International Journal of Pure and Applied Mathematics
Volume 57 No. 3 2009, 341-349

STABILITY AND HOPF BIFURCATION FOR AN APPROACHABLE HAEMATOPOIETIC STEM CELLS MODEL WITH DIFFUSIONS

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Abstract: This paper is concerned with an approachable haematopoietic stem cells model with a delay and diffusions. The stability of the equilibria are first considered by analyzing the distribution of the roots of associated characteristic equation. We then consider the impact of the diffusions on bifurcated periodic solution, and find that only small diffusions effect on the numbers of the Hopf bifurcation critical point under certain conditions.

AMS Subject Classification: 34C23, 34C25, 92D25
Key Words: cells model, time delay, diffusion, stability, Hopf bifurcation

1. Introduction

The population of haematopoietic stem cells (HSC) gives rise to all of the differentiated elements of the blood, which may be either actively proliferating or in a resting phase. After entering the proliferating phase, a cell is committed to undergo cell division at a fixed time τ later. The generation time τ is assumed to consist of four phases, G_1 the pre-synthesis phase, S the DNA synthesis phase, G_2 the post-synthesis phase and M the mitotic phase. Just after the division, both daughter cells go into the resting phase. Once in this phase, they can either return to the proliferating phase and complete the cycle

Received: October 18, 2009

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or die before ending the cycle. The dynamics of the (HSC) are governed by the coupled differential delay equations (see [1])

$$\begin{cases} N'(t) = -\delta N(t) - \alpha(N(t)) + 2e^{-\gamma\tau}\alpha(N(t-\tau)), \\ P'(t) = -\gamma P(t) + \alpha(N(t)) - e^{-\gamma\tau}\alpha(N(t-\tau)), \end{cases} \tag{1}$$

where $\alpha(N) = \beta(N)N$, β is a monotone decreasing function of N and has the explicit form of a Hill function:

$$\beta(N) = \beta_0 \frac{\theta^n}{\theta^n + N^n}.$$

N is the number of cells in non-proliferative phase, P the number of cycling proliferating cells. For more symbols of system (1) (see [1], [5], [6]).

In [1], Alaoui and Yafia made the following hypotheses:

(H0) $\delta < \frac{\beta_0}{2}$;

(H1) $a(\tau) < 0$ and $|b(\tau)| < -a(\tau)$ for all $\tau > 0$;

(H2) $\tau a(\tau) < 1$ and $|a(\tau)| \le |b(\tau)|$ for all $\tau > 0$,

where

$$a(\tau) = -(\delta + \alpha'(N^*)), \quad b(\tau) = 2e^{-\gamma\tau}\alpha'(N^*)$$

and

$$\alpha'(N^*) = \frac{\delta}{\beta_0(2e^{-\gamma\tau} - 1)^2}[\beta_0(1-n)(2e^{-\gamma\tau} - 1) + n\delta].$$

Denote $\bar{\tau} = \frac{1}{\gamma}\ln\left(\frac{2}{1+\frac{2\delta}{\beta_0}}\right)$, then (H0) implies that $\bar{\tau} > 0$ and $\beta_0(2e^{-\gamma\tau} - 1) > \delta$ when $0 < \tau < \bar{\tau}$. Clearly, this system has equilibrium $(0,0)$ and a unique positive equilibrium (N^*, P^*), where

$$N^* = \theta\left(\frac{\beta_0(2e^{-\gamma\tau} - 1) - \delta}{\delta}\right)^{\frac{1}{n}}, \quad \text{and} \quad P^* = \frac{\delta N^*}{\gamma}\left(\frac{1 - e^{-\gamma\tau}}{2e^{-\gamma\tau} - 1}\right). \tag{2}$$

It is easy to see that $E^*(\tau) = (N^*, P^*)$ is depending on the delay. Their main results are following.

Lemma 1. *For system* (1), *assume that* (H0) *holds. Then:*

(i) The trivial equilibrium $(0,0)$ *is unstable for* $0 < \tau < \bar{\tau}$*;*

(ii) i) *If* a *and* b *satisfy* (H1), $E^*(\tau)$ *is asymptotically stable for* $0 < \tau < \bar{\tau}$*;*

ii) *If* a *and* b *satisfy* (H2) *and* n *sufficiently large and* γ *close to 0, there exists a unique* τ_0 *in* $(0, \bar{\tau})$ *such that* $E^*(\tau)$ *is asymptotically stable when* $\tau \in (0, \tau_0)$ *and unstable when* $\tau \in (\tau_0, \bar{\tau})$.

