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Spatiotemporal patterns of a structured spruce budworm diffusive model

Hongying Shu [a,b], Wanxiao Xu [b], Xiang-Sheng Wang [c,*], Jianhong Wu [d]

[a] *School of Mathematics and Statistics, Shaanxi Normal University, Xi'an 710062, PR China*
[b] *School of Mathematical Sciences, Tongji University, Shanghai 200092, PR China*
[c] *Department of Mathematics, University of Louisiana at Lafayette, Lafayette, LA 70503, USA*
[d] *Department of Mathematics and Statistics, York University, Toronto, Ontario, M3J 1P3, Canada*

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Abstract

We formulate and analyze a general reaction-diffusion equation with delay, inspired by age-structured spruce budworm population dynamics with spatial diffusion by matured individuals. The model has its particular feature for bistability due to the incorporation of a nonlinear birth function (Ricker's function) and a Holling type function of predation by birds. Here we establish some results about the global dynamics, in particular, the stability of and global Hopf bifurcation from the spatially homogeneous steady state when the maturation delay is taken as a bifurcation parameter. We also use a degree theoretical argument to identify intervals for the diffusion rate when the model system has a spatially heterogeneous steady state. Numerical experiments presented show interesting spatialtemporal patterns.

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Keywords: Spruce budworm; Reaction-diffusion equation; Age structure model; Time delay; Global Hopf bifurcation

* Corresponding author.
E-mail addresses: hshu@snnu.edu.cn (H. Shu), wanxiao@tongji.edu.cn (W. Xu), xiangsheng.wang@louisiana.edu (X.-S. Wang), wujh@mathstat.yorku.ca (J. Wu).

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1. Introduction

The spruce budworm is an insect commonly observed in North American forests [7,4,14,15, 29,34]. Even though many efforts have been made (including insecticides) to control the spruce budworm population, the outbreak of the spruce budworm occurs every 30-60 years and lasts 5-15 years, causing massive tree mortality and tremendous economic loss to forest industry [4,13, 20,21,23,24,29]. It is thus important to understand the complex dynamics of the spruce budworm population via mathematical models [5,9,11,12,27,28,32,33].

In this paper, we propose to study a spruce budworm model with age structure and spatial diffusion. Assume that the spruce budworms live in a bounded spatial habitat $\Omega \subset \mathbb{R}^n$ with a smooth boundary $\partial\Omega$. Denote by $u(x,t,a)$ the density of budworm population at location $x \in \Omega$, time $t \in \mathbb{R}$, and age $a \geq 0$. Let $\tau > 0$ be the maturation age. For the immatured budworms, we consider the standard equation with age structure [26]:

$$\partial_t u(x,t,a) + \partial_a u(x,t,a) = -\delta u(x,t,a), \quad a \in (0,\tau).$$

For the matured budworms, we incorporate spatial diffusion and predation into the age structure model:

$$\partial_t u(x,t,a) + \partial_a u(x,t,a) = d\Delta u(x,t,a) - \gamma u(x,t,a) - \frac{g(w)}{w} u(x,t,a), \; a \geq \tau.$$

Here, δ and γ are the death rates of immatured and matured budworms, $d > 0$ is the diffusion rate of matured budworms,

$$w(x,t) = \int_\tau^\infty u(x,t,a)da$$

is the total population of matured budworms, and $g(w)$ is the predation rate. Note that in our model assumptions, the immatured budworms do not diffuse and the predators (birds) only consume the matured budworms. The birth rate is assumed to be a nonlinear function of the matured budworm population $u(x,t,0) = f(w(x,t))$ which satisfies the following conditions.

(H$_1$) $f(w) \in C^1$, $f(0) = \lim_{w\to\infty} f(w) = 0$; $f(w) > 0$ for $w > 0$; there exists $\bar{c} > 0$ such that $f'(\bar{c}) = 0$ and $(w - \bar{c})f'(w) < 0$ for $w > 0$ and $w \neq \bar{c}$; $f''(w) < 0$ for $w \in [0, \bar{c}]$.

We also assume that $u(x,t,\infty) = 0$. It is easily seen from the above equations that $u(x,t,\tau) = u(x,t-\tau,0)e^{-\delta\tau} = e^{-\delta\tau} f(w(x,t-\tau))$, and hence,

$$\begin{aligned}\frac{\partial w(x,t)}{\partial t} &= \int_\tau^\infty \left(d\Delta u - \gamma u - \frac{g(w)}{w}u - \partial_a u\right)da \\ &= d\Delta w(x,t) - \gamma w(x,t) - g(w(x,t)) + e^{-\delta\tau} f(w(x,t-\tau)).\end{aligned}$$

Since the dynamics of the budworm population is much faster than the dynamics of the predators (birds), we assume the bird population is constant, which implies that the predation rate saturates when the budworm population is large. In mathematical formula, we have $g(\infty) = \beta > 0$. On the other hand, when the budworm population increases from a low population, the birds start to learn how to search for budworms, and the predation rate increases faster than a linear function. This means that $g(w)/w \to 0$ as $w \to 0^+$. A nature selection of such a predation rate is the Holling type II functional response [12]:

$$g(w) = \frac{\beta w^2}{\alpha^2 + w^2},$$

where $\beta = g(\infty) > 0$ is the saturated predation rate, and $\alpha > 0$ is the budworm population size at which the birds consume at half of the saturate rates: $g(\alpha) = \beta/2$. To reduce the number of parameters, we may assume without loss of generality that $\alpha = \beta = 1$ upon a rescaling on the state variable w and the time variable t. Hence, we have the following model

$$\frac{\partial w(x,t)}{\partial t} = d\Delta w(x,t) - \gamma w(x,t) - \frac{w^2(x,t)}{1 + w^2(x,t)} + e^{-\delta\tau} f(w(x,t-\tau)) \tag{1.1}$$

for $x \in \Omega$ and $t > 0$. For biological applications, it is nature to impose non-negative initial condition

$$w(x,\theta) = w_0(x,\theta) \geq 0, \quad x \in \Omega, \ \theta \in [-\tau, 0],$$

and no-flux boundary condition

$$\partial_\nu w(x,t) = 0, \quad x \in \partial\Omega, \ t > 0.$$

Our model generalizes those considered in [9,28,32].

The spruce budworm equation is well-known for its bi-stability behaviors. However, when time delay is present and when the survival rate during the immaturation period depends on the maturation time, the intermediate equilibrium may lose its stability, leading to the initiation of a local branch of Hopf bifurcation of spatially homogeneous periodic solutions. How this local branch continues when the maturation delay moves away from the critical bifurcation value is a very difficult yet important task to understand the global dynamics. This issue will be addressed in Section 4 below, where we use the global Hopf bifurcation theory to characterize the global continuation of such a local branch. Due to the random movement of the matured individuals, a spatially heterogeneous equilibrium may exit, and in Section 5 below, we use a degree-theoretical argument to find the union of non-overlap intervals for the diffusion rate when such a spatially heterogeneous steady state can be ensured.

The rest of this paper is organized as follows. In Section 2, we present some preliminary results and basic dynamics of our model system. In Section 3, we choose the birth function $f(w)$ to be Ricker's function and investigate the complex dynamics of the model. In Section 4, we conduct local and global bifurcation analysis of the model. In Section 5, we establish the existence theory of positive heterogeneous steady state for a general elliptic equation. In Section 6, we use numerical simulations to illustrate our theoretical results. In Section 7, we conclude our paper with a summary.

2. Preliminaries and basic dynamics

Denote by $X = C(\bar{\Omega})$ the Banach space of continuous functions with the supremum norm. Let $\mathcal{C} := C([-\tau, 0], X)$ be the Banach space of continuous map from $[-\tau, 0]$ to X with the supremum norm, and $\mathcal{C}^+$ the nonnegative cone of $\mathcal{C}$. Given a continuous function $w(x,t)$ on $\Omega \times [-\tau, \infty)$, we define $w_t \in \mathcal{C}$ as $w_t(\theta) = w(\cdot, t+\theta)$ for $\theta \in [-\tau, 0]$. As a preliminary result, we shall establish the existence, uniqueness and boundedness of the solution to (1.1).

Proposition 2.1. *For any continuous, nonnegative, and nontrivial initial condition $w_0(x,\theta) \geq 0 (\not\equiv 0)$, system (1.1) admits a unique solution $w(x,t)$. Moreover, $w(x,t) > 0$ for all $(x,t) \in \bar{\Omega} \times (0, \infty)$ and*

$$\limsup_{t\to\infty} w(x,t) \leq M < e^{-\delta\tau} f(\bar{c})/\gamma,$$

where $M > 0$ is uniquely determined by the nonlinear equation $e^{-\delta\tau} f(\bar{c}) = \gamma M + M^2/(1+M^2)$.

Proof. Denote $q(u) = \gamma u + u^2/(1+u^2)$. Clearly, $q(0) = 0, q(\infty) = +\infty$ and $q'(u) > 0$ for $u \geq 0$. Then there exists an unique positive M such that $q(u) = e^{-\delta\tau} f(\bar{c}) > 0$. Let $w_1(t)$ be the unique solution to

$$w_1'(t) = e^{-\delta\tau} f(\bar{c}) - \gamma w_1(t) - \frac{w_1^2(t)}{1+w_1^2(t)}, \quad w_1(0) = \sup_{\Omega\times[-\tau,0]} w_0(x,\theta).$$

It is readily seen that $\limsup_{t\to\infty} w_1(t) \leq M < e^{-\delta\tau} f(\bar{c})/\gamma$. Since $\overline{w}(x,t) = w_1(t)$ and $\underline{w}(x,t) = 0$ are a pair of upper-solution and lower-solution to (1.1), we obtain from [18, Theorem 3.1] that (1.1) admits a unique global solution $w(x,t)$ satisfying $0 \leq w(x,t) \leq w_1(t)$ for all $(x,t) \in \bar{\Omega} \times [0, \infty)$. Hence, $\limsup_{t\to\infty} w(x,t) \leq \limsup_{t\to\infty} w_1(t) \leq M$. The strong maximum principle implies that $w(x,t) > 0$ for all $(x,t) \in \bar{\Omega} \times (0,\infty)$. This ends the proof. □

Clearly, system (1.1) always has a trivial steady state 0. Based on the linearized model about the trivial steady state, we define the basic reproduction ratio as

$$R_0 = \frac{f'(0)e^{-\delta\tau}}{\gamma}. \tag{2.1}$$

A positive spatially homogeneous steady state is a solution to the nonlinear algebraic equation $\gamma + w/(1+w^2) = e^{-\delta\tau} f(w)/w$. Note that $\gamma + \frac{w}{1+w^2}$ is increasing in [0,1] and decreasing in $[1, \infty)$ with $\lim_{w\to\infty} \gamma + \frac{w}{1+w^2} = \gamma$. Moreover, it follows from ($\mathbf{H}_1$) that $f(w)/w$ is decreasing in $[0, \infty)$ with $\lim_{w\to 0} f(w)/w = f'(0)$. Thus, 0 is the unique nonnegative spatially homogeneous steady state if and only if $R_0 \leq 1$, and the model (1.1) admits at least one positive spatially homogeneous steady state if $R_0 > 1$.

Linearizing (1.1) at a spatially homogeneous steady state $\widehat{w}$, we obtain

$$\frac{\partial w(x,t)}{\partial t} = d\Delta w(x,t) - \left(\gamma + \frac{2\widehat{w}}{(1+\widehat{w}^2)^2}\right) w(x,t) + e^{-\delta\tau} f'(\widehat{w}) w(x, t-\tau). \tag{2.2}$$

The corresponding characteristic equation is given by

$$\lambda + d\mu_n + \gamma + \frac{2\widehat{w}}{(1+\widehat{w}^2)^2} - e^{-\delta\tau} f'(\widehat{w})e^{-\lambda\tau} = 0, \; n = 0, 1, 2\cdots, \tag{2.3}$$

where

$$0 = \mu_0 < \mu_1 \le \cdots \le \mu_n \le \mu_{n+1} \le \cdots \text{and} \lim_{n\to\infty} \mu_n = \infty \tag{2.4}$$

are the eigenvalues of $-\Delta$ in Ω with Neumann boundary condition. When $\widehat{w} = 0$, the characteristic equation becomes $\lambda + d\mu_n + \gamma - f'(0)e^{-\delta\tau}e^{-\lambda\tau} = 0$. It follows from [25, Lemma 6] that all eigenvalues have negative real parts if $R_0 < 1$, and there exists at least one positive eigenvalue if $R_0 > 1$. Thus, 0 is locally asymptotically stable if $R_0 < 1$, and unstable if $R_0 > 1$.

