of Lemma 2.8 and the above discussion, we can conclude that when $\frac{1}{\tau} \le A$, Eq. (2.13) has no purely imaginary roots for any $n \in \mathbb{N}$.

Next, we focus on $\frac{1}{\tau} > A$. Note that (2.37) still holds for any $n \in \mathbb{N}$. Hence, the sign of $\kappa(\sigma, n^2)$ is determined by its numerator. Then, a simple calculation yields

$$\kappa(\sigma, n^2) > 0 \Longleftrightarrow \sigma > \sigma_* \text{ and } A > \xi(\sigma, n^2), \tag{2.38}$$

where σ_* and $\xi(\sigma, n^2)$ are defined by (2.32) and (2.33), respectively. This, combined with Lemma 2.8, implies that when $0 < \sigma \le \sigma_*$, Eq. (2.13) has no purely imaginary roots for any $n \in \mathbb{N}$.

When $\sigma > \sigma_*$, it is easy to verify that $\xi(\sigma, n^2) < \xi(\sigma, (n+1)^2)$ for $n \in \mathbb{N}$. Consequently, if $A \le \xi(\sigma, 1)$, then $A \le \xi(\sigma, n)$ for any $n \in \mathbb{N}$. It therefore follows from (2.38) and Lemma 2.8 that Eq. (2.13) has no purely imaginary roots for any $n \in \mathbb{N}$. This concludes $(II)(i)$.

When $\sigma > \sigma_*$, if there exists some $N_* \in \mathbb{N}$ such that $\xi(\sigma, N_*^2) < A \le \xi(\sigma, (N_*+1)^2)$, then $A > \xi(\sigma, n^2)$ for any $1 \le n \le N_*$ and $A \le \xi(\sigma, n^2)$ for any $n \ge N_* + 1$, which, along with (2.38) and Lemma 2.8, proves $(II)(ii)$. This completes the proof. □

Remark 2.2. When $B = 0$, Eq. (2.13) has also been studied in [11]. Lemmas 2.5 and 2.9 contain the results in [11] for the case of the weak kernel.

From the above lemma, we know that when $(H2)$ and the assumptions of (II) of Lemma 2.10 or $(II)(ii)$ of Lemma 2.11 are satisfied, Eq. (2.13) has a pair of purely imaginary roots provided that $d_2 = d_2^H(\sigma, n^2)$. Then, taking d_2 as a bifurcation parameter and assuming that $\lambda(d_2)$ is the root of Eq. (2.13), we have

$$\left.\frac{d\mathrm{Re}\lambda(d_2)}{dd_2}\right|_{d_2=d_2^H(\sigma,n^2)} = -\frac{u_* n^2\sigma^2(2\tau d_1\frac{n^2}{\ell^2} + 1 - \tau A)}{2\ell^2(\sigma^2\tau^2\omega_n^2 + P_n^2)} \begin{cases} > 0, & d_2 \ge 0,\ 1 \le n \le N_H - 1, \\ < 0, & d_2 < 0,\ 1 \le n \le N_*. \end{cases} \tag{2.39}$$

Using Lemmas 2.5, 2.9–2.11 and the transversality conditions (2.23) and (2.39), we arrive at the following theorems.

Theorem 2.2. *Assume that $(H1)$ holds, $h_1(t,\tau) = \frac{1}{\tau}e^{-\frac{t}{\tau}}$, $h_2(t,\sigma) = \frac{1}{\sigma}e^{-\frac{t}{\sigma}}$, and, $d_{2,1}^T(\sigma, n^2)$ and N_T are defined by (2.18) and (2.19), respectively. For system (1.5), we have*

- *(I) if $d_2 \ge 0$, then the positive constant steady state u_* is asymptotically stable;*
- *(II) if $d_2 < 0$, then the positive constant steady state u_* is asymptotically stable for $d_{2,1}^T(\sigma, N_T^2) < d_2 < 0$ and unstable for $d_2 < d_{2,1}^T(\sigma, N_T^2)$; moreover, there is no Hopf bifurcation and system (1.5) undergoes steady state bifurcation at $d_2 = d_{2,1}^T(\sigma, N_T^2)$ provided that $d_{2,1}^T(\sigma, N_T^2) \ne d_{2,1}^T(\sigma, (N_T+1)^2)$.*

Theorem 2.3. *Assume that $(H2)$ holds, $h_1(t,\tau) = \frac{1}{\tau}e^{-\frac{t}{\tau}}$, $h_2(t,\sigma) = \frac{1}{\sigma}e^{-\frac{t}{\sigma}}$, and, $d_{2,1}^T(\sigma, n^2)$, $d_2^H(\sigma, n^2)$, $\xi(\sigma, n^2)$, N_T, N_H and σ_* are defined by (2.18), (2.28), (2.33), (2.19), (2.30) and (2.32), respectively. For system (1.5), we have the following statements.*

- *(I) When $d_2 \ge 0$, we have*
  - *(i) if $\frac{1}{\tau} \ge A - \frac{2d_1}{\ell^2}$, then the positive constant steady state u_* is asymptotically stable;*
  - *(ii) if $\frac{1}{\tau} < A - \frac{2d_1}{\ell^2}$, then the positive constant steady state u_* is asymptotically stable for $0 \le d_2 < \min_{1\le n\le N_H-1}\{d_2^H(\sigma, n^2)\}$ and unstable for $d_2 > \min_{1\le n\le N_H-1}\{d_2^H(\sigma, n^2)\}$; moreover, there is no steady state bifurcation and system (1.5) undergoes Hopf bifurcation at $d_2 = d_2^H(\sigma, n^2)$, $1 \le n \le N_H - 1$, provided that $d_2^H(\sigma, n^2) \ne d_2^H(\sigma, m^2)$ for $m \ne n$ and $1 \le m \le N_H - 1$.*
- *(II) When $d_2 < 0$, we have*
  - *(i) if $\frac{1}{\tau} \le A$, then the positive constant steady state u_* is asymptotically stable for $d_{2,1}^T(\sigma, N_T^2) < d_2 < 0$ and unstable for $d_2 < d_{2,1}^T(\sigma, N_T^2)$; moreover, there is no Hopf bifurcation and system (1.5) undergoes steady state bifurcation at $d_2 = d_{2,1}^T(\sigma, N_T^2)$ provided that $d_{2,1}^T(\sigma, N_T^2) \ne d_{2,1}^T(\sigma, (N_T+1)^2)$;*
  - *(ii) if $\frac{1}{\tau} > A$, then we have:*
    - *(a) if either $0 < \sigma \le \sigma_*$, or $\sigma > \sigma_*$ and $A \le \xi(\sigma, 1)$, then the positive constant steady state u_* is asymptotically stable for $d_{2,1}^T(\sigma, N_T^2) < d_2 < 0$ and unstable for $d_2 < d_{2,1}^T(\sigma, N_T^2)$; moreover, there is no Hopf bifurcation and system (1.5) undergoes steady state bifurcation at $d_2 = d_{2,1}^T(\sigma, N_T^2)$ provided that $d_{2,1}^T(\sigma, N_T^2) \ne d_{2,1}^T(\sigma, (N_T+1)^2)$;*
    - *(b) if $\sigma > \sigma_*$ and $\xi(\sigma, N_*^2) < A \le \xi(\sigma, (N_*+1)^2)$ for some $N_* \in \mathbb{N}$, then the positive constant steady state u_* is asymptotically stable for $\max\left\{d_{2,1}^T(\sigma, N_T^2), \max_{1\le n\le N_*} d_2^H(\sigma, n^2)\right\} < d_2 < 0$ and unstable for $d_2 < \max\left\{d_{2,1}^T(\sigma, N_T^2), \max_{1\le n\le N_*} d_2^H(\sigma, n^2)\right\}$; moreover, system (1.5) undergoes steady state bifurcation at $d_2 = d_{2,1}^T(\sigma, N_T^2)$*

Table 1
Stability of the positive steady state u_* and possible bifurcations for Case (I)

	$d_2 \ge 0$		$d_2 < 0$	
	Conditions for τ	Stability and bifurcations	Conditions for τ	Stability and bifurcations
$(H1)$ holds	$\tau > 0$	stable	$\tau > 0$	SSB
$(H2)$ holds	$\frac{1}{\tau} \ge A - \frac{2d_1}{\ell^2}$	stable	$\frac{1}{\tau} > A$	SSB, HB
	$\frac{1}{\tau} < A - \frac{2d_1}{\ell^2}$	HB	$\frac{1}{\tau} \le A$	SSB

" SSB" and "HB" denote steady state bifurcation and Hopf bifurcation, respectively.

provided that $d^T_{2,1}(\sigma, N_T^2) \ne d^T_{2,1}(\sigma, (N_T+1)^2)$ *and* $d^T_{2,1}(\sigma, N_T^2) \ne d^H_2(\sigma, n^2)$, $1 \le n \le N_*$, *and Hopf bifurcation at* $d_2 = d^H_2(\sigma, n^2)$, $1 \le n \le N_*$, *provided that* $d^H_2(\sigma, n^2) \ne d^T_{2,1}(\sigma, k^2)$ *for* $k \in \mathbb{N}$ *and* $d^H_2(\sigma, n^2) \ne d^H_2(\sigma, m^2)$ *for* $m \ne n$ *and* $1 \le m \le N_*$.

