Transient oscillatory patterns in the diffusive non-local blowfly equation with delay under the zero-flux boundary condition

2014 Nonlinearity 27 87

(http://iopscience.iop.org/0951-7715/27/1/87)

IOP Publishing | London Mathematical Society Nonlinearity

Nonlinearity **27** (2014) 87–104 doi:10.1088/0951-7715/27/1/87

Transient oscillatory patterns in the diffusive non-local blowfly equation with delay under the zero-flux boundary condition

Ying Su[1,2] and Xingfu Zou[2]

[1] Department of Mathematics, Harbin Institute of Technology, Harbin, Heilongjiang, 150001, People's Republic of China
[2] Department of Applied Mathematics, University of Western Ontario, London, Ontario, N6A 5B7, Canada

E-mail: ysu62@uwo.ca and xzou@uwo.ca

Received 9 April 2013, revised 8 November 2013
Accepted for publication 22 November 2013
Published 17 December 2013

Recommended by M J Field

Abstract

In this paper, we study the spatial-temporal patterns of the solutions to the diffusive non-local Nicholson's blowflies equations with time delay (maturation time) subject to the no flux boundary condition. We establish the existence of both spatially homogeneous periodic solutions and various spatially inhomogeneous periodic solutions by investigating the Hopf bifurcations at the spatially homogeneous steady state. We also compute the normal form on the centre manifold, by which the bifurcation direction and stability of the bifurcated periodic solutions can be determined. The results show that the bifurcated *homogeneous* periodic solutions are stable, while the bifurcated *inhomogeneous* periodic solutions can only be stable on the corresponding centre manifold, implying that generically the model can only allow *transient* oscillatory patterns. Finally, we present some numerical simulations to demonstrate the theoretic results. For these transient patterns, we derive approximation formulas which are confirmed by numerical simulations.
Mathematics Subject Classification: 35B32, 35K57, 92B05

(Some figures may appear in colour only in the online journal)

1. Introduction

Gurney *et al* [5] proposed the time delayed ODE model

$$\frac{\mathrm{d}w(t)}{\mathrm{d}t} = -\mathrm{d}w(t) + pw(t-\tau)\mathrm{e}^{-qw(t-\tau)} \tag{1.1}$$

to describe the population dynamics of blowflies, hoping to explain the oscillatory phenomena in Nicholson's laboratory experiments [17]. Here $w(t)$ is the size of the mature blowfly population at time t, p is the maximum per capita daily egg production rate, $1/q$ is the size at which the blowfly population reproduces at its maximum rate, d is the per capita daily adult death rate and τ is the maturation time. Since [5], (1.1) has been widely quoted as the Nicholson blowflies equation and has been extensively studied in the literature (see, e.g., [1, 10–12, 23, 28] and references therein).

In fact, (1.1) can be derived from the following age-structured population model (see, e.g., [19])

$$\begin{cases} \dfrac{\partial u(t,a)}{\partial t} + \dfrac{\partial u(t,a)}{\partial a} = -d(a)u(t,a), & t>0,\ a>0, \\ u(t,0) = b\big(w(t)\big), & t>0, \end{cases} \tag{1.2}$$

where $u(t,a)$ is the population density of age a at time t, $d(a)$ is the age-dependent death rate, $w(t) = \int_\tau^{+\infty} u(t,a)\,\mathrm{d}a$ is the total density of the mature population at time t, τ is the maturation time and $b(w)$ is the Ricker type's birth function: $b(w) = pw\mathrm{e}^{-qw}$.

Taking into account spatial diffusion of the population in a one dimensional domain $\Omega \subset \mathbb{R}$, parallel to (1.2), one can obtain a general diffusive age-structured model given by (see, e.g., [15])

$$\begin{cases} \dfrac{\partial u(t,a,x)}{\partial t} + \dfrac{\partial u(t,a,x)}{\partial a}, & t>0,\ a>0,\ x\in\Omega\subset\mathbb{R}, \\ = D(a)\dfrac{\partial^2 u(t,a,x)}{\partial x^2} - d(a)u(t,a,x) & \\ u(t,0,x) = b\big(w(t,x)\big), & t>0,\ x\in\Omega\subset\mathbb{R}, \end{cases} \tag{1.3}$$

where $u(t,a,x)$ now is the population density of age a at time t and location x, $D(a)$ is the age-dependent diffusion rate, $w(t,x) = \int_\tau^{+\infty} u(t,a,x)\,\mathrm{d}a$ is the total density of the mature population at time t and location x. For fundamental theory and many interesting topics on age-structured models, we refer to [16, 26, 27].

Under the assumption that the diffusion rate and death rate of the mature population are age-independent, that is,

$$D(a) = D_m, \qquad d(a) = d \quad \text{for all } a \geqslant \tau,$$

one can derive the following equation from (1.3) for the mature population $w(t,x)$:

$$\frac{\partial w(t,x)}{\partial t} = D_m\frac{\partial^2 w(t,x)}{\partial x^2} - \mathrm{d}w(t,x) + \varepsilon\int_\Omega K_\alpha(x,y)b(w(t-\tau,y))\,\mathrm{d}y, \quad t>0, \quad x\in\Omega, \tag{1.4}$$

where $\alpha = \int_0^\tau D(a)\,\mathrm{d}a$ measures the mobility of the immature population and $\varepsilon = \exp(-\int_0^\tau \mathrm{d}(a)\,\mathrm{d}a)$ is the survival factor accounting for the proportion of individuals that can survive the immature period, while the kernel function $K_\alpha(x,y)$ depends on the boundary condition, accounting for the probability that an individual born in location y will have moved to location x after τ units of time (maturation time). Thus, the last term on the right hand side of (1.4) sums up all individuals born in the domain τ time units ago who have moved to location x at maturation. There is one thing in common for the kernel function $K_\alpha(x,y)$ under various boundary conditions, that is, as $\alpha \to 0$, $K_\alpha(x, y)$ tends to the Dirac delta function of $x - y$: $K_\alpha(x, y) = \delta(x - y)$, reducing (1.4) to the spatially local equation:

$$\frac{\partial w(t,x)}{\partial t} = D_m \frac{\partial w^2(t,x)}{\partial x^2} - \mathrm{d}w(t,x) + \varepsilon b(w(t-\tau,x)), \qquad t > 0, \quad x \in \Omega. \tag{1.5}$$

For $\Omega = \mathbb{R}$, So *et al* [21] showed that K_α is nothing but the heat kernel function with the parameter α determining its flatness. There have been many works on (1.4) or some special cases of (1.4) (including (1.5)), dealing with such interesting topics as stability of the constant steady states, travelling wave fronts connecting two constant steady states and the stability of these fronts, as well as the asymptotic speed of spread. Such an unbounded domain case is not the concern of this paper, and hence, we will not go further along this line. An interested reader is referred to, for example, [2, 14, 21, 24, 36] and the references therein.

For $\Omega = [0, L]$, Liang *et al* [13] obtained the explicit forms of $K_\alpha(x, y)$ under some common boundary conditions (including Neumann, Dirichlet, Robin and periodic conditions) at the two ends $x = 0$, L and explored numerical methods for the solutions to the resulting non-local reaction–diffusion equations. For the special case (1.5) (i.e., $\alpha \to 0$), under zero Dirichlet boundary condition (a scenario for hostile boundary), So and Yang [22] investigated the global stability of the steady states of (1.5), So *et al* [20] numerically explored Hopf bifurcation of (1.5), and Su *et al* [25] analysed the existence and nonexistence of the positive steady state of (1.5); while under zero-flux boundary condition, Yang and So [31] studied the stability of the steady states and the existence of Hopf bifurcation, Yi *et al* [32] and Yi and Zou [34, 35] identified some ranges of the parameters within which the delay τ has no impact on the global dynamics of (1.5). For the true non-local case, Xu and Zhao [30], Zhao [38] and Yi and Zou [37] have obtained some results on the threshold dyanamics of (1.4) under zero Dirichlet/Neumann boundary condition which support convergence of solutions to steady states.

In this paper, we consider the true non-local equation (1.4) with the Ricker type birth function $b(w) = pw\mathrm{e}^{-qw}$ on the domain $\Omega = [0, \pi]$ subject to the zero-flux boundary condition. By the results in [30, 34, 35, 38], it is known that when $1 < p\varepsilon/d < \mathrm{e}^2$, the equation has a positive constant steady state $E^+(p\varepsilon/d)$ which attracts all positive solutions to this boundary value problem, and therefore there will be no temporal and/or spatial patterns arising from (1.4). It is natural to ask what will happen when $p\varepsilon/d > \mathrm{e}^2$, and addressing this question constitutes the goal of this paper.

To proceed, we note that for $\Omega = [0, \pi]$ and with the zero-flux boundary condition, [13] has shown that the kernel function $K_\alpha(x, y)$ in (1.4) is

$$K_\alpha(x, y) = \frac{1}{\pi}\left[1 + \sum_{n=1}^{+\infty} (\cos n(x+y) + \cos n(x-y))\, \mathrm{e}^{-\alpha n^2}\right].$$

Plugging this into (1.4), re-scaling by

$$\hat{w}(\hat{t}) = qw\left(\frac{t}{\tau}\right), \qquad \hat{D}_m = \tau D_m, \qquad \hat{\tau} = \mathrm{d}\tau, \qquad \text{and} \qquad \beta = \frac{p\varepsilon}{d}$$

and dropping the hats for the simplicity of notations , we obtain

$$\begin{cases} \dfrac{\partial w(t,x)}{\partial t} = D_m \dfrac{\partial^2 w(t,x)}{\partial x^2} - \tau w(t,x) + \dfrac{\beta\tau}{\pi}\displaystyle\int_0^\pi w(t-1,y)\exp\{-w(t-1,y)\} \\ \times\left[1 + \displaystyle\sum_{n=1}^{+\infty}\big(\cos n(x+y) + \cos n(x-y)\big)\mathrm{e}^{-\alpha n^2}\right]\mathrm{d}y, \quad x \in [0,\pi], \\ \dfrac{\partial w(t,0)}{\partial x} = \dfrac{\partial w(t,\pi)}{\partial x} = 0. \end{cases} \tag{1.6}$$

As such, in the rest of this paper we only need to focus on the boundary value problem (1.6) in the range $\beta \in (e^2, \infty)$.