For the critical case when $R_0 = 1$, 0 is the only real eigenvalue for the characteristic equation with $n = 0$, and all other eigenvalues have negative real parts. We investigate the stability of 0 by using the normal forms for partial functional differential equations [3]. Let

$$\Lambda = \{\lambda \in \mathbb{C}, \lambda \text{ is an eigenvalue of (2.3) with } \mathrm{Re}\lambda = 0\}. \tag{2.5}$$

Clearly, $\Lambda = \{0\}$ if $R_0 = 1$, and (1.1) satisfies the nonresonance condition relative to Λ. We write (1.1) as an abstract equation $\dot{w}_t = A_0 w_t + F_0(w_t)$ on $\mathcal{C}$, where A_0 is a linear operator defined as $(A_0\phi)(\theta) = \phi'(\theta)$ for $\theta \in [-\tau, 0)$ and $(A_0\phi)(0) = d\Delta\phi(0) - \gamma\phi(0) + e^{-\delta\tau} f'(0)\phi(-\tau)$, and F_0 is a nonlinear operator defined as $(F_0(\phi))(\theta) = 0$ for $\theta \in [-\tau, 0)$ and

$$(F_0(\phi))(0) = e^{-\delta\tau} f(\phi(-\tau)) - e^{-\delta\tau} f'(0)\phi(-\tau) - \frac{\phi^2(0)}{1+\phi^2(0)}.$$

For $\psi \in C([0, \tau], X)$ and $\phi \in \mathcal{C}$, we introduce a bilinear form

$$\langle \psi, \phi \rangle = \int_\Omega \left[\psi(0)\phi(0) + e^{-\delta\tau} f'(0) \int_{-\tau}^{0} \psi(\theta+\tau)\phi(\theta)d\theta \right] dx.$$

We then choose $\psi = 1$ and $\phi = 1$ to be the left and right eigenfunctions of A_0 with respect to the eigenvalue 0, respectively. By using the decomposition $w_t = z\phi + y$ with $\langle \psi, y \rangle = 0$, we obtain from $A_0\phi = 0$ and $\langle \psi, A_0 y \rangle = 0$ that $\dot{z}\langle \psi, \phi \rangle = \langle \psi, F_0(z\phi + y) \rangle$. Thus, we have

$$\dot{z} \int_\Omega (1 + e^{-\delta\tau} f'(0)\tau) dx = \int_\Omega (F_0(z\phi + y))(0)dx.$$

If the initial value is a small perturbation of 0, then z is also small with positive initial value $z(0)$ and $y = O(z^2)$. By Taylor expansion, we obtain $(F_0(z\phi+y))(0) = e^{-\delta\tau} f''(0)z^2/2 - z^2 + O(z^3)$. Thus, the solution semiflow projected on the center manifold is given by

$$\dot{z} = -\frac{1 - \frac{1}{2}e^{-\delta\tau} f''(0)}{1+\gamma\tau} z^2 + O(z^3).$$

Note that $f''(0) < 0$, thus the zero solution of the above equation with positive initial value is locally asymptotically stable. This proves the local asymptotic stability of 0 if $R_0 = 1$.

We next show that 0 is globally attractive in $\mathcal{C}^+$ if $R_0 \le 1$. Define a Lyapunov functional $\mathbb{L}_1 : \mathcal{C}^+ \to \mathbb{R}$ as

$$\mathbb{L}_1(\phi) = \int_\Omega \phi(0)dx + e^{-\delta\tau} \int_\Omega \int_{-\tau}^0 f(\phi(\theta))d\theta dx \text{ for } \phi \in \mathcal{C}^+.$$

Calculating $d\mathbb{L}_1/dt$ along solutions of (1.1), we obtain from $f(w) \le f'(0)w$ for $w \ge 0$ that

$$\frac{d\mathbb{L}_1}{dt} \le (f'(0)e^{-\delta\tau} - \gamma) \int_\Omega w(x,t)dx \le 0 \text{ if } R_0 \le 1.$$

The maximal invariant subset of $d\mathbb{L}_1/dt = 0$ is the singleton $\{0\}$. By LaSalle-Lyapunov invariance principle [6], 0 is globally attractive in $\mathcal{C}^+$. We thus obtain the global asymptotic stability of 0. To summarize, we have the following results on stability of the trivial steady state.

Theorem 2.2. *If $R_0 \le 1$, then the trivial steady state 0 of the (1.1) is globally asymptotically stable in $\mathcal{C}^+$; whereas if $R_0 > 1$, then 0 is unstable, and the model (1.1) admits at least one positive spatially homogeneous steady state.*

To ensure the uniqueness of positive spatially homogeneous steady state, we make the assumption:

($\mathbf{H}_2$) $(1 + w^2)f(w)/w$ is nonincreasing on $[0, \infty)$.

Remark 2.3. If $f(w)$ is chosen as Ricker's function [22]: $f(w) = bwe^{-aw}$, or the Beverton-Holt function [2]: $f(w) = \frac{bw}{1+aw^2}$, where $a, b > 0$, then ($\mathbf{H}_2$) holds if and only if $a \ge 1$.

Denote

$$\tau_{max} := \frac{1}{\delta} \ln \frac{f'(0)}{\gamma}, \quad \widehat{\tau} := \max\{\frac{1}{\delta} \ln \frac{f(\bar{c})}{\gamma\bar{c} + \bar{c}^2/(1+\bar{c}^2)}, 0\}. \tag{2.6}$$

Obviously, $R_0 > 1$ if and only if $f'(0) > \gamma$ and $\tau \in [0, \tau_{max})$. It also follows from $f(\bar{c})/\bar{c} < f'(0)$ that $\widehat{\tau} < \tau_{max}$. Let w^* be a positive spatially homogeneous steady state of (1.1). Then we have

$$\frac{f(w^*)[1 + (w^*)^2]}{w^*} \cdot \frac{1}{\gamma[1 + (w^*)^2] + w^*} = e^{\delta\tau}.$$

In view of ($\mathbf{H}_2$), w^* is a decreasing function of τ and $w^* \to 0$ as $\tau \to \tau_{max}$. If $\widehat{\tau} = 0$, then

$$\frac{f(\bar{c})(1 + \bar{c}^2)}{\bar{c}} \cdot \frac{1}{\gamma(1 + \bar{c}^2) + \bar{c}} \le 0,$$

which implies that $w^* \le \bar{c}$ for all $\tau \ge 0$. If $\widehat{\tau} > 0$, then $w^* \to \bar{c}$ as $\tau \to \widehat{\tau}$. Thus,

$$\widehat{\tau} \le \tau < \tau_{max} \text{ is equivalent to } 0 < w^* \le \bar{c}. \tag{2.7}$$

Theorem 2.4. *Assume that $R_0 > 1$ and ($\boldsymbol{H}_2$) hold. Then (1.1) admits a unique positive spatially homogeneous steady state w^*. Moreover, all solutions of (1.1) with nontrivial and nonnegative initial conditions converge to w^* for $\tau \in [\widehat{\tau}, \tau_{max})$, where $\widehat{\tau}$ and τ_{max} are defined in (2.6).*

Proof. A positive spatially homogeneous steady state w^* exists if and only if $h(w^*) = 0$, where $h(w) = \gamma(1 + w^2) + w - e^{-\delta\tau}(1 + w^2)f(w)/w$. Since $R_0 > 1$, we obtain from ($\mathbf{H}_2$) that $h(0) = \gamma - f'(0)e^{-\delta\tau} < 0$, $\lim_{w\to\infty} h(w) = \infty$, and $h'(w) > 0$ on $(0, \infty)$. Thus, there exists a unique positive spatially homogeneous steady state w^* to (1.1). It follows from (2.2) that the characteristic equation at w^* is

$$\lambda + a_n - b_n e^{-\lambda\tau} = 0,\ n = 0, 1, 2 \cdots, \tag{2.8}$$

where

$$a_n = d\mu_n + \gamma + \frac{2w^*}{(1 + w^{*2})^2} > 0,\ b_n = e^{-\delta\tau} f'(w^*). \tag{2.9}$$

For $\tau \in [\widehat{\tau}, \tau_{max})$, (2.7) implies that $w^* \in (0, \bar{c}]$. Hence, $b_n \ge 0$. Denote

$$h_0(w) = h_1(w) - e^{-\delta\tau} f(w) \text{ and } h_1(w) = \gamma w + \frac{w^2}{1 + w^2}. \tag{2.10}$$

Clearly, $h_0(w^*) = 0$ and $h_0(\infty) = \infty$. By ($\mathbf{H}_2$), we obtain $h_0'(w^*) > 0$. Thus, we have $a_n - b_n = d\mu_n + h_0'(w^*) > 0$ for all $n \ge 0$. This, together with $b_n \ge 0$ and Lemma 6 in [25], implies that all eigenvalues of (2.8) have negative real parts. Therefore, the unique positive spatially homogeneous steady state w^* is locally asymptotically stable.

We next show that w^* is globally attractive in $\mathcal{C}^+ \setminus \{0\}$. Since $w^* \in (0, \bar{c}]$ is the unique positive zero of $h_0(w)$ and $h_0(\infty) = \infty$, we have $h_0(\bar{c}) \ge 0$ and $h_1(\bar{c}) \ge e^{-\delta\tau} f(\bar{c}) = h_1(M)$, where M is defined in Proposition 2.1. Thus, we obtain $M \le \bar{c}$. It then follows from Proposition 2.1 that $\limsup_{t\to\infty} w(x, t) \le M \le \bar{c}$. Hence, $\Gamma_0 = \{\phi \in \mathcal{C}^+ : \phi \not\equiv 0, \|\phi\| \le \bar{c}\}$ is positively invariant and attracts all solutions of (1.1) with nontrivial initial conditions. We then consider the solution map restricted on Γ_0 and show that w^* attracts all initial profiles in Γ_0. Define a Lyapunov functional $\mathbb{L}_2 : \Gamma_0 \to \mathbb{R}$ as

$$\mathbb{L}_2(\phi) = \int_\Omega \big(\phi(0) - w^* \ln \phi(0)\big)\, dx + e^{-\delta\tau} \int_\Omega \int_{-\tau}^{0} f(\phi(\theta)) - f(w^*) \ln f(\phi(\theta)) d\theta dx$$

for $\phi \in \mathcal{C}^+$. Calculating $d\mathbb{L}_2/dt$ along the positive solutions of model (1.1), we obtain

$$\begin{aligned}\frac{d\mathbb{L}_2}{dt} =& - dw^* \int_\Omega \frac{|\nabla w(x,t)|^2}{w^2(x,t)} dx \\ &+ \int_\Omega \Bigg(e^{-\delta\tau} f(w(x,t)) + h_1(w(x,t)) (\frac{w^*}{w(x,t)} - 1) \\ &- e^{-\delta\tau} f(w(x,t-\tau)) \frac{w^*}{w(x,t)} + e^{-\delta\tau} f(w^*) \ln \frac{f(w(x,t-\tau))}{f(w(x,t))} \Bigg) dx,\end{aligned}$$

where h_1 is defined in (2.10). Using $h_1(w^*) = e^{-\delta\tau} f(w^*)$ and denote $L(u) = u - 1 - \ln u$ for $u > 0$, we obtain

$$\begin{aligned}\frac{d\mathbb{L}_2}{dt} =& - dw^* \int_\Omega \frac{|\nabla w(x,t)|^2}{w^2(x,t)} dx \\ &- h_1(w^*) \int_\Omega \left(L\left(\frac{f(w^*) w(x,t)}{f(w(x,t)) w^*} \right) + L\left(\frac{w^* f(w(x,t-\tau))}{w(x,t) f(w^*)} \right) \right) dx \\ &+ \int_\Omega h_1(w(x,t)) \left(\frac{f(w(x,t))}{f(w^*)} - 1 \right) \left(\frac{h_1(w^*)}{h_1(w(x,t))} - \frac{f(w^*)}{f(w(x,t))} \right) dx \\ &+ \int_\Omega h_1(w^*) \left(\frac{f(w^*))}{f(w(x,t))} - \frac{w^*}{w(x,t)} \right) \left(\frac{w(x,t)}{w^*} - \frac{h_1(w(x,t))}{h_1(w^*)} \right) dx.\end{aligned}$$

($\mathbf{H}_2$) implies that $f'(w) \le (1 - w^2) f(w) / (w(1 + w^2))$ for $w > 0$. This, together with $f'(\bar{c}) = 0$, leads to $0 < \bar{c} \le 1$. Thus, $h_1(w)/w$ is strictly increasing on $[0, \bar{c}]$. Since $f(w)$ is strictly increasing on $[0, \bar{c}]$ and $f(w)/w$ is strictly decreasing on $[0, \infty)$, we obtain

$$\begin{aligned}\left(\frac{f(w(x,t))}{f(w^*)} - 1 \right) \left(\frac{h_1(w^*)}{h_1(w(x,t))} - \frac{f(w^*)}{f(w(x,t))} \right) \le 0, \\ \left(\frac{f(w^*))}{f(w(x,t))} - \frac{w^*}{w(x,t)} \right) \left(\frac{w(x,t)}{w^*} - \frac{h_1(w(x,t))}{h_1(w^*)} \right) \le 0,\end{aligned}$$

for all $0 < w(x,t) \le \bar{c}$, and the equalities hold only if $w(x,t) \equiv w^*$. Note that $L(u) \ge 0$ for $u > 0$ and $L(u) = 0$ if and only if $u = 1$. Hence, $d\mathbb{L}_2/dt \le 0$ for all $w_t \in \Gamma_0$, and the maximal invariant subset of $d\mathbb{L}_2/dt = 0$ is the singleton $\{w^*\}$. By LaSalle-Lyapunov invariance principle [6], we conclude that w^* is globally asymptotically stable in $\mathcal{C}^+ \setminus \{0\}$ for $\tau \in [\widehat{\tau}, \tau_{max})$. □

3. Spatially homogeneous equilibria and bistability

Throughout this section, we choose the birth function as Ricker's function:

$$f(w) = bwe^{-aw},$$

where $b > 0$ is the maximum possible per capita egg production rate, and $1/a > 0$ is the population size at which the birth rate achieves its maximum. If w is a positive spatially homogeneous steady state of (1.1), then $u = aw$ is a positive root of the nonlinear function

$$p(u) = \frac{1}{R_0} + \frac{ru}{a^2 + u^2} - e^{-u}, \text{ where } r = \frac{ae^{\delta\tau}}{b} \text{ and } R_0 = \frac{be^{-\delta\tau}}{\gamma}. \tag{3.1}$$

If $R_0 \le 1$, then $p(u) \ge 1 - e^{-u} > 0$ for all $u > 0$. If $R_0 > 1$, then $p(0) = 1/R_0 - 1 < 0$ and $p(u) \to 1/R_0 > 0$ as $u \to \infty$. Hence, the model (1.1) possesses at least one positive equilibrium if and only if $R_0 > 1$. Assume $R_0 > 1$ and $u > 0$ is a positive solution to the equation $p(u) = 0$. We have

$$p'(u) = \frac{rp_1(u)}{(a^2 + u^2)^2} + \frac{1}{R_0}, \text{ where } p_1(u) = u^3 - u^2 + a^2u + a^2. \tag{3.2}$$

Note that $p_1'(u) = 3u^2 - 2u + a^2$. If $a^2 \ge 1/3$, then $p_1'(u) \ge 0$ and hence $p_1(u) \ge p_1(0) = a^2 > 0$ for all $u \ge 0$. This implies that $p'(u) > 0$ for $u > 0$. The model (1.1) possesses exactly one positive equilibrium if $R_0 > 1$ and $a^2 \ge 1/3$.

