Applied Mathematical Modelling 34 (2010) 1068–1077

Contents lists available at ScienceDirect

Applied Mathematical Modelling

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

Bifurcation analysis in an age-structured model of a single species living in two identical patches ☆

Chunbo Yu [a], Junjie Wei [a,*], Xingfu Zou [b]

[a] Department of Mathematics, Harbin Institute of Technology, Harbin 150001, PR China
[b] Department of Applied Mathematics, University of Western Ontario, London, Ontario, Canada N6A 5B7

ARTICLE INFO

Article history:
Received 9 February 2008
Received in revised form 26 July 2009
Accepted 31 July 2009
Available online 6 August 2009

Keywords:
Age-structured model
Delay
Homogeneous equilibrium
Hopf bifurcation
Periodic solutions

ABSTRACT

In this paper, we consider the age-structured model of a single species living in two identical patches derived in So et al. [J.W.-H. So, J. Wu, X. Zou, Structured population on two patches: modeling dispersal and delay, J. Math. Biol. 43 (2001) 37–51]. We chose a birth function that is frequently used but different from the one used in So et al. which leads to a different structure of the homogeneous equilibria. We investigate the stability of these equilibria and Hopf bifurcations by analyzing the distribution of the roots of associated characteristic equation. By the theory of normal form and center manifold, an explicit algorithm for determining the direction of the Hopf bifurcation and stability of the bifurcating periodic solutions are derived. Finally, some numerical simulations are carried out for supporting the analytic results.

1. Introduction

Maturation delay and spatial dispersion are two important factors in population dynamics. By employing the basic age structure equation (see e.g., Metz and Diekmann [1]) and the idea of characteristics (see e.g., Smith [2]) in terms of time and age, So et al. [3] derived a system of delay differential equations to model the growth of the matured population in two patches:

$$
\begin{aligned}
\frac{dx(t)}{dt} &= -d_{1,m}x(t) + D_{2,m}y(t) - D_{1,m}x(t) \\
&\quad + e^{*}\left[1 - \int_0^{\tau} e^{-\int_{\theta}^{\tau}\widehat{D}(a)da} D_1(\theta)d\theta\right] b_1(x(t-\tau)) \\
&\quad + e^{*}\left[\int_0^{\tau} e^{-\int_{\theta}^{\tau}\widehat{D}(a)da} D_2(\theta)d\theta\right] b_2(y(t-\tau)), \\
\frac{dy(t)}{dt} &= -d_{2,m}y(t) + D_{1,m}x(t) - D_{2,m}y(t) \\
&\quad + e^{*}\left[1 - \int_0^{\tau} e^{-\int_{\theta}^{\tau}\widehat{D}(a)da} D_2(\theta)d\theta\right] b_2(y(t-\tau)) \\
&\quad + e^{*}\left[\int_0^{\tau} e^{-\int_{\theta}^{\tau}\widehat{D}(a)da} D_1(\theta)d\theta\right] b_1(x(t-\tau)).
\end{aligned} \tag{1}
$$

☆ Supported by the National Natural Science Foundation of China (No. 10771045), Program of Excellent Team in HIT, NSERC of Canada, and a Premiers Research Excellence Award of Ontario.

* Corresponding author. Tel.: +86 451 86417440; fax: +86 451 86415647.
E-mail address: weijj@hit.edu.cn (J. Wei).

0307-904X/$ - see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.apm.2009.07.018

Here x and $d_{1,m} > 0$ (y and $d_{2,m}$) denote the density and death rate of mature population in patch 1 (patch 2), τ denotes the maturation age, b_i denote the birth functions in patch i, $i = 1,2$, $D_{i,m} > 0$ denote the migration rate of mature population from patch $i (i = 1,2)$ to the other patch. The parameter $e^* = e^{-\int_0^\tau d_I(a)da}$ with $d_I(a)$ denotes the death rate of individuals at age a which is independent of the patch considered is called the survival rate, giving the probability that a new born individual can survive to adult. $D_i(a)$ denote the migration rate of age a from patch i to patch j, $\widehat{D}(a) = D_1(a) + D_2(a), 0 \leqslant a \leqslant \tau$. The term $e^*[\int_0^\tau e^{-\int_\theta^\tau \widehat{D}(a)da} D_1(\theta)d\theta]b_1(x(t-\tau))$ denotes the portion of the mature population which was born in the first patch at time $t-\tau$ but is in the second patch at the current time t, and the term $e^*[\int_0^\tau e^{-\int_\theta^\tau \widehat{D}(a)da} D_2(\theta)d\theta]b_2(y(t-\tau))$ denotes the portion of the mature population which was born in the second patch at time $t-\tau$ but is in the first patch at the current time t. This term is usually ignored in the literature before [3].

In the case that the two patches are identical: $d_{i,m} = d_m =: d, D_{i,m} = D_m =: D, b_i(s) = b(s)$ and $D_i(a) = D_I(a)$ for $i = 1,2$ and for $0 \leqslant a \leqslant \tau$, system (1) becomes

$$\begin{aligned} \frac{dx(t)}{dt} &= -dx(t) + D(y(t) - x(t)) \\ &\quad + e^*(1-r)b(x(t-\tau)) + e^* rb(y(t-\tau)), \\ \frac{dy(t)}{dt} &= -dy(t) + D(x(t) - y(t)) \\ &\quad + e^*(1-r)b(y(t-\tau)) + e^* rb(x(t-\tau)), \end{aligned} \tag{2}$$

where

$$r = \frac{1}{2}\left[1 - e^{-2\int_0^\tau D_I(a)da}\right].$$

Clearly $0 < r < 1/2$.

In [3], the authors chose the following birth function:

$$b(s) = s^2 e^{-\beta s}, \quad \beta > 0 \tag{3}$$

and showed that varying the immature death rate can alter the behaviors of the homogeneous equilibria. Indeed, they numerically observed transient oscillations around an intermediate equilibrium, as well as bifurcation of non-homogeneous equilibria. They also theoretically showed the existence of Hopf bifurcation near the largest equilibrium.

In this paper, we also consider system (2), but we will choose an another important birth function, called Ricker's function, given by

$$b(s) = se^{-\beta s}, \quad \beta > 0. \tag{4}$$

This birth function has also been widely used in population dynamics, particularly in modeling fish population. See e.g., Cooke et al. [4] and the references therein. This change of the birth function leads to change of the structure of homogeneous equilibria, and raises a natural question of how does this affect the population dynamics described by the model. In this paper, address this question by analyzing the structure and the stability of homogeneous equilibria, and the associated Hopf bifurcation of homogeneous periodic orbits.

We point out that when the dispersion channels between the two patches are cut off, meaning that $D_{i,m} = D_m = 0, D_i(a) = D_I(a) = 0$ for $i = 1,2$, system (2) reduces to two decoupled scalar equations of the form

$$\frac{dx(t)}{dt} = -dx(t) + e^{-d_I\tau} b(x(t-\tau)), \tag{5}$$

which was proposed in Cooke et al. [4]. With the birth function given by (4), is have been shown that the positive equilibrium of (5) may experience double switches for its stability as τ increases: there are $0 < \tau_1 < \tau_2$ such that when $\tau \in [0, \tau_1)$ or $\tau \in (\tau_2, \infty)$, the positive equilibrium is stable while when $\tau \in (\tau_1, \tau_2)$, it is unstable. A similar result is also obtained for the patch model (2) in this paper. The global bifurcation of (5) with (4) has been further studied in Wei and Zou [5].

The rest of the paper is organized as follows: in Section 2, we focus mainly on the positive homogeneous equilibria, and analyze its stability. Using the approach of Beretta and Kuang [6], we show that the positive steady-state can be destabilized through a Hopf bifurcation. In Section 3, the direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions are determined by using the normal form theory and center manifold argument presented in Hassard et al. [7]. Finally, some numerical simulations are given to illustrate the theoretical results obtained.

2. Stability and local Hopf bifurcation

In this section, we shall employ the result due to Beretta and Kuang [6] to study the stability of the positive homogeneous equilibrium and existence of local Hopf bifurcation. Assume that $d_I(a)$ is age independent, that is $d_I(a) = d_I > 0$. Then we have $e^* = e^{-d_I\tau}$.

Our main concern is the homogeneous equilibrium (x,y) which is one with $x = y \stackrel{\text{def}}{=} x^*$. The homogeneous equilibria of system (2) are obtained from the solutions of the scalar equation

$$dx^* = e^* x^* e^{-\beta x^*}. \tag{6}$$

Clearly, Eq. (6) has two fixed points if $e^* > d$. The first one is the origin $E_0 = (0,0)$. The second one is given by

$$E_1 = (x,y) = (\bar{x},\bar{x}), \quad \bar{x} = \frac{1}{\beta}\ln\frac{e^*}{d}.$$

Through out this paper, we always assume that $e^* > d$. The linearization of Eq. (2) around $E^* = (x^*,x^*)(x^* = 0 \text{ or } \bar{x})$ is given by

$$\begin{aligned}\frac{dx(t)}{ddt} &= -dx(t) + D(y(t) - x(t)) + e^* r(1-\beta x^*)e^{-\beta x^*} y(t-\tau)\\ &\quad + e^*(1-r)(1-\beta x^*)e^{-\beta x^*} x(t-\tau),\\ \frac{dy(t)}{dt} &= -dy(t) + D(x(t) - y(t)) + e^* r(1-\beta x^*)e^{-\beta x^*} x(t-\tau)\\ &\quad + e^*(1-r)(1-\beta x^*)e^{-\beta x^*} y(t-\tau).\end{aligned}$$

Its characteristic equation is

$$[\lambda + d - e^*(1-\beta x^*)e^{-\beta x^*}e^{-\lambda\tau}] \times [\lambda + d + 2D - e^*(1-2r)(1-\beta x^*)e^{-\beta x^*}e^{-\lambda\tau}] = 0,$$

which is equivalent to

$$\lambda + d - e^*(1-\beta x^*)e^{-\beta x^*}e^{-\lambda\tau} = 0 \tag{7}$$

and

$$\lambda + d + 2D - e^* e^{-2\int_0^\tau D_I(a)da}(1-\beta x^*)e^{-\beta x^*}e^{-\lambda\tau} = 0. \tag{8}$$

Since Eq. (7) with $x^* = 0$ always has a positive real root, we conclude that the equilibrium E_0 is unstable. Now we consider the stability of the positive homogeneous equilibrium.

Let

$$\begin{aligned} I_1 &= \left\{\tau | \tau \in [0,\tau_1), \tau_1 = -\frac{2+\ln d}{d_I}\right\},\\ I_2 &= \left\{\tau | \tau \in [0,\tau_2), \tau_2 = -\frac{k+\ln d}{d_I}, k = \frac{2[D+(1-r)d]}{(1-2r)d}\right\}.\end{aligned} \tag{9}$$

Note that $0 < r < \frac{1}{2}$, it follows that $I_2 \subset I_1$, I_1 and I_2 are non-empty under the following assumption:

$$(\text{A1}) \quad \ln d < -\frac{2(1-r)}{1-2r} \quad \text{and} \quad D < \frac{d}{2}[(1+\ln d)(2r-1) - 1].$$

For convenience, we make the following hypotheses:

$$(\text{A1}^*) \quad \ln d < -2.$$

Eqs. (7) and (8) take the general form as

$$P_j(\lambda,\tau) + Q_j(\lambda,\tau)e^{\lambda\tau} = 0, \quad j = 1,2 \tag{10}$$

with

$$P_1(\lambda,\tau) = \lambda + d, \quad Q_1(\lambda,\tau) = d(\beta\bar{x} - 1) \tag{11}$$

and

$$P_2(\lambda,\tau) = \lambda + d + 2D, \quad Q_2(\lambda,\tau) = d(\beta\bar{x} - 1)(1-2r). \tag{12}$$

When $\tau = 0$, the root of Eq. (10) with $j = 1$ is given by $\lambda = -d\beta\bar{x} < 0$, and with $j = 2$ is given by $\lambda = -2D - 2dr - (1-2r)d\beta\bar{x} < 0$. Hence, we have the following result.