Based on Theorems 2.2 and 2.3, the influence of d_2 and τ on the stability of the positive steady state of (1.5) for Case (I) is shown in Table 1.

2.2. Other temporal kernels

For other three cases: (II) strong/weak; (III) weak/strong; (IV) strong/strong, one can analyze the stability and bifurcation using the similar method as for Case (I), but the specific analysis is very complicated. Here, instead of the comprehensive and cumbersome analysis, we only give some preliminary results for these three types of temporal kernels. For Cases (II), (III) and (IV), the corresponding characteristic equation can be written as

$$\begin{aligned}&\left(\lambda + d_1\tfrac{n^2}{\ell^2} - A\right)\left(1+\tau d_1\tfrac{n^2}{\ell^2}+\tau\lambda\right)^2\left(1+\sigma d_1\tfrac{n^2}{\ell^2}+\sigma\lambda\right) + d_2 u_* \tfrac{n^2}{\ell^2}\left(1+\sigma d_1\tfrac{n^2}{\ell^2}+\sigma\lambda\right)\\ &-B\left(1+\tau d_1\tfrac{n^2}{\ell^2}+\tau\lambda\right)^2 = 0,\end{aligned} \tag{2.40}$$

$$\begin{aligned}&\left(\lambda + d_1\tfrac{n^2}{\ell^2} - A\right)\left(1+\tau d_1\tfrac{n^2}{\ell^2}+\tau\lambda\right)\left(1+\sigma d_1\tfrac{n^2}{\ell^2}+\sigma\lambda\right)^2 + d_2 u_* \tfrac{n^2}{\ell^2}\left(1+\sigma d_1\tfrac{n^2}{\ell^2}+\sigma\lambda\right)^2\\ &-B\left(1+\tau d_1\tfrac{n^2}{\ell^2}+\tau\lambda\right) = 0,\end{aligned} \tag{2.41}$$

and

$$\begin{aligned}&\left(\lambda + d_1\tfrac{n^2}{\ell^2} - A\right)\left(1+\tau d_1\tfrac{n^2}{\ell^2}+\tau\lambda\right)^2\left(1+\sigma d_1\tfrac{n^2}{\ell^2}+\sigma\lambda\right)^2 + d_2 u_* \tfrac{n^2}{\ell^2}\left(1+\sigma d_1\tfrac{n^2}{\ell^2}+\sigma\lambda\right)^2\\ &-B\left(1+\tau d_1\tfrac{n^2}{\ell^2}+\tau\lambda\right)^2 = 0,\end{aligned} \tag{2.42}$$

respectively.

By Lemma 2.1, we find that for $n = 0$, all roots of Eq. (2.40) have negative real parts provided that $(H1)$ or $(H2)$ holds, and all roots of Eq. (2.41) or Eq. (2.42) have negative real parts provided that either $(H1)$ or $(H3)$ holds, where

$$(H3)\ B<0 \text{ and } (\sigma, A) \in \left\{(\sigma, A)\middle| 0<\sigma \le -\frac{1}{2B}, A < -B\right\} \cup \left\{(\sigma, A)\middle| \sigma > -\frac{1}{2B},\ A < \frac{1}{\sigma} - \sqrt{-\frac{B}{2\sigma}}\right\}.$$

According to Lemma 2.1, these hypotheses imply that the positive steady state u_* of system (2.7) is asymptotically stable. Under these hypotheses, we investigate possible bifurcations induced by d_2 and τ. Note that steady state bifurcation is related to zero roots. In fact, 0 is a root of (2.40)–(2.42), respectively, provided that

$$\left(d_1\frac{n^2}{\ell^2} - A\right)\left(1+\tau d_1\frac{n^2}{\ell^2}\right)^2\left(1+\sigma d_1\frac{n^2}{\ell^2}\right) + d_2 u_* \frac{n^2}{\ell^2}\left(1+\sigma d_1\frac{n^2}{\ell^2}\right) - B\left(1+\tau d_1\frac{n^2}{\ell^2}\right)^2 = 0, \tag{2.43}$$

$$\left(d_1\frac{n^2}{\ell^2} - A\right)\left(1+\tau d_1\frac{n^2}{\ell^2}\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2 + d_2 u_* \frac{n^2}{\ell^2}\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2 - B\left(1+\tau d_1\frac{n^2}{\ell^2}\right) = 0, \tag{2.44}$$

or

$$\left(d_1\frac{n^2}{\ell^2} - A\right)\left(1+\tau d_1\frac{n^2}{\ell^2}\right)^2\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2 + d_2 u_* \frac{n^2}{\ell^2}\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2 - B\left(1+\tau d_1\frac{n^2}{\ell^2}\right)^2 = 0. \tag{2.45}$$

Furthermore, (2.43)–(2.45) are equivalent to $d_2 = d^T_{2,2}(\sigma, n^2)$, $d_2 = d^T_{2,3}(\sigma, n^2)$ and $d_2 = d^T_{2,4}(\sigma, n^2)$, respectively, where

$$d^T_{2,2}(\sigma, n^2) = \frac{\left(1+\tau d_1\frac{n^2}{\ell^2}\right)^2\left(B - \left(d_1\frac{n^2}{\ell^2} - A\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)\right)}{u_*\frac{n^2}{\ell^2}\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)},\quad n\in\mathbb{N}, \tag{2.46}$$

$$d_{2,3}^T(\sigma,n^2)=\frac{\left(1+\tau d_1\frac{n^2}{\ell^2}\right)\left(B-\left(d_1\frac{n^2}{\ell^2}-A\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2\right)}{u_*\frac{n^2}{\ell^2}\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2},\ n\in\mathbb{N}, \tag{2.47}$$

and

$$d_{2,4}^T(\sigma,n^2)=\frac{\left(1+\tau d_1\frac{n^2}{\ell^2}\right)^2\left(B-\left(d_1\frac{n^2}{\ell^2}-A\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2\right)}{u_*\frac{n^2}{\ell^2}\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2},\ n\in\mathbb{N}. \tag{2.48}$$

Utilizing $(H1)$ or $(H2)$, we obtain $d_{2,2}^T(\sigma,n^2)<0$, while applying $(H1)$ or $(H3)$, we find that $d_{2,3}^T(\sigma,n^2)<0$ and $d_{2,4}^T(\sigma,n^2)<0$.

Assuming that 0 is a simple root of (2.40)–(2.42), respectively, we have

$$\left.\frac{d\lambda}{dd_2}\right|_{d_2=d_{2,2}^T(\sigma,n^2)} = \frac{-u_*\frac{n^2}{\ell^2}\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)}{\left(1+\tau d_1\frac{n^2}{\ell^2}\right)^2\left(1-\sigma A+2\sigma d_1\frac{n^2}{\ell^2}\right)+2\tau\left(1+\tau d_1\frac{n^2}{\ell^2}\right)\left(\left(d_1\frac{n^2}{\ell^2}-A\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)-B\right)+\sigma d_2u_*\frac{n^2}{\ell^2}} \neq 0,$$

$$\left.\frac{d\lambda}{dd_2}\right|_{d_2=d_{2,3}^T(\sigma,n^2)} = \frac{-u_*\frac{n^2}{\ell^2}\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2}{\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2\left(1-\tau A+2\tau d_1\frac{n^2}{\ell^2}\right)+2\sigma\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)\left(\left(d_1\frac{n^2}{\ell^2}-A\right)\left(1+\tau d_1\frac{n^2}{\ell^2}\right)+d_2u_*\frac{n^2}{\ell^2}\right)-B\tau} \neq 0,$$

or

$$\left.\frac{d\lambda}{dd_2}\right|_{d_2=d_{2,4}^T(\sigma,n^2)}=\frac{-u_*\frac{n^2}{\ell^2}\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2}{\chi}\neq 0,$$

where

$$\begin{aligned}\chi\ =\ &\left(1+\tau d_1\frac{n^2}{\ell^2}\right)^2\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2+2\tau\left(1+\tau d_1\frac{n^2}{\ell^2}\right)\left(\left(d_1\frac{n^2}{\ell^2}-A\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)^2-B\right)\\ &+2\sigma\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)\left(\left(d_1\frac{n^2}{\ell^2}-A\right)\left(1+\tau d_1\frac{n^2}{\ell^2}\right)^2+d_2u_*\frac{n^2}{\ell^2}\right).\end{aligned}$$

To summarize the above, we obtain the following result on steady state bifurcation.