Now, we assume that $R_0 > 1$ and $a^2 < 1/3$. $p_1'(u) = 0$ has two positive roots $a_\pm = (1 \pm \sqrt{1 - 3a^2})/3$. Since $p_1(0) = a^2 > 0$ and the leading coefficient of the cubic function $p_1(u)$ is positive, we find that $p_1(u) \ge 0$ for all $u \ge 0$ if and only if

$$0 \le p_1(a_+) = a_+^3 - a_+^2 - (a_+ + 1)(3a_+^2 - 2a_+) = -2a_+(a_+^2 + a_+ - 1),$$

if and only if $a_+ \le (\sqrt{5} - 1)/2$, if and only if $a^2 \ge (5\sqrt{5} - 11)/2 \approx 0.09$. Thus, the model (1.1) possesses exactly one positive equilibrium if $R_0 > 1$ and $a^2 \ge (5\sqrt{5} - 11)/2$.

In the next step, we assume that $R_0 > 1$ and $a^2 < (5\sqrt{5} - 11)/2$. The cubic function $p_1(u)$ has exactly two positive roots, denoted by $a_1 < a_2$. Since $p_1(a) = 2a^3 > 0$, $p_1(1) = 2a^2 > 0$, $p_1(a_+) < 0$, and $a < a_+ < 1$, we have $a < a_1 < a_+ < a_2 < 1$. Note that $p_1(u) > 0$ for $u \in (0, a_1) \cup (a_2, \infty)$. We obtain from (3.2) that $p(u)$ is strictly increasing for u in each of the intervals $(0, a_1)$ and (a_2, ∞). Recall that $p(0) < 0$ and $p(\infty) > 0$. To count the number of positive equilibria, we shall investigate the zeros of $p(u)$ in $[a_1, a_2]$. If $p(u) = 0$ for some $u \in [a_1, a_2]$, we can eliminate r in (3.2) and rewrite

$$p'(u) = \frac{u^2 - a^2}{u(a^2 + u^2)} \left[\frac{1}{R_0} + \frac{e^{-u}p_1(u)}{u^2 - a^2} \right]. \tag{3.3}$$

Recall the definition of $p_1(u)$ in (3.2). A simple calculation gives

$$\left[\frac{e^{-u}p_1(u)}{u^2 - a^2} \right]' = \frac{-ue^{-u}p_2(u)}{(u^2 - a^2)^2}, \text{ where } p_2(u) = u^4 - 2u^3 + 6a^2u - a^4. \tag{3.4}$$

For $u \in [a_1, a_2]$, we have $p_1(u) = u^3 - u^2 + a^2u + a^2 < 0$ and hence $p_2'(u) = 4u^3 - 6u^2 + 6a^2 < -2(u^2 - a^2) - 4a^2u < 0$. This implies that $p_2(u)$ is strictly decreasing in $[a_1, a_2]$. On the other hand, since $p_1(u) < 0$ for all $u \in (a_1, a_2)$ and $p_1(a_1) = p_1(a_2) = 0$, we have $p_2(a_1) > 0 > p_2(a_2)$. Hence, the equation $p_2(u) = 0$ has a unique solution, denoted by a_3, in $[a_1, a_2]$. The minimum of the function $e^{-u}p_1(u)/(u^2 - a^2)$ in the interval $[a_1, a_2]$ is achieved at a_3. If

$R_0 \le (a^2 - a_3^2)e^{a_3}/p_1(a_3)$, then $p'(u) \ge 0$ for any $u \in [a_1, a_2]$ such that $p(u) = 0$. Consequently, the model (1.1) possesses exactly one positive equilibrium if $R_0 > 1$, $a^2 < (5\sqrt{5} - 11)/2$, and $R_0 \le (a^2 - a_3^2)e^{a_3}/p_1(a_3)$.

Finally, we assume that $R_0 > 1$, $a^2 < (5\sqrt{5} - 11)/2$, and $R_0 > (a^2 - a_3^2)e^{a_3}/p_1(a_3)$. Recall from the previous step that $p_2(u) > 0$ for $u \in (a_1, a_3)$ and $p_2(u) < 0$ for $u \in (a_3, a_2)$. The function $e^{-u}p_1(u)/(u^2 - a^2) + 1/R_0$ is decreasing in (a_1, a_3) and increasing in (a_3, a_2). Moreover, the minimum of this function at a_3 is negative. Hence, it has exactly two roots, denoted by c_1 and c_2 respectively in the two intervals (a_1, a_3) and (a_3, a_2). In other words, the function $p'(u)$ has exactly two roots c_1 and c_2 in the interval $[a_1, a_2]$. Moreover, $p'(u) < 0$ for $u \in (c_1, c_2)$ and $p'(u) > 0$ for $u \in [0, c_1) \cup (c_2, \infty)$. Depending on the signs of $p(c_1)$ and $p(c_2)$, we have the following results. If $p(c_1) > 0 > p(c_2)$; namely,

$$\frac{(e^{-c_1} - 1/R_0)(a^2 + c_1^2)}{c_1} < r < \frac{(e^{-c_2} - 1/R_0)(a^2 + c_2^2)}{c_2}, \tag{3.5}$$

then the model (1.1) possesses exactly three positive equilibria in the intervals $(0, c_1)$, (c_1, c_2), and (c_2, ∞), respectively. If $p(c_1) = 0$; namely,

$$r = \frac{(e^{-c_1} - 1/R_0)(a^2 + c_1^2)}{c_1}, \tag{3.6}$$

then the model (1.1) possesses exactly two positive equilibria: one is c_1, and the other lies in (c_2, ∞). If $p(c_2) = 0$; namely,

$$r = \frac{(e^{-c_2} - 1/R_0)(a^2 + c_2^2)}{c_2}, \tag{3.7}$$

then the model (1.1) possesses exactly two positive equilibria: one is c_2, and the other lies in $(0, c_1)$. If $p(c_1) < 0$; namely,

$$r < \frac{(e^{-c_1} - 1/R_0)(a^2 + c_1^2)}{c_1}, \tag{3.8}$$

then the model (1.1) possesses exactly one positive equilibrium which lies in (c_2, ∞). If $p(c_2) > 0$; namely,

$$r > \frac{(e^{-c_2} - 1/R_0)(a^2 + c_2^2)}{c_2}, \tag{3.9}$$

then the model (1.1) possesses exactly one positive equilibrium which lies in $(0, c_1)$. We summarize our results in the following theorem.

Theorem 3.1. *Consider the model* (1.1) *with* $f(w) = bwe^{-aw}$. R_0 *is defined in* (2.1).

(i) *If* $R_0 \le 1$, *then the model* (1.1) *has no positive spatially homogeneous steady state, and the trivial steady state* 0 *of* (1.1) *is globally asymptotically stable in* $\mathcal{C}^+$.

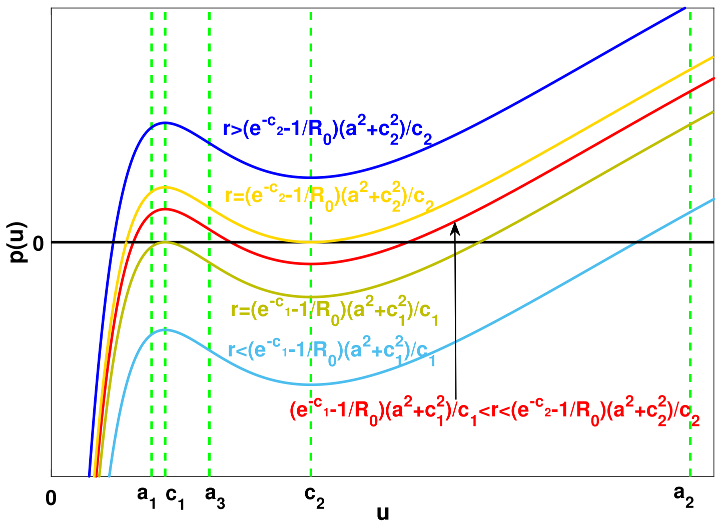


Fig. 1. The graph of $p(u)$.

(ii) *If* $R_0 > 1$ *and* $a^2 \geq (5\sqrt{5} - 11)/2$*, then the model* (1.1) *has exactly one positive spatially homogeneous steady state.*

(iii) *If* $R_0 > 1$ *and* $a^2 < (5\sqrt{5} - 11)/2$*, then the cubic function* $p_1(u) = u^3 - u^2 + a^2 u + a^2$ *has exactly two positive roots, denoted by* $a_1 < a_2 < 1$*. Moreover, the quartic function* $p_2(u) = u^4 - 2u^3 + 6a^2 u - a^4$ *has a unique solution, denoted by* a_3*, in* $[a_1, a_2]$*.*

(iii.a) *If* $R_0 \leq (a^2 - a_3^2)e^{a_3}/p_1(a_3)$*, then the model* (1.1) *has exactly one positive spatially homogeneous steady state.*

(iii.b) *If* $R_0 > (a^2 - a_3^2)e^{a_3}/p_1(a_3)$*, then the function* $e^{-u}p_1(u)/(u^2 - a^2) + 1/R_0$ *has exactly two roots, denoted by* c_1 *and* c_2 *respectively in the two intervals* (a_1, a_3) *and* (a_3, a_2)*. The model* (1.1) *has exactly one positive spatially homogeneous steady state if either* (3.8) *or* (3.9) *is satisfied, exactly two spatially homogeneous steady states if either* (3.6) *or* (3.7) *is satisfied, and exactly three spatially homogeneous steady states if* (3.5) *is satisfied.*

For cases (ii) and (iii.a) in Theorem 3.1, $p(u)$ defined in (3.1) is strictly increasing on $[0, \infty)$. We use Fig. 1 to illustrate the graph of $p(u)$ for the case (iii.b) in Theorem 3.1.

Now, we are ready to discuss the stability of the positive spatially homogeneous steady state. For convenience, we make the following assumptions.

($\mathbf{A}_1$) One of the following conditions holds: (i) $a^2 \geq (5\sqrt{5} - 11)/2$; (ii) $a^2 < (5\sqrt{5} - 11)/2$ and $R_0 \leq (a^2 - a_3^2)e^{a_3}/p_1(a_3)$; (iii) $a^2 < (5\sqrt{5} - 11)/2$, $R_0 > (a^2 - a_3^2)e^{a_3}/p_1(a_3)$ and either (3.8) or (3.9) is satisfied.

($\mathbf{A}_2$) $R_0 > (a^2 - a_3^2)e^{a_3}/p_1(a_3)$ and $a^2 < (5\sqrt{5} - 11)/2$.

For Ricker's function, we obtain from (2.6) that $\bar{c} = 1/a$ and $f'(0) = \gamma$. Hence, we have

$$\tau_{max} = \frac{1}{\delta} \ln \frac{b}{\gamma} \quad \text{and} \quad \widehat{\tau} = \max\{\frac{1}{\delta} \ln \frac{b}{e(\gamma + \frac{a}{a^2+1})}, 0\}. \tag{3.10}$$

To obtain the global stability of w^*, we shall assume that $\bar{c} \le 1$, that is, $a \ge 1$. By using the same arguments as in the proof of Theorem 2.4, we obtain the following results.

Theorem 3.2. *Consider the model* (1.1) *with* $f(w) = bwe^{-aw}$. *Assume that* $R_0 > 1$, $\tau \in [\widehat{\tau}, \tau_{max})$, *and* $(\boldsymbol{A}_1)$ *holds. The unique positive spatially homogeneous steady state* w^* *of* (1.1) *is locally asymptotically stable. If further* $a \ge 1$, *then all solutions of* (1.1) *with nontrivial initial conditions converge to* w^*.