Section 2 is devoted to a thorough Hopf bifurcation analysis for (1.6), using $\beta \in (e^2, \infty)$ as a bifurcation parameter. We show that there is a sequence of critical values for β at which Hopf bifurcations occur. Among these critical values, the first one presents Hopf bifurcation generating *spatially homogeneous* periodic solutions around the spatially homogeneous positive steady state $E^+(\beta)$, while the rest give rise to periodic solutions that are *spatially inhomogeneous*, demonstrating various spatial patterns. By applying the centre manifold theory and the normal form method, we are also able to provide, in the appendix, an explicit algorithm for determining the direction of the Hopf bifurcation and stability of the bifurcating periodic solutions. We also study the dependence of Hopf bifurcation points and the bifurcated oscillations on some model parameters including the diffusion rates of the mature and immature populations. We prove that there exist spatially heterogeneous periodic solutions which are $\cos(nx)$-perturbations of $E^+(\beta)$; and show that for some parameter values, they can be stable on the centre manifold but unstable in the whole phase space. Therefore, *generically* (1.6) only allows transient spatial patterns. In section 3, we present numerical simulations which demonstrate our theoretical results; in particular, the simulations show that a solution with a $\cos(nx)$-like initial function tends to a $\cos(nx)$-like time-periodic solution in a relatively long time, and then it eventually converges to a spatially homogeneous periodic solution. The numerical simulations shows that the non-locality caused by the mobility of the immature population (measured by α) will shorten the duration of such transient spatial patterns, and to our best knowledge, this is the first time that such an effect is observed/reported.

To end this introduction, we point out that Gourley and Ruan [4] generalized (1.5) to the following equation by introducing distributed delay

$$\frac{\partial w(t,x)}{\partial t} = D_m \frac{\partial w^2(t,x)}{\partial x^2} - \mathrm{d}w(t,x) + \varepsilon b \left(\int_{-\infty}^{0} f(s) w(t+s,x)\, \mathrm{d}s \right). \quad (1.7)$$

Hu and Yuan [8] further generalized (1.7) to a spatially non-local version

$$\frac{\partial w(t,x)}{\partial t} = D_m \frac{\partial w^2(t,x)}{\partial x^2} - \mathrm{d}w(t,x) + \varepsilon b \left(\int_{-\infty}^{0} \int_{\Omega} f(s,x,y) w(t+s,y)\, \mathrm{d}y\, \mathrm{d}s \right). \quad (1.8)$$

In both [4, 8], by using delay as the bifurcation parameter, the authors considered Hopf bifurcations at the positive constant steady state, but only explored *spatially homogeneous* periodic solutions. Note that for a PDE system subject to zero-flux boundary condition, a bifurcated *spatially homogeneous* periodic solution can also be bifurcated in the corresponding kinetic equation (equation without diffusion), the effect of diffusion cannot be reflected by such bifurcations. Overall, *spatially inhomogeneous* time-periodic solutions in reaction–diffusion systems subject to zero-flux boundary condition have been overlooked. The recent work Yi *et al* [33] is an exception, where for a PDE model without delay, the authors observed that the bifurcated *spatially inhomogeneous* periodic solution are unstable. But here we have gone further by showing that such a *spatially inhomogeneous* periodic solution can be stable in the corresponding centre manifold, and can be numerically observable in a relatively long time period if the initial distribution is close to the central manifold (being a $\cos nx$-like shape). We would also like to point out that the system (1.8) was *proposed* as a mathematical generalization of (1.7), and hence, of (1.5); our model (1.6) is *rigorously derived* from the standard age structured PDE model (1.3), and thus, all terms and parameters in (1.6) have clear biological explanations.

2. Characteristic equations and Hopf bifurcations

In this section, we study the local stability of the spatially homogeneous positive steady state and Hopf bifurcations for (1.6). Unlike in [4, 8] where delay was used as the bifurcation parameter, we will use β as the bifurcation parameter.

Denote $X := \{\phi \in W^{2,2}(0,\pi), \phi'(0) = \phi'(\pi) = 0\}$ and let $C = C([-1,0], X)$ be the Banach space of continuous X-values functions on $[-1,0]$ equipped with the sup norm. From [29] or [7], (1.6) with the following initial condition

$$w(t,x) = \eta(\theta,x) \in C\big([-1,0],\quad W^{1,2}(0,\pi)\big),\qquad t \in [-1,0]$$

have a unique local solution. By an easy calculation we know that (1.6) has a spatially homogeneous steady state $E^+ = \ln\beta$. Since we always assume that $\beta > \mathrm{e}^2$ in the rest of this paper, it follows that E^+ is indeed a positive steady state. The linearization of (1.6) about E^+ is

$$\begin{cases} \dfrac{\partial w(t,x)}{\partial t} = D_m \dfrac{\partial^2 w(t,x)}{\partial x^2} - \tau w(t,x) + \dfrac{(1-\ln\beta)\tau}{\pi}\left(\displaystyle\int_0^\pi w(t-1,y)\right. \\ \left.\times\left[1 + \sum_{n=1}^{+\infty}\big(\cos n(x+y) + \cos n(x-y)\big)\mathrm{e}^{-\alpha n^2}\right]\mathrm{d}y,\qquad x\in[0,\pi],\quad t>0 \\ \dfrac{\partial w(t,0)}{\partial x} = \dfrac{\partial w(t,\pi)}{\partial x} = 0,\qquad t>0. \end{cases} \tag{2.1}$$

It is well known that the eigenvalue problem

$$\phi''(x) = \nu\phi(x),\qquad \phi'(0) = \phi'(\pi) = 0,$$

has eigenvalues $\nu = -n^2$, $n \in \mathbb{N}_0$, with the corresponding normalized eigenfunctions $\rho_n\cos(nx)$, where $\rho_0 = \sqrt{1/\pi}$ and $\rho_n = \sqrt{2/\pi}$ for $n > 0$, and $\{\rho_n\cos(nx)\}_{n=0}^{\infty}$ forms a complete and orthonormal basis for X. Here and in the sequel, we follow the tradition to denote by $\mathbb{N}$ the set of all natural numbers and $\mathbb{N}_0 = \mathbb{N}\bigcup\{0\}$.

To explore the stability of E^+, we plug the trial function $w(t,x) = \mathrm{e}^{\lambda t}\phi(x)$ into (2.1). Before this, we note that $\phi(x)$ can be expressed in terms of $\{\rho_n\cos(nx)\}_{n=0}^{\infty}$ as

$$\phi(x) = \sum_{n=0}^{+\infty} c_n\rho_n\cos(nx).$$

Making use of the orthogonality of $\{\rho_n\cos(nx)\}_{n=0}^{\infty}$ after plugging, we are led to

$$c_n\big(\lambda + \tau + D_m n^2 - \tau(1-\ln\beta)\mathrm{e}^{-\lambda}\mathrm{e}^{-\alpha n^2}\big) = 0,\qquad n\in\mathbb{N}_0. \tag{2.2}$$

Denote $\Delta_n(\lambda) = \lambda + \tau + D_m n^2 - \tau(1-\ln\beta)\mathrm{e}^{-\lambda}\mathrm{e}^{-\alpha n^2}$. Note that $\phi(x)$ is non-trivial if and only if $c_n \neq 0$ for some $n \in\in \mathbb{N}_0$, implying that λ is an eigenvalue of the linearization equation (2.1) if and only if there exists $n \in \mathbb{N}_0$ such that $\Delta_n(\lambda) = 0$. Thus, (2.1) has the following set of characteristic equations:

$$\Delta_n(\lambda) = 0,\qquad n\in\mathbb{N}_0. \tag{2.3}$$

It is easy to see that $\lambda = 0$ is not an eigenvalue. If $\lambda = \pm\mathrm{i}\omega$ $(\omega > 0)$ are the solutions of (2.3), then substituting it into (2.3) and separating the real and imaginary parts, we obtain the following equations

$$\begin{cases} \omega = \tau(\ln\beta - 1)\mathrm{e}^{-\alpha n^2}\sin\omega, \\ \tau + D_m n^2 = \tau(1-\ln\beta)\mathrm{e}^{-\alpha n^2}\cos\omega, \end{cases}\qquad n\in\mathbb{N}_0. \tag{2.4}$$

For fixed τ, D_m and α, let $\omega_n^j \in (\frac{\pi}{2} + 2j\pi, \pi + 2j\pi)$ be the solution of the following equation

$$\tan\omega = -\frac{\omega}{\tau + D_m n^2},\qquad n\in\mathbb{N}_0,\quad j\in\mathbb{N}_0 \tag{2.5}$$

and

$$\beta_n^j = \exp\left\{1 - \frac{\tau + D_m n^2}{\tau e^{-\alpha n^2} \cos \omega_n^j}\right\}, \qquad n \in \mathbb{N}_0, \quad j \in \mathbb{N}_0. \tag{2.6}$$

From the definitions of ω_n^j and β_n^j, we know that $\pm i\omega_n^j$ are the roots of $\Delta_n(\lambda) = 0$ with $\beta = \beta_n^j$ and β_n^j can also be expressed as

$$\beta_n^j = \exp\left\{1 + \frac{\omega_n^j}{\tau e^{-\alpha n^2} \sin \omega_n^j}\right\}, \qquad n \in \mathbb{N}_0, \quad j \in \mathbb{N}_0. \tag{2.7}$$

It is obvious that w_n^j is increasing in τ and D_m for $n \in \mathbb{N}$ and $j \in \mathbb{N}_0$, and is independent of α, and $\beta_0^0 > e^2$. From the above discussions, we can easily obtain following further information about w_n^j and β_n^j.

Lemma 2.1. *The following statements hold.*

(i) $\pm i\omega_n^j, \ \ n \in \mathbb{N}_0, \ \ j \in \mathbb{N}_0$ *are the purely imaginary roots of (2.3) with* $\beta = \beta_n^j$*, and (2.3) has no other purely imaginary root*

(ii) *For any fixed* $n \in \mathbb{N}_0$, $\beta_n^j < \beta_n^k$ *if* $j < k$. *For any fixed* $j \in \mathbb{N}_0$, $\beta_n^j < \beta_m^j$ *if* $n < m$. *Therefore,* $\beta_n^j < \beta_m^k$ *if* $n \leqslant m$, $j \leqslant k$ *and* $(n, j) \neq (m, k)$

(iii) $\beta_0^j, \ \ j \in \mathbb{N}_0$ *is independent on* D_m *and* α. *For any fixed* $n \in \mathbb{N}$ *and* $j \in \mathbb{N}_0$, β_n^j *is a increasing function of* D_m *and* α.

Let $\lambda(\beta) = \gamma(\beta) + i\omega(\beta)$ be the root of (2.3) satisfying $\gamma(\beta_n^k) = 0$ and $\omega(\beta_n^k) = \omega_n^k$, when β is close to β_n^k, for $n \in \mathbb{N}_0, \ k \in \mathbb{N}_0$. Then we have the following transversality result.

Lemma 2.2. $\gamma'(\beta_n^k) > 0$*, for any* $n \in \mathbb{N}_0, \ k \in \mathbb{N}_0$.

Proof. Taking the derivative on both side of (2.3) with respect to β, and replacing β by β_n^k, we have

$$\frac{d\lambda}{d\beta}(\beta_n^k) = \frac{-\tau e^{-i\omega_n^k} e^{-\alpha n^2}}{\beta_n^k[1 + \tau(1 - \ln \beta_n^k) e^{-i\omega_n^k} e^{-\alpha n^2}]}. \tag{2.8}$$

Using the fact that $\lambda = i\omega_n^k$ is the solution of (2.3), replacing $\tau(1 - \ln \beta_n^k) e^{-i\omega_n^k} e^{-\alpha n^2}$ by $i\omega_n^k + \tau + D_m n^2$ and matching the real parts of both sides of the resulting equation yields

$$\gamma'(\beta_n^k) = -\frac{\tau e^{-\alpha n^2}[\cos \omega_n^k (1 + \tau + D_m n^2) - \omega_n^k \sin \omega_n^k]}{\beta_n^k[(1 + \tau + D_m n^2)^2 + (\omega_n^k)^2]} > 0. \tag{2.9}$$

□

From lemmas 2.1 and 2.2 and using the result of Ruan and Wei [18, corollary 2.4], we now are in the position to state a conclusion on the distribution of roots of (2.3).

Lemma 2.3. *The following statements hold.*

(i) *If* $\beta \in (e^2, \beta_0^0)$ *(note that* $\beta_0^0 > e^2$*), then all roots of (2.3) have negative real parts.*

(ii) *For* $n \in \mathbb{N}_0$, *(2.3) has purely imaginary roots if and only if* $\beta = \beta_n^j, \ \ j \in \mathbb{N}_0$. *When* $\beta = \beta_0^0$, *all the roots of (2.3), except* $\pm i\omega_0^0$, *have negative real parts.*

(iii) *If* $\beta > \beta_0^0$, *then (2.3) has at least one pair of roots with positive real parts.*

The following result on the stability of the spatially homogeneous steady state $E^+ = \ln \beta$ follows directly from the above lemma.

Theorem 2.4. *For any fixed* τ*, the spatially homogeneous steady state* $E^+ = \ln\beta$ *is asymptotically stable when* $\beta \in (e^2, \beta_0^0)$ *and unstable when* $\beta > \beta_0^0$*. Moreover, (1.6) undergoes a Hopf bifurcation at* $w = \ln\beta$ *and* $\beta = \beta_0^0$*.*

Remark 2.5. The first Hopf bifurcation value β_0^0 is independent of diffusion coefficients D_m and α, so is the stability of the spatially homogeneous steady state E^+.

In what follows, we always impose the following assumption when we study Hopf bifurcations around $\beta = \beta_n^k$ for $k,\ n \in \mathbb{N}_0$.

(H_n^k) Equation $\Delta_n(\lambda) = 0$ with $\beta = \beta_n^k$ has only one pair of purely imaginary roots $\pm i\omega_n^k$.

This assumption is equivalent to the following condition due to lemma 2.1:

$(H_n^k)^*$ $\beta_n^k \neq \beta_m^j$, $\forall (m, j) \in \{(m, j) : m > n, j < k\} \cup \{(m, j) : m < n, j > k\}$.

With the above preparation, we have the following theorem.

Theorem 2.6. *If* $(H_n^k)^*$ *holds for* $n, k \in \mathbb{N}_0$*, then (1.6) undergoes a Hopf bifurcation at* $w = \ln\beta_n^k$ *when* $\beta = \beta_n^k$*, and the bifurcating periodic solutions can be written as*

$$w(t, x) = \ln\beta + 2\sqrt{-\frac{(\beta - \beta_n^k)\gamma'(\beta_n^k)}{\mathrm{Re}\{C_1^{nk}(0)\}}}\rho_n \cos\left(\frac{2\pi t}{T}\right)\cos(nx) + O(\beta - \beta_n^k), \tag{2.10}$$

where

$$T = \frac{2\pi}{\omega_n^k}\left[1 - \tau_2^{nk}\frac{\gamma'(\beta_n^k)(\beta - \beta_n^k)}{\mathrm{Re}\{C_1^{nk}(0)\}} + O\big((\beta - \beta_n^k)^2\big)\right],$$

$$\tau_2^{nk} = -\frac{1}{\omega_n^k}\left[\mathrm{Im}\{C_1^{nk}(0)\} - \frac{\mathrm{Re}\{C_1^{nk}(0)\}\omega'(\beta_n^k)}{\gamma'(\beta_n^k)}\right],$$

and $C_1^{nk}(0)$ *is a constant in the normal form which is calculated in the appendix.*

Proof. The existence of Hopf bifucation at $\beta = \beta_n^k$ directly follows from lemmas 2.1–2.2 and the expression (2.10), and the formulas for T and τ_2^{nk} are direct result of applying the centre manifold theorem in [3] and normal form method in [6], with detailed derivation given in the appendix. □

Remark 2.7. Based on the above discussions, we also have the following remarks.

(i) If (H_n^k) with $n \neq 0$ holds and $\mathrm{Re}C_1^{nk}(0) \neq 0$, then (1.6) admits spatially inhomogeneous periodic solutions with form (2.10) in a left or right neighbourhood of β_n^k. From expression (2.10), we see that at time t these solutions are $\cos(nx)$-perturbations of the spatially homogeneous steady state $\ln\beta$.

(ii) Using lemma (2.3)-(iii), we know that when $\beta > \beta_0$, an unstable manifold in a small neighbourhood of the steady state always exists. Therefore, all inhomogeneous periodic solutions arising from local Hopf bifurcations are unstable in the phase space. But its stability on the centre manifold is determined by the sign of the corresponding $\mathrm{Re}C_1^{nk}(0)$.

(iii) From lemma (2.1), we see that for any fixed $n \geqslant 1$ the critical value β_n^0, from which $\cos(nx)$-like time-periodic solutions are bifurcated, is increasing both with respect to the mature diffusion coefficients D_m and in the immature mobility constant α. Therefore, increasing α may will enlarge β_n^0 and therefore, may help eliminate $\cos(nx)$-like oscillations in time around the steady state.

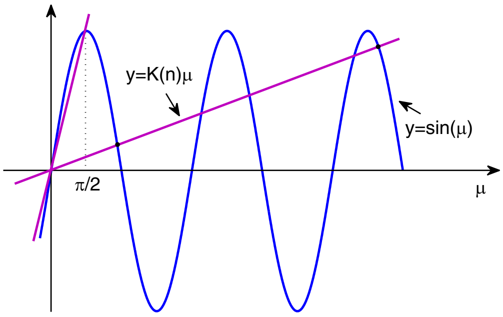

Figure 1. Illustration of the solution of the first equation of (2.11)

Next we explore in more detail the impact of the mature diffusion rate D_m on the existence of imaginary roots in spatially inhomogeneous periodic solutions. To this end, we use D_m as a parameter. We have seen from lemmas 2.1 and 2.3 that if $\beta \leqslant \beta_0^0$, then (2.3) has no purely imaginary roots for all $D_m > 0$ and $\alpha \geqslant 0$. Thus, in the sequel we only need to consider those $\beta > \beta_0^0$ with $\beta \neq \beta_0^j$, since $\beta_0^j,\ \ j \in \mathbb{N}$ are critical values for β that are independent of D_m at which, only spatially homogeneous periodic solutions are bifurcated. For convenience, we set $M = \{\beta : \ \beta > \beta_0^0 \text{ and } \beta \neq \beta_0^j,\ \ j \in \mathbb{N}\}$.

Assume that $\lambda = \pm \mathrm{i}\mu$ are a pair of purely imaginary roots of $\Delta_n(\lambda) = 0$. Then, the real parts in the equation $\Delta_n(\mathrm{i}\mu) = 0$ lead to

$$K(n)\mu = \sin(\mu) \tag{2.11}$$

and the imaginary parts result in

$$(\tau + D_m n^2)K(n) = -\cos(\mu) \tag{2.12}$$

where

$$K(n) = \frac{\mathrm{e}^{\alpha n^2}}{\tau(\ln\beta - 1)}.$$

Note that $K(n) > 0$ (since $\beta \in M$) and $K(n)$ is increasing in n with $K(\infty) = \infty$ if $\alpha > 0$. Thus, if $K(1) \geqslant 2/\pi$, then (2.11) cannot have any root $\mu > 0$ at which $\cos\mu < 0$ (see figure 1), implying that $\Delta_n(\lambda) = 0$ cannot have purely imaginary roots for all $n \in \mathbb{N}$.