Proposition 2.1. *The positive homogeneous equilibrium E_1 of (2) is asymptotically stable when $\tau = 0$.*

In what following, we will investigate the existence of purely imaginary roots $\lambda = i\omega_1(\omega_1 > 0)$ to Eq. (7) and $\lambda = i\omega_2(\omega_2 > 0)$ to Eq. (8). Since Eqs. (7) and (8) are equations with delay-dependent coefficients, we shall apply the approach due to Beretta and Kuang [6]. Similar to the process in Qu and Wei [10], we first verify the following properties for all $\tau \in I_j (j = 1,2)$.

(i) $P_j(0,\tau) + Q_j(0,\tau) \neq 0$.
(ii) $P_j(i\omega_j,\tau) + Q_j(i\omega_j,\tau) \neq 0$.

(iii) $\limsup\{|Q_j(\lambda,\tau)/P_j(\lambda,\tau)|; |\lambda| \to \infty, \mathrm{Re}\lambda \geqslant 0\} < 1$ for any τ.
(iv) $F_j(\omega_j,\tau) =: |P_j(i\omega_j,\tau)|^2 - |Q_j(i\omega_j,\tau)|^2$ has a finite number of zeros.
(v) Each positive root $\omega_j(\tau)$ of $F_j(\omega_j,\tau) = 0$ is continuous and differentiable in τ whenever it exists.

From the definitions of P_j and Q_j in (11) and (12), respectively, we can get that

$$\begin{aligned}
&P_1(0,\tau) + Q_1(0,\tau) = d\beta\bar{x} > 0,\\
&P_2(0,\tau) + Q_2(0,\tau) = (1-2r)d\beta\bar{x} + 2D + 2dr > 0,\\
&P_1(i\omega_1,\tau) + Q_1(i\omega_1,\tau) = i\omega_1 + d\beta\bar{x} \neq 0,\\
&P_2(i\omega_2,\tau) + Q_2(i\omega_2,\tau) = i\omega_2 + d(1-2r)(\beta\bar{x}-1) + d + 2D \neq 0,\\
&\lim_{|\lambda|\to\infty}\left|\frac{Q_1(\lambda,\tau)}{P_1(\lambda,\tau)}\right| = \lim_{|\lambda|\to\infty}\left|\frac{d(\beta\bar{x}-1)}{\lambda+d}\right| = 0,\\
&\lim_{|\lambda|\to\infty}\left|\frac{Q_2(\lambda,\tau)}{P_2(\lambda,\tau)}\right| = \lim_{|\lambda|\to\infty}\left|\frac{d(\beta\bar{x}-1)(1-2r)}{\lambda+d+2D}\right| = 0.
\end{aligned}$$

These imply that (i), (ii) and (iii) are satisfied.

Let F be defined as in (iv). From Eqs. (11) and (12), we have

$$\begin{aligned}
&F_1(\omega_1,\tau) = \omega_1^2 - d^2\beta\bar{x}(\beta\bar{x}-2),\\
&F_2(\omega_2,\tau) = \omega_2^2 - d^2(1-2r)^2(\beta\bar{x}-1)^2 + (d+2D)^2.
\end{aligned}$$

It is obvious that property (iv) is satisfied, and by Implicit Function Theorem, (v) is also satisfied.

Substituting $\lambda = i\omega_1$ into Eq. (7) and separating the real and imaginary parts yields

$$\begin{aligned}
&d = d(1-\beta\bar{x})\cos\omega_1\tau,\\
&-\omega_1 = d(1-\beta\bar{x})\sin\omega_1\tau.
\end{aligned}$$

Hence

$$\begin{aligned}
&\cos\omega_1\tau = \frac{1}{1-\beta\bar{x}},\\
&\sin\omega_1\tau = -\frac{\omega_1}{d(1-\beta\bar{x})}.
\end{aligned} \tag{13}$$

In the same way, we have

$$\begin{aligned}
&\cos\omega_2\tau = \frac{d+2D}{d(1-2r)(1-\beta\bar{x})},\\
&\sin\omega_2\tau = -\frac{\omega_2}{d(1-2r)(1-\beta\bar{x})}.
\end{aligned} \tag{14}$$

By the definitions of P_j and Q_j as in (11) and (12), and applying the property (i), (13) and (14) can be written as

$$\begin{aligned}
&\cos\omega_j\tau = -\mathrm{Re}\frac{P_j(i\omega_j,\tau)}{Q_j(i\omega_j,\tau)},\\
&\sin\omega_j\tau = \mathrm{Im}\frac{P_j(i\omega_j,\tau)}{Q_j(i\omega_j,\tau)},
\end{aligned}$$

which yields $|P_j(i\omega_j,\tau)|^2 = |Q_j(i\omega_j,\tau)|^2$. That is,

$$F_j(\omega_j,\tau) = 0. \tag{15}$$

For $\tau \in I_1$

$$\omega_1 = \omega_1(\tau) = d\sqrt{\beta\bar{x}(\beta\bar{x}-2)}$$

makes sense, and hence ω_1 is a root of Eq. (12) with $j = 1$. Similarly,

$$\omega_2 = \omega_2(\tau) = \sqrt{[(1-2r)d\beta\bar{x} + 2rd + 2D][(1-2r)d\beta\bar{x} + 2(r-1)d - 2D]}$$

makes sense for $\tau \in I_2$, and hence ω_2 is a root of (15) with $j = 2$. Then, let $\theta_j(\tau) \in [0, 2\pi]$ be defined for $\tau \in I_j$ by

$$\begin{aligned}
&\cos\theta_j(\tau) = -\mathrm{Re}\frac{P_j(i\omega_j,\tau)}{Q_j(i\omega_j,\tau)},\\
&\sin\theta_j(\tau) = \mathrm{Im}\frac{P_j(i\omega_j,\tau)}{Q_j(i\omega_j,\tau)},
\end{aligned} \tag{16}$$

where $\omega_j = \omega_j(\tau)$ and $j = 1, 2$. Since $F_j(\omega_j(\tau), \tau) = 0$ for $\tau \in I_j$, it follows that $\theta_j(\tau)$ is well and uniquely defined for all $\tau \in I_j$.