Next, we investigate the stability of positive spatially homogeneous steady states when the model (1.1) has two or three positive spatially homogeneous steady states.

Theorem 3.3. *Consider the model* (1.1) *with* $f(w) = bwe^{-aw}$. *Assume that* $R_0 > 1$ *and* $(\boldsymbol{A}_2)$ *holds. Let* $c_1 < c_2 < 1$ *and* $\widehat{\tau}$ *be defined in Theorem* 3.1 *and* (3.10), *respectively.*

- (i) *If* (3.5) *holds, then the model* (1.1) *has exactly three positive spatially homogeneous steady states* $w_1 < w_2 < w_3$, *where* $w_1 \in (0, c_1/a)$ *is locally asymptotically stable,* $w_2 \in (c_1/a, c_2/a)$ *is unstable, and* $w_3 \in (c_2/a, \infty)$ *is locally asymptotically stable provided* $\tau \in [\widehat{\tau}, \tau_{max})$.
- (ii) *If* (3.6) *holds, then the model* (1.1) *has two positive spatially homogeneous steady states* $w_1^* = c_1/a$ *and* $w_3 \in (c_2/a, \infty)$, *where* w_1^* *is unstable, and* w_3 *is locally asymptotically stable provided* $\tau \in [\widehat{\tau}, \tau_{max})$.
- (iii) *If* (3.7) *holds, then the model* (1.1) *has two positive spatially homogeneous steady states* $w_1 \in (0, c_1/a)$ *and* $w_2^* = c_2/a$, *where* w_1 *is locally asymptotically stable, and* w_2^* *is unstable.*

Proof. (i) Theorem 3.1 gives the existence of three positive spatially homogeneous steady states $w_1 \in (0, c_1/a)$, $w_2 \in (c_1/a, c_2/a)$ and $w_3 \in (c_2/a, \infty)$. The characteristic equation at w_i is

$$\lambda + a_n(w_i) - b_n(w_i)e^{-\lambda\tau} = 0 \quad \text{for integer } n \ge 0 \text{ and } i = 1, 2, 3, \tag{3.11}$$

where $a_n(w_i) = d\mu_n + \gamma + 2w_i/(1 + w_i^2)^2 > 0$ and $b_n(w_i) = e^{-\delta\tau} f'(w_i)$. Note that $w_1 < w_2 < 1/a$. Then $b_n(w_1) > 0$ and $b_n(w_2) > 0$. A simple calculation gives

$$a_n(w_i) - b_n(w_i) = d\mu_n + be^{-\delta\tau} aw_i p'(aw_i) \text{ for integer } n \ge 0 \text{ and } i = 1, 2, 3.$$

Since $p'(aw_1) > 0$, we have $a_n(w_1) - b_n(w_1) > 0$. Note that $a_n(w_1) > 0$ and $b_n(w_1) > 0$. It then follows from [25, Lemma 6] that all eigenvalues of (3.11) with $i = 1$ have negative real parts. Hence, w_1 is locally asymptotically stable. Clearly, $p'(aw_2) < 0$ and $a_0(w_2) - b_0(w_2) < 0$. Since $a_0(w_1) > 0$ and $b_0(w_2) > 0$, we obtain from [25, Lemma 6] that the characteristic equation with $i = 2$ and $n = 0$ admits at least one positive eigenvalue. Thus, w_2 is unstable. Note from $p'(aw_3) > 0$ that $a_n(w_3) - b_n(w_3) > 0$. It is also readily seen that $a_n(w_3) > 0$. Furthermore, $b_n(w_3) \ge 0$ if and only if $w_3 \le 1/a$. By using a similar argument as in the proof of Theorem 2.4, we can show that w_3 is locally asymptotically stable if $\tau \in [\widehat{\tau}, \tau_{max})$.

(ii) If (3.6) holds, we obtain from Theorem 3.1 and the argument in the previous case that (1.1) has two positive spatially homogeneous steady states $w_1^* = c_1/a < 1/a$ and $w_3 \in (c_2/a, \infty)$, where w_3 is locally asymptotically stable provided $\tau \in [\widehat{\tau}, \tau_{max})$. To analyze the stability of w_1^*, we shall investigate the characteristic equation in (3.11) with $i = 1$. It is easy to show that

$a_n(w_1^*) > 0$ and $b_n(w_1^*) = e^{-\delta\tau} f'(w_1^*) > 0$ for all integer $n \geq 0$. Moreover, $a_0(w_1^*) - b_0(w_1^*) = 0$ and $a_n(w_1^*) - b_n(w_1^*) = d\mu_n > 0$ for integer $n \geq 1$. Thus, 0 is the only real eigenvalue for $n = 0$ and all other eigenvalues have negative real parts. By (2.5), we have $\Lambda = \{0\}$ and (1.1) satisfies the nonresonance condition relative to Λ. We will investigate the local stability of w_1^* by normal form. Let $v = w - w_1^*$ and rewrite (1.1) as an abstract equation $\dot{v_t} = A_1 v_t + F_1(v_t)$ on $\mathcal{C}$, where A_1 is defined as $(A_1\phi)(\theta) = \phi'(\theta)$ for $\theta \in [-\tau, 0)$ and

$$(A_1\phi)(0) = d\Delta\phi(0) - (\gamma + \frac{2w_1^*}{(1+w_1^{*2})^2})\phi(0) + e^{-\delta\tau} f'(w_1^*)\phi(-\tau).$$

The nonlinear operator F_1 is defined by $(F_1(\phi))(\theta) = 0$ for $\theta \in [-\tau, 0)$ and

$$\begin{aligned}(F_1(\phi))(0) =& e^{-\delta\tau} f(w_1^* + \phi(-\tau)) - e^{-\delta\tau} f'(w_1^*)\phi(-\tau) - \gamma w_1^* \\ & - \frac{(w_1^* + \phi(0))^2}{1 + (w_1^* + \phi(0))^2} + \frac{2w_1^*}{(1+w_1^{*2})^2}\phi(0).\end{aligned}$$

For $\psi \in C([0, \tau], X)$ and $\phi \in \mathcal{C}$, we define a bilinear form

$$\langle \psi, \phi \rangle = \int_\Omega \left[\psi(0)\phi(0) + e^{-\delta\tau} f'(w_1^*) \int_{-\tau}^{0} \psi(\theta + \tau)\phi(\theta) d\theta \right] dx.$$

We choose $\psi = 1$ and $\varphi = 1$ to be the left and right eigenfunctions of A_1 with respect to the eigenvalue 0, respectively. We decompose v_t as $v_t = z\varphi + y$ with $\langle \psi, y \rangle = 0$. By using $A_1\varphi = 0$ and $\langle \psi, A_1 y \rangle = 0$, we obtain $\dot{z}\langle \psi, \varphi \rangle = \langle \psi, F_1(z\varphi + y) \rangle$, that is,

$$\dot{z} \int_\Omega (1 + \tau e^{-\delta\tau} f'(w_1^*)) dx = \int_\Omega (F_1(z\varphi + y))(0) dx.$$

The initial value is a small perturbation of w_1, then z is small and $y = O(z^2)$. By using Taylor expansion, we have

$$\begin{aligned}(F_1(z\phi + y))(0) =& \left(\frac{e^{-\delta\tau}}{2} f''(w_1^*) - \frac{1 - 3w_1^{*2}}{(1+w_1^{*2})^3} \right) z^2 + O(z^3) \\ =& \frac{a^2 c_1 p_2(c_1)}{2(a^2 + c_1^2)^3} z^2 + O(z^3),\end{aligned}$$

where $p_2(c_1) > 0$ is defined in Theorem 3.1. Thus, the flow on the center manifold is

$$\dot{z} = \frac{a^2 c_1 p_2(c_1)}{2(a^2 + c_1^2)^3 (1 + \tau e^{-\delta\tau} f'(w_1^*))} z^2 + O(z^3),$$

where $f'(w_1^*) > 0$. Hence, the spatially homogeneous steady state $w_1^* = c_1/a$ of (1.1) is unstable.

(iii) If (3.7) holds, we obtain from Theorem 3.1 that (1.1) has two positive spatially homogeneous steady states $w_1 \in (0, c_1/a)$ and $w_3^* = c_2/a$. From the proof of (i), we obtain the local asymptotical stability of w_1. We use a similar argument as in (ii) to calculate the normal form of (1.1) at $w_2^* = c_2/a$. The resulting equation is given by

$$\dot{z} = \frac{a^2 c_2 p_2(c_2)}{2(a^2 + c_2^2)^3 (1 + \tau e^{-\delta\tau} f'(w_2^*))} z^2 + O(z^3),$$

where $p_2(c_2) < 0$ and $f'(w_2^*) > 0$. Therefore, the spatially homogeneous steady state w_2^* of (1.1) is unstable. This completes this proof. □

4. Hopf bifurcation analysis

In this section, we use the delay $\tau > 0$ as the bifurcation parameter to analyze periodic solutions of (1.1) bifurcating from the positive spatially homogeneous steady state. For the model (1.1) with a general birth function satisfying $(\mathbf{H}_2)$, Hopf bifurcation may occur at the unique positive spatially homogeneous steady state w^* only if $\tau \in [0, \widehat{\tau})$. Throughout this section, we assume that $\tau \in [0, \widehat{\tau})$, which in view of (2.7) is the same as $w^* > \bar{c}$. Hence, by $(\mathbf{H}_1)$ and (2.9), we have $b_n < 0 < a_n$ for all integers $n \geq 0$.

4.1. Existence of Hopf bifurcations

Recall that w^* is locally asymptotically stable when $\tau = 0$ and 0 cannot be an eigenvalue of (2.8) for any $\tau \geq 0$. Thus, the stability of w^* changes only when at least a pair of eigenvalues of (2.8) cross the imaginary axis to the right. This suggests us to find a pair of purely imaginary eigenvalues for some $\tau > 0$. Substituting $\lambda = i\nu$ with $\nu > 0$ into (2.8) yields

$$\sin \nu\tau = -\frac{\nu}{b_n}, \ \cos \nu\tau = \frac{a_n}{b_n}, \quad P_n(\nu, \tau) := \nu^2 - b_n^2 + a_n^2 = 0, \ n \geq 0. \tag{4.1}$$

Note that $b_n - a_n < 0$ for all $n \geq 0$, and $b_n + a_n$ is increasing in n. Hence, $P_n(\nu, \tau)$ has no positive zeros for all $n \geq 0$ if and only if $b_0 + a_0 \geq 0$. On the other hand, $P_n(\nu, \tau)$ has a unique positive zero

$$\nu_n(\tau) = \sqrt{b_n^2 - a_n^2} \tag{4.2}$$

for some $n \geq 0$ if and only if $b_0 + a_0 = \gamma + \frac{2w^*}{(1+w^{*2})^2} + e^{-\delta\tau} f'(w^*) < 0$; namely,

$$\gamma + \frac{2w^*}{(1 + w^{*2})^2} + f'(w^*) < 0 \ \text{ and } \ \tau < \widetilde{\tau} := \frac{1}{\delta} \ln\left(\frac{-f'(w^*)}{\gamma + 2w^*/(1 + w^{*2})^2}\right). \tag{4.3}$$

Set

$$I_n = \{\tau \in [0, \widehat{\tau}) \ \text{ such that } \ b_n + a_n < 0\}. \tag{4.4}$$

We have the following lemma.

Lemma 4.1. *$I_0 = \emptyset$ if and only if either $\gamma + \frac{2w^*}{(1+w^{*2})^2} + f'(w^*) \geq 0$ or $\widetilde{\tau} \geq \widehat{\tau}$, where $\widehat{\tau}$ and $\widetilde{\tau}$ are defined in* (3.10) *and* (4.3)*, respectively.*

Clearly, $I_0 = \emptyset$ implies that $I_n = \emptyset$ for all integer $n \geq 0$. In the following, we assume that $I_0 \neq \emptyset$, that is, $\gamma + 2w^*/(1+w^{*2})^2 + f'(w^*) < 0$ and $\widetilde{\tau} < \widehat{\tau}$. Then there exists an integer $N_1 \geq 0$ such that $I_0 \supset I_1 \supset \cdots \supset I_{N_1} \neq \emptyset$ and $I_n = \emptyset$ for $n \geq N_1 + 1$. For $\tau \in I_n$, let $\theta_n(\tau)$ be the unique solution of $\sin\theta_n(\tau) = -\nu_n(\tau)/b_n > 0$ and $\cos\theta_n(\tau) = a_n/b_n < 0$ in $(0, 2\pi]$, that is,

$$\theta_n(\tau) = \arccos(a_n/b_n) \in (\pi/2, \pi).$$

For $n \in [0, N_1]$ and $k \geq 0$, we define

$$S_n^k(\tau) = \tau\nu_n(\tau) - (\theta_n(\tau) + 2k\pi) \text{ for } \tau \in I_n. \tag{4.5}$$

Clearly, $\nu_n(\tau)$ in (4.2) is strictly decreasing in n and $\theta_n(\tau)$ is strictly increasing in n. Thus, $S_n^k > S_n^{k+1}$ for $\tau \in I_n$, and $S_n^k > S_{n+1}^k$ for $\tau \in I_{n+1}$. It can be verified that for each integer $0 \leq n \leq N_1$, $\pm i\nu_n(\tau_n^*)$ are a pair of purely imaginary eigenvalues of (2.8) if and only if τ_n^* is the zero of $S_n^k(\tau)$ for some integer $k \geq 0$. The local stability of w^* of model (1.1) when $\tau = 0$ implies $S_0^0(0) < 0$. For all integer $n \in [0, N_1]$, denote

$$\widehat{\tau}_n = \sup I_n = \sup\{\tau \in [0, \widehat{\tau}) \;\text{ such that }\; b_n + a_n < 0\}.$$

Clearly, $\widehat{\tau}_n$ is decreasing in n and $a_n(\widehat{\tau}_n) + b_n(\widehat{\tau}_n) = 0$. Hence, as $\tau \to \widehat{\tau}_n^-$, we have $\nu_n(\tau) \to 0$, $\sin\theta_n(\tau) \to 0$, $\cos\theta_n(\tau) \to -1$, $\theta_n(\tau) \to \pi$, and $S_n^k(\tau) \to -(2k+1)\pi$. By [1, Theorem 2.2], we obtain

$$\text{Sign}\frac{dRe\lambda(\tau_n^*)}{d\tau} = \text{Sign}\Big(\frac{\partial P_n}{\partial \nu}(\nu_n(\tau_n^*), \tau_n^*)\Big)\text{Sign}\frac{dS_n^k(\tau_n^*)}{d\tau} = \text{Sign}\frac{dS_n^k(\tau_n^*)}{d\tau}. \tag{4.6}$$

Moreover, the pair of purely imaginary roots $\pm i\nu_n(\tau_n^*)$ cross the imaginary axis from left to right at $\tau = \tau_n^*$ if $(S_n^k)'(\tau_n^*) > 0$ and from right to left if $(S_n^k)'(\tau_n^*) < 0$.