Theorem 2.4. *Assume that the positive steady state u_* of system (2.7) is asymptotically stable and $d_{2,2}^T(\sigma,n^2)$, $d_{2,3}^T(\sigma,n^2)$ and $d_{2,4}^T(\sigma,n^2)$ are defined by (2.46)–(2.48), respectively.*

(I) If $d_2\ge 0$, then there is no steady state bifurcation for Cases (II), (III) and (IV).
(II) If $d_2<0$, then system (1.5) undergoes steady state bifurcation at $d_2=d_{2,j}^T(\sigma,n^2)$ provided that $d_{2,j}^T(\sigma,n_1^2)\neq d_{2,j}^T(\sigma,n_2^2)$ for $n_1,n_2\in\mathbb{N}$ and $n_1\neq n_2$. Here, $d_{2,j}^T(\sigma,n^2)$ with $j=2,3,4$, correspond to the bifurcation values of Cases (II), (III) and (IV), respectively.

By Theorems 2.2–2.4, it is easy to see that as far as steady state bifurcation is concerned, the influence of these types of temporal kernels is very similar and the main difference is that the critical values of steady state bifurcation are different. Notice that $d_{2,1}^T(\sigma,n^2)$ can be rewritten as follows

$$d_{2,1}^T(\sigma,n^2)=\frac{\left(1+\tau d_1\frac{n^2}{\ell^2}\right)\left(B-\left(d_1\frac{n^2}{\ell^2}-A\right)\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)\right)}{u_*\frac{n^2}{\ell^2}\left(1+\sigma d_1\frac{n^2}{\ell^2}\right)}<0,\ n\in\mathbb{N},$$

which, together with (2.46) and $0<\left(1+\tau d_1\frac{n^2}{\ell^2}\right)<\left(1+\tau d_1\frac{n^2}{\ell^2}\right)^2$, implies that

$$d_{2,2}^T(\sigma,n^2)<d_{2,1}^T(\sigma,n^2)<0. \tag{2.49}$$

Moreover, using (2.47), (2.48) and $0 < \left(1+\tau d_1 \frac{n^2}{\ell^2}\right) < \left(1+\tau d_1 \frac{n^2}{\ell^2}\right)^2$, we have

$$d_{2,4}^T(\sigma, n^2) < d_{2,3}^T(\sigma, n^2) < 0. \tag{2.50}$$

By (2.49) and (2.50), we can conclude that for the same temporal kernel in reaction and the same wave number n, the critical value of steady state bifurcation of system (1.5) with the "weak" memory-based temporal kernel is larger than that of system (1.5) with the "strong" memory-based temporal kernel.

The Hopf bifurcation analysis for Cases (II)-(IV) is very complicated, although the method is very similar to Case (I). Therefore, we do not make the specific theoretical analysis. The numerical simulations in Section 3.2 show that when (H2) holds, $d_2 \geq 0$ and $\frac{1}{\tau} \geq A - \frac{2d_1}{\ell^2}$, the positive steady state u_* is asymptotically stable in Case (I) and Hopf bifurcation will occur in other three cases.

3. Applications

In [12], Shi and Shivaji considered a diffusive logistic model with predation and Dirichlet boundary condition, which has the form

$$\begin{cases} \dfrac{\partial u}{\partial t} = d\Delta u + ru\left(1-\dfrac{u}{k}\right) - \dfrac{Eu}{1+Fu}, & x \in \Omega,\ t > 0, \\ u(x,t) = 0, & x \in \partial\Omega,\ t > 0, \end{cases} \tag{3.1}$$

where $d, r, k > 0$, and d, r and k stand for the diffusion rate, the intrinsic growth rate and the carrying capacity, respectively. The term $\dfrac{Eu}{1+Fu}$ with $E \geq 0, F > 0$ reflects the influence of a satiating generalist predator, or the behaviour of seeking a mate [12]. Spatially homogeneous and inhomogeneous steady states and global bifurcation were discussed in [12].

In this section, we introduce the spatial memory and spatiotemporal delays into (3.1) and consider the following revised version of (3.1) under Neumann boundary condition on one dimensional spatial domain $\Omega = (0, \ell\pi)$:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 u_{xx} + d_2 (uv_x)_x + u(1-w) - \dfrac{Eu}{1+Fu}, & x \in (0,\ell\pi),\ t > 0, \\ u_x(0,t) = u_x(\ell\pi, t) = 0, & t > 0, \end{cases} \tag{3.2}$$

where $d_1 > 0$, $d_2 \in \mathbb{R}$, and $v = g_1 ** u$ and $w = g_2 ** u$ are defined as in (1.3) and (1.4), respectively.

3.1. Two weak temporal kernels: $h_1(t,\tau) = \frac{1}{\tau}e^{-\frac{t}{\tau}}$ and $h_2(t,\sigma) = \frac{1}{\sigma}e^{-\frac{t}{\sigma}}$

3.1.1. $E = 0$

When $E = 0$, it is easy to verify that system (3.2) possesses two constant steady states: $u_0 \equiv 0$ and $u_* \equiv 1$. It is easy to show that $u_0 \equiv 0$ is always unstable. For $u_* \equiv 1$, we have $A = 0$ and $B = -1$. Thus, (H2) holds, and $A - \frac{2d_1}{\ell^2} < A < \frac{1}{\tau}$ for any $\ell, d_1, \tau > 0$. It then follows from $(I)(i)$ of Theorem 2.3 that when $d_2 \geq 0$, $u_* \equiv 1$ is asymptotically stable for any $\ell, d_1, \sigma, \tau > 0$. On the other hand, when $d_2 < 0$, the stability of $u_* \equiv 1$ is dependent of the choice of parameters.

When $d_2 < 0$, taking $d_1 = 0.5$, $\ell = 2$, $\tau = 1$, restricting the range of σ to $0 < \sigma \leq 20$ and noting $\frac{1}{\tau} > A = 0$, we discuss the stability of $u_* \equiv 1$ in terms of $(II)(ii)$ of Theorem 2.3. It follows from (2.32), (2.19) and (2.33) that $\sigma_* = 2$,

$$N_T = \begin{cases} 3, & \text{for } 0 < \sigma < 4.3431, \\ 2, & \text{for } 4.3431 < \sigma \leq 20, \end{cases}$$

and

$$\xi(\sigma, 1) = \begin{cases} \geq 0, & \text{for } 0 < \sigma \leq 3.6515, \\ < 0, & \text{for } 3.6515 < \sigma \leq 20. \end{cases} \tag{3.3}$$

Notice that for each $n \in \mathbb{N}$, $\xi(\sigma, n^2)$ attains its minimum at $\sigma_n^\sharp = 2\tau + \frac{\ell^2}{d_1 n^2}$. Therefore, we have $\xi(\sigma, 2^2) \geq \xi(\sigma_2^\sharp, 2^2) = \frac{5}{3} > 0$. This, together with (3.3) and $A = 0$, implies that $A \leq \xi(\sigma, 1)$ for $\sigma_* < \sigma \leq 3.6515$, while for $3.6515 < \sigma \leq 20$, $\xi(\sigma, 1) < A \leq \xi(\sigma, 2^2)$ and then

$$N_* = 1.$$

The numerical calculation shows that $d_2^H(\sigma, 1) < \min\left\{d_{2,1}^T(\sigma, 2^2), d_{2,1}^T(\sigma, 3^2)\right\}$ for $3.6515 < \sigma \leq 20$. Then, by $(II)(ii)$ of Theorem 2.3, we have the following stability results on $u_* \equiv 1$.

Proposition 3.1. *Assume that $E = 0$, $d_1 = 0.5$, $\ell = 2$, $\tau = 1$ and $0 < \sigma \leq 20$.*

(I) For $0 < \sigma \leq 4.3413$, $u_* \equiv 1$ is asymptotically stable for any $d_2 > d_{2,1}^T(\sigma, 3^2)$.