Meanwhile, the authors investigated the Hopf bifurcation depending on time delay occuring at the non-trivial state. Let

(H3) $\bar{\tau}a(\tau_0) < 1$ and $|a(\tau)| \le |b(\tau)|$ for $0 < \tau < \bar{\tau}$.

Lemma 2. *Assume* (H0) *and* (H3). *For* n *sufficiently large and* γ *close to 0,* $E^*(\tau_0)$ *is the Hopf bifurcation critical point of system* (1).

Models involving delays and also spatial diffusion are increasingly applied to the study of a variety of situations (see [2], [4], [8], [9], [10]). For this reason, we consider the delayed reaction-diffusion system with Neumann conditions, resulting from considering one spatial variable and adding diffusion terms $d_1 \triangle N$, $d_2 \triangle P$, $d_1, d_2 > 0$, respectively, to the first and second equations of system (1):

$$\begin{cases} \frac{\partial N(t,x)}{\partial t} = d_1 \frac{\partial^2 N(t,x)}{\partial x^2} - \delta N(t,x) - \alpha(N(t,x)) + 2e^{-\gamma\tau}\alpha(N(t-\tau,x)), \\ \frac{\partial P(t,x)}{\partial t} = d_2 \frac{\partial^2 P(t,x)}{\partial x^2} - \gamma P(t,x) + \alpha(N(t,x)) - e^{-\gamma\tau}\alpha(N(t-\tau,x)), \\ \qquad\qquad t > 0, x \in (0,\pi), \\ \frac{\partial N(t,x)}{\partial x} = \frac{\partial P(t,x)}{\partial x} = 0, \qquad x = 0, \pi. \end{cases} \tag{3}$$

2. Stability for Equilibria and Hopf Bifurcation

Suppose (H0) hold. Then Alaoui and Yafia [1] proved that system (1) has a unique interior equilibrium $E^*(\tau) = (N^*, P^*)$ when $0 < \tau < \bar{\tau}$, where N^* and P^* satisfy (2). Clearly, $E^*(\tau)$ is also the unique positive stationary solution for (3), and system (3) can be given in abstract form by

$$\begin{cases} \frac{d}{dt}u(t) = \tau d_1 \triangle u(t) + \tau[-\delta u(t) - \alpha(u(t)) + 2e^{-\gamma\tau}\alpha(u(t-1))], \\ \frac{d}{dt}v(t) = \tau d_2 \triangle u(t) + \tau[-\gamma v(t) + \alpha(u(t)) - e^{-\gamma\tau}\alpha(u(t-1))], \end{cases} \tag{4}$$

where, for simplification of notation, we use $u(t)$ for $N(t,x)$ and $v(t)$ for $P(t,x)$ and $(u(t), v(t)) = (N(t,x), P(t,x))$ is in a suitable Hilbert space X. For example, we can take

$$X = \left\{(u,v) : u, v \in H^2(0,\pi); \frac{du}{dx} = \frac{dv}{dx} = 0, x = 0, \pi\right\}.$$

Now we consider the stability of the equilibria.

Since the eigenvalues of $d_i \triangle$ on X are $\mu_k^i = -d_i k^2$, $i = 1, 2$, $k = 0, 1, 2, \cdots$, so the characteristic equations of the linearized equation of (4) around equilibrium $E(u,v)$ is given by

$$(\lambda + d_2\tau k^2 + \tau\gamma)(\lambda + d_1\tau k^2 - \tau a(\tau) - \tau b(\tau)e^{-\lambda}) = 0 \tag{5}$$

with $a(\tau) = -(\delta + \alpha'(u))$, $b(\tau) = 2e^{-\gamma\tau}\alpha'(u)$.

(i) Consider the equilibrium $E(0,0)$.