From $\omega_j(\tau)\tau = \theta_j(\tau) + 2n\pi$, one can check that $i\omega^*$, with $\omega^* = \omega(\tau^*) > 0$, is a purely imaginary zero of (7) if and only if τ^* is a root of the function S_j^n, defined by

$$S_1^n(\tau) = \tau - \frac{\theta_1(\tau) + 2n\pi}{\omega_1(\tau)}, \quad \tau \in I, \ n \in Z \tag{17}$$

and $i\omega^*$, with $\omega^* = \omega(\tau^*) > 0$, is a purely imaginary zero of (8) if and only if τ^* is a root of the function S_j^n, defined by

$$S_2^n(\tau) = \tau - \frac{\theta_2(\tau) + 2n\pi}{\omega_2(\tau)}, \quad \tau \in I, \ n \in Z. \tag{18}$$

In order to investigate the zeros of S_j^n, we state a theorem is due to Beretta and Kuang [6].

Theorem 2.2. *Assume that the function $S_1^n(\tau)$ (rep. $S_2^n(\tau)$) has a positive root $\tau^* \in I_1$ (rep. I_2), for some $n \in N$. Then a pair of simple conjugate pure imaginary roots $\pm i\omega(\tau^*)$ of Eq. (7) (rep. Eq. (8)) exists at $\tau = \tau^*$ which crosses the imaginary axis from left to right if $\delta_1(\tau^*) > 0$ (rep. $\delta_2(\tau^*) > 0$) and the imaginary axis from right to left if $\delta_1(\tau^*) < 0$ (rep. $\delta_2(\tau^*) < 0$), where*

$$\delta_j(\tau^*) = Sign\left\{\frac{dRe(\lambda)}{d\tau}\bigg|_{\lambda = i\omega(\tau^*)}\right\} = Sign\left\{\frac{\partial F_j}{\partial \omega}(\omega(\tau^*), \tau^*)\right\} Sign\left\{\frac{dS_j^n(\tau)}{d\tau}\bigg|_{\tau=\tau^*}\right\}, \quad j = 1, 2. \tag{19}$$

Since $\partial F_j / \partial \omega_j(\omega_j, \tau) = 2\omega_j > 0 (j = 1, 2)$, (19) is equivalent to

$$\delta_j(\tau^*) = Sign\left\{\frac{dRe(\lambda)}{d\tau}\bigg|_{\lambda = i\omega_j(\tau^*)}\right\} = Sign\left\{\frac{dS_j^n(\tau)}{d\tau}\bigg|_{\tau=\tau^*}\right\}.$$

We can easily observe that $S_j^n(0) < 0$. Moreover, for all $\tau \in I_j, S_j^n(\tau) > S_j^{n+1}(\tau)$ with $n \in Z$. Therefore, if S_j^0 has no zero in I_j, then the functions S_j^n have no zero in I_j. If the function $S_j^{n^*}(\tau)$ has positive zeros $\tau \in I_j$for $n^* \in N$, there exists at least one zero satisfying $dS_j^n(\tau^*)/d\tau > 0$, where $n < n^*, S_j^n(\tau^*) = 0$.

Furthermore, from (15) it follows that:

$$\lim_{\tau \to \tau_j} \omega_j(\tau) = 0, \quad j = 1, 2,$$

where τ_1 and τ_2 are defined as in (6). And hence,

$$\lim_{\tau \to \tau_j} \sin\theta_j(\tau) = 0 \quad \text{and} \quad \lim_{\tau \to \tau_j} \cos\theta_j(\tau) = -1, \quad j = 1, 2.$$

This implies that, $\lim_{\tau \to \tau_j} \theta_j(\tau) = \pi$. Therefore, by (17) and (18) it follows that:

$$\lim_{\tau \to \tau_j} S_j^n(\tau) = -\infty, \quad j = 1, 2.$$

Define

$$\begin{aligned}
&X = \{\tau : S_j^n(\tau) = 0, n \in Z, j = 1, 2, \tau \in I_2\}, \\
&\tilde{\tau} = \min\{\tau : \tau \in X\}, \quad \bar{\tau} = \max\{\tau : \tau \in X\}, \\
&X_j = \{\tau : S_j^n(\tau) = 0, n \in Z, \tau \in I_j\}, \\
&\tilde{\tau}_j = \min\{\tau : \tau \in X_j\}, \quad \bar{\tau}_j = \max\{\tau : \tau \in X_j\}, \quad j = 1, 2.
\end{aligned}$$

For convenience, we assume that

$$\text{(A2)} \quad \frac{dS_j^n(\tau)}{d\tau}\bigg|_{\tau \in X} \neq 0 \quad \forall n \in N, \ j = 1, 2,$$

$$\text{(A2}^*\text{)} \quad \frac{dS_1^n(\tau)}{d\tau}\bigg|_{\tau \in X_1} \neq 0 \quad \forall n \in N.$$

Applying the Hopf bifurcation theorem for functional differential equations (see Hale [8], Chapter 11, Theorem 1.1), we can conclude the existence of Hopf bifurcation as stated in the following theorem.