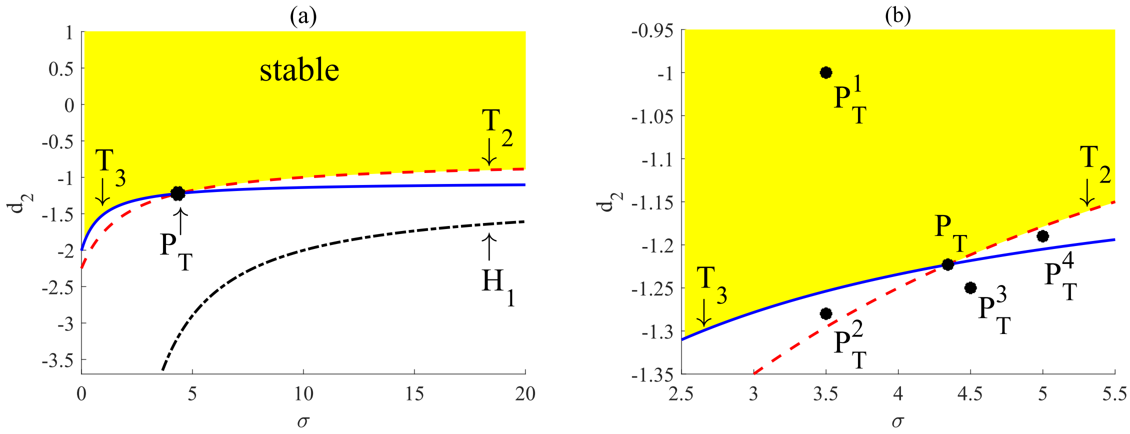

Fig. 1. (a) Stability region and bifurcation curves for the positive constant steady state $u_* \equiv 1$ of system (3.2) with $d_1 = 0.5,\ \ell = 2,\ \tau = 1,\ E = 0$ and $0 < \sigma \le 20$ in the $\sigma - d_2$ plane. T_2 and T_3 are steady state bifurcation curves and H_1 is Hopf bifurcation curve. (b) The enlargement of (a) for $2.5 \le \sigma \le 5.5$ and $-1.35 \le d_2 \le -0.95$, and the points $P_T^1 - P_T^4$ are chosen for numerical simulations.

(II) For $4.3413 < \sigma \le 20$, $u_* \equiv 1$ *is asymptotically stable for any* $d_2 > d_{2,1}^T(\sigma, 2^2)$.

In $\sigma - d_2$ plane, we display graphically steady state bifurcation curves $T_3 : d_2 = d_{2,1}^T(\sigma, 3^2)$, $T_2 : d_2 = d_{2,1}^T(\sigma, 2^2)$ and Hopf bifurcation curve $H_1 : d_2 = d_2^H(\sigma, 1), \sigma > 3.6515$, as shown in Fig. 1(a). As we can see from Fig. 1(a), when $0 < \sigma \le 20$, the boundaries of the stable region consist of steady state bifurcation curves T_3 and T_2.

Furthermore, steady state bifurcation curves T_3 and T_2 intersect at $P_T = (4.3431, -1.2230)$, which is a codimension-2 spatial resonance bifurcation point. We numerically investigate the dynamics of system (3.2) near P_T. Fig. 1(b) is the enlargement of the region near P_T of Fig. 1(a) and we numerically describe the solutions of system (3.2) for different points $P_T^1 - P_T^4$, where

$$P_T^1 = (3.5, -1), P_T^2 = (3.5, -1.28), P_T^3 = (4.5, -1.25), P_T^4 = (5, -1.19).$$

Fig. 2(a)–(d) illustrate the solutions for $P_T^1 - P_T^4$, respectively. Fig. 2(a) shows the stable positive constant steady state, while Fig. 2(b) and Fig. 2(d) display the spatially inhomogeneous steady states shaped like $\cos\frac{3x}{2}$ and $\cos x$, respectively. It is observed in Fig. 2(c) that the solution with an initial shape of $\cos\frac{3x}{2}$ converges to the solution with a different shape as time increases. For the fixed time $t = 500$, Fig. 3 describes the spatial shape of the solutions of Fig. 2.

3.1.2. $E > 0$

When $E > 0$, $u_0 \equiv 0$ is still a constant steady state of system (3.2) and the existence of the positive constant steady state depends on the relationship between E and F. The following proposition is concerned with the existence of the positive constant steady state.

Proposition 3.2. *Assume that* $E > 0$.

(I) If $E < 1$, *then system (3.2) has a unique positive constant steady state* $u_*^{(1)}$, *where*

$$u_*^{(1)} = \frac{F - 1 + \sqrt{(F-1)^2 + 4F(1-E)}}{2F}. \tag{3.4}$$

(II) If $E = 1$, *then system (3.2) has no positive constant steady states for* $F \le 1$ *and has a unique positive constant steady state* $u_*^{(1)}$ *for* $F > 1$, *where* $u_*^{(1)}$ *is defined by (3.4).*

(III) If $E > 1$, *then system (3.2) has no positive constant steady states for* $F \le 1$, *or for* $F > 1$ *and* $(F+1)^2/(4F) < E$, *and has two positive constant steady states* $u_*^{(1)}$ *and* $u_*^{(2)}$ *for* $F > 1$ *and* $(F+1)^2/(4F) \ge E$, *where* $u_*^{(1)}$ *is defined by (3.4) and*

$$u_*^{(2)} = \frac{F - 1 - \sqrt{(F-1)^2 + 4F(1-E)}}{2F}. \tag{3.5}$$

Moreover, if $F > 1$ *and* $(F+1)^2/(4F) = E$, *then* $u_*^{(1)} = u_*^{(2)}$.

We can graphically describe Proposition 3.2 in Fig. 4, where the existence of the positive constant steady state is shown in $F - E$ plane. It is easy to verify that $u_0 \equiv 0$ is unstable for $E < 1$ and asymptotically stable for $E > 1$. In addition, if $u_*^{(2)}$ exists, then it is always unstable.

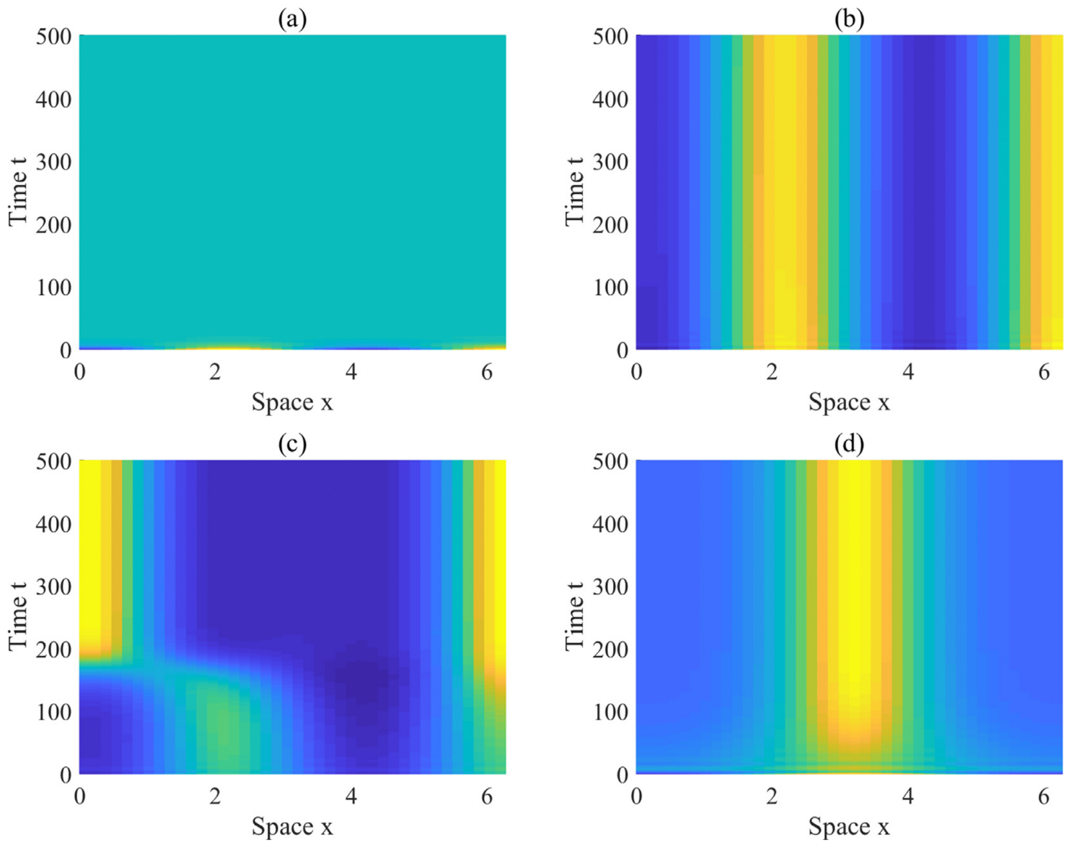

Fig. 2. (a)–(d) illustrate the projection of the solutions of system (3.2) in the $x-t$ plane, respectively, for $P_T^1 - P_T^4$ that are near P_T and shown in Fig. 1(b).

Taking $d_1 = 0.5,\ \ell = 5,\ \tau = 10,\ E = 1$ and $F = 2$, system (3.2) admits a unique positive steady state $u_*^{(1)} = 0.5$. Then, it is easily shown that $A = 0.25,\ B = -0.5 < 0$ and $A - \frac{2d_1}{\ell^2} = 0.21$. Moreover, $u_*^{(1)}$ is unstable for $\sigma > 4$ according to Theorem 2.1. When $0 < \sigma < \frac{1}{A} = 4$, (H2) holds. Then, we have

$$\ell\sqrt{\frac{\tau A - 1}{2\tau d_1}} = 1.9365,$$

which, together with (2.30), gives $N_H = 2$. Furthermore, from (2.19), numerical computation shows that $N_T = 3$ for $0 < \sigma < 4$. Note that $\frac{1}{\tau} = 0.1 < A - \frac{2d_1}{\ell^2} < A$. Therefore, using Theorem 2.3, we have the following result.