Note that $f'(0)e^{-\delta\tau} > \gamma$ if and only if $f'(0) > \gamma$ and $0 \leq \tau < \tau_{max} := \ln(f'(0)/\gamma)/\delta$. If $\sup_{\tau \in I_0} S_0^0(\tau) < 0$, then $S_n^k(\tau)$ has no zeros in I_n for any $n \in [0, N_1]$ and $k \geq 0$. Hence, w^* is locally asymptotically stable for all $\tau \in [0, \tau_{max})$. If $\sup_{\tau \in I_0} S_0^0(\tau) = 0$, then $S_0^0(\tau)$ has a zero τ^* of even multiplicity in I_0. By (4.6), there is no eigenvalue crossing the imaginary axis to the right. Thus, w^* is locally asymptotically stable for $\tau \in [0, \tau_{max})$. To ensure the existence of Hopf bifurcation at w^*, we assume that

($\mathbf{H}_3$) $\sup_{\tau \in I_0} S_0^0(\tau) > 0$ and $S_n^k(\tau)$ has at most two zeros (counting multiplicity) for each $n \in [0, N_1]$ and $k \geq 0$.

Condition ($\mathbf{H}_3$) implies that there exists an integer $N_0 \in [0, N_1]$ such that, for any integer $n \in [0, N_0]$, there exists an integer $K_n \geq 1$ such that $S_n^i(\tau)$ has two simple zeros $(\tau_n^i, \tau_n^{2K_n-i-1})$ if $0 \leq i \leq K_n - 1$ and no zeros if $i \geq K_n$. Since $S_n^k(0) < 0$ and $S_n^k(\widehat{\tau}_n) < 0$, then for each $n \in [0, N_0]$, there are $2K_n$ simple zeros τ_n^j of $S_n^k(\tau)$ for all $k \geq 0$ and $0 < \tau_n^0 < \tau_n^1 < \tau_n^2 < \cdots < \tau_n^{2K_n-1} < \widehat{\tau}_n$. From (4.6), we have $dS_n^i(\tau_n^i)/d\tau > 0$ and $dS_n^{2K_n-i-1}(\tau_n^i)/d\tau < 0$ for each $0 \leq i \leq K_n - 1$.

Next, we consider the collection of all τ_n^i with integers $(n, i) \in [0, N_0] \times [0, K_n]$. If a value appears more than once in the collection, then there are at least two pairs of purely imaginary roots and thus the condition of Hopf bifurcation is violated. For this reason, we only keep the values which appear exactly once in the collection and rearrange them in increasing order. Denote the new set by

$$\Sigma_H = \{\tau_i^H : 0 \leq i \leq 2K - 1\} \text{ with an integer } 0 < K \leq \sum_{j=0}^{N_2} K_j. \tag{4.7}$$

Clearly, τ_0^H and τ_{2K-1}^H are two simple zeros of $S_0^0(\tau)$, system (1.1) undergoes a Hopf bifurcation at w^* when $\tau = \tau_i^H$ for each $0 \leq i \leq 2K - 1$. Furthermore, w^* is locally asymptotically stable for $\tau \in [0, \tau_0^H) \cup (\tau_{2K-1}^H, \tau_{max})$, and unstable for $\tau \in (\tau_0^H, \tau_{2K-1}^H)$. To summarize, we have the following results on the stability of w^* and the existence of Hopf bifurcation.

Theorem 4.2. *Consider the model (1.1) with a general birth function satisfying ($\boldsymbol{H}_2$). Assume that $R_0 > 1$. Let I_n, $S_n^k(\tau)$ and Σ_H be defined in (4.4), (4.5) and (4.7), respectively.*

- (i) *If either $I_0 = \emptyset$ or $\sup_{\tau \in I_0} S_0^0(\tau) \leq 0$, then w^* is locally asymptotically stable for all $\tau \in [0, \tau_{max})$.*
- (ii) *If ($\boldsymbol{H}_3$) holds, then there exist exactly $2K$ local Hopf bifurcation values, namely, $0 < \tau_0^H < \tau_1^H < \cdots < \tau_{2K-1}^H < \widehat{\tau}$. w^* is locally asymptotically stable for $\tau \in [0, \tau_0^H) \cup (\tau_{2K-1}^H, \tau_{max})$, and unstable for $\tau \in (\tau_0^H, \tau_{2K-1}^H)$. Moreover, the periodic solutions bifurcating at $\tau \in \Sigma_0^H$ are spatially homogeneous, which coincide with the periodic orbits of the corresponding ODE system; and the periodic solutions bifurcating at $\tau \in \Sigma_H \setminus \Sigma_0^H$ are spatially heterogeneous, where $\Sigma_0^H = \{\tau \in \Sigma_H : S_0^k(\tau) = 0$ for some integer $k \in [0, k_0]\}$.*

For the model (1.1) with Ricker's birth function $f(w) = bwe^{-aw}$, Hopf bifurcation may occur only if $R_0 > 1$ and $\tau \in [0, \widehat{\tau})$. Moreover, if ($\mathbf{A}_1$) holds, then periodic solutions may bifurcate from the unique positive spatially homogeneous steady state w^*; if ($\mathbf{A}_2$) holds and either (3.5) or (3.6) is satisfied, then periodic solutions may bifurcate from the largest positive spatially homogeneous steady state w_3, we denote $w^* = w_3$ in this case.

Remark 4.3. Consider the model (1.1) with $f(w) = bwe^{-aw}$.

- (i) If we replace the condition ($\mathbf{H}_2$) in Theorem 4.2 with ($\mathbf{A}_1$), we have same results in Theorem 4.2 at the unique positive spatially homogeneous steady state w^*.
- (ii) If we replace the condition ($\mathbf{H}_2$) in Theorem 4.2 with ($\mathbf{A}_2$), and either (3.5) or (3.6), we have same results in Theorem 4.2 at the largest positive spatially homogeneous steady state w_3.

4.2. Global Hopf bifurcation analysis

Theorem 4.2 states that periodic solutions can bifurcate from w^* when τ is near the local Hopf bifurcation values $\tau_i^H \in \Sigma_H$. In this subsection, we study the global continuation of these local bifurcating periodic solutions via the global Hopf bifurcation theorem [31]. Let $z(t) = w(\cdot, \tau t) - w^*$. System (1.1) can be written as the following semilinear functional differential equation

$$z'(t) = Az(t) + F(z_t, \tau, T), (t, \tau, T) \in \mathbb{R}_+ \times [0, \widehat{\tau}) \times \mathbb{R}_+, \tag{4.8}$$

where $z_t \in C([-1, 0], X)$ with $z_t(\theta) = z(t+\theta)$ for $\theta \in [-1, 0]$, $A = \tau d\Delta - \tau\gamma$ and

$$F(z_t) = \tau e^{-\delta\tau} f(z_t(-1) + w^*) - \frac{\tau(z_t(0) + w^*)^2}{1 + (z_t(0) + w^*)^2}.$$

Denote by $\{T(t)\}_{t\geq 0}$ the semigroup generated by the operator A with Neumann boundary condition on Ω. Clearly, $T(t) \to 0$ as $t \to \infty$, and the solution of (4.8) satisfies

$$z(t) = T(t)z(0) + \int_0^t T(t-s)F(z_s)ds. \tag{4.9}$$

If $z(t)$ is a periodic solution of (4.8) with period κ, it then follows from the above equation that

$$z(t) = T(t + n\kappa)z(0) + \int_{-n\kappa}^{t} T(t-s)F(z_s)ds.$$

Since $T(t + n\kappa)z(0) \to 0$ as $n \to \infty$, the above equation is equivalent to

$$z(t) = \int_{-\infty}^{t} T(t-s)F(z_s)ds. \tag{4.10}$$

Thus, a periodic solution of (4.10) is also a periodic solution (4.9). From Chapter 6.5 in [30], the integral operator on the right-hand side of (4.10) is differential, completely continuous and G-equivariant. Theorem 2.4 and Corollary 5.2 imply that w^* is the unique positive steady state of (1.1). Note that $a_n - b_n > 0$ for all integer $n \geq 0$ and $\tau \in [0, \widehat{\tau})$, then 0 is not an eigenvalue of (2.8) if $R_0 > 1$ and $(\mathbf{H}_2)$ holds. Hence, the condition (H1) in [30, Chapter 6.5] holds. By Theorem 4.2, when $\tau = \tau_i^H$ for some integer $i \in [0, 2K-1]$, the characteristic equation (2.8) has exactly one pair of purely imaginary eigenvalues $\pm i\nu_n(\tau_i^H)$ for some $n \in [0, N_0]$. Then, the condition (H2) in [30, Chapter 6.5] holds. For $(\tau, \omega) \in [\tau_i^H - \epsilon_1, \tau_i^H + \epsilon_1] \times [\nu_n(\tau_i^H) - \epsilon_2, \nu_n(\tau_i^H) + \epsilon_2]$ with sufficiently small $\epsilon_1, \epsilon_2 > 0$, $\pm i\nu_n(\tau_i^H)$ are a pair of eigenvalues of (2.8) if and only if $\tau = \tau_i^H$ and $\nu = \nu_n(\tau_i^H)$. Thus, the smoothness condition (H3) in [30, Chapter 6.5] is satisfied, and $(w^*, \tau_H^i, 2\pi/(\tau_i^H \nu_n(\tau_i^H)))$ is an isolated singular point. From the transversality condition (4.6), the crossing number $\eta(w^*, \tau_H^i, 2\pi/(\tau_i^H \nu_n(\tau_i^H)))$ at each of these centers is

$$\eta_i(w^*, \tau_i^H, \frac{2\pi}{\nu_n(\tau_i^H)\tau_i^H}) = -\text{Sign}(\text{Re}\lambda'(\tau_i^H)) = \begin{cases} -1, & 0 \leq i \leq K-1, \\ 1, & K \leq i \leq 2K-1. \end{cases}$$

Hence, the condition (H4) in [30, Chapter 6.5] is satisfied. We next define a closed subset Γ of $X \times \mathbb{R}_+^2$ by

$$\Gamma = \mathcal{C}l\{(z, \tau, T) \in X \times \mathbb{R}_+^2 : z \text{ is a nontrivial } T\text{-periodic solution of (4.8)}\}.$$

Let $\mathcal{P}_i(w^*, \tau_i^H, T_i)$ be the connected component of (w^*, τ_i^H, T_i) in Γ for each integer $i \in [0, 2K-1]$. Theorem 4.2 (ii) ensures that $\mathcal{P}_i(w^*, \tau_i^H, T_i)$ is a nonempty subset of Γ.

To find the interval of τ in which periodic solutions exist, we shall further investigate the properties of periodic solutions of (4.8).

Lemma 4.4. *Consider the model* (1.1) *with a general birth function satisfying* ($\boldsymbol{H}_2$). *Assume that* $R_0 > 1$. *Let* M *be defined as in Proposition* 2.1. *There exists a constant* $m > 0$ *such that* $m \le w(x,t) \le M$ *for all* $(x,t) \in \bar{\Omega} \times \mathbb{R}_+$, *where* $w(x,t)$ *is any nonnegative periodic solution of* (1.1).

Proof. We claim that $w(x,t) \le M$ for all $(x,t) \in \bar{\Omega} \times \mathbb{R}_+$. Otherwise, if there exists $(x_1, t_1) \in \bar{\Omega} \times \mathbb{R}_+$ such that $w(x_1, t_1) > M$, then $\lim_{n\to\infty} w(x_1, t_1 + n\kappa) = w(x_1, t_1) > M$, where κ is the period of the periodic solution. This contradicts $\limsup_{t\to\infty} w(x,t) \le M$ for all $x \in \bar{\Omega}$ in Proposition 2.1. Hence, M is a uniform upper bound of $w(x,t)$.