When $K(1) < 2/\pi$, there is an $N \geqslant 1$ such that $K(n) < 2/\pi$ for $n \leqslant N$ and $K(n) \geqslant 2/\pi$ for $n > N$. In such a case, for each $n \leqslant N$, define

$$I_n = \max\left\{j \in \mathbb{N}_0 : \ (2.11) \text{ has a solution } \ \mu_n^j \ \text{ in the interval } \ (\pi/2 + 2j\pi, \pi + 2j\pi)\right\}. \tag{2.13}$$

Then, for $0 \leqslant j < k \leqslant I_n$, we have

$$-\cos(\mu_n^0) \geqslant -\cos(\mu_n^j) > -\cos(\mu_n^k) \geqslant -\cos(\mu_n^{I_n}).$$

Note that

$$(\tau + D_m n^2)K(n) = \frac{\mathrm{e}^{\alpha n^2}(\tau + D_m n^2)}{\tau(\ln\beta - 1)} > \frac{\mathrm{e}^{\alpha}(\tau + D_m)}{\tau(\ln\beta - 1)} > \frac{\mathrm{e}^{\alpha}}{\ln\beta - 1}.$$

Thus, if

$$\frac{\mathrm{e}^{\alpha}}{\ln\beta - 1} \geqslant -\cos(\mu_n^0) \tag{2.14}$$

then none of the μ_n^j, $j = 0, 1, \cdots, I_n$, can satisfy (2.12), implying that (2.3) cannot have purely imaginary roots for $D_m > 0$. On the other hand, if (2.14) is reversed, i.e.,

$$\frac{\mathrm{e}^{\alpha}}{\ln\beta - 1} < -\cos(\mu_n^0), \tag{2.15}$$

then, there exists a $J_n \in \mathbb{N}$ with $J_n < I_n$ such that

$$(D_m)_n^j := [\tau(1-\ln\beta)\cos(\mu_n^j)\mathrm{e}^{-\alpha n^2} - \tau](n^2)^{-1} > 0. \tag{2.16}$$

In other words, μ_n^j also satisfies (2.12) when $D_m = (D_m)_n^j$ for $0 \leqslant j \leqslant J_n$, meaning that $i\mu_n^j$, $0 \leqslant j \leqslant J_n$, are roots of (2.3). One can also easily see that for any fixed $n \leqslant N$, $(D_m)_n^j < (D_m)_n^k$, if j, $k \leqslant J_n$ with $j > k$; and for any fixed $j \leqslant J_n$, $(D_m)_n^j < (D_m)_m^j$, if $m < n \leqslant N$.

Summarizing the above analysis and noting that $K(1) \geqslant 2/\pi$ is equivalent to $\beta \leqslant \exp(\frac{\pi}{2\tau}\mathrm{e}^{\alpha} + 1)$, we obtain the following lemma.

Lemma 2.8. *The following statements hold.*

(i) When $\beta \leqslant \exp(\frac{\pi}{2\tau}\mathrm{e}^{\alpha} + 1)$, (2.3) has no purely imaginary root for any $D_m > 0$.

(ii) When $\beta > \exp(\frac{\pi}{2\tau}\mathrm{e}^{\alpha} + 1)$, there exists an $N > 1$ such that for every $n \leqslant N$, I_n in (2.13) is well-defined. Moreover,

(ii)-1 if $(1-\ln\beta)\cos(\mu_1^0)\mathrm{e}^{-\alpha} \leqslant 1$, then (2.3) has no purely imaginary root for any $D_m > 0$;

(ii)-2 if $(1-\ln\beta)\cos(\mu_1^0)\mathrm{e}^{-\alpha} > 1$, then there exists an $J_n \in \mathbb{N}$ with $J_n < I_n$ such that $(D_m)_n^j$ given by (2.16) is positive for $0 \leqslant j \leqslant J_n$, and $\mathrm{i}\mu_n^j$, $0 \leqslant j \leqslant J_n$, are roots of (2.3) for $D_m = (D_m)_n^j$.

In the case of (ii)-2, for any fixed $1 \leqslant n \leqslant N$, let $\lambda(D_m) = \xi(D_m) + \mathrm{i}\mu(D_m)$ be the root of $\Delta(\lambda, n) = 0$ satisfying $\xi((D_m)_n^k) = 0$ and $\mu((D_m)_n^k) = \mu_n^k$, when D_m is close to $(D_m)_n^k$, for $0 \leqslant k \leqslant J_n$. A calculation similar to the proof of lemma 2.2 verifies the transversality condition as stated below.

Lemma 2.9. *For any fixed $1 \leqslant n \leqslant N$, $\xi'((D_m)_n^k) < 0$, $\forall\, k = 0, \ldots, J_n$.*

By the above two lemmas, we have the following theorem confirming the bifurcation of spatially inhomogeneous periodic solutions, in terms of the diffusion rate D_m.

Theorem 2.10. *In addition to the assumptions for (ii)-2 in lemma 2.8, further assume that except for the pair $\lambda = \pm\mathrm{i}\mu_n^k$, there is no other purely imaginary root for the characteristic equation $\Delta_n(\lambda) = 0$ when $D_m = (D_m)_n^k$. Then (1.6) undergoes a Hopf bifurcation at $w = \ln\beta$ at $D_m = (D_m)_n^k$, and the bifurcating periodic solutions can be written as*

$$w(t,x) = \ln\beta + 2\sqrt{-\frac{(D_m - (D_m)_n^k)\xi'(0)}{\mathrm{Re}\{\tilde{C}_1^{nk}(0)\}}}\rho_n \cos\left(\frac{2\pi t}{\tilde{T}}\right)\cos(nx) + O(D_m - (D_m)_n^k), \tag{2.17}$$

with

$$\tilde{T} = \frac{2\pi}{\mu_n^k}\left[1 - \tilde{\tau}_2^{nk}\frac{\xi'((D_m)_n^k)(D_m - (D_m)_n^k)}{\mathrm{Re}\{\tilde{C}_1^{nk}(0)\}} + O\big((D_m - (D_m)_n^k)^2\big)\right],$$

$$\tilde{\tau}_2^{nk} = -\frac{1}{\mu_n^k}\left[\mathrm{Im}\{\tilde{C}_1^{nk}(0)\} - \frac{\mathrm{Re}\{\tilde{C}_1^{nk}(0)\}\mu'((D_m)_n^k)}{\xi'((D_m)_n^k)}\right],$$

where $\tilde{C}_1^{nk}(0)$ is given by the same formula (4.22) as for $C_1^{nk}(0)$ in the appendix with β_n^k being replaced by β and D_m replaced by $(D_m)_n^k$.

Remark 2.11. From lemma 2.8-(i), for any fixed β and τ, Hopf bifurcation will not occur for large $\alpha = \int_0^{\tau} D(a)\,\mathrm{d}a$. This suggests that large diffusion rate of immature individuals tends to destroy spatially inhomogeneous patterns. Also note that $(D_m)_n^k < (D_m)_m^k$, for $m < n \leqslant N$. This implies that the smaller D_m may lead to more complicated spatial patterns.

Table 1. Critical values.

n	ω_n^0	β_n^0	β_n^1	$\mathrm{Re}C_1^{n0}(0)$
0	2.4556	9.8976	49.9956	−1.6299
1	2.4570	10.0561	—	−1.7625
2	2.4611	10.5590	—	−1.6715
3	2.4677	11.4993	—	−1.5284
4	2.4768	13.0730	—	−1.3409

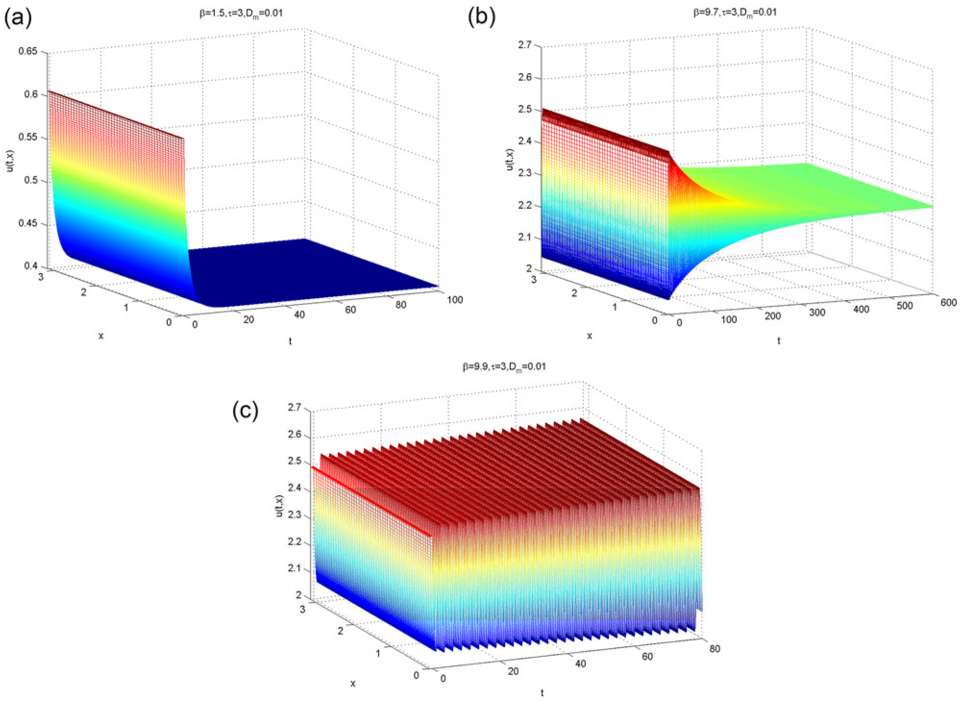

Figure 2. Numerical simulations of (1.6) with $\tau = 3$, $D_m = 0.01$, $\alpha = 0$ and initial function $\ln\beta + 0.2$. (*a*) $\beta = 1.5$, the solution approaches to the steady state. (*b*) $\beta = 9.7$, the solution still approaches to the steady state but with noticeable oscillations. (*c*) $\beta = 9.9$, the solution tends to a spatially homogeneous periodic solution.

3. Numerical analysis and discuss

In this section we present some numerical simulations for (1.6) to illustrate the obtained analytic results.

Firstly, we choose $\alpha = 0$, $\tau = 3$ and $D_m = 0.01$. By using formulas (2.5), (2.6), (4.21) and (4.22), we can obtain table 1 for the related critical values of bifurcations. Note that $\beta_0^1 = 49.9956$, which is greater than all β_n^0 for $n \leqslant 4$. It follows that assumption (H_n^0) holds for $n \leqslant 4$. Therefore, from the theoretic results in the last section, we see that for (1.6) the spatially homogeneous steady state is asymptotically stable if $\beta < 9.8976$ and unstable if $\beta > 9.8976$. Moreover, stable spatially homogeneous periodic solutions occur when β crosses through 9.8976 and $\cos(nx)$-like, $n = 1, 2, 3, 4$ periodic solutions appear when β crosses through 10.0561, 10.5590, 11.4993 and 13.0730, respectively, and they are stable on the centre manifolds.