Proposition 3.3. *Assume that $d_1 = 0.5,\ \ell = 5,\ \tau = 10,\ E = 1,\ F = 2$ and $0 < \sigma < 4$. The positive constant steady state $u_*^{(1)}$ of system (3.2) is asymptotically stable for $d_{2,1}^T(\sigma, 3^2) < d_2 < d_2^H(\sigma, 1)$ and unstable for $d_2 \in \left(-\infty, d_{2,1}^T(\sigma, 3^2)\right) \cup \left(d_2^H(\sigma, 1), +\infty\right)$.*

Proposition 3.3 implies that the boundaries of the stable region of $u_*^{(1)}$ in the $\sigma - d_2$ plane consist of steady state bifurcation curve $T_3 : d_2 = d_{2,1}^T(\sigma, 3^2)$, Hopf bifurcation curve $H_1 : d_2 = d_2^H(\sigma, 1)$ and Hopf bifurcation line $H_0 : \sigma = 4$, as shown in Fig. 5(a). As we can see from Fig. 5(a), the intersection of Hopf bifurcation curve H_1 and Hopf bifurcation line H_0 is $P_H = (4, 14.9273)$, which is a double Hopf bifurcation point, while the intersection of steady state bifurcation curve T_3 and Hopf bifurcation line H_0 is $P_{TH} = (4, -3.4331)$, which is a steady state-Hopf bifurcation point.

Since we are interested in the spatiotemporal dynamics of system (3.2) near the double Hopf bifurcation point P_H and steady state-Hopf bifurcation point P_{TH}, the regions near these two codimension-two point are magnified in Figs. 5(b) and (c), respectively. We next choose the points $P_H^1 - P_H^6$ in Fig. 5(b) and $P_{TH}^1 - P_{TH}^5$ in Fig. 5(c) for numerical simulations, where

$$\begin{aligned} &P_H^1 = (4.01, 14.1), \quad P_H^2 = (3.8, 15), \quad P_H^3 = (3.95, 16.8), \\ &P_H^4 = (4.03, 15.5), \quad P_H^5 = (4.03, 15), \quad P_H^6 = (4.03, 14.5), \end{aligned}$$

and

$$\begin{aligned} &P_{TH}^1 = (3.9, -3.5), \quad P_{TH}^2 = (3.9, -3.2), \quad P_{TH}^3 = (4.05, -3.2), \\ &P_{TH}^4 = (4.05, -3.45), \quad P_{TH}^5 = (4.05, -3.6). \end{aligned}$$

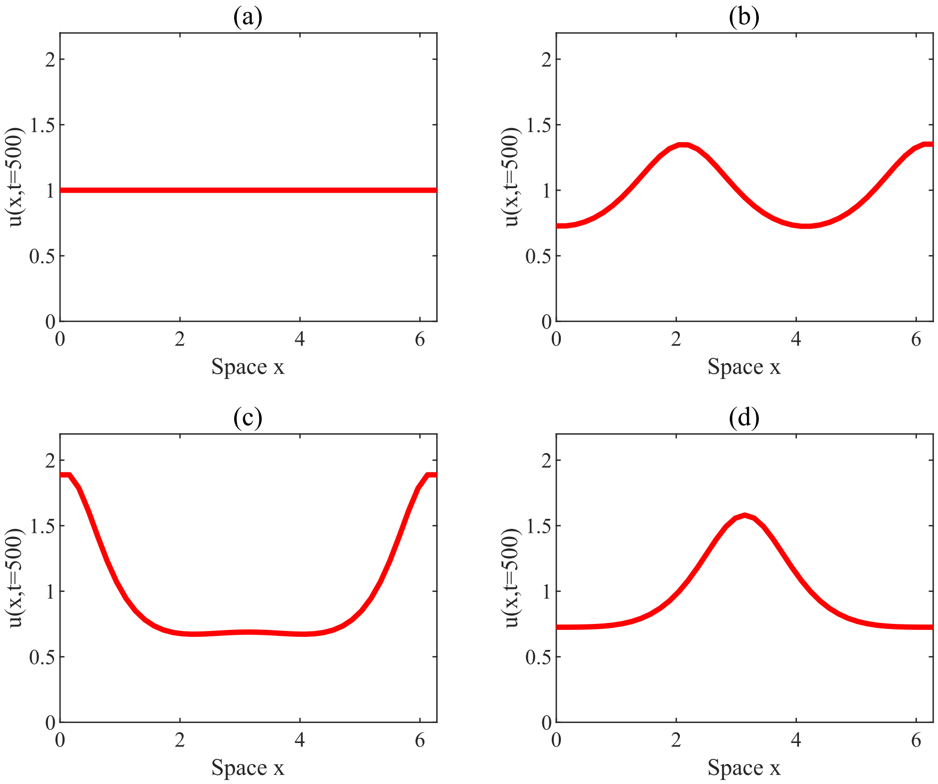

Fig. 3. (a)–(d) are the truncated curves of $u(x,t)$ of Fig. 2(a)–(d) in the direction of space for the fixed time $t = 500$, respectively.

In Fig. 6, (a)–(f) depict the solutions of system (3.2) for $P_H^1 - P_H^6$, respectively. More specifically, Figs. 6(a) and (c) illustrate the spatially homogeneous periodic solution and the spatially inhomogeneous periodic solution with a spatial shape like $\cos \frac{x}{5}$, respectively, while (b) shows the stable positive constant steady state. As we can see from Fig. 6(d)–(f), system (3.2) possesses spatially inhomogeneous quasi-periodic solutions. For the fixed spatial variable $x = \pi$, Fig. 7(a)–(f) show the evolution of the solution $u(x,t)$ of Fig. 6(a)–(f) in the direction of time t, respectively.

In Fig. 8, (a)–(d) describe the respective solutions of system (3.2) for $P_{TH}^1 - P_{TH}^4$, respectively. More specifically, Figs. 8(a) and (b) depict the spatially inhomogeneous steady state shaped like $\cos \frac{3x}{5}$ and the stable positive constant steady state, respectively, while Figs. 8(c) and (d) illustrate the spatially homogeneous periodic solution and the spatially inhomogeneous periodic solution with a spatial mode like $\cos \frac{3x}{5}$, respectively. When (σ, d_2) is chosen to be P_{TH}^5, there exists a spatially inhomogeneous quasi-periodic solution with a drift of the maximum of the solution in the spatial direction along with the increasing of time, as shown in Fig. 9. We would like to mention that when the parameters are very close to the Turing bifurcation curve, the spatial profile of the solution is very similar to the eigenfunction of the linear problem. Although P_{TH}^4 and P_{TH}^5 are located in the same region near the bifurcation point in Fig. 5(c), but the solutions look different. Since the point P_{TH}^4 is close to the steady state bifurcation curve T_3, the spatial profile of the solution seems to look like $\cos \frac{3x}{5}$. However, the P_{TH}^5 is far away from the steady state bifurcation curve T_3, we do not predict what the spatial profile of the solution looks like.

3.2. Other temporal kernels

In this subsection, we numerically investigate the influence of different temporal kernels on the dynamics of system (3.2) for $E = 0, d_1 = 0.5, \ell = 2, \tau = 1, \sigma = 2$ and $d_2 = 15$. It follows from the discussion of Section 3.1.1 that for Case (I), the positive steady state $u_* \equiv 1$ of system (3.2) with $E = 0$ is asymptotically stable. However, for other three cases, spatially homogeneous/inhomogeneous periodic solutions may occur. Fig. 10 (a)–(c) are the solutions of system (3.2) for Cases (II)–(IV), respectively. In Fig. 10, (a) and (c) show the spatially inhomogeneous periodic solutions, while (b) illustrates the spatially homogeneous periodic solution. Note that in Fig. 10, (a) and (c) are related to the strong kernel in the spatial memory diffusion, while (b) is related to the weak kernel in the spatial memory diffusion. This indicates that the strong kernel in the spatial memory diffusion can intensify the diversity of the spatial distribution of the population. Moreover, Fig. 11(a)–(c) are the truncated curves of $u(\pi,t)$ of Fig. 10(a)–(c) in the direction of time t, respectively.