Theorem 2.3. *For system (2), the following conclusions hold:*

(1) *Suppose one of the following is satisfied.*
- (i) (A1*) *does not hold*;
- (ii) (A1*) *holds, but* (A1) *does not hold*, $X_1 = \emptyset$.
- (iii) (A1) *holds*, $X_2 = X_1 = \emptyset$.

Then the positive homogeneous equilibrium E_1 is asymptotically stable for all $\tau > 0$.

(2) *The assumption* (A1*) *holds.* $X_1 \neq \emptyset$, *and one of the following holds:*
 (i) (A1) *does not hold*;
 (ii) (A1) *holds*, $X_2 = \emptyset$.
 (A2*) *holds. Then* E_1 *is asymptotically stable for* $\tau \in [0, \tilde{\tau}_1)$, *and becomes unstable for* $\tau \in (\tilde{\tau}_1, \bar{\tau}_1)$, *and back to asymptotically stable when* $\tau \in (\bar{\tau}_1, \tau_1)$ *with two Hopf bifurcation points* $\tau = \tilde{\tau}_1, \bar{\tau}_1$.

(3) *The assumption* (A1) *holds.* $X_1 = \emptyset$, $X_2 \neq \emptyset$. (A2) *holds. Then* E_1 *is asymptotically stable for* $\tau \in [0, \tilde{\tau}_2)$, *and becomes unstable for* $\tau \in (\tilde{\tau}_2, \bar{\tau}_2)$, *and back to asymptotically stable when* $\tau \in (\bar{\tau}_2, \tau_2)$ *with two Hopf bifurcation points* $\tau = \tilde{\tau}_2, \bar{\tau}_2$.

(4) *The assumption* (A1) *holds.* $X_1 \neq \emptyset$, $X_2 \neq \emptyset$. (A2) *holds. Then:*
 (i) E_1 *is asymptotically stable for* $\tau \in [0, \tilde{\tau})$;
 (ii) *If*

 $S_1^0(\tau_2) > 0,$

 then E_1 *is unstable for* $\tau \in (\tilde{\tau}, \tau_2)$, *with a Hopf bifurcation occurring when* $\tau = \tilde{\tau}$;
 (iii) *If*

 $S_1^0(\tau_2) < 0,$

 then E_1 *is unstable for* $\tau \in (\tilde{\tau}, \bar{\tau})$, *and becomes asymptotically stable when* $\tau \in (\bar{\tau}, \tau_2)$, *with two Hopf bifurcation points* $\tau = \tilde{\tau}, \bar{\tau}$.

3. Direction and stability of the Hopf bifurcation

In the previous section, we have already obtained some sufficient conditions ensuring system (2) undergoes a Hopf bifurcation at the positive homogeneous equilibrium $E_1 = (\bar{x}, \bar{x})$. In this section we shall study the direction of the Hopf bifurcation, and the stability of the bifurcating periodic solutions under the conditions of Theorem 2.3, using techniques of the normal form and center manifold theory (see e.g., Hassard et al.[7]).

Without loss of generality, we let $\hat{\tau}$ be the critical value of τ at which system (2) undergoes a Hopf bifurcation at E_1. Let $\tau = \hat{\tau} + \alpha$, then $\alpha = 0$ is the Hopf bifurcation value of system (2).

For convenience, let $t = s\tau$, and still denote time t, system (2) can be rewritten as

$$\begin{pmatrix} \dot{x}(t) \\ \dot{y}(t) \end{pmatrix} = \tau A \begin{pmatrix} x(t) \\ y(t) \end{pmatrix} + \tau B \begin{pmatrix} x(t-1) \\ y(t-1) \end{pmatrix} + f, \tag{20}$$

where

$$A = \begin{pmatrix} -d-D & D \\ D & -d-D \end{pmatrix}, \quad B = d(1-\beta\bar{x}) \begin{pmatrix} 1-r & r \\ r & 1-r \end{pmatrix},$$

$$f = \tau d \begin{pmatrix} (1-r)\left[\left(\frac{1}{2}\bar{x}\beta - 1\right)\beta x^2(t-1) + \frac{1}{2}\left(1 - \frac{1}{3}\bar{x}\beta\right)\beta^2 x^3(t-1)\right] \\ \quad + r\left[\left(\frac{1}{2}\bar{x}\beta - 1\right)\beta y^2(t-1) + \frac{1}{2}\left(1 - \frac{1}{3}\bar{x}\beta\right)\beta^2 y^3(t-1)\right] + O(x^4, y^4) \\ (1-r)\left[\left(\frac{1}{2}\bar{x}\beta - 1\right)\beta y^2(t-1) + \frac{1}{2}\left(1 - \frac{1}{3}\bar{x}\beta\right)\beta^2 y^3(t-1)\right] \\ \quad + r\left[\left(\frac{1}{2}\bar{x}\beta - 1\right)\beta x^2(t-1) + \frac{1}{2}\left(1 - \frac{1}{3}\bar{x}\beta\right)\beta^2 x^3(t-1)\right] + O(x^4, y^4) \end{pmatrix}.$$

Choose the phase space as $C = C([-1, 0], R^2)$, for any $\phi = (\phi_1, \phi_2)^T \in C$ let

$$L_\alpha(\phi) = (\hat{\tau} + \alpha)A\phi(0) + (\hat{\tau} + \alpha)B\phi(-1).$$

By the Riesz representation theorem, there exists a matrix whose components are bounded variation function $\eta(\theta, \alpha) : [-1, 0] \to R^{2^2}$ in $\theta \in [-1, 0]$ such that

$$L_\alpha \phi = \int_{-1}^{0} d\eta(\theta, \alpha)\phi(\theta) \quad \text{for } \phi \in C. \tag{21}$$

In fact, we can choose $\eta(\theta, \alpha) = (\hat{\tau} + \alpha)A\delta(\theta) + (\hat{\tau} + \alpha)B\delta(\theta + 1)$, where

$$\delta(\theta) = \begin{cases} 1, & \theta = 0, \\ 0, & \theta \neq 0. \end{cases}$$

Then Eq. (21) is satisfied.