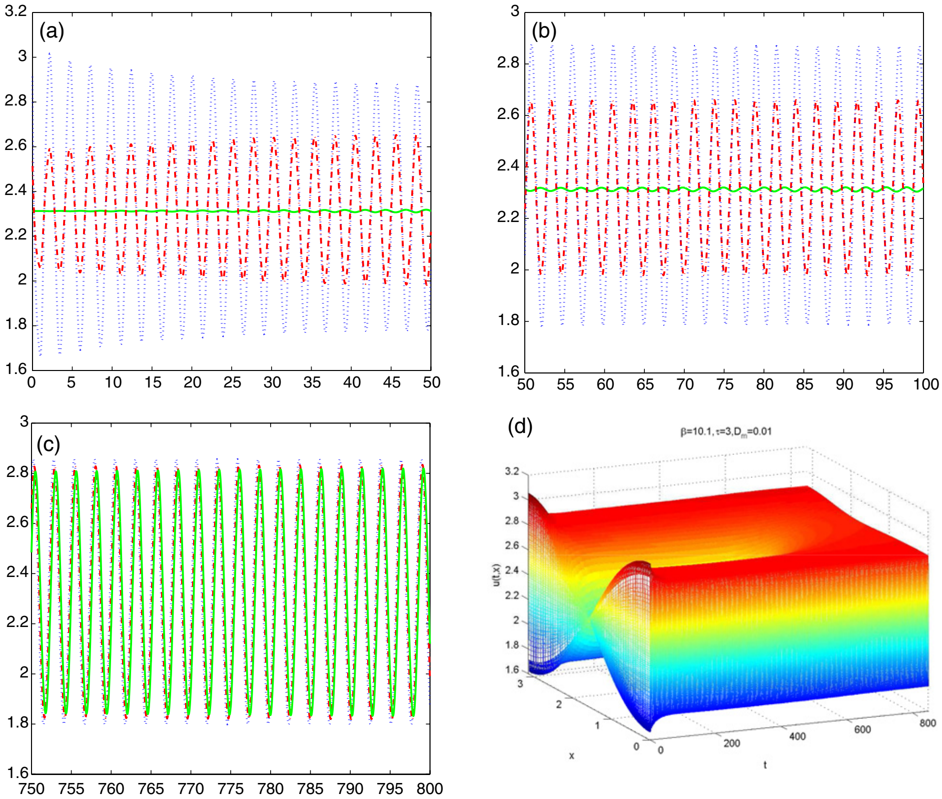

Figure 3. Numerical simulations of (1.6) with $\tau = 3$, $D_m = 0.01$, $\beta = 10.1$, $\alpha = 0$ and initial function $\ln\beta + 0.6\cos(x)$. (*a*), (*b*) and (*c*) describe the solution in locations $x = 0$ (blue), $x = \frac{\pi}{2}$ (green) and $x = \frac{2\pi}{5}$ (red); (*d*) solution follows a $\cos(x)$-like periodic pattern with time period 2.56 which is close to $\frac{2\pi}{\omega_1^0} = 2.5572$ first, then approaches a homogeneous periodic solution, demonstrating transient oscillatory patterns.

When $1 < \beta < \beta_0^0$ the spatially homogeneous steady state is asymptotically stable, as shown in figures 2(*a*) and (*b*). When β crosses through β_0^0, Hopf bifurcation occurs and the bifurcated periodic solutions are stable as shown in figure 2(*c*). Besides, the bifurcated periodic solution is spatially homogeneous.

In figure 3, we use the initial function which is a $\cos(x)$-perturbation of the spatially homogeneous steady state. Figure 3(*a*) plots the solutions at $x = 0$ (blue), $x = \frac{\pi}{2}$ (green) and $x = \frac{2\pi}{5}$ (red) in the time interval [0, 50]. Figures 3(*b*) and (*c*) are for time intervals [50, 100] and [750, 800], respectively. Figure 3 shows that the solution is spatially inhomogeneous at first, and then it tends to a $\cos(x)$-like periodic solution as shown in figure 3(*d*). Further, the period of the periodic solution is about 2.56 which is close to the period of the bifurcated periodic solution $\frac{2\pi}{\omega_1^0} = 2.5572$ (see figure 3(*b*)). Moreover, the solution approaches to a spatially homogeneous periodic solution with the same period after around time 700.

Since the $\cos(nx)$-like bifurcated periodic solutions are stable on the centre manifolds, we can see from figures 4 and 5(*b*) that they can be observed for a relatively long period if we choose a perturbation of $\cos(nx)$ as the initial function, when the parameter β crosses

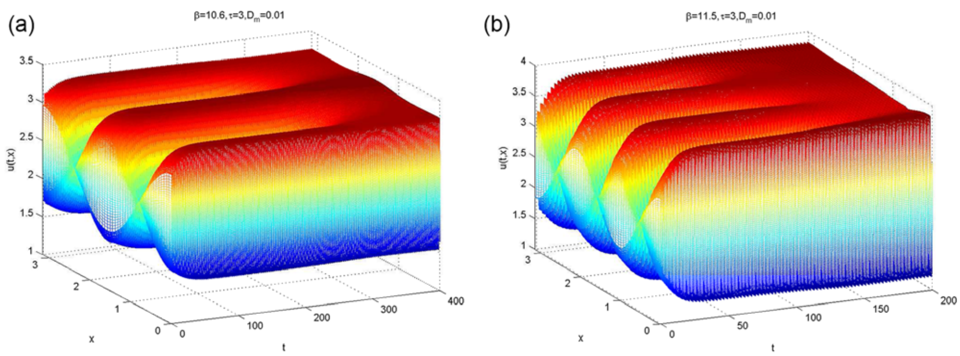

Figure 4. Numerical simulations of (1.6) with $\tau = 3$, $D_m = 0.01$ and $\alpha = 0$. (a) $\beta = 10.6$, initial function $\ln\beta + 0.6\cos(2x)$, the solution follows a $\cos(2x)$-like pattern for some time and then approaches a uniform periodic solution. (b) $\beta = 11.5$, initial function $\ln\beta + 0.6\cos(3x)$, the solution follows a $\cos(3x)$-like pattern for some time and then tends to a uniform periodic solution.

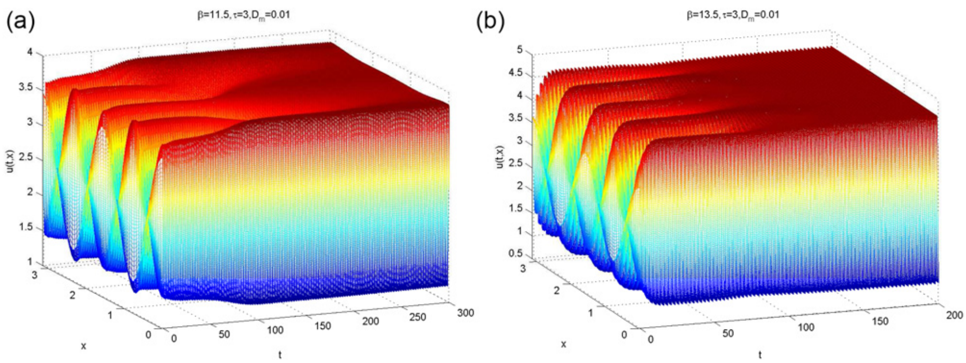

Figure 5. Numerical simulations of (1.6) with $\tau = 3$, $D_m = 0.01$ and $\alpha = 0$. (a) $\beta = 11.5$, initial function $\ln\beta + \cos(4x)$, the solution directly approaches to a uniform periodic solution. (b) $\beta = 13.5$, the solution follows a $\cos(4x)$-like periodic pattern for some time before approaching a homogeneous periodic solution.

through the critical values β_n^0. Figure 5(a) shows that a solution with initial function being a $\cos(4x)$-perturbation of the steady state will not converge to any $\cos(4x)$-like periodic solution, instead it will tend to a spatially homogeneous periodic solution directly when β is less than the critical value β_4^0. Figures 3, 4 and 5 suggest that the spatially homogeneous periodic solution exists for a wide range of the parameter β and it is stable.

Now, we explore the effect of the non-locality caused by the mobility of the immature population. To this end, we choose $\alpha = 0.1$, $\tau = 3$ and $D_m = 0.01$. Similarly, we can obtain table 2 for related critical values of bifurcations. From table 2 and the theoretic results we know that: for (1.6) the spatially homogeneous steady state is asymptotically stable if $\beta < 9.8976$ and unstable if $\beta > 9.8976$; $\cos(nx)$-like, $n = 1, 2$, periodic solutions appear when β crosses through 11.3744 and 19.0092, respectively, and they are stable in on the corresponding centre manifolds.