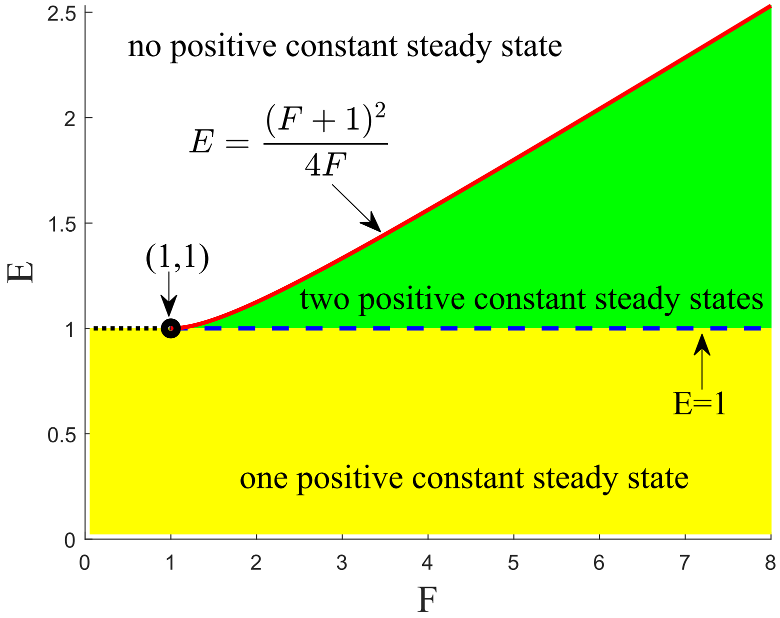

Fig. 4. The existence and nonexistence of the positive constant steady states of system (3.2) for $E > 0$.

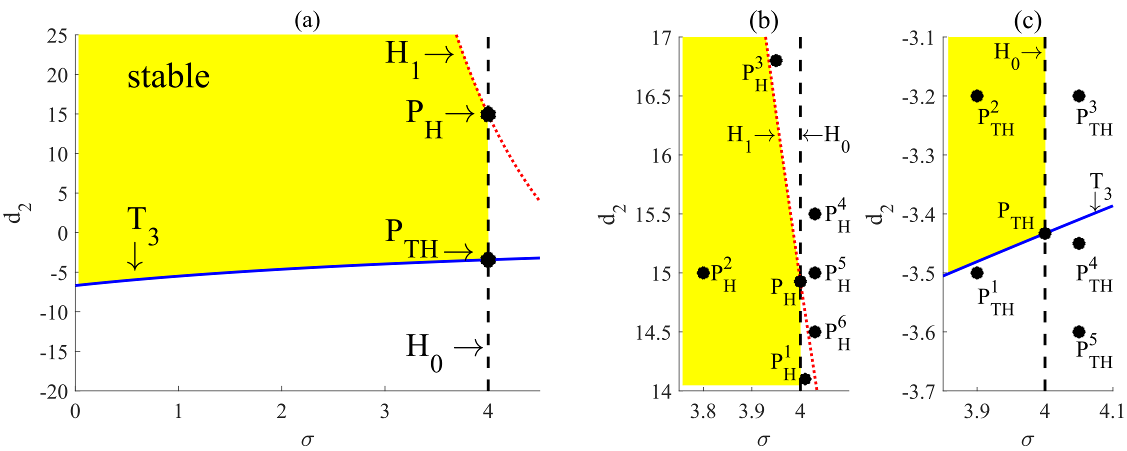

Fig. 5. (a) Stability region and bifurcation curves for the positive constant steady state $u_*^{(1)}$ of system (3.2) with $d_1 = 0.5$, $\ell = 5$, $\tau = 10$, $E = 1$ and $F = 2$ in the $\sigma - d_2$ plane. T_3 is steady state bifurcation curve, H_0 is Hopf bifurcation line and H_1 is Hopf bifurcation curve. (b) The enlargement of the region near the double Hopf bifurcation point P_H of (a). (c) The enlargement of the region near the steady state-Hopf bifurcation point P_{TH} of (a).

4. Discussion

Spatial memory naturally exists and is inevitable in any animal movement model. Delay is the most explicit way to incorporate the memory effect, and furthermore distributed delay is more realistic than discrete delay to describe the accumulated memory. The delay in reaction represents factors like gestation, food digestion or maturation period, and obviously the distributed format is also more realistic. Hence, in this paper we propose a general diffusive single-species model with spatiotemporal distributed delays in diffusion and reaction.

We explore the dynamics for different temporal kernels in spatiotemporal delays. Through stability and bifurcation analysis, we investigate the effects of the spatial memory-based diffusion coefficient and the spatiotemporal delays on the stability of the positive constant steady state of model (1.5) and possible bifurcations. We find that no matter which kernel is considered, steady state bifurcation occurs for $d_2 < 0$ and cannot occur for $d_2 \geq 0$. Thus, we can conclude that the behaviour of the animals leaving away from low density to high density (corresponding to $d_2 < 0$) is beneficial to the diversity of the spatial distribution of the population.

In particular, if the memory-based temporal kernel and the maturation-based temporal kernel are both "weak", i.e., $h_1(t,\tau) = \frac{1}{\tau}e^{-\frac{t}{\tau}}$ and $h_2(t,\sigma) = \frac{1}{\sigma}e^{-\frac{t}{\sigma}}$, then the conditions for the occurrence of steady state and Hopf bifurcations are

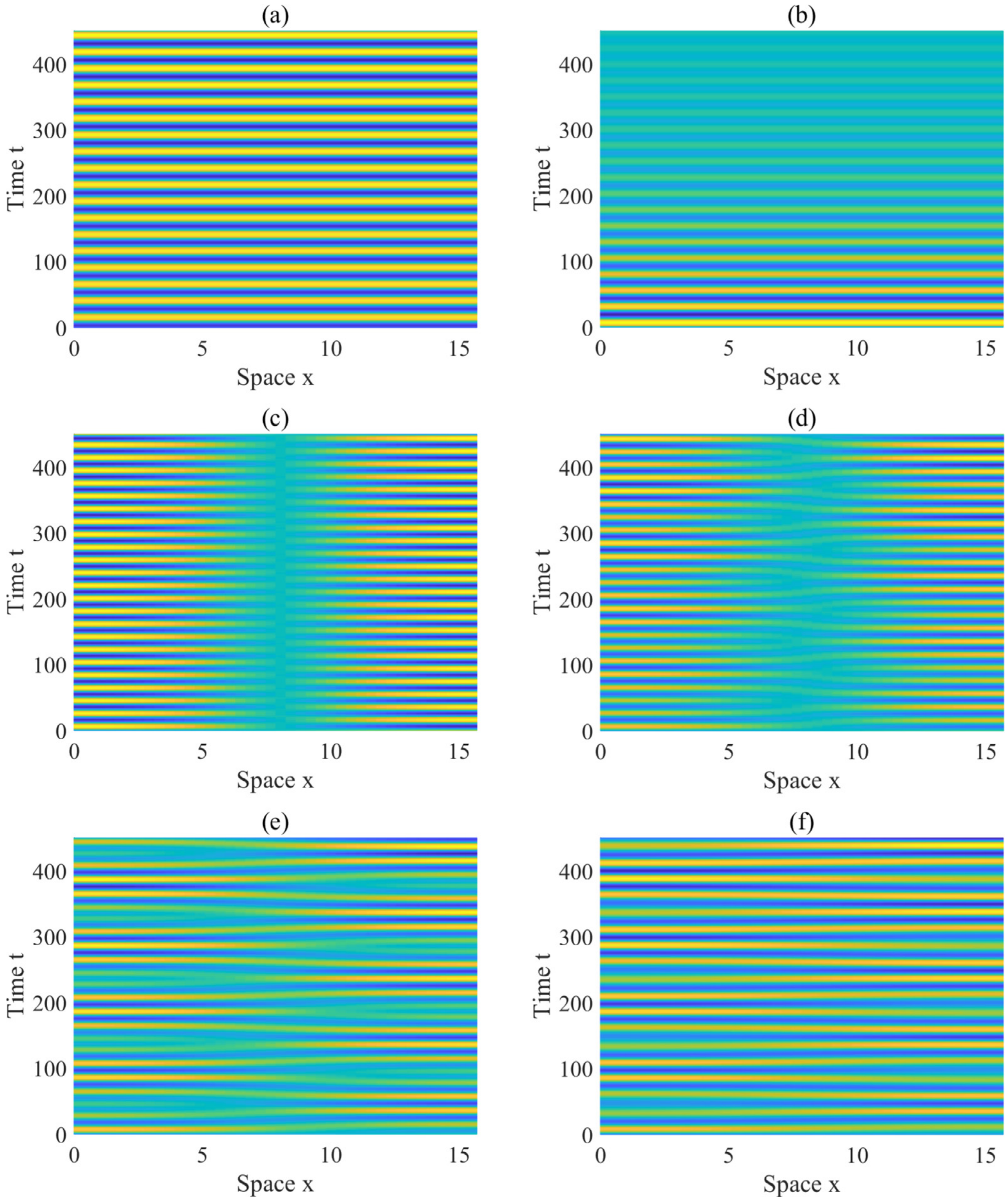

Fig. 6. (a)-(f) are the projection of the solutions of system (3.2) in the $x - t$ plane, respectively, for the points $P_H^1 - P_H^6$.

determined according to the coefficient d_2 of the spatial memory-based diffusion and the average delay τ in the spatial memory-based diffusion (see Theorems 2.2 and 2.3 and Table 1). The theoretical results show that the dynamics for $d_2 > 0$ is similar to the case of $d_2 = 0$. This implies that when the animals leave away from high density to low density (corresponding to $d_2 > 0$), the spatial memory-based diffusion has nearly no obvious effects on the evolution of the population. However, when $d_2 < 0$, the dynamics are different from the case of $d_2 = 0$, and whatever the average delay τ is small or large, the positive constant steady state always loses its stability via the occurrence of steady state or Hopf bifurcations as the spatial memory-based diffusion coefficient d_2 decreases.