From (4), it is easy to obtain that the characteristic equations of the linearized equation of (4) around equilibrium $(0,0)$ is given by

$$(\lambda + d_2\tau k^2 + \tau\gamma)(\lambda + d_1\tau k^2 + \tau\delta + \tau\beta_0 - 2\tau\beta_0 e^{-\gamma\tau}e^{-\lambda}) = 0. \tag{6}$$

For any $k = 0, 1, 2, \cdots$, $d_2\tau k^2 + \tau\gamma > 0$, then the stability of the $(0,0)$ follows from the study of roots of the following the sequence of equations:

$$\lambda + d_1\tau k^2 + \tau\delta + \tau\beta_0 - 2\tau\beta_0 e^{-\gamma\tau}e^{-\lambda} = 0. \tag{7}$$

From (H0), for each $0 < \tau < \bar{\tau}$, $\beta_0(2e^{-\gamma\tau} - 1) > 2\delta > \delta$, so we have $2\tau\beta_0 e^{-\gamma\tau} > \tau\delta + \tau\beta_0$, this implies that at least one of the straight lines with equations $y_k = \lambda + d_1\tau k^2 + \tau\delta + \tau\beta_0$ intersects the curve $y = 2\tau\beta_0 e^{-\gamma\tau}e^{-\lambda}$ for $\lambda > 0$. Thus, (7) has at least one real root which is positive and $(0,0)$ is unstable.

(ii) Consider the equilibrium $E^*(u^*, v^*)$.

The characteristic equations of the linearized equation of (4) around equilibrium E^* is

$$(\lambda + d_2\tau k^2 + \tau\gamma)(\lambda + d_1\tau k^2 - \tau a(\tau) - \tau b(\tau)e^{-\lambda}) = 0 \tag{8}$$

with $a(\tau) = -(\delta + \alpha'(u^*))$, $b(\tau) = 2e^{-\gamma\tau}\alpha'(u^*)$.

As $d_2\tau k^2 + \tau\gamma > 0$, the stability of E^* follows from the study of roots of the following equations

$$\Delta(\lambda, \tau) = \lambda + d_1\tau k^2 - \tau a(\tau) - \tau b(\tau)e^{-\lambda} = 0. \tag{9}$$

Suppose $\lambda = \mu + i\nu$ $(\mu \geq 0)$ is a root of (9) for $0 < \tau < \bar{\tau}$, then

$$\begin{cases} \mu + d_1\tau k^2 - \tau a(\tau) - \tau b(\tau)e^{-\mu}\cos\nu = 0, \\ \nu + \tau b(\tau)e^{-\mu}\sin\nu = 0, \end{cases} \tag{10}$$

from the first equation of (10), we obtain $d_1k^2 - a(\tau) \leq b(\tau)e^{-\mu}\cos\nu$.

Notice that under the hypothesis (H0), $\alpha'(u^*) < 0$ for each $0 < \tau < \bar{\tau}$, $-1 \leq \cos\nu \leq 1$ and $0 < e^{-\mu} < 1$, we have $-a(\tau) \leq d_1k^2 - a(\tau) \leq |b(\tau)|$, which contradict the assumption (H1), i.e., for all $0 < \tau < \bar{\tau}$, the roots of (8) have negative real parts. Summarizing the above discussion and combining Lemma 1, we have the following theorem on the stability of equilibria.

Theorem 3. *For system* (3), *assume that* (H0) *holds. Then:*

(i) The trivial equilibrium $(0,0)$ *is unstable for* $0 < \tau < \bar{\tau}$.

(ii) If a *and* b *satisfy* (H1), $E^*(\tau)$ *is asymptotically stable for* $0 < \tau < \bar{\tau}$.

Remark 4. For system (1) with $0 < \tau < \bar{\tau}$, the diffusion terms do not have effect on the stability of $(0,0)$ under hypothesis (H0) and the stability of $E^*(\tau)$ under hypotheses (H0) and (H1).

In the following, we shall investigate the switch of stability of $E^*(\tau)$ when $0<\tau<\bar{\tau}$. For this reason, one needs to find the imaginary root of equation (9). Let $\lambda=i\omega(\omega>0)$ be a root of (9), then $\Delta(i\omega,\tau)=0$, it must be that

$$\omega=\arccos\left(\frac{d_1k^2-a(\tau)}{b(\tau)}\right)\in(0,\pi),\qquad 0<\left|\frac{d_1k^2-a(\tau)}{b(\tau)}\right|<1, \tag{11}$$

and

$$\tau\sqrt{b^2(\tau)-(d_1k^2-a(\tau))^2}=\arccos\left(\frac{d_1k^2-a(\tau)}{b(\tau)}\right). \tag{12}$$

When $k=0$, (12) becomes

$$\tau\sqrt{b^2(\tau)-a^2(\tau)}=\arccos\left(\frac{-a(\tau)}{b(\tau)}\right). \tag{13}$$

If (H0) and (H2) hold, then for n sufficiently large and γ close to 0, we see from [1] that there exist a unique τ_0 in $(0,\bar{\tau})$ which a solution equation (13). (H2) implies that $a(\tau)=0$ or $0<\tau a(\tau)<1$ or $a(\tau)<0$. In what follows, we always assume that $a(\tau)<0$ and $|a(\tau)|<|b(\tau)|$ in (H2).

When $k\geq 1$, observe that

$$|d_1k^2-a(\tau)|=|d_1k^2|+|a(\tau)|\geq d_1+|a(\tau)|.$$

Therefore, letting $d_1>|b(\tau)|-|a(\tau)|$ leads us to

$$d_1+|a(\tau)|>|b(\tau)|\Longrightarrow\left|\frac{d_1k^2-a(\tau)}{b(\tau)}\right|>1,$$

it implies that equation (11) has not solutions.

Follow Lemma 1 and Lemma 2 above in Section 1. Notice that $\tau(a(\tau)-d_1k^2)<1$ and $a(\tau_0)-d_1k^2<\frac{1}{\bar{\tau}}$. We have the following result.

Theorem 5. *For system* (3)*, assume that* $d_1>|b(\tau)|-|a(\tau)|$ *holds.*

(i) If (H0) *and* (H2) *hold, then for* n *sufficiently large and* γ *close to 0, there exists a unique* τ_0 *in* $(0,\bar{\tau})$ *such that* $E^*(\tau)$ *is asymptotically stable when* $\tau\in(0,\tau_0)$ *and unstable when* $\tau\in(\tau_0,\bar{\tau})$.

(ii) $\tau=\tau_0$ *is the Hopf bifurcation value of system* (3).

Remark 6. For system (1) with $0<\tau<\bar{\tau}$, the diffusion terms do not have effect on the stability of $E^*(\tau)$ under hypotheses (H0) and (H2) and Hopf bifurcation under hypotheses (H0) and (H2) when $d_1>|b(\tau)|-|a(\tau)|$.

3. Effect of Diffusion

In Section 2, we have discussed how the diffusion terms do not have effect on the stability of equilibrium and the Hopf bifurcation under certain conditions. In the following, we discuss the effect of diffusion on Hopf bifurcation for system (1) when the condition $d_1 > |b(\tau)| - |a(\tau)|$ fails.

Consider the following one of the characteristic equations (9) of system (3)

$$\Delta_1(\lambda, \tau) = \lambda + d_1\tau - \tau a(\tau) - \tau b(\tau)e^{-\lambda} = 0. \tag{14}$$

Suppose $\lambda = i\omega(\omega > 0)$ is a root of (14), then

$$\omega = \arccos\left(\frac{d_1 - a(\tau)}{b(\tau)}\right) \in (0, \pi), \quad 0 < \left|\frac{d_1 - a(\tau)}{b(\tau)}\right| < 1, \tag{15}$$

and

$$\tau\sqrt{b^2(\tau) - (d_1 - a(\tau))^2} = \arccos\left(\frac{d_1 - a(\tau)}{b(\tau)}\right). \tag{16}$$

When $d_1 < |b(\tau)| - |a(\tau)|$, we have

$$|d_1 - a(\tau)| \leq d_1 + |a(\tau)| < |b(\tau)|.$$

Define τ_1 by $\tau_1\sqrt{b^2(\tau_1) - (d_1 - a(\tau_1))^2} = \arccos\left(\frac{d_1 - a(\tau_1)}{b(\tau_1)}\right)$, we can obtain:

Theorem 7. *Assume that* (H0) *and* (H2) *hold. If* $d_1 < |b(\tau)| - |a(\tau)|$, *then for* n *sufficiently large and* γ *close to 0, there exists at least a solution* τ_1 *of equation* (16) *in* $(0, \bar{\tau})$ *such that* $i\omega_1$ *is a purely imaginary root of equation* (14), *with* $\omega_1 = \arccos\left(\frac{d_1 - a(\tau_1)}{b(\tau_1)}\right)$.

Proof. Under (H0) and (H2), a root of equation (16) solves the following equation

$$\tau = -\frac{\arccos\left(\frac{d_1 - a(\tau)}{b(\tau)}\right)}{b(\tau)\sin\left(\arccos\left(\frac{d_1 - a(\tau)}{b(\tau)}\right)\right)}. \tag{17}$$

Let $y(\tau) = \arccos\left(\frac{d_1 - a(\tau)}{b(\tau)}\right)$, $F(\tau) = -\frac{y(\tau)}{b(\tau)\sin(y(\tau))}$. As $F(0) > 0$ for sufficiently large n and $F(\bar{\tau}) < \bar{\tau}$ for γ close to 0, the continuity of F imply that there exists at least $\tau_1 \in (0, \bar{\tau})$ such that $F(\tau_1) = \tau_1$. □

In the next we will show that system (3) has a Hopf bifurcation at $\tau = \tau_1$. Consider the abstract form of system (3)

$$\begin{cases} \frac{d}{dt}u(t) = \tau d_1 \triangle u(t) + \tau[-\delta u(t) - \alpha(u(t)) + 2e^{-\gamma\tau}\alpha(u(t-1))], \\ \frac{d}{dt}v(t) = \tau d_2 \triangle u(t) + \tau[-\gamma v(t) + \alpha(u(t)) - e^{-\gamma\tau}\alpha(u(t-1))], \end{cases} \tag{18}$$

where, for simplification of notation, we use $u(t)$ for $P(t,x)$ and $v(t)$ for $N(t,x)$ and $(u(t),v(t)) = (P(t,x),N(t,x))$ is in a suitable Hilbert space X. We can take X as stated in Section 2. Translating $E^*(\tau_1)$ to the origin by setting $U(t) = (u(t),v(t)) - E^*(\tau_1) \in X$, (18) is transformed into the equation in $\mathcal{C} = C([-1,0];X)$

$$\frac{d}{dt}U(t) = \tau d\triangle U(t) + \tau L(U_t) + \tau f(U_t), \tag{19}$$

where $d = (d_1\triangle, d_2\triangle)$ and

$$L(\varphi) = \begin{pmatrix} -(\delta+\alpha'(u^*))\varphi_1(0) + 2e^{-\gamma\tau_1}\alpha'(u^*)\varphi_1(-1) \\ -\gamma\varphi_2(0) + \alpha'(u^*)\varphi_1(0) - e^{-\gamma\tau_1}\alpha'(u^*)\varphi_1(-1) \end{pmatrix},$$

$$f(\varphi) = \begin{pmatrix} -\alpha(\varphi_1(0)+u^*) + \alpha'(u^*)\varphi_1(0) - 2e^{-\gamma\tau_1}\alpha'(u^*)\varphi_1(-1) \\ +2e^{-\gamma\tau_1}\alpha(\varphi_1(-1)+u^*) - \delta u^* \\ \\ \alpha(\varphi_1(0)+u^*) - \alpha'(u^*)\varphi_1(0) - e^{-\gamma\tau_1}\alpha(\varphi_1(-1)+u^*) \\ +e^{-\gamma\tau_1}\alpha'(u^*)\varphi_1(-1) - \gamma u^* \end{pmatrix},$$

for $\varphi = (\varphi_1,\varphi_2) \in \mathcal{C}$.

Notice that $f(0) = Df(0) = 0$ for all $\tau > 0$, the characteristic equation for the linear equation (19) around $E^*(\tau_1)$ is equivalent to

$$\Delta_k(\lambda,\tau) = \lambda + d_1\tau k^2 - \tau a(\tau_1) - \tau b(\tau_1)e^{-\lambda} = 0. \tag{20}$$

Under (H0) and (H2), from Lemma 1, $\lambda - \tau a(\tau_1) - \tau b(\tau_1)e^{-\lambda} = 0$ has no root $i\omega$, so we can know $\Delta_0(i\omega,\tau) \neq 0$ for any $\omega > 0$; from the discussion above, if $d_1 > |b(\tau)| - |a(\tau)|$ failed, then find a pure imaginary root of equation (19) is equivalent to find a pure imaginary root of the equation

$$\Delta_1(\lambda,\tau) = \lambda + d_1\tau - \tau a(\tau_1) - \tau b(\tau_1)e^{-\lambda} = 0. \tag{21}$$

From (16) and Theorem 7, we can find at least $\tau_1 \in (0,\bar{\tau})$, such that $\Delta_1(i\omega_1,\tau) = 0$, in which $\omega_1 = \arccos\left(\frac{d_1 - a(\tau_1)}{b(\tau_1)}\right)$. So (20) has at least a pair of simple imaginary roots $\pm i\omega_1$ at $\tau = \tau_1$.