To find a uniform lower bound for $w(x,t)$, we note from Proposition 2.1 that $w(x,t)$ should be strictly positive, and thus possesses a positive minimum $w_m > 0$ at (x_2, t_2); namely $w_m = \min_{\bar{\Omega}\times\mathbb{R}_+} w(x,t) = w(x_2, t_2)$. We then have $\partial w(x_2, t_2)/\partial t = 0$ and $\Delta w(x_2, t_2) \ge 0$. It follows from (1.1) that

$$e^{-\delta\tau} f(w(x_2, t_2 - \tau)) \le h_1(w_m), \quad \text{where } h_1(w) = \gamma w + \frac{w^2}{1 + w^2}.$$

If $w_m \le w(x_2, t_2 - \tau) < w^*$, then $h_1(m) \le h_1(w(x_2, t_2 - \tau)) < e^{-\delta\tau} f(w(x_2, t_2 - \tau))$, a contradiction. Hence, we have $1/a \le w^* \le w(x_2, t_2 - \tau) \le M$. Consequently, $h_1(w_m) \ge e^{-\delta\tau} f(w(x_2, t_2 - \tau)) \ge e^{-\delta\tau} f(M)$ and $w_m \ge m := h_1^{-1}(e^{-\delta\tau} f(M))$. This ends the proof. □

Lemma 4.5. *Consider the model* (1.1) *with a general birth function satisfying* ($\boldsymbol{H}_2$). *If* $R_0 > 1$, *then system* (1.1) *has no nontrivial periodic solution of period* τ.

Proof. Assume to the contrary, $w(x,t)$ is a nontrivial periodic solution of (1.1) with period τ, that is, $w(x, t - \tau) = w(x,t)$. Then it satisfies the following equation

$$\frac{\partial w(x,t)}{\partial t} = d\Delta w(x,t) - \gamma w(x,t) - \frac{w^2(x,t)}{1 + w^2(x,t)} + e^{-\delta\tau} f(w(x,t)) \tag{4.11}$$

with positive initial condition and Neumann boundary condition. We claim that $\lim_{t\to\infty} w(x,t) = w^*$. To prove this claim, we consider the ordinary differential equation

$$v'(t) = h_2(v(t)) := e^{-\delta\tau} f(v(t)) - \gamma v(t) - \frac{v^2(t)}{1 + v^2(t)}. \tag{4.12}$$

Clearly, the above equation has two equilibria $v = 0$ and $v = w^* > 0$. Moreover, $h_2(v) > 0$ for $v \in (0, w^*)$, and $h_2(v) < 0$ for $v > w^*$. Thus, the solution of (4.12) with positive initial condition converges to the unique positive equilibrium w^*, that is, $\lim_{t\to\infty} v(t, v_0) = w^*$ for any $v_0 > 0$. Let $M_0 = \max_{\bar{\Omega}} w(x, 0)$, then $\overline{w}(x,t) = v(t, M_0)$ and $\underline{w}(x,t) = 0$ are upper solution and lower solution of (4.11), respectively. Thus, system (4.11) has a unique solution $w(x,t)$ which satisfies $0 \le w(x,t) \le v(t, M_0)$. It then follows from the strong maximum principle that $w(x,t) > 0$ for any $(x,t) \in \bar{\Omega} \times \mathbb{R}_+$. Fix any $t_1 > 0$, then $u(x,t) := w(x, t + t_1)$ satisfies the following system

$$
\begin{aligned}
&\frac{\partial u(x,t)}{\partial t} = d\Delta u(x,t) - \gamma u(x,t) - \frac{u^2(x,t)}{1+u^2(x,t)} + e^{-\delta\tau} f(u(x,t)),\ x \in \Omega, t > 0,\\
&\partial_\nu u(x,t) = 0, \quad x \in \partial\Omega,\ t > 0,\\
&u(x,0) = w(x,t_1) > 0, \quad x \in \Omega.
\end{aligned}
$$

Denote $m_1 := \min_{\bar{\Omega}} w(x, t_1) > 0$ and $M_1 := \max_{\bar{\Omega}} w(x, t_1) > 0$. Thus, $v(t, M_1)$ and $v(t, m_1)$ are upper solution and lower solution of the above system, respectively. Hence, we have $v(t, m_1) \le u(x,t) = w(x, t+t_1) \le v(t, M_1)$. This, together with $\lim_{t\to\infty} v(t, m_1) = \lim_{t\to\infty} v(t, M_1) = w^*$, leads to $\lim_{t\to\infty} w(x,t) = w^*$. This precludes the existence of nontrivial periodic solution of system (4.11). Hence, system (1.1) has no nontrivial periodic solution of period τ. $\square$

We are now ready to analyze the structure of $\mathcal{P}_i(w^*, \tau_i^H, T_i)$ and prove global existence of periodic solutions of (4.8). For each $0 \le j \le K_0$, we denote

$$
\Sigma_H^j = \{\tau \in \Sigma_H : S_n^j(\tau) = 0 \text{ for some } n \in [0, N_0]\}. \tag{4.13}
$$

Lemma 4.5 shows that model (4.8) has no nontrivial periodic solution with period 1 and thus has no nontrivial periodic solution with period $1/j$ for any positive integer j. When τ is close to the bifurcation point $\tau_i \in \Sigma_H^j$, we obtain from local Hopf bifurcation theorem that $\nu_j\tau \in (2j\pi + \pi/2, 2j\pi + \pi) \subset (2j\pi, 2j\pi + \pi)$. Thus, the period $T = 2\pi/(\nu_j\tau) \in (1/(j+1), 1/j)$ for $j \ge 1$, and $T > 1$ for $j = 0$. For $j \ge 1$, system (4.8) has no nontrivial periodic solution of period $1/j$ or $1/(j+1)$. It then follows from the continuity of Hopf bifurcation branch that the periods on $\mathcal{P}_i$ are bounded by $1/j$ and $1/(j+1)$. For $j = 0$, the periods on $\mathcal{P}_i$ are always greater than 1. Therefore, any two global Hopf branches do not intersect: $\mathcal{P}_{i_1} \cap \mathcal{P}_{i_2} = \emptyset$ with $\tau_{i_1} \in \Sigma_H^{j_1}$, $\tau_{i_2} \in \Sigma_H^{j_2}$ and $j_1 \ne j_2$.

By using an argument similar to [17, Theorem 4.12], we arrive at our conclusion concerning the global existence of periodic solutions and the properties of the global Hopf branches.

Theorem 4.6. *Consider the model (1.1) with a general birth function satisfying ($\boldsymbol{H}_2$). Assume that $R_0 > 1$ and ($\boldsymbol{H}_3$) holds. For each integer $i \in [0, 2K-1]$, denote by $\mathcal{P}_i := \mathcal{P}_i(w^*, \tau_i^H, T_i)$ the connected component of (w^*, τ_i^H, T_i) in Γ. We have the following results.*

(i) *For $\tau_i \in \Sigma_H^j$ with $j \ge 1$ and $i \in [0, 2K-1]$, the global Hopf branch $\mathcal{P}_i$ is bounded with bounded τ-component in $[0, \widehat{\tau})$, bounded solution component in $[m, M]$, and bounded period component in $(1/(j+1), 1/j)$.*

(ii) *For* $\tau_{i_1} \in \Sigma_H^{j_1}$, $\tau_{i_2} \in \Sigma_H^{j_2}$ *with* $i_1, i_2 \in [0, 2K-1]$ *and* $j_1, j_2 \in [0, K_0]$, *we have* $\mathcal{P}_{i_1} \cap \mathcal{P}_{i_2} = \emptyset$ *if* $j_1 \neq j_2$.

(iii) *For any* $\tau \in (\min_{1 \le j \le K_0} \Sigma_H^j, \max_{1 \le j \le K_0} \Sigma_H^j)$, *there exists at least one periodic solution for system* (1.1).

Note that if the periods of any nontrivial periodic solutions of (1.1) are bounded from the above, then all global Hopf branches $\mathcal{P}_i$ with integer $i \in [0, 2K-1]$ are bounded, and for each $\tau \in (\tau_0, \tau_{2K-1})$, there exists at least one periodic solution for system (1.1). We leave the proof of upper boundedness of the periods of any nontrivial periodic solutions of (1.1) as an open problem.

Remark 4.7. Consider the model (1.1) with Ricker's birth function $f(w) = bwe^{-aw}$. The statements in Theorem 4.6 remain valid if we replace the condition $(\mathbf{H}_2)$ with $(\mathbf{A}_1)$.

5. The positive heterogeneous steady states

The steady state of (1.1) satisfies the following elliptic equation

$$\begin{aligned} -d\Delta w(x) &= e^{-\delta\tau} f(w(x)) - \gamma w(x) - \frac{w^2(x)}{1+w^2(x)}, \quad x \in \Omega, \\ \partial_\nu w(x) &= 0, \quad x \in \partial\Omega. \end{aligned} \tag{5.1}$$

The strong maximum principle implies that any nonnegative heterogeneous steady state $w(x)$ of (5.1) is positive; namely, $w(x) > 0$ for all $x \in \bar{\Omega}$. We now provide a general result on the nonexistence of positive heterogeneous solutions for the following general elliptic equation.

$$-d\Delta z(x) = G(z(x)) \ \text{ in } \ \Omega, \ \ \partial_\nu z(x) = 0 \ \text{ on } \ \partial\Omega \tag{5.2}$$

Here, $d > 0$, Ω is an open and bounded domain with sufficiently smooth boundary (for instance, the boundary is C^1 and satisfies the interior ball condition) in a Euclidean space.

Theorem 5.1. *Assume that* $G(z) \in C^1(\mathbb{R})$ *has finite number of zeros, and there exists* $z_1 > 0$ *such that* $G(z)(z - z_1) \le 0$ *for all* $z \ge 0$. *Then the elliptic equation* (5.2) *has no positive heterogeneous solution.*

Proof. Let $z(x)$ be a positive solution of (5.2). Multiplying (5.2) by $z(x) - z_1$ and integrating over Ω, we obtain from Green's identity that

$$0 \le d \int_\Omega |\nabla z(x)|^2 dx = \int_\Omega G(z(x))(z(x) - z_1) dx \le 0.$$

Hence, $z(x) \equiv$ constant. This ends the proof. □

If $R_0 \le 1$, it follows from the global stability of the trivial steady state in Theorem 2.2 that there does not exist any positive heterogeneous steady states of (1.1). If $R_0 > 1$ and the model

(1.1) admits one or two positive spatially homogeneous steady states, we denote by $\widehat{w}$ the largest positive spatially homogeneous steady state and find

$$(e^{-\delta\tau} f(w) - \gamma w - \frac{w^2}{1+w^2})(w - \widehat{w}) \le 0$$

for all $w \ge 0$. This together with Theorem 5.1 gives the following corollary.

Corollary 5.2. *If the model (1.1) admits zero, one, or two positive spatially homogeneous steady states, then it has no positive heterogeneous steady state.*

The existence conditions for the positive heterogeneous steady state of (5.2) are stated in the following theorem.

Theorem 5.3. *Let $G(z) \in C^1(\mathbb{R}_+)$ and $\overline{z} \ge \underline{z} > 0$ such that $G(z) > 0$ for $z \in (0, \underline{z})$ and $G(z) < 0$ for $z \in (\overline{z}, \infty)$. Choose $L > 0$ such that $|G'(z)| \le L$ for all $z \in [\underline{z}, \overline{z}]$. Let $0 = \lambda_0 < \lambda_1 < \lambda_2 < \cdots$ be the odd eigenvalues of $-\Delta$ on Ω with Neumann boundary condition. Denote by $\underline{\lambda}$ the smallest positive eigenvalue of $-\Delta$ on Ω with Neumann boundary condition. We have the following results.*

- (i) *Any nonnegative and nontrivial solution of (5.2) satisfies $\underline{z} \le z(x) \le \overline{z}$ for all $x \in \Omega$.*
- (ii) *If $d > L/\underline{\lambda}$, then all nonnegative solutions of (5.2) are constant solutions.*
- (iii) *The equation (5.2) possesses at least one positive spatially heterogeneous solution if there exists a positive root z^* of $G(z)$ such that $G'(z^*) > 0$ and*

$$d \in \bigcup_{k\ge 1} (\frac{G'(z^*)}{\lambda_{2k}}, \frac{G'(z^*)}{\lambda_{2k-1}}). \tag{5.3}$$

Proof. The first statement is a direct consequence of [10, Proposition 2.2] or [19, Lemmas 2.3-2.4]. If $z(x)$ is a nonnegative and nontrivial solution of (5.2), then the strong maximum principle implies that $z(x) > 0$ for all $x \in \Omega$. We claim that $z(x) \le \overline{z}$ for all $x \in \Omega$. Assume to the contrary that $M := \max_{x\in\bar{\Omega}} z(x) > \overline{z}$. Since $G(M) < 0$, we have from the maximum principle that $z(x_0) = M$ for some $x_0 \in \partial\Omega$. The Hopf lemma implies that $\partial_\nu z(x_0) > 0$, which contradicts the Neumann boundary condition. Hence, we obtain $z(x) \le \overline{z}$ for all $x \in \Omega$. In a similar manner, we can show that $z(x) \ge \underline{z}$ for all $x \in \Omega$.