For $\phi \in C^1([-1, 0], R^2)$, define

$$A(\alpha)\phi = \begin{cases} d\phi(\theta)/d\theta, & \theta \in [-1,0), \\ \int_{-1}^{0} d\eta(t,\alpha)\phi(t), & \theta = 0, \end{cases}$$
$$R(\alpha)\phi = \begin{cases} 0, & \theta \in [-1,0), \\ f(\alpha,\phi), & \theta = 0. \end{cases}$$

Then system (20) can be rewritten in the following form:

$$\dot{u}_t = A(\alpha)u_t + R(\alpha)u_t,$$

where $u_t = u(t+\theta)$ for $\theta \in [-1,0]$.

For $\psi \in C^1([0,1],(C^2)^*)$, define

$$A^*\psi(s) = \begin{cases} -d\psi(s)/ds, & s \in (0,1], \\ \int_{-1}^{0} d^T\eta(t,0)\psi(-t), & s = 0. \end{cases}$$

For $\phi \in C([-1,0],C^2)$ and $\psi \in C([0,1],(C^2)^*)$, define

$$\langle \psi, \phi \rangle = \bar{\psi}(0)\phi(0) - \int_{-1}^{0}\int_{0}^{\theta} \bar{\psi}(\xi-\theta)d\eta(\theta)\phi(\xi)d\xi,$$

where $\eta(\theta) = \eta(\theta,0)$. Then A^* and $A(0)$ are adjoint operators. Let $q(\theta)$ and $q^*(s)$ are eigenvector of A and A^* corresponding to $i\hat{\tau}\omega_0$ and $-i\hat{\tau}\omega_0$, respectively, where

$$\omega_0 = \begin{cases} \omega_1, & \text{if } S_1^n(\hat{\tau}) = 0, \\ \omega_2, & \text{if } S_2^n(\hat{\tau}) = 0, \end{cases} \quad n \in N.$$

By direct computation, we obtain that

$$q(\theta) = (1,1)^T e^{i\hat{\tau}\omega_0\theta},$$
$$q^*(s) = D_0(1,1)e^{i\hat{\tau}\omega_0 s},$$

where

$$\overline{D_0} = \left[2 + 2\hat{\tau}d(1-\beta\bar{x})e^{-i\hat{\tau}\omega_0}\right]^{-1}.$$

Moreover, $\langle q^*(s), q(\theta)\rangle = 1$ and $\langle q^*(s), \bar{q}(\theta)\rangle = 0$.

Following the algorithms in Hassard et al. [7] and using a computation process similar to what stated in Wei and Ruan [9], we can obtain the coefficients which will be used in determining the important quantities:

$$g_{20} = D_0\hat{\tau}d\beta(\beta\bar{x}-2)e^{-2i\hat{\tau}\omega_0},$$
$$g_{11} = 2D_0\hat{\tau}d\beta(\beta\bar{x}-2),$$
$$g_{02} = D_0\hat{\tau}d\beta(\beta\bar{x}-2)e^{2i\hat{\tau}\omega_0},$$
$$g_{21} = D_0\hat{\tau}d\beta^2(3-\beta\bar{x})e^{-i\hat{\tau}\omega_0} + D_0\hat{\tau}d\beta(\beta\bar{x}-2),$$
$$\left[e^{-i\hat{\tau}\omega_0}(W_{11}^1(-1) + W_{11}^2(-1)) + e^{i\hat{\tau}\omega_0}(W_{20}^1(-1) + W_{20}^2(-1))\right],$$

where

$$W_{20}(-1) = \frac{ig_{20}}{\hat{\tau}\omega_0}q(0)e^{-i\hat{\tau}\omega_0} + \frac{i\bar{g}_{20}}{3\hat{\tau}\omega_0}\bar{q}(0)e^{i\hat{\tau}\omega_0} + \begin{pmatrix} E_1^1 \\ E_1^1 \end{pmatrix} e^{-2i\hat{\tau}\omega_0},$$
$$E_1^1 = E_1^2 = \frac{d\beta(\beta\bar{x}-2)e^{-2i\hat{\tau}\omega_0}}{2i\omega_0 + d - d(1-\beta\hat{x})e^{-2i\hat{\tau}\omega_0}},$$
$$W_{11}(-1) = -\frac{ig_{11}}{\hat{\tau}\omega_0}q(0)e^{-i\hat{\tau}\omega_0} + \frac{i\bar{g}_{11}}{\hat{\tau}\omega_0}\bar{q}(0)e^{i\hat{\tau}\omega_0} + \begin{pmatrix} E_2^1 \\ E_2^1 \end{pmatrix},$$
$$E_2^1 = E_2^2 = \frac{\beta\bar{x}-2}{\bar{x}}.$$

Since each g_{ij} above is determined by the parameters and delays in system (20), we can compute the following quantities:

$$C_1(0) = \frac{i}{2\omega_0\hat{\tau}}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2\right) + \frac{g_{21}}{2},$$
$$\mu_2 = -\frac{\mathrm{Re}\{C_1(0)\}}{\mathrm{Re}\lambda'(\hat{\tau})},$$
$$\beta_2 = 2\mathrm{Re}\{C_1(0)\},$$
$$T_2 = -\frac{\mathrm{Im}C_1(0) + \mu_2\mathrm{Im}(\lambda'(\hat{\tau}))}{\omega_0\hat{\tau}}.$$

We know that (see Hassard et al. [7]) μ_2 determines the direction of the Hopf bifurcation: if $\mu_2 > 0(< 0)$, then the bifurcating periodic solutions exist for $\tau > \hat{\tau}(< \hat{\tau})$. β_2 determines the stability of the bifurcating periodic solution: if $\beta_2 < 0(> 0)$ the bifurcating periodic solutions are stable(unstable). T_2 determines the period of the bifurcating periodic solutions: the period increase (decrease) if $T_2 > 0(T_2 < 0)$. Particularly, the direction of the Hopf bifurcation and stability of the bifurcating periodic solutions on the center manifold are coincidence with that of system (2) at the first bifurcation value $\hat{\tau}$, since all the roots of the characteristic equation with $\tau = \hat{\tau}$ have negative real parts except $\pm i\omega_0$.