To apply the Hopf Bifurcation Theorem to system (19), we also need the transversality condition to be satisfied.

From (21), $\Delta_1(i\omega_1,\tau_1) = 0$ and $\frac{\partial}{\partial\lambda}\Delta_1(i\omega_1,\tau_1) = 1 + d_1\tau_1 - \tau_1 a(\tau_1) + i\omega_1 \neq 0$. According to the implicit function theorem, there exists a complex function $\lambda = \lambda(\tau)$ defined in a neighborhood of τ_1, such that $\lambda(\tau_1) = i\omega$ and $\Delta_1(\lambda(\tau),\tau) = 0$, and

$$\lambda'(\tau) = -\frac{\partial\Delta_1(\lambda,\tau)/\partial\tau}{\partial\Delta_1(\lambda,\tau)/\partial\lambda} \tag{22}$$

when all τ close to τ_1. Suppose $\lambda(\tau) = p(\tau) + iq(\tau)$, then we can easy to obtain

$$p'(\tau) \mid_{\tau=\tau_1} = -\frac{\tau_1[b^2(\tau_1) - (d_1 - a(\tau_1))^2]}{(1 + \tau_1 b(\tau_1)\cos\omega_1)^2 + (\tau_1 b(\tau_1)\sin\omega_1)^2}.$$

Let

(H4) $\bar{\tau} a(\tau_1) < 1$ and $|a(\tau)| \leq |b(\tau)|$ for $0 < \tau < \bar{\tau}$.

Notice that (H4) imply $d_1 - a(\tau_1) > 1/\tau_1$; $d_1 > |b(\tau)| - |a(\tau)|$ imply $|d_1 - a(\tau_1)| > |b(\tau_1)|$, and $a(\tau) < 0$ for each $0 < \tau < \bar{\tau}$. So, we deduce that $p'(\tau) \mid_{\tau=\tau_1} > 0$.

According to the discussion above and apply Hopf Bifurcation Theorem introduced in [7], we have the following result.

Theorem 8. *For system* (3)*, assume that* $d_1 < |b(\tau)| - |a(\tau)|$ *holds. If* (H0), (H2) *and* (H4) *hold, then for* n *sufficiently large and* γ *close to 0, there exist at least* τ_1 *in* $(0, \bar{\tau})$ *such that* $E^*(\tau_1)$ *is a Hopf bifurcation critical point.*

Remark 9. For system (1) with $0 < \tau < \bar{\tau}$, if $d_1 < |b(\tau)| - |a(\tau)|$, the diffusion terms effect on the numbers of the Hopf bifurcation critical point under certain conditions.

4. Discussions

In Sections 2 and 3 of this paper it is showm that the diffusion coefficient d_2 cannot effect the stability of $E^*(\tau_0)$ and the Hopf bifurcation. Under the conditions $d_1 > |b(\tau)| - |a(\tau)|$, one of diffusion terms d_1 cannot effect the stability of $E^*(\tau_0)$ and the Hopf bifurcation, but when $d_1 < |b(\tau)| - |a(\tau)|$, the other Hopf bifurcation will happen at $E^*(\tau_1)$, although we cannot give any result of stability of $E^*(\tau_1)$, because the dependance of $E^*(\tau)$ on the delay τ. From Lemma 1, $E^*(\tau_0)$ is only Hopf bifurcation critical point of model without diffusion, but Theorem 8 implies that $E^*(\tau_1)$ is Hopf bifurcation critical point of model with diffusion, which means that under the condition that diffusion creates Hopf bifurcation.

In our present model (3), in view of the biology significance for HSC, we assume that (3) subject to homogeneous Neumann boundary condition indicates that this system is self-contained with zero population flux across the boundary. From Theorem 5 and Theorem 8, we can see that only small diffusion terms effect on the Hopf bifurcation of model (1). The results proposed in this paper should hopefully improve the understanding of the qualitative properties of the description delivered by model (1) with delay but no diffusion.

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