Now, we assume $d > L/\underline{\lambda}$ and let $z(x)$ be any positive solution of (5.2). Denote $c := \int_\Omega z(x)dx/|\Omega| \in [\underline{z}, \overline{z}]$ such that $\int_\Omega (z(x) - c)dx = 0$. It then follows from (5.2) and Green's formula that

$$d \int_\Omega |\nabla(z(x) - c)|^2 dx = \int_\Omega [G(z(x)) - G(c)][z(x) - c]dx.$$

By mean value theorem, we have $|G(z(x)) - G(c)| \le L|z(x) - c|$. We then obtain from Poincaré's inequality that

$$d\underline{\lambda}\int_\Omega |z(x)-c|^2dx \le d\int_\Omega |\nabla(z(x)-c)|^2dx \le L\int_\Omega |z(x)-c|^2dx.$$

Since $d > L/\underline{\lambda}$, the above inequalities are valid only if $z(x) \equiv c$ is a constant solution.

Next, we will use Leray-Schauder's theory [8] to prove the existence of positive spatially heterogeneous solutions of (5.2) if (5.3) is satisfied. Note that the solution of (5.2) is the same as the fixed point of the nonlinear compact operator

$$\mathcal{G}_d(z) := (L - d\Delta)^{-1}(Lz + G(z))$$

in the open set

$$U := \{z \in C^2(\Omega) \cap C^1(\bar{\Omega}) :\ \partial_\nu z|_{\partial\Omega} = 0,\ \underline{z}/2 < z(x) < 2\overline{z}\}.$$

Since all positive solutions of (5.2) are bounded by $\underline{z}$ from below and $\overline{z}$ from the above, $\mathcal{G}_d$ does not possess any fixed point on ∂U. Consequently, the Leray-Schauder degree

$$\deg(I - \mathcal{G}_d, U, 0) = \deg(I - \mathcal{G}_0, U, 0) = \deg(-G, U, 0) = 1 \tag{5.4}$$

is independent of $d \ge 0$, where the last equality follows from the fact that $G(\underline{z}/2) > 0 > G(2\overline{z})$. Now, we assume d satisfies (5.3) and prove by contradiction that (5.2) possesses at least one positive heterogeneous solution. If not, then all positive solutions of (5.2) are constants which correspond to the positive roots of $G(z)$. In this case, we have

$$\deg(I - \mathcal{G}_d, U, 0) = \sum_{z^*>0, G(z^*)=0} \deg(I - \mathcal{G}_d, U_\varepsilon(z^*), 0),$$

where $U_\varepsilon(z^*)$ is a small neighborhood of z^* in U. Let

$$D\mathcal{G}_d(z^*) = (L - d\Delta)^{-1}(L + G'(z^*))$$

be the linearized operator of $\mathcal{G}_d$ about z^*. We shall consider the following four cases.

(a) If $G'(z^*) < 0$, then all eigenvalues of $D\mathcal{G}_d(z^*)$ are less than one, and hence

$$\deg(I - \mathcal{G}_d, U_\varepsilon(z^*), 0) = \deg(I - D\mathcal{G}_d(z^*), U_\varepsilon(z^*), 0) = 1.$$

(b) If $G'(z^*) = 0$ and z^* is an even root of $G(z)$, then we can find a small perturbation of G that does not change sign in $[z^* - \varepsilon, z^* + \varepsilon]$ for all sufficiently small $\varepsilon > 0$. By homotopy property of the Leray-Schauder degree [16], we then have

$$\deg(I - \mathcal{G}_d, U_\varepsilon(z^*), 0) = 0.$$

(c) If $G'(z^*) = 0$ and z^* is an odd root of $G(z)$, then we can find a small perturbation of G, denoted by G_δ, which has a simple root $z^*_\delta \in (z^* - \varepsilon, z^* + \varepsilon)$ for a sufficiently small $\varepsilon > 0$. By homotopy property of the Leray-Schauder degree, we then have

$$\deg(I-\mathcal{G}_d, U_\varepsilon(z^*), 0) = \deg(I-\mathcal{G}_{d,\delta}, U_\varepsilon(z^*), 0) = \deg(I-D\mathcal{G}_{d,\delta}, U_\varepsilon(z^*), 0),$$

where $\mathcal{G}_{d,\delta}(z) := (L-d\Delta)^{-1}(Lz+G_\delta(z))$ and $D\mathcal{G}_{d,\delta} := (L-d\Delta)^{-1}(L+G'_\delta(z^*_\delta))$ are small perturbations of $\mathcal{G}_d$ and $D\mathcal{G}_d$, respectively. We choose the perturbation parameter $\delta > 0$ to be sufficiently small such that $|G'_\delta(z^*_\delta)| < d\underline{\lambda}$. If $G(z)(z-z^*) \le 0$ for $z \in (z^*-\varepsilon, z^*+\varepsilon)$, then $G'_\delta(z^*_\delta) < 0$ and all eigenvalues of $D\mathcal{G}_{d,\delta}(z^*)$ are less than one. Consequently,

$$\deg(I-\mathcal{G}_d, U_\varepsilon(z^*), 0) = \deg(I-D\mathcal{G}_{d,\delta}, U_\varepsilon(z^*), 0) = 1.$$

If $G(z)(z-z^*) \ge 0$ for $z \in (z^*-\varepsilon, z^*+\varepsilon)$, then $G'_\delta(z^*_\delta) > 0$ and the principal eigenvalue of $D\mathcal{G}_{d,\delta}(z^*)$ is $1 + G'_\delta(z^*_\delta)/L > 1$ while all other eigenvalues of $D\mathcal{G}_{d,\delta}(z^*)$ are less than one. Consequently,

$$\deg(I-\mathcal{G}_d, U_\varepsilon(z^*), 0) = \deg(I-D\mathcal{G}_{d,\delta}, U_\varepsilon(z^*), 0) = -1.$$

(d) If $G'(z^*) > 0$, then

$$\deg(I-\mathcal{G}_d, U_\varepsilon(z^*), 0) = \deg(I-D\mathcal{G}_d(z^*), U_\varepsilon(z^*), 0) \ge -1.$$

If further, $G'(z^*)/\lambda_{2k} < d < G'(z^*)/\lambda_{2k-1}$ for some $k \ge 1$, then the set of odd eigenvalues of $D\mathcal{G}_{d,\delta}(z^*)$ which are greater than one is given by

$$\bigcup_{0\le l\le 2k-1}\{\frac{L+G'(z^*)}{L+d\lambda_l}\},$$

and consequently,

$$\deg(I-\mathcal{G}_d, U_\varepsilon(z^*), 0) = \deg(I-D\mathcal{G}_d(z^*), U_\varepsilon(z^*), 0) = (-1)^{2k} = 1.$$

Let $0 < z_1 < z_2 < \cdots < z_{2m+1}$ be the odd roots of $G(z)$ in $(\underline{z}/2, 2\overline{z})$. Since $G(\underline{z}/2) > 0$ and $G(2\overline{z}) < 0$, we have $G(z)(z-z_{2j+1}) \le 0$ for $z \in (z_{2j}, z_{2j+2})$ (where for convenience we have denoted $z_0 = 0$ and $z_{2m+2} = \infty$) and $G(z)(z-z_{2j}) \ge 0$ for $z \in (z_{2j-1}, z_{2j+1})$. From the above arguments, we obtain $\deg(I-\mathcal{G}_d, U_\varepsilon(z_{2j+1}), 0) = 1$ and $\deg(I-\mathcal{G}_d, U_\varepsilon(z_{2j}), 0) \ge -1$. Moreover, there exists j such that $\deg(I-\mathcal{G}_d, U_\varepsilon(z_{2j}), 0) = 1$. Consequently,

$$\begin{aligned}\deg(I-\mathcal{G}_d, U, 0) &= \sum_{j=0}^{m}\deg(I-\mathcal{G}_d, U_\varepsilon(z_{2j+1}), 0) + \sum_{j=1}^{m}\deg(I-\mathcal{G}_d, U_\varepsilon(z_{2j}), 0)\\ &\ge (m+1)-(m-2) = 3.\end{aligned}$$

This contradicts (5.4). Therefore, the elliptic equation (5.2) possesses at least one positive heterogeneous solution if (5.3) is satisfied. The proof is completed. □

Corollary 5.4. *If $d > d^* := (f'(0)e^{-\delta\tau} - \gamma)/\mu_1$, where μ_1 is defined in* (2.4)*, then the model* (1.1) *has no positive heterogeneous steady states.*

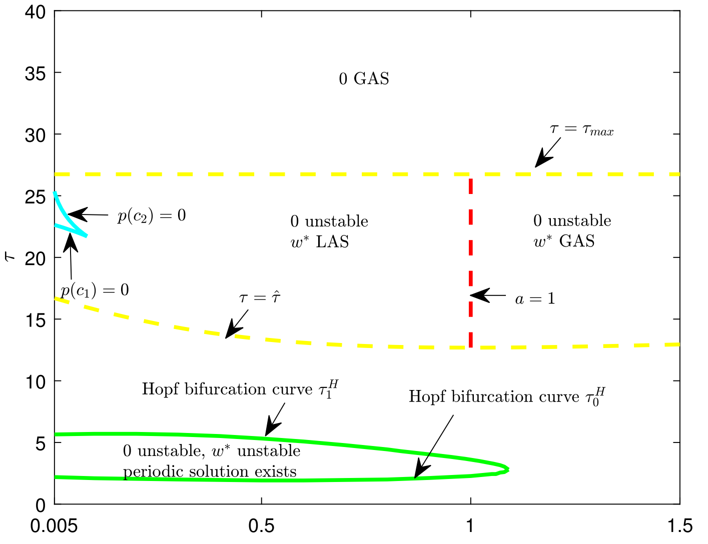


Fig. 2. The existence and stability regions of equilibria of (1.1) in the $a - \tau$ plane.

Corollary 5.5. *Let* $0 = \lambda_0 < \lambda_1 < \lambda_2 < \cdots$ *be the odd eigenvalues of* $-\Delta$ *on* Ω *with Neumann boundary condition. If there exists* $w^* > 0$ *such that* $e^{-\delta\tau} f(w^*) = \gamma w^* + (w^*)^2/(1 + (w^*)^2)$ *and*

$$d\lambda_{2k-1} < e^{-\delta\tau} f'(w^*) - \gamma - \frac{2w^*}{(1 + (w^*)^2)^2} < d\lambda_{2k}$$

for some $k \geq 1$, *then* (1.1) *possesses at least one positive heterogeneous steady state.*

Note that Corollary 5.5 gives a sufficient condition for the existence of a positive heterogeneous steady state, which can be satisfied only when the model (1.1) has at least three positive spatially homogeneous steady states.

6. Numerical exploration

In this section, we use numerical exploration to illustrate our theoretical results on the model dynamics. We set $\Omega = (0, \pi)$ and choose the birth function as $f(w) = bwe^{-aw}$. The parameter values as given as $d = 1, \gamma = 1, \delta = 0.1, b = 14.5$. The regions for the existence and stability of equilibria of system (1.1) in the $a - \tau$ plane are plotted in Fig. 2. No positive equilibrium shall exist in the region above the horizontal line with $\tau = \tau_{max}$. There exist two positive equilibria on the two curves defined by $p(c_1) = 0$ and $p(c_2) = 0$, respectively. There are three positive equilibria in the regions bounded by the these two curves. In the other regions, there exists exactly one positive equilibrium w^*, which is locally asymptotically stable when $\tau \geq \hat{\tau}$. Moreover, the positive equilibrium w^* is globally asymptotically stable if $\tau \in [\hat{\tau}, \tau_{\max})$ and $a \geq 1$.

Now, we choose $a = 0.8$ to explore the stability of the unique positive spatially homogeneous steady state w^*. A simple calculation gives $\widehat{\tau} \approx 12.77$, $\tau_{max} \approx 26.74$, $\sup I_0 \approx 5.43$ and $I_n = \varnothing$ for $n \geq 1$. We further obtain that $\sup_{I_0} S_0^0(\tau) \approx 0.49 > 0$, and $S_0^0(\tau)$ has exactly two zeros in I_0: $\tau_0^H \approx 2.01$ and $\tau_1^H \approx 4.45$. The dynamics of system (1.1) are summarized as follows.

(i) If $\tau \in [\tau_{max}, \infty)$, then 0 is globally asymptotically stable; see Fig. 3(a).
(ii) If $\tau \in (0, \tau_0^H) \cup (\tau_1^H, \tau_{max})$, then w^* is locally asymptotically stable; see Fig. 3(b).
(iii) If $\tau \in (\tau_0^H, \tau_1^H)$, then 0 and w^* are unstable. Moreover, there exists a periodic solution bifurcated from w^*; see Fig. 3(c). System (1.1) undergoes a Hopf bifurcation at w^* when $\tau = \tau_i^H$ for $i = 0, 1$.

Next, we choose $a = 0.02$, $\tau = 23.48$ to explore the stability of three positive spatially homogeneous equilibria obtained in Theorem 3.3. By a simple calculation, we have $\widehat{\tau} \approx 16.54$, $\tau_{max} \approx 26.74$, $c_1/a \approx 1.09$, $c_2/a \approx 7.67$, and $w_1 \approx 0.45 \in (0, c_1/a)$, $w_2 \approx 2.91 \in (c_1/a, c_2/a)$, $w_3 \approx 12.48 \in (c_2/a, \infty)$. The dynamics of system (1.1) are summarized as follows.