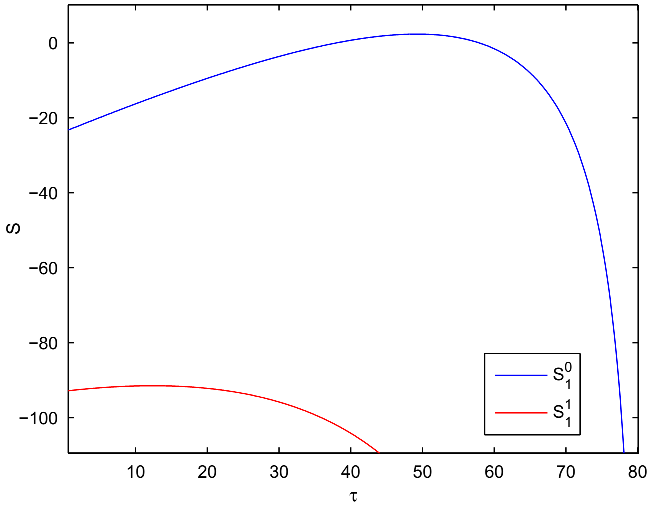

Fig. 1. Graph of functions S_1^0 and S_1^1 for $\tau \in [0, 81.3411)$.

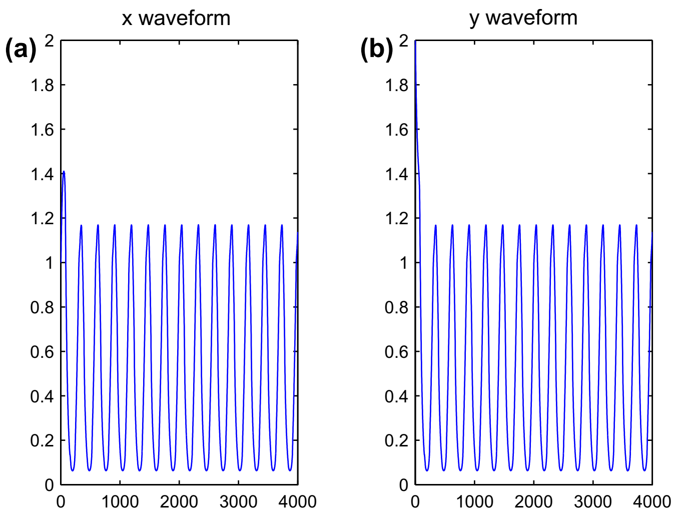

Fig. 2. Waveform for system (2) when $\tau = 40 > \tilde{\tau} = 38.0610$.

4. Computer simulation

In this section, we present some numerical results to Eq. (1) at different values of d, d_I, D, β, r and τ.

If we choose $d = 0.06, d_I = 0.01, D = 2, \beta = 10, r = 0.02$, it is easy to verify that $I_1 = [0, 81.3411), I_2 = \emptyset$, and the assumptions (A1*) and (A2*) hold. $S_1^0(\tau)$ has positive zero in I_1, $\tilde{\tau}_1 = 38.0610, \bar{\tau}_1 = 57.8658$. We draw the graph of S_1^0 and S_1^1 versus τ on I_1 in Fig. 1.

From Theorem 2.3(2), we conclude that the positive homogeneous equilibrium E_1 is asymptotically stable for $\tau \in [0, 38.0610)$, and becomes unstable for $\tau \in (38.0610, 57.8658)$, and back to asymptotically stable when $\tau \in (57.8658, 81.3411)$ with two Hopf bifurcation points $\tau = 38.0610, 57.8658$.

If we choose $\hat{\tau} = 38.0610$, we can get that $\lambda\prime(\hat{\tau}) \doteq 0.00068, g_{20} \doteq -0.1857 + 7.2030i, g_{11} \doteq 14.4108, g_{02} \doteq -0.1857 - 7.2030i$ and $g_{21} \doteq -48.1846 - 26.2981i$, and hence

$$C_1(0) \doteq -46.241 - 106.04i, \quad \mu_2 \doteq 67999,$$
$$\beta_2 \doteq -92.4815, \quad T_2 \doteq 45.2507.$$

Therefore, the bifurcating periodic solutions exist for $\tau > \hat{\tau}$ and the bifurcating periodic solutions are orbitally asymptotically stable (see Fig. 2).

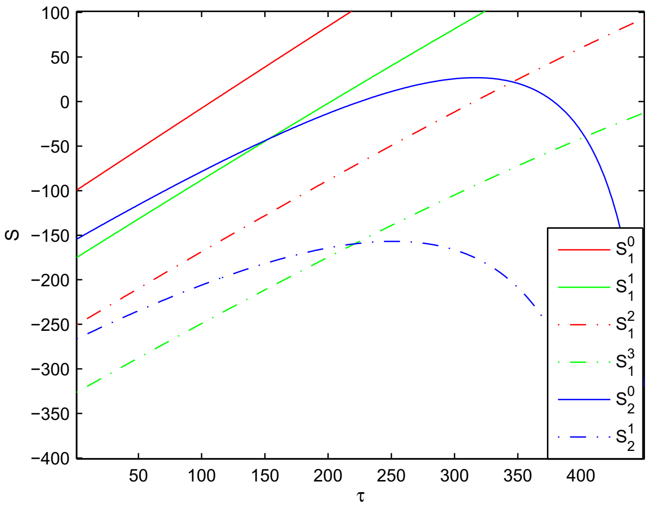

Fig. 3. Graph of functions $S_1^0, S_1^1, S_1^2, S_3^1$, S_2^0 and S_2^1 for $\tau \in [0, 472.8132)$.

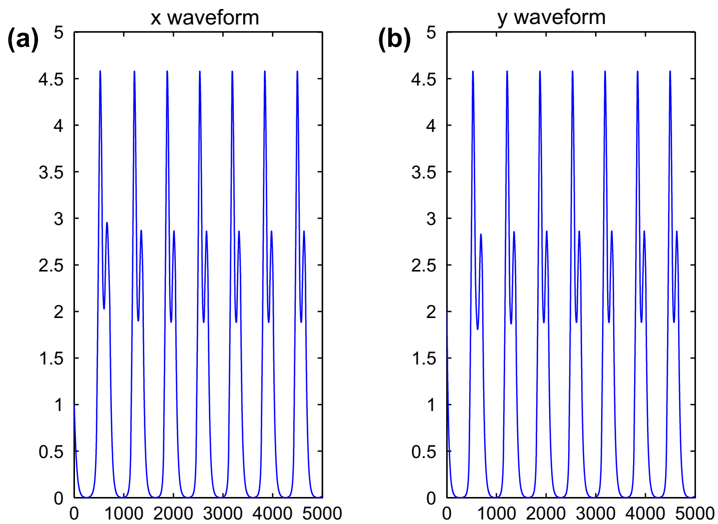

Fig. 4. Waveform for system (2) with $\tau = 120 > \tilde{\tau} = 118.6664$.

If we choose $d = 0.045, d_I = 0.001, D = 0.0119, \beta = 50, r = 0.03$, it is easy to verify that $I_2 = [0, 472.8132)$, the assumptions (A1) and (A2) hold. $S_1^0(472.8132) > 0$. Both $S_1^0(\tau)$ and $S_2^0(\tau)$ have positive zero in I_2, $\tilde{\tau} = 118.6664$. We draw the graph of $S_1^0, S_1^1, S_1^2, S_3^1, S_2^0$ and S_2^1 versus τ on I_2 in Fig. 3.

From Theorem 2.3(4), we conclude that the positive homogeneous equilibrium E_1 is asymptotically stable for $\tau \in [0, 118.6664)$, and becomes unstable for $\tau \in (118.6664, 472.8132)$ with two Hopf bifurcation points $\tau = 118.6664$.

If we choose $\hat{\tau} = 118.6664$, we can get that $\lambda'(\hat{\tau}) \doteq 0.0003, g_{20} \doteq 110.66 + 70.671i, g_{11} \doteq 262.6053, g_{02} \doteq 110.66 - 70.671i$ and $g_{21} \doteq -3521.6 + 4094.8i$, and hence

$$C_1(0) \doteq -2776.0 - 4221.8i, \quad \mu_2 \doteq 9167700,$$
$$\beta_2 \doteq -5552, \quad T_2 \doteq 461.8764.$$

Therefore, the bifurcating periodic solutions exist for $\tau > \hat{\tau}$ and the bifurcating periodic solutions are orbitally asymptotically stable (see Fig. 4).

5. Conclusion

The dynamical behavior of the age-structured model of a single species living in two identical patches derived in So et al. [3] has been investigated. We chose a birth function that is frequently used but different from the one used in So et al. [3], which leads to a different structure of the homogeneous equilibria. The stability of these equilibria and existence of Hopf bifurcations are obtained by analyzing the distribution of the roots of associated characteristic equation, using the approach introduced by Beretta and Kuang [6]. It is found that there are stability switches when time delay varies. By the theory of normal form and center manifold presented in Hassard et al. [7], an explicit algorithm for determining the direction of the Hopf bifurcation and stability of the bifurcating periodic solutions is derived. Some numerical simulations are carried out for supporting the analytic results.

The results we obtained show that there exist periodic solutions when the time delay is near the Hopf bifurcation values. A question of mathematical and biological interest is whether the periodic solutions exist when the delay is far away from the critical values? Future work will study the global existence of periodic solutions.

Acknowledgements

The authors wish to thank Professor M. Cross and the referees for their valuable comments and suggestions that led to truly significant improvement of the manuscript.

References

[1] J.A.J. Metz, O. Diekmann, in: J.A.J. Metz, O. Diekmann (Eds.), The Dynamics of Physiologically Structured Populations, Springer-Verlag, New York, 1986.
[2] H.L. Smith, A structured population model and a related functional-differential equation: global attractors and uniform persistence, J. Dyn. Diff. Eq. 6 (1994) 71–99.
[3] J.W.-H. So, J. Wu, X. Zou, Structured population on two patches: modeling dispersal and delay, J. Math. Biol. 43 (2001) 37–51.
[4] K. Cooke, P. van den Driessch, X. Zou, Interaction of maturation delay and nonlinear birth in population and epidemic models, J. Math. Biol. 39 (1999) 332–352.
[5] J. Wei, X. Zou, Birfurcation analysis of a population model and the resulting sis epidemic model with delay, J. Comput. Appl. Math. 197 (2006) 169–187.
[6] E. Beretta, Y. Kuang, Geometric stability switch criteria in delay differential systems with delay dependant parameters, SIAM J. Math. Anal. 33 (2002) 1144–1165.
[7] B.D. Hassard, N.D. Kazarinoff, Y.H. Wan, Theory and Applications of Hopf Bifurcation, Cambridge University Press, Cambridge, 1981.
[8] J. Hale, Theory of Functional Differential Equations, Springer, New York, 1977.
[9] J. Wei, S. Ruan, Stability and bifurcation in a neural network model with two delays, Phys. D 130 (1999) 225–272.
[10] Y. Qu, J. Wei, Bifurcation analysis in a time-delay model for prey–predator growth with stage-structure, Nonlinear Dyn. 49 (2007) 285–294.