As an application of the theoretical results, we investigate a modified diffusive logistic model with predation (model (3.2)). When the memory-based temporal kernel and the maturation-based temporal kernel are both “weak”, we treat σ and d_2 as bifurcation parameters and sketch the bifurcation diagram of the positive constant steady state in Figs. 1 and 5, where the codimension-2 spatial resonance, double Hopf and steady state-Hopf bifurcations are observed. We numerically investigate the dynamics near these codimension-2 points, and obtain the stable spatially inhomogeneous steady states, spatially homogeneous and inhomogeneous periodic solutions, and spatially inhomogeneous quasi-periodic solutions. For the

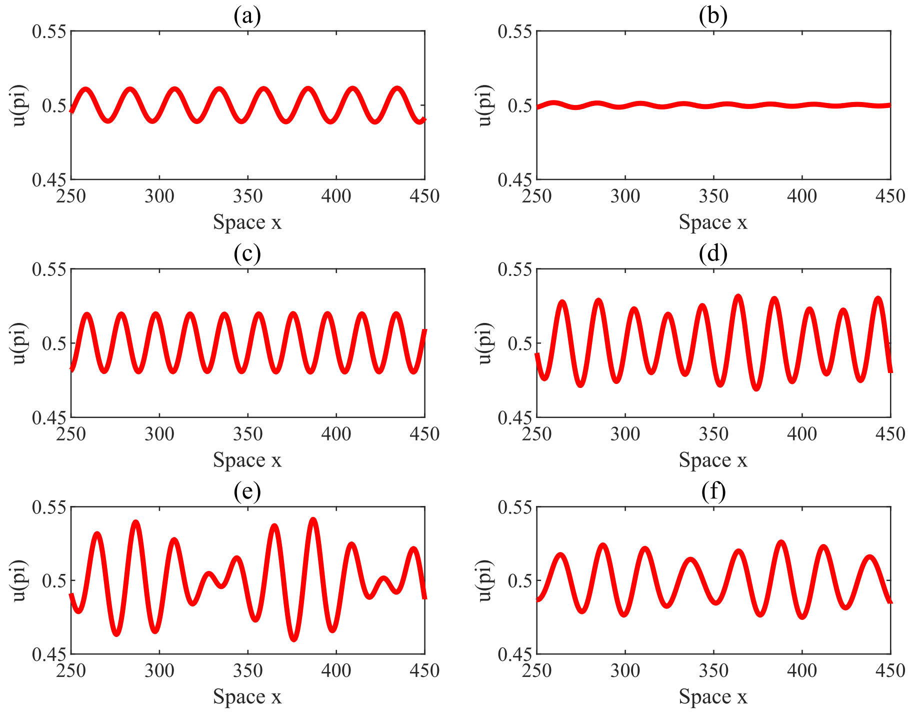

Fig. 7. (a)–(f) are the truncated curves of $u(x,t)$ of Fig. 6(a)–(f) in the direction of time t for the fixed spatial variable $x = \pi$, respectively.

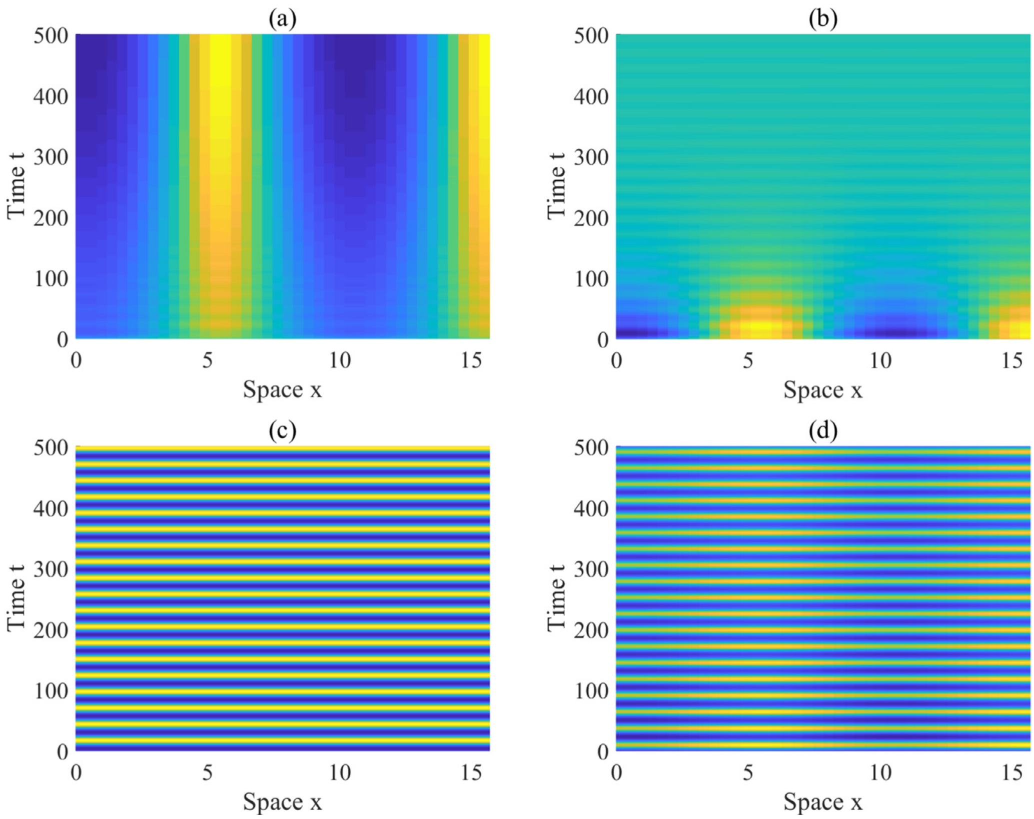

Fig. 8. (a)-(d) are the projection of the solutions of system (3.2) in the $x - t$ plane, respectively, for the points $P^1_{TH} - P^4_{TH}$.

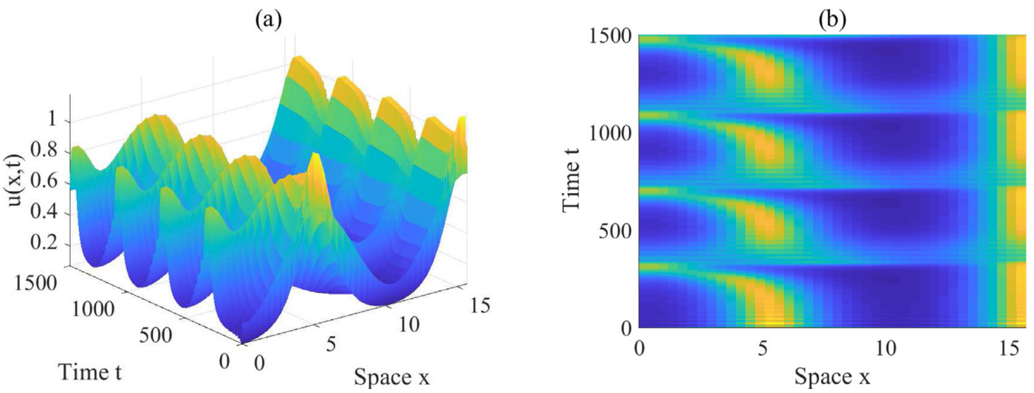

Fig. 9. (a) The spatially inhomogeneous quasi-periodic solution of system (3.2) for P_{TH}^5. (b) The projection of the solution of (a) on the $x-t$ plane.

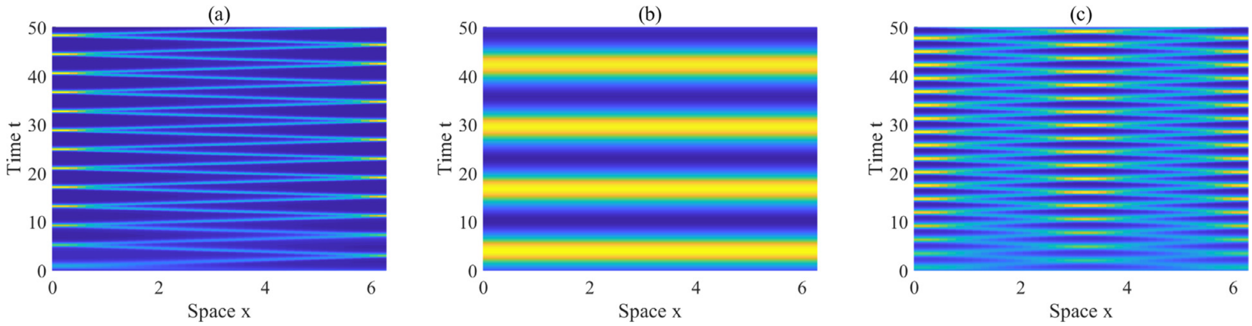

Fig. 10. (a)-(c) are the projection of the solutions of system (3.2) in the $x-t$ plane, respectively, for Cases (II)-(IV). Here, $d_1 = 0.5$, $\ell = 2$, $\tau = 1$, $E = 0$, $\sigma = 2$ and $d_2 = 15$.