(i) w_1 is locally asymptotically stable; see Fig. 3(d).
(ii) w_2 is unstable, for instance, the solution of (1.1) converges to w_3 by choosing an initial condition close to w_2; see Fig. 3(e).
(iii) w_3 is locally asymptotically stable for $\tau \in [\widehat{\tau}, \tau_{max})$; see Fig. 3(f).

Corollary 5.5 gives sufficient conditions for the existence of positive heterogeneous steady states. We set $d = 0.1, \gamma = 1, \delta = 0.01, a = 0.04, b = 4.21, \tau = 100.1$, $\Omega = (0, 3\pi)$ and $w_0(x, \theta) = 1.571 + 0.1 \cos x$. There are three positive equilibria $w_1 \approx 0.864$, $w_2 \approx 1.571$, $w_3 \approx 8.015$. For $k = 2$, two simple eigenvalues of $-\Delta$ in Ω with Neumann boundary condition are $\lambda_3 = 1$, $\lambda_4 = 16/9$ and then $d\lambda_3 < e^{-\delta\tau} f'(w_2) - \gamma - \frac{2w_2}{(1+w_2^2)^2} \approx 0.1004 < d\lambda_4$. It then follows from Corollary 5.5 that system (1.1) has at least one positive heterogeneous solution; see Fig. 4.

To demonstrate the existence of multiple global Hopf branches, we choose $\Omega = (0, \pi)$ and

$$d = 0.2, \gamma = 1, \delta = 0.1, a = 11, b = 50.$$

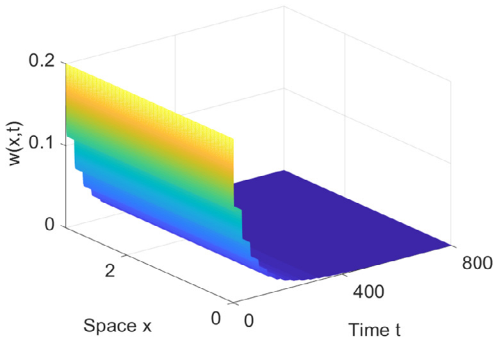
It follows from Section 4 that $\sup I_0 \approx 15.94$, $\sup I_1 \approx 14.08$, $\sup I_2 \approx 8.82$, $\sup I_3 \approx 0.8$ and $I_n = \emptyset$ for $n \geq 4$. By Theorem 4.2 and 4.6, there are exactly 12 Hopf bifurcation values (see Fig. 5):

$$\begin{aligned} \tau_0^H &\approx 0.68 < \tau_1^H \approx 0.74 < \tau_2^H \approx 1 < \tau_3^H \approx 3.24 < \tau_4^H \approx 3.5 \\ &< \tau_5^H \approx 8 < \tau_6^H \approx 8.6 < \tau_7^H \approx 11.04 < \tau_8^H \approx 12.74 \\ &< \tau_9^H \approx 13.94 < \tau_{10}^H \approx 14.72 < \tau_{11}^H \approx 15.8. \end{aligned}$$

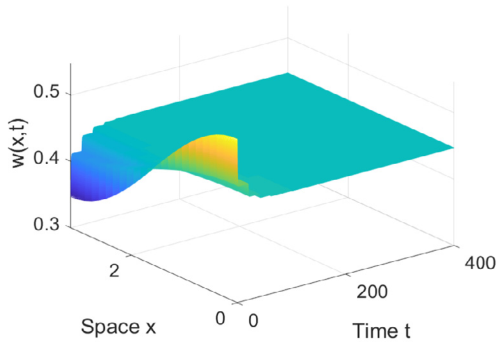
By Theorem 4.2, the unique positive spatially homogeneous steady state w^* is locally asymptotically stable for $\tau \in [0, \tau_0^H) \cup (\tau_{11}^H, \tau_{max})$, and unstable for $\tau \in (\tau_0^H, \tau_{11}^H)$. Moreover, the model (1.1) has at least one periodic solution for $\tau \in (\tau_0^H, \tau_{11}^H)$. The periodic solutions bifurcated from $\tau \in \{\tau_0^H, \tau_3^H, \tau_5^H, \tau_7^H, \tau_{10}^H, \tau_{11}^H\}$ are spatially homogeneous, and the periodic solutions bifurcated from $\tau \in \{\tau_1^H, \tau_2^H, \tau_4^H, \tau_6^H, \tau_8^H, \tau_9^H\}$ are spatially nonhomogeneous, see Fig. 6. One can also observe from numerical simulations that the periods of the periodic solution for (1.1) are bounded. It then follows from Theorem 4.6 that all global Hopf branches are bounded and connected by a pair of Hopf bifurcation values.

7. Summary and discussion

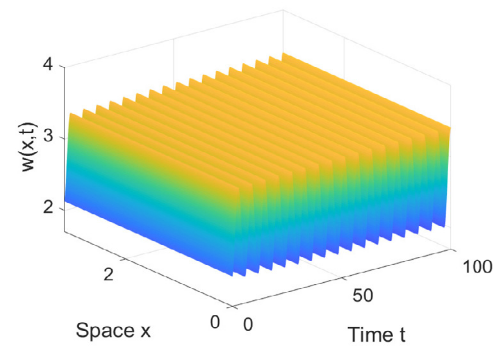
In this paper, we derive a general delayed diffusive spruce budworm model from an age structure system. When the basic reproduction number is no more than one, we prove global



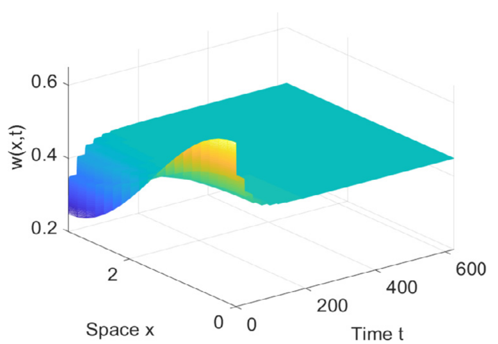
(a) $a = 0.8, \tau = 30 > \tau_{max}$, 0 is locally asymptotically stable.



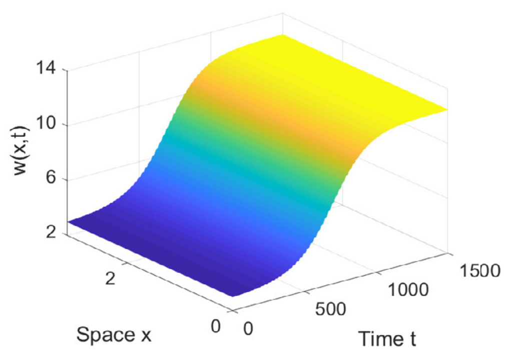
(b) $a = 0.8, \tau = 20 \in (\widehat{\tau}, \tau_{max})$, $w^* \approx 0.45$ is locally asymptotically stable.



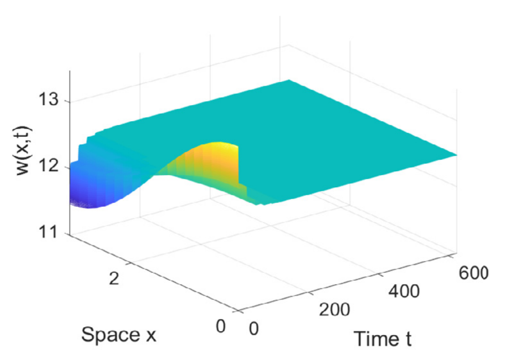
(c) $a = 0.8, \tau = 2.3 \in (\tau_0^H, \tau_1^H)$, a periodic solution is bifurcated from $w^* \approx 2.70$.



(d) $a = 0.02, \tau = 23.48$, $w_1 \approx 0.45$ is locally asymptotically stable.



(e) $a = 0.02, \tau = 23.48$, $w_2 \approx 2.91$ is unstable.



(f) $a = 0.02, \tau = 23.48 \in [\widehat{\tau}, \tau_{max})$, $w_3 \approx 12.48$ is locally asymptotically stable.

Fig. 3. The dynamics of system (1.1) with different values of a and τ. The initial conditions are: $w_0(x, \theta) = 0.2$ for (a); $w_0(x, \theta) = w^* + 0.1 \cos x$ for (b) and (c); $w_0(x, \theta) = w_1 + 0.2 \cos x$ for (d); $w_0(x, \theta) = 3 + 0.01 \cos x$ for (e); and $w_0(x, \theta) = w_3 + \cos x$ for (f).

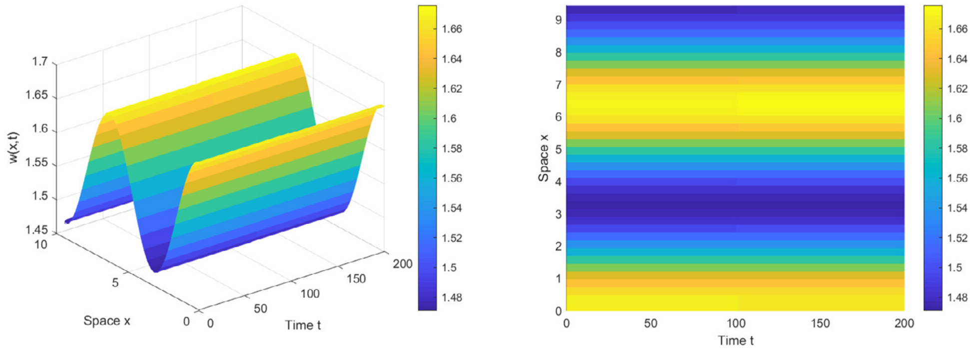


Fig. 4. The solution $w(x,t)$ and its projection on $x-t$ plane. Parameter values are $d=0.1, \gamma=1, \delta=0.01, a=0.04, b=4.21, \tau=100.1$, $\Omega=(0,3\pi)$ and $w_0(x,\theta)=1.571+0.1\cos x$, $\theta\in[-\tau,0]$. (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)

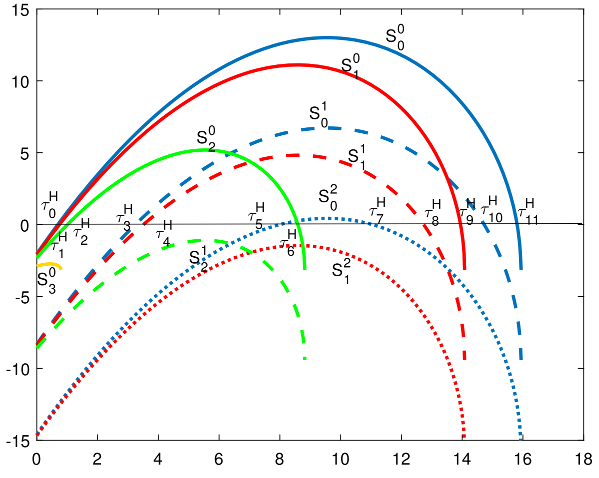


Fig. 5. The graphs of S_n^k for $0\le n,k\le 2$, and the Hopf bifurcation values τ_j^H for $0\le j\le 11$.

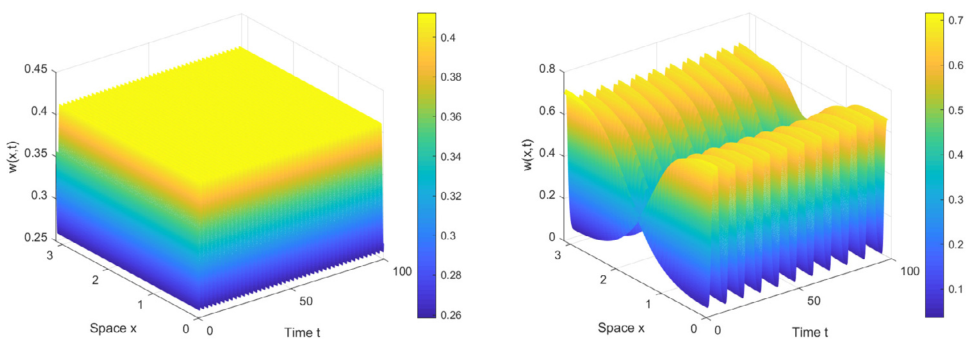


Fig. 6. Left: $\tau=0.72\in(\tau_0^H,\tau_1^H)$, a bifurcating spatially homogeneous periodic solution exists. Right: $\tau=4.144\in(\tau_4^H,\tau_5^H)$, a bifurcating spatially non-homogeneous periodic solution exists.

asymptotic stability of the trivial steady state via the Lyapunov functional technique and LaSalle invariance principle. When the basic reproduction number is greater than one, we analyze the nonlinear functions in the model system and establish necessary and sufficient conditions for the existence of one, two, and three positive spatially homogeneous steady states, respectively. By Leray-Schauder's theory, we establish existence conditions of positive spatially heterogeneous steady states for a general elliptic equation with Neumann boundary condition. To examine the onset and termination of periodic solutions bifurcated from the positive spatially homogeneous steady state, we use the maturation delay as the bifurcation parameter and prove the existence and boundedness of the global Hopf branches.

Data availability

No data was used for the research described in the article.

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