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Global dynamics and Hopf bifurcation of a structured population model

Dashun Xu*

Department of Mathematics and Statistics, Memorial University of Newfoundland, Rank Str. 11, St Johns, Nfld, Canada A1C 5S7

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Abstract

In this paper, we consider a system of delay differential equations which describes a structured single species population distributed over a two-patch environment. For a large class of birth functions, we obtain sufficient conditions for uniform persistence and global stabilities of equilibria. A Hopf bifurcation in this system is also discussed when the birth function takes a specific form, and the stability of the bifurcated periodic solutions and the bifurcation direction are investigated in detail. Finally, some numerical simulations of the system are given.

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1. Introduction

In general, a single species population in a homogeneous environment is modelled by a logistic equation. If a delayed growth of the species is considered, a time delay is added to the equation. The delayed growth may be caused by different hatching times, different rates of maturation and/or gestation. Moreover, when we consider a single species living in an n -patch and non-homogeneous environment, the dynamics of the population is very complicated. To describe the dynamics, Smith and Thieme [7] derived a system of delay

* Tel.: +709 7378521; fax: +709 7373010.

E-mail address: dxu@math.mun.ca (D. Xu).

differential equations as follows:

$$\dot{u}_j(t) = \sum_{k=1}^n \alpha_{jk} u_k(t) + \sum_{k=1}^n (e^{\tau_j A})_{jk} b_k(u_k(t - \tau_k)), \quad j = 1, 2, \dots, n, \tag{1.1}$$

where $A = (\alpha_{jk})_{n \times n}$ with

$$\alpha_{jk} = D_{jk} - \left(\sum_{i=1}^n D_{ij} + d_j \right) \delta_{jk}$$

and δ_{jk} are Kronecker symbols. d_j and b_j denote the death rates of the individuals and the birth function in the j th patch, respectively. τ_j represents the maturation age in patch j and D_{jk} corresponds to the migration rate from patch k to patch j . Under certain assumptions, Smith and Thieme [7] established the generic convergence for system (1.1) by applying the theories of monotone dynamical systems.

When $n = 2$, assuming that $\tau_1 = \tau_2 = r$, and

$$d_j(a) = \begin{cases} d_1(a), & 0 \leq a \leq r, \\ d_j \equiv \text{constant}, & a > r, \end{cases} \quad D_{jk}(a) = \begin{cases} D_j(a), & 0 \leq a \leq r, \\ D_j \equiv \text{constant}, & a > r, \end{cases}$$

where $j, k = 1, 2, j \neq k$, and by applying the method similar to [7], So, Wu and Zou [9] derived the following system:

$$\begin{aligned} \frac{du_1(t)}{dt} &= -d_1 u_1(t) + D_2 u_2(t) - D_1 u_1(t) \\ &\quad + e^* \left[1 - \int_0^r e^{-\int_\theta^r \hat{D}(a) da} D_1(\theta) d\theta \right] b_1(u_1(t - r)) \\ &\quad + e^* \int_0^r e^{-\int_\theta^r \hat{D}(a) da} D_2(\theta) d\theta b_2(u_2(t - r)), \\ \frac{du_2(t)}{dt} &= -d_2 u_2(t) + D_1 u_1(t) - D_2 u_2(t) \\ &\quad + e^* \int_0^r e^{-\int_\theta^r \hat{D}(a) da} D_1(\theta) d\theta b_1(u_1(t - r)) \\ &\quad + e^* \left[1 - \int_0^r e^{-\int_\theta^r \hat{D}(a) da} D_2(\theta) d\theta \right] b_2(u_2(t - r)), \end{aligned} \tag{1.2}$$

where $\hat{D}(a) = D_1(a) + D_2(a)$, and $\alpha = (e^*)^{-1}$ represents the immature death rate. So, Wu and Zou [9] analyzed the dynamics of system (1.2) in the case where two patches are identical and the birth functions take $b(u) = u^2 e^{-\beta u}$. They showed that the immature death rate α significantly affects the dynamics of the mature population. The variations of the immature death rate α not only result in the variation of positive homogeneous equilibria, but also may lead to stable periodic solutions.

This paper deals with system (1.2) in the case of identical patches with a large class of birth functions. In Section 2, we obtain sufficient conditions for uniform persistence and the global stability of equilibria by appealing to persistence theory and the theory of

monotone dynamical systems. In Section 3, in the case where the birth function is of the form $b(u) = ue^{-\beta u}$, we give some formulas to determine the type of Hopf bifurcation, and provide some numerical simulations to illustrate the Hopf bifurcation.