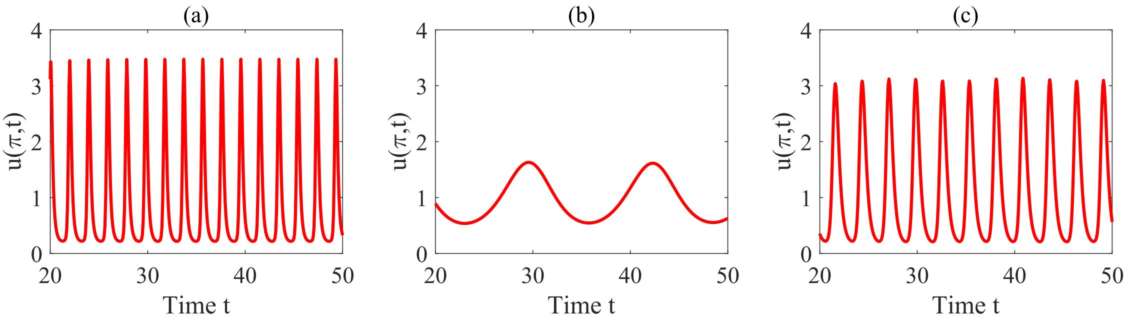

Fig. 11. (a)-(c) are the truncated curves of $u(\pi, t)$ of Fig. 10(a)–(c) in the direction of time t, respectively.

parameter far away from the steady state-Hopf bifurcation point, the numerical simulation shows the existence of a spatially inhomogeneous quasi-periodic solution with a drift of the maximum of the solution in the spatial direction. Numerical results for other temporal kernels indicate that the strong kernel in the spatial memory diffusion can intensify the diversity of the spatial distribution of the population.

The reaction-diffusion equations with discrete delay have been widely investigated in the literature. As far as bifurcations are concerned, the discrete delay leads to the occurrence of Hopf bifurcation and there is no steady state bifurcation for the reaction-diffusion equations with discrete delay regardless of whether the spatial memory-based diffusion exists or not (see, for example, [13,14,19] and references therein). A reaction-diffusion equation with spatiotemporal delay or distributed delay in reaction only without the spatial memory-based diffusion has been investigated in [20,21], where there is still no steady state bifurcation. In [11], Shi et al. investigated a single-species model with a memory-based spatiotemporal delay but without maturation-based delay. They found that if the temporal kernel is “weak”, then steady state bifurcation occurs for $d_2 < 0$ and there is no Hopf bifurcation, while if the temporal kernel is “strong”, then steady state and Hopf bifurcations occur for $d_2 > 0$ and $d_2 < 0$, respectively, and there is no interaction of these two bifurcations. In this paper, our theoretical and numerical results suggest that in the presence of maturation-based delay, the “weak” kernel even induces the complex dynamics, such as steady state, Hopf, double Hopf and steady state-Hopf bifurcations.

The theoretical analysis of the present paper focuses on the case when the memory-based temporal kernel and the maturation-based temporal kernel are both "weak". Even for this simple case, to understand the dynamical classification near the obtained codimension-two double Hopf and steady state-Hopf bifurcations, the associated norm forms should be calculated. Although the theory of the normal form for the reaction-diffusion equations and the algorithm for calculating the normal form of Turing-Hopf bifurcation have been developed in [5,15], they cannot be directly applied to differential equations with memory-based diffusion and spatiotemporal delay. In addition, when there is at least one strong temporal kernel, the associated characteristic equations are complicated and the Hopf bifurcation analysis is fairly difficult. These tasks would be challenging and intriguing to study in future.

Acknowledgements

The authors thank an anonymous reviewer and editor for helpful comments which improved the initial draft of the paper. This work was partially supported by grants from Zhejiang Provincial Natural Science Foundation of China (No. LY19A010010), National Natural Science Foundation of China (Nos. 11971143 and 12071105), and Natural Sciences and Engineering Research Council of Canada (Discovery Grant RGPIN-2020-03911 and Accelerator Grant RGPAS-2020-00090).

References

[1] W.F. Fagan, M.A. Lewis, M. Auger-Méthé, T. Avgar, S. Benhamou, G. Breed, L. LaDage, U.E. Schlägel, W.W. Tang, Y.P. Papastamatiou, J. Forester, Spatial memory and animal movement, Ecol. Lett. 16 (10) (2014) 1316–1329.
[2] P. Ashwin, M.V. Bartuccelli, T.J. Bridges, S.A. Gourley, Travelling fronts for the KPP equation with spatio-temporal delay, Z. Angew. Math. Phys. 53 (1) (2002) 103–122.
[3] N.F. Britton, Spatial structures and periodic travelling waves in an integro-differential reaction-diffusion population model, SIAM J. Appl. Math. 50 (6) (1990) 1663–1688.
[4] S. Chen, J. Yu, Stability analysis of a reaction-diffusion equation with spatiotemporal delay and Dirichlet boundary condition, J. Dyn. Differ. Equ. 28 (3–4) (2016) 857–866.
[5] T. Faria, Normal forms and Hopf bifurcation for partial differential equations with delays, Trans. Am. Math. Soc. 352 (5) (2000) 2217–2238.
[6] S.A. Gourley, M.V. Bartuccelli, Parameter domains for instability of uniform states in systems with many delays, J. Math. Biol. 35 (7) (1997) 843–867.
[7] S.A. Gourley, N.F. Britton, A predator-prey reaction-diffusion system with nonlocal effects, J. Math. Biol. 34 (3) (1996) 297–333.
[8] S.A. Gourley, J.W.H. So, Dynamics of a food-limited population model incorporating nonlocal delays on a finite domain, J. Math. Biol. 44 (1) (2002) 49–78.
[9] R. Hu, Y. Yuan, Stability and Hopf bifurcation analysis for Nicholson's blowflies equation with non-local delay, Eur. J. Appl. Math. 23 (6) (2012) 777–796.
[10] D. Liang, J.W.-H. So, F. Zhang, X. Zou, Population dynamic models with nonlocal delay on bounded domains and their numerical computations, Differ. Equ. Dyn. Syst. 11 (1–2) (2003) 117–139.
[11] Q. Shi, J. Shi, H. Wang, Spatial movement with distributed memory, J. Math. Biol. 82 (4) (2021) 33.
[12] J. Shi, R. Shivaji, Persistence in reaction diffusion models with weak Allee effect, J. Math. Biol. 52 (6) (2006) 807–829.
[13] J. Shi, C. Wang, H. Wang, Diffusive spatial movement with memory and maturation delays, Nonlinearity 32 (9) (2019) 3188–3208.
[14] J. Shi, C. Wang, H. Wang, X. Yan, Diffusive spatial movement with memory, J. Dyn. Differ. Equ. 32 (2) (2020) 979–1002.
[15] Y. Song, H. Jiang, Y. Yuan, Turing-Hopf bifurcation in the reaction-diffusion system with delay and application to a diffusive predator-prey model, J. Appl. Anal. Comput. 9 (3) (2019) 1132–1164.
[16] Y. Song, S. Wu, H. Wang, Spatiotemporal dynamics in the single population model with memory-based diffusion and nonlocal effect, J. Differ. Equ. 267 (11) (2019) 6316–6351.
[17] Y. Su, X. Zou, Transient oscillatory patterns in the diffusive non-local blowfly equation with delay under the zero-flux boundary condition, Nonlinearity 27 (1) (2014) 87–104.
[18] Z. Wang, W. Li, S. Ruan, Travelling wave fronts in reaction-diffusion systems with spatio-temporal delays, J. Differ. Equ. 222 (1) (2006) 185–232.
[19] J. Wu, Theory and applications of partial functional-differential equations, Appl. Math. Sci., 119, Springer-Verlag, New York, 1996.
[20] W. Zuo, Y. Song, Stability and bifurcation analysis of a reaction-diffusion equation with distributed delay, Nonlinear Dyn. 79 (1) (2015) 437–454.
[21] W. Zuo, Y. Song, Stability and bifurcation analysis of a reaction-diffusion equation with spatio-temporal delay, J. Math. Anal. Appl. 430 (1) (2015) 243–261.