In figure 6, we use a $\cos(x)$-perturbation of the spatially homogeneous steady state as the initial function. Figures 6(a) and (b) illustrate that the spatially homogeneous steady state is

Table 2. Critical values.

n	ω_n^0	β_n^0	β_n^1	$\mathrm{Re}C_1^{n0}(0)$
0	2.4556	9.8976	49.9956	−1.6299
1	2.4570	11.3744	—	−1.5036
2	2.4611	19.0092	—	−0.8333
3	2.4677	69.5551	—	—

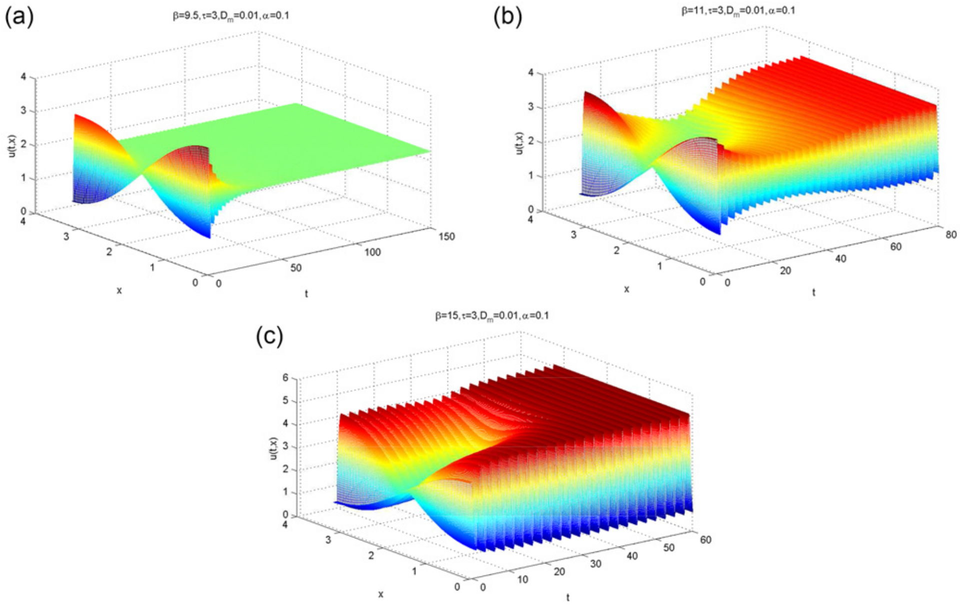

Figure 6. Numerical simulations of (1.6) with $\tau = 3$, $D_m = 0.01$, $\alpha = 0.1$ and initial function $\ln\beta + 1.5\cos(x)$. (*a*) $\beta = 9.5$, the solution approaches to the steady state. (*b*) $\beta = 10$, the solution tends to a spatially homogeneous periodic solution. (*c*) $\beta = 15$, the solution first follows a $\cos(x)$-like inhomogeneous periodic solution for some time and then approaches a uniform periodic solution.

asymptotically stable if $\beta < 9.8976$ and unstable if $\beta > 9.8976$, respectively. Figure 6(*b*) further illustrates that there is no transient spatial pattern if $\beta < 11.3744$. Figure 6(*c*) shows that the solution follows a spatially inhomogeneous and time-periodic pattern for some time before it eventually converges to a spatially homogeneous periodic solution. Comparing the numerical results for $\alpha = 0$ and $\alpha = 0.1$, we find that the spatial non-locality may shorten the duration of the transient spatial patterns.

Acknowledgments

The authors would like to thank the anonymous referees for their comments which led to an improvement in the presentation of the paper. Research supported by the Natural Science and Engineering Council of Canada and National Natural Science Foundation of China (no. 11201096).

Appendix: Normal form

Assume (H_n^k) holds and let $\beta = \beta_n^k + \mu,\ \mu \in \mathbb{R}$. Then $\mu = 0$ is a Hopf bifurcation value for (1.6). For $\phi \in C$, denote

$$L_\mu \phi := -\tau\phi(0) + \frac{(1 - \ln(\beta_n^k + \mu))\tau}{\pi} \times \int_0^\pi \phi(-1)\left[1 + \sum_{n=1}^{+\infty}\big(\cos n(x+y) + \cos n(x-y)\big)\mathrm{e}^{-\alpha n^2}\right]\mathrm{d}y,$$

$$f_\mu \phi := \frac{\tau}{\pi}\left\{\int_0^\pi \left[\left(\frac{1}{2}\ln(\beta_n^k + \mu) - 1\right)\phi^2(-1) + \left(\frac{1}{2} - \frac{1}{6}\ln(\beta_n^k + \mu)\right)\phi^3(-1) + O\big(\phi^4(-1)\big)\right]\right. \times \left[1 + \sum_{n=1}^{+\infty}\big(\cos n(x+y) + \cos n(x-y)\big)\mathrm{e}^{-\alpha n^2}\right]\mathrm{d}y,$$

$A(\mu)\phi = \dot\phi + X_0[L_\mu(\phi) + D_m \frac{\partial^2 \phi}{\partial x^2}(0) - \dot\phi(0)]$ and $R(\mu)\phi := X_0 f_\mu(\phi)$, where

$$X_0 = \begin{cases} 0, & \theta \in [-1, 0) \\ 1, & \theta = 0. \end{cases}$$

Then (1.6) can be rewrite as the following

$$w'(t) = A(\mu)w_t + R(\mu)w_t, \tag{4.1}$$

where '′' is the derivative with respect to t and $w_t = w(t+\theta)$ for $\theta \in [-1, 0]$.

For $\psi \in C([0, 1], X)$ and $\phi \in C([-1, 0], X)$, we define a bilinear form as following

$$(\psi, \phi) = \int_0^\pi \bar\psi(0)\phi(0)\,\mathrm{d}y + \int_{-1}^0\int_0^\pi \frac{(1 - \ln\beta_n^k)}{\pi}\left[\int_0^\pi \bar\psi(s+1, z)\right. \times \left[1 + \sum_{n=1}^{+\infty}\big(\cos m(y+z) + \cos m(y-z)\big)\mathrm{e}^{-\alpha n^2}\right]\mathrm{d}z\phi(s, y)\,\mathrm{d}y\,\mathrm{d}s. \tag{4.2}$$

In the rest of this section, we always use similar notations to those used in Hassard *et al* [6]. Define $q_{nk}(\theta) = \mathrm{e}^{\mathrm{i}\omega_n^k\theta}\rho_n\cos(nx)$, and $q_{nk}^*(s) = P_n^k \mathrm{e}^{\mathrm{i}\omega_n^k s}\rho_n\cos(nx)$, $n \in \mathbb{N}_0,\ k \in \mathbb{N}_0$, where

$$P_n^k = (1 + \tau + D_m n^2 - \mathrm{i}\omega_n^k)^{-1}.$$

Then by direct computations we have

$$(q_{nk}^*, q_{nk}) = (\bar q_{nk}^*, \bar q_{nk}) = 1 \quad \text{and} \quad (q_{nk}^*, \bar q_{nk}) = (\bar q_{nk}^*, q_{nk}) = 0.$$

Let w_t be the solution of (1.6) when $\mu = 0$ and define $z_{nk}(t) = (q_{nk}, w_t)$ and $W^{nk}(t, \theta, x) = w_t(\theta) - 2\mathrm{Re}\{z_{nk}(t)q_{nk}\}$. Using the definitions of z_{nk}, W^{nk} and the bilinear form, it is not difficult to verify that (1.6) is reduced to the following system:

$$\begin{cases} z_{nk}'(t) = \mathrm{i}\omega_n^k z_{nk} + \displaystyle\int_0^\pi \bar q_{nk}^*(0) f_0\,\mathrm{d}y, \\ (W^{nk})'(t) = A(0)W^{nk} - 2\mathrm{Re}\left\{\displaystyle\int_0^\pi \bar q_{nk}^*(0) f_0\,\mathrm{d}y q_{nk}(\theta)\right\} + X_0 f_0, \quad \theta \in [-1, 0], \end{cases} \tag{4.3}$$

where $f_0 = f_0\big(2\mathrm{Re}\{z_{nk}(t)q_{nk}\} + W(t, \theta)\big)$. Denote

$$g_{nk}(z_{nk}, \bar z_{nk}) = \int_0^\pi \bar q_{nk}^*(0) f_0\,\mathrm{d}y := g_{20}^{nk}\frac{z_{nk}^2}{2} + g_{11}^{nk} z_{nk}\bar z_{nk} + g_{02}^{nk}\frac{\bar z_{nk}^2}{2} + g_{21}^{nk}\frac{z_{nk}^2 \bar z_{nk}}{2} + \cdots. \tag{4.4}$$

Then, the Poincaré normal form for (1.6) has the following form:

$$z'_{nk} = \lambda(\mu)z + C_1^{nk}(\mu)z^2\bar{z} + \text{h.o.t.}, \tag{4.5}$$

and

$$C_1^{nk}(0) = \frac{\mathrm{i}}{2\omega_n^k}\left(g_{20}^{nk}g_{11}^{nk} - 2|g_{11}^{nk}|^2 - \frac{1}{3}|g_{02}^{nk}|^2\right) + \frac{g_{21}^{nk}}{2}. \tag{4.6}$$

To obtain the existence of the non-trivial periodic solutions, the only remaining thing is the calculations of C_1^{nk}.

Using the centre manifold theorem given in [3], we know that on the centre manifold $W^{nk}(t,\theta)$ has the following form

$$W^{nk} = W_{20}^{nk}(\theta,x)\frac{z_{nk}^2}{2} + W_{11}^{nk}(\theta,x)z_{nk}\bar{z}_{nk} + W_{02}^{nk}(\theta,x)\frac{\bar{z}_{nk}^2}{2} + \cdots. \tag{4.7}$$

By expanding the series and comparing the corresponding coefficients, we have

$$g_{20}^{nk} = \begin{cases} \dfrac{2\tau}{\sqrt{\pi}}\bar{P}_n^k\left(\dfrac{1}{2}\ln\beta_0^k - 1\right)\mathrm{e}^{-2\mathrm{i}\omega_0^k}, & n = 0\\ 0, & n \neq 0, \end{cases} \tag{4.8}$$

$$g_{02}^{nk} = \begin{cases} \dfrac{2\tau}{\sqrt{\pi}}\bar{P}_n^k\left(\dfrac{1}{2}\ln\beta_0^k - 1\right)\mathrm{e}^{2\mathrm{i}\omega_0^k}, & n = 0\\ 0, & n \neq 0, \end{cases} \tag{4.9}$$

$$g_{11}^{nk} = \begin{cases} \dfrac{2\tau}{\sqrt{\pi}}\bar{P}_n^k\left(\dfrac{1}{2}\ln\beta_0^k - 1\right), & n = 0\\ 0, & n \neq 0, \end{cases} \tag{4.10}$$

$$g_{21}^{0k} = \frac{2\tau}{\pi}\bar{P}_0^k\left(\frac{1}{2}\ln\beta_0^k - 1\right)\int_0^\pi [\mathrm{e}^{\mathrm{i}\omega_0^k}W_{20}^{0k}(-1) + 2\mathrm{e}^{-\mathrm{i}\omega_0^k}W_{11}^{0k}(-1)]\,\mathrm{d}y + \frac{\tau}{\pi}\bar{P}_0^k(3 - \ln\beta_0^k)\mathrm{e}^{-\mathrm{i}\omega_0^k} \tag{4.11}$$

and

$$\begin{aligned} g_{21}^{nk} = {} & \frac{8\tau}{\pi^2}\bar{P}_n^k\left(\frac{1}{2}\ln\beta_n^k - 1\right)\int_0^\pi \cos(ny)\int_0^\pi \cos(nz)\Bigg(\frac{1}{2}\mathrm{e}^{\mathrm{i}\omega_n^k}W_{20}^{nk}(-1)\\ & + \mathrm{e}^{-\mathrm{i}\omega_n^k}W_{11}^{nk}(-1)\Bigg)\sum_{m=1}^{+\infty}\big(\cos m(y+z) + \cos m(y-z)\big)\mathrm{e}^{-\alpha m^2}\,\mathrm{d}z\,\mathrm{d}y\\ & + \frac{9\tau}{\pi}\bar{P}_n^k\left(\frac{1}{2} - \frac{1}{6}\ln\beta_n^k\right)\mathrm{e}^{-\mathrm{i}\omega_n^k}\mathrm{e}^{-\alpha n^2}, \qquad n \neq 0. \end{aligned} \tag{4.12}$$

Next we calculate the centre manifold. Let

$$\begin{aligned} H_{nk}(z_{nk},\bar{z}_{nk},\theta) &= -2\mathrm{Re}\left\{\int_0^\pi \bar{q}_{nk}^*(0)f_0\,\mathrm{d}y q_{nk}(\theta)\right\} + X_0 f_0\\ &:= H_{20}^{nk}(\theta)\frac{z_{nk}^2}{2} + H_{11}^{nk}(\theta)z_{nk}\bar{z}_{nk} + H_{02}^{nk}(\theta)\frac{\bar{z}_{nk}^2}{2} + H_{21}^{nk}(\theta)\frac{z_{nk}^2\bar{z}_{nk}}{2} + \cdots. \end{aligned} \tag{4.13}$$

Expanding both sides of the second equation of (4.3) and comparing the corresponding coefficients, we can obtain that

$$(2\mathrm{i}\omega_n^k - A(0))W_{20}^{nk} = H_{20}^{nk}, \tag{4.14}$$

$$A(0)W_{11}^{nk} = -H_{11}^{nk}, \tag{4.15}$$

$$(2\mathrm{i}\omega_n^k + A(0))W_{02}^{nk} = -H_{02}^{nk}. \tag{4.16}$$

By comparing coefficients of the both sides of (4.13), we have that for $\theta \in [-1, 0)$,

$$H_{20}^{nk}(\theta) = -g_{20}^{nk} q_{nk}(\theta) - \bar{g}_{02}^{nk} \bar{q}_{nk}(\theta),$$
$$H_{11}^{nk}(\theta) = -g_{11}^{nk} q_{nk}(\theta) - \bar{g}_{11}^{nk} \bar{q}_{nk}(\theta).$$

Substituting the above equations into (4.14) and (4.15) respectively, leads to

$$\dot{W}_{20}^{nk}(\theta) = 2i\omega_n^k W_{20}^{nk}(\theta) + g_{20}^{nk}\rho_n \cos(nx)\mathrm{e}^{\mathrm{i}\omega_n^k\theta} + \bar{g}_{02}^{nk}\rho_n \cos(nx)\mathrm{e}^{-\mathrm{i}\omega_n^k\theta},$$
$$\dot{W}_{11}^{nk}(\theta) = g_{11}^{nk}\rho_n \cos(nx)\mathrm{e}^{\mathrm{i}\omega_n^k\theta} + \bar{g}_{11}^{nk}\rho_n \cos(nx)\mathrm{e}^{-\mathrm{i}\omega_n^k\theta}.$$

Solving the above equations, we obtain,

$$W_{20}^{nk}(\theta) = -\frac{g_{20}^{nk}}{\mathrm{i}\omega_n^k}\rho_n \cos(nx)\mathrm{e}^{\mathrm{i}\omega_n^k\theta} - \frac{\bar{g}_{02}^{nk}}{3\mathrm{i}\omega_n^k}\rho_n \cos(nx)\mathrm{e}^{-\mathrm{i}\omega_n^k\theta} + E^{nk}(x)\mathrm{e}^{2\mathrm{i}\omega_n^k\theta},$$

$$W_{11}^{nk}(\theta) = \frac{g_{11}^{nk}}{\mathrm{i}\omega_n^k}\rho_n \cos(nx)\mathrm{e}^{\mathrm{i}\omega_n^k\theta} - \frac{\bar{g}_{11}^{nk}}{\mathrm{i}\omega_n^k}\rho_n \cos(nx)\mathrm{e}^{-\mathrm{i}\omega_n^k\theta} + F^{nk}(x),$$

where $E^{nk}(x)$ and $F^{nk}(x)$ can be expressed as $E^{nk}(x) = \sum_{m=0}^{+\infty} E_m^{nk}\cos(mx)$ and $F^{nk}(x) = \sum_{m=0}^{+\infty} F_m^{nk}\cos(mx)$, respectively, and E_m^{nk} and F_m^{nk} $(m,\ n \in \mathbb{N}_0)$ are constants for fixed parameters. However,

$$H_{20}^{0k} = -g_{20}^{0k}\sqrt{\frac{1}{\pi}} - \bar{g}_{02}^{0k}\sqrt{\frac{1}{\pi}} + \frac{2\tau}{\pi}\left(\frac{1}{2}\ln\beta - 1\right)\mathrm{e}^{-2\mathrm{i}\omega_0^k}, \tag{4.17}$$

$$\begin{aligned} H_{20}^{nk} = &- g_{20}^{nk}\sqrt{\frac{2}{\pi}}\cos(nx) - \bar{g}_{02}^{nk}\sqrt{\frac{2}{\pi}}\cos(nx) + \frac{2\tau}{\pi}\left(\frac{1}{2}\ln\beta - 1\right)\mathrm{e}^{-2\mathrm{i}\omega_n^k} \\ &+ \frac{2\tau}{\pi}\left(\frac{1}{2}\ln\beta - 1\right)\mathrm{e}^{-2\mathrm{i}\omega_n^k}\mathrm{e}^{-4\alpha n^2}\cos(2nx), \qquad n \neq 0, \end{aligned} \tag{4.18}$$

$$H_{11}^{0k} = -g_{11}^{0k}\sqrt{\frac{1}{\pi}} - \bar{g}_{11}^{0k}\sqrt{\frac{1}{\pi}} + \frac{2\tau}{\pi}\left(\frac{1}{2}\ln\beta - 1\right), \tag{4.19}$$

$$\begin{aligned} H_{11}^{nk} = &- g_{11}^{nk}\sqrt{\frac{2}{\pi}}\cos(nx) - \bar{g}_{11}^{nk}\sqrt{\frac{2}{\pi}}\cos(nx) + \frac{2\tau}{\pi}\left(\frac{1}{2}\ln\beta - 1\right) \\ &+ \frac{2\tau}{\pi}\left(\frac{1}{2}\ln\beta - 1\right)\mathrm{e}^{-4\alpha n^2}\cos(2nx), \qquad n \neq 0. \end{aligned} \tag{4.20}$$

Substituting (4.17) and (4.19) into (4.14) and (4.15), respectively, we then have for $n = 0$,

$$E^{0k} = \frac{2\tau(\frac{1}{2}\ln\beta_0^k - 1)\mathrm{e}^{-2\mathrm{i}\omega_0^k}}{\pi[2\mathrm{i}\omega_0^k + \tau - (1 - \ln\beta_0^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_0^k}]} + \sum_{p=1}^{+\infty} E_p^{0k}\cos(px)$$

and

$$F^{0k} = \frac{2(\frac{1}{2}\ln\beta_0^k - 1)}{\pi\ln\beta_0^k} + \sum_{p=1}^{+\infty} F_p^{0k}\cos(px).$$

Similarly, we can obtain that for $n > 0$,

$$\begin{aligned} E^{nk} = &\frac{2\tau(\frac{1}{2}\ln\beta_n^k - 1)\mathrm{e}^{-2\mathrm{i}\omega_n^k}}{\pi[2\mathrm{i}\omega_n^k + \tau - (1 - \ln\beta_n^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_n^k}]} \\ &+ \frac{2\tau(\frac{1}{2}\ln\beta_n^k - 1)\mathrm{e}^{-2\mathrm{i}\omega_n^k}\mathrm{e}^{-4\alpha n^2}\cos(2nx)}{\pi[2\mathrm{i}\omega_n^k + 4D_m n^2 + \tau - (1 - \ln\beta_n^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_n^k}\mathrm{e}^{-4\alpha n^2}]} + \sum_{p=1,\,p\neq 2n}^{+\infty} E_p^{nk}\cos(px) \end{aligned}$$

and

$$F^{nk} = \frac{2(\frac{1}{2}\ln\beta_n^k - 1)}{\pi\ln\beta_n^k} + \frac{2\tau(\frac{1}{2}\ln\beta_n^k - 1)\mathrm{e}^{-4\alpha n^2}\cos(2nx)}{\pi[4D_m n^2 + \tau - (1-\ln\beta_n^k)\tau\mathrm{e}^{-4\alpha n^2}]} + \sum_{p=1,p\neq 2n}^{+\infty} F_p^{nk}\cos(px).$$

Then, we have

$$g_{21}^{0k} = \frac{\tau}{\pi}\bar{P}_0^k(3-\ln\beta_0^k)\mathrm{e}^{-\mathrm{i}\omega_0^k} + 4\tau^2\bar{P}_0^k\left(\frac{1}{2}\ln\beta_0^k - 1\right)^2\left[\frac{\bar{P}_0^k}{\mathrm{i}\omega_0^k}\mathrm{e}^{-2\mathrm{i}\omega_0^k} - \frac{7P_0^k}{3\mathrm{i}\omega_0^k} + \frac{\mathrm{e}^{-3\mathrm{i}\omega_0^k}}{\pi[2\mathrm{i}\omega_0^k + \tau - (1-\ln\beta_0^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_0^k}]} + \frac{2\mathrm{e}^{-\mathrm{i}\omega_0^k}}{\pi\tau\ln\beta_0^k}\right],$$

$$\begin{aligned} g_{21}^{nk} &= 2\tau^2\bar{P}_n^k\left(\frac{1}{2}\ln\beta_n^k - 1\right)^2\mathrm{e}^{-\alpha n^2}\left[\frac{2\mathrm{e}^{-3\mathrm{i}\omega_n^k}}{\pi[2\mathrm{i}\omega_n^k + \tau - (1-\ln\beta_n^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_n^k}]} + \frac{4\mathrm{e}^{-\mathrm{i}\omega_n^k}}{\pi\tau\ln\beta_n^k}\right] \\ &\quad + \tau^2\bar{P}_n^k\left(\frac{1}{2}\ln\beta_n^k - 1\right)^2\mathrm{e}^{-5\alpha n^2}\left[\frac{2\mathrm{e}^{-3\mathrm{i}\omega_n^k}}{\pi[2\mathrm{i}\omega_n^k + 4D_m n^2 + \tau - (1-\ln\beta_n^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_n^k}\mathrm{e}^{-4\alpha n^2}]} \right. \\ &\quad \left. + \frac{4\mathrm{e}^{-\mathrm{i}\omega_n^k}}{\pi[4D_m n^2 + \tau - (1-\ln\beta_n^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_n^k}\mathrm{e}^{-4\alpha n^2}]}\right], \qquad \text{for } n \neq 0. \end{aligned}$$

Therefore,

$$C_1^{0k}(0) = 2\tau^2\bar{P}_0^k\left(\frac{1}{2}\ln\beta_0^k - 1\right)^2\left[\frac{\mathrm{e}^{-3\mathrm{i}\omega_0^k}}{\pi[2\mathrm{i}\omega_0^k + \tau - (1-\ln\beta_0^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_0^k}]} + \frac{2\mathrm{e}^{-\mathrm{i}\omega_0^k}}{\pi\tau\ln\beta_0^k}\right] + \frac{\tau}{2\pi}\bar{P}_0^k(3-\ln\beta_0^k)\mathrm{e}^{-\mathrm{i}\omega_0^k}, \tag{4.21}$$

$$\begin{aligned} C_1^{nk}(0) &= 2\tau^2\bar{P}_n^k\left(\frac{1}{2}\ln\beta_n^k - 1\right)^2\mathrm{e}^{-\alpha n^2}\left[\frac{\mathrm{e}^{-3\mathrm{i}\omega_n^k}}{\pi[2\mathrm{i}\omega_n^k + \tau - (1-\ln\beta_n^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_n^k}]} + \frac{2\mathrm{e}^{-\mathrm{i}\omega_n^k}}{\pi\tau\ln\beta_n^k}\right] \\ &\quad + \tau^2\bar{P}_n^k\left(\frac{1}{2}\ln\beta_n^k - 1\right)^2\mathrm{e}^{-5\alpha n^2}\left[\frac{\mathrm{e}^{-3\mathrm{i}\omega_n^k}}{\pi[2\mathrm{i}\omega_n^k + 4D_m n^2 + \tau - (1-\ln\beta_n^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_n^k}\mathrm{e}^{-4\alpha n^2}]} \right. \\ &\quad \left. + \frac{2\mathrm{e}^{-\mathrm{i}\omega_n^k}}{\pi[4D_m n^2 + \tau - (1-\ln\beta_n^k)\tau\mathrm{e}^{-2\mathrm{i}\omega_n^k}\mathrm{e}^{-4\alpha n^2}]}\right], \qquad \text{for } n \neq 0. \end{aligned} \tag{4.22}$$

References

[1] Berezansky L, Braverman E and Idels L 2010 Nicholson's blowflies differential equations revisited: main results and open problems *Appl. Math. Model.* **34** 1405–17

[2] Fang J and Zhao X 2010 Existence and uniqueness of traveling waves for non-monotone integral equations with applications *J. Diff. Eqns* **248** 2199–226

[3] Faria T, Huang W and Wu J 2002 Smoothness of center manifolds for maps and formal adjoints for semilinear FDEs in general Banach spaces *SIAM J. Math. Anal.* **34** 173–203

[4] Gourley S A and Ruan S 2000 Dynamics of the diffusive Nicholson's blowflies equation with distributed delay *Proc. R. Phys. Soc. Edinb.* A **130** 1275–91

[5] Gurney M S, Blythe S P and Nisbet R M 1980 Nicholson's bowflies revisited *Nature* **287** 17–21

[6] Hassard B, Kazarinoff N and Wan Y 1981 *Theory and Applications of Hopf Bifurcation* (Cambridge: Cambridge University Press)

[7] Henry D 1981 *Geometric Theory of Semilinear Parabolic Equations* (*Lecture Notes in Mathematics* vol 840) (Berlin: Springer)

[8] Hu R and Yuan Y 2012 Stability and Hopf bifurcation analysis for Nicolson's blowflies equation with non-local delay *Eur. J. Appl. Math.* **23** 777–96

[9] Jin Y and Zhao X 2009 Spatial dynamics of a nonlocal periodic reaction–diffusion model with stage structure *SIAM J. Math. Anal.* **40** 2496–516

[10] Kuang Y 1992 Global attractivity and periodic solutions in delay-differential equations related to models in physiology and population biology *Japan J. Indust. Appl. Math.* **9** 205–38

[11] Kulenovic M R S and Ladas G 1987 Linearized oscillations in population dynamics *Bull. Math. Biol.* **49** 615–27

[12] Li J 1996 Global attractivity in Nicholson's blowflies *Appl. Math.* B **11** 425–34

[13] Liang D, So J, Zhang F and Zou X 2003 Population dynamic models with nonlocal delay on bounded fields and their numeric computations *Diff. Eqns Dyn. Syst.* **11** 117–39

[14] Mei M, So J W-H, Li M Y and Shen S 2004 Asymptotic stability of travelling waves for Nicholson's blowflies equation with diffusion *Proc. R. Soc. Edinb.* A **134** 579–94

[15] Metz J A J and Diekmann O 1986 *The Dynamics of Physiologically Structured Populations* (New York: Springer)

[16] Magal P and Ruan S 2009 Center manifolds for semilinear equations with non-dense domain and applications on Hopf bifurcation in age structured models *Mem. Am. Math. Soc.* **202** 951

[17] Nicholson A J 1954 Compensatory reactions of populations to stresses, and their evolutionary significance *Aust. J. Zool.* **2** 1–8

[18] Ruan S and Wei J 2003 On the zeros of transcendental functions with applications to stability of delay differential equations with two delays *Dyn. Contin. Discrete Impulsive Syst.* A **10** 863–74

[19] Smith H L 1994 A structured population model and related function-differential equation: global attractors and uniform persistence *J. Dyn. Diff. Eqns* **6** 71–99

[20] So J W-H, Wu J and Yang Y 2000 Numerical steady-state and Hopf bifurcation analysis on the diffusive Nicholson's blowflies equation *Appl. Math. Comput.* **111** 33–51

[21] So J W-H, Wu J and Zou X 2001 A reaction–diffusion model for a single species with age structure: I. Travelling wavefronts on unbounded domains *Proc. R. Soc. Lond.* A **457** 1841–53

[22] So J W-H and Yang Y 1998 Dirichlet problem for the diffusive Nicholson's blowflies equation *J. Diff. Eqns* **150** 317–34

[23] So J W-H and Yu J S 1994 Global attractivity and uniform persistence in Nicholson's blowflies *Differ. Eqns Dyn. Syst.* **2** 11–8

[24] So J W-H and Zou X 2001 Traveling waves for the diffusive Nicholson's blowflies equation *Appl. Math. Comput.* **122** 385–92

[25] Su Y, Wei J and Shi J 2010 Bifurcation analysis in a delayed diffusive Nicholson's blowflies equation *Nonlinear Anal. RWA* **11** 1692–703

[26] Thieme H R 1990 Semiflows generated by Lipschitz perturbations of non-densely defined operators *Diff. Integr. Eqns* **3** 1035–66

[27] Webb G F 1985 *Theory of Nonlinear Age-Dependent Population Dynamics* (*Monographs and Textbooks in Pure and Applied Mathematics* vol 89) (New York: Marcel Dekker, Inc.)

[28] Wei J and Li M Y 2005 Hopf bifurcation analysis in a delayed Nicholson's blowflies equation *Nonlinear Anal. TMA* **60** 1351–67

[29] Wu J 1996 *Theory and Applications of Partial Functional-Differential Equations* (New York: Springer)

[30] Xu D and Zhao X 2003 A nonlocal reaction–diffusion population model with stage structure *Can. Appl. Math. Q.* **11** 303–19

[31] Yang Y and So J W-H 1998 Dynamics of the diffusive Nicholson's blowflies equation *Proc. Int. Conf. Dynamical Systems and Differential Equations* (*Springfield, MI, 1996*) vol II, ed W Chen and S Hu, an added volume to *Discrete Contin. Dyn. Syst.* pp 333–52

[32] Yi T, Chen Y and Wu J 2009 Threshold dynamics of a delayed reaction–diffusion equation subject to the Dirichlet condition *J. Biol. Dyn.* **3** 331–41

[33] Yi F, Wei J and Shi J 2009 Bifurcation and spatiotemporal patterns in a homogeneous diffusive predator–prey system *J. Diff. Eqns* **246** 1944–77

[34] Yi T and Zou X 2008 Global attractivity of the diffusive Nicholson blowflies equation with Neumann boundary condition: a non-monotone case *J. Diff. Eqns* **245** 3376–88

[35] Yi T and Zou X 2010 Map dynamics versus dynamics of associated delay R-D equation with Neumann boundary condition *Proc. R. Soc. Lond.* A **466** 2955–73

[36] Yi T and Zou X 2011 Global dynamics of a delay differential equation with spatial non-locality in an unbounded domain *J. Diff. Eqns* **251** 2598–611

[37] Yi T and Zou X On Dirichlet problem for a class of delayed reaction–diffusion equations with spatial nonlocality *J. Dyn. Diff. Eqns* **25** 959–79

[38] Zhao X 2009 Global attractivity of a class of nonmonotone reaction–diffusin equation with time delay *Can. Appl. Math. Q.* **17** 271–81