2. Global dynamics for two identical patches

In this section, we consider system (1.2) in two identical patches; namely, we assume that $d_i = d$, $D_i = D$, $b_i(u) = b(u)$, $D_i(a) = D(a)$ for $a \in (0, r)$, where $i = 1, 2$. Then system (1.2) reduces to

$$\begin{cases} \frac{du_1(t)}{dt} = -du_1(t) + D(u_2(t) - u_1(t)) + e^*(1-r^*)b(u_1(t-r)) + e^*r^*b(u_2(t-r)), \\ \frac{du_2(t)}{dt} = -du_2(t) + D(u_1(t) - u_2(t)) + e^*r^*b(u_1(t-r)) + e^*(1-r^*)b(u_2(t-r)), \end{cases} \quad (2.1)$$

where

$$r^* = \int_0^r e^{-\int_0^r \hat{D}(a) da} D(\theta) d\theta = \frac{1}{2}(1 - e^{-2\int_0^r D(a) da}).$$

Then $r^* \in (0, \frac{1}{2})$.

We assume that

(H) $b(u) = ug(u)$, $g(u) > 0$, $g'(u) < 0$ for all $u \geq 0$.

Hence, $b(u) < ug(0)$ for $u > 0$, and $g(u)$ is a strictly decreasing function.

Let \tilde{u} be the number such that $b'(\tilde{u}) = g(\tilde{u}) + \tilde{u}g'(\tilde{u}) = 0$. \tilde{u} denotes the unique solution of $g(\tilde{u}) = d\alpha$ in the case of $g(\infty) < d\alpha < g(0)$, where $\alpha = (e^*)^{-1}$ represents the death rate of the immature population. Then $\tilde{u}, \tilde{u} > 0$, $b'(u) > 0$ if $u \in [0, \tilde{u})$, and $b'(u) < 0$ if $u \in (\tilde{u}, +\infty)$. In addition, it is easy to see that system (2.1) has a positive homogeneous equilibrium (\bar{u}, \bar{u}) in the case of $g(\infty) < d\alpha < g(0)$.

Let $X = C([-r, 0], R_+^2)$. Then, for any $\varphi \in X$, there exists a unique solution $u(t, \varphi) = (u_1(t, \varphi), u_2(t, \varphi))$ ($t \geq 0$) of system (2.1) with $u(s, \varphi) = \varphi(s)$, $s \in [-r, 0]$ (see e.g. [5]). Let $u_t(\varphi)$ be the solution semiflow of system (2.1), where $u_t(\varphi)(s) = u(t + s, \varphi)$, $s \in [-r, 0]$, $t \geq 0$. Note that every solution $u(t, \varphi)$ of system (2.1) is non-negative for $\varphi \in X$ (see [6, Theorem 5.2.1]). Hereafter, by a solution $u(t, \varphi)$ of system (2.1) we always mean a non-negative solution $u(t, \varphi)$.

Theorem 2.1. *Assume (H) holds.*

(i) *If $d\alpha > g(0)$ (i.e. $d > e^*g(0)$), the trivial equilibrium of system (2.1) is globally asymptotically stable.*

(ii) *If $d\alpha < g(0)$, system (2.1) is uniformly persistent in the sense that there exists a $\delta > 0$ such that each solution $(u_1(t, \varphi), u_2(t, \varphi))$ of system (2.1) with $\varphi \in X$ satisfies $\liminf_{t \rightarrow \infty} u_i(t, \varphi) \geq \delta$, $i = 1, 2$. If, in addition, $d\alpha > g(\infty)$ and $\bar{u} \leq \tilde{u}$, then the positive homogeneous equilibrium (\bar{u}, \bar{u}) is globally asymptotically stable.*

Biologically, case (i) implies that the species will die out, while case (ii) implies that the species in two patches will be persistent, and will stabilize at the positive equilibrium (\bar{u}, \bar{u})

under the additional conditions. Obviously, the immature death rate α and the mature death rate d jointly determine the eventual states of the mature populations. Note that the global stability in Theorem 2.1 is very different in spirit from the one in [7]. This stability result holds for all delays, but makes certain restrictions. The result in [7] provides global stability without these restrictions provided that the delay is small enough.

Proof of Theorem 2.1. (i) Clearly, system (2.1) has a trivial equilibrium $(0, 0)$. Let $u = u_1 + u_2$, then

$$\begin{aligned} \dot{u}(t) &= -du + e^*(b(u_1(t-r)) + b(u_2(t-r))) \\ &\leq -du + e^*g(0)u(t-r). \end{aligned}$$

The zero solution is globally asymptotically stable for the linear equation $\dot{x}(t) = -dx(t) + e^*g(0)x(t-r)$ when $d > e^*g(0)$. Therefore, by the standard comparison theorem (see [6, Theorem 5.1.1]), every solution of system (2.1) goes to zero as t goes to infinity. Thus, the trivial equilibrium of system (2.1) is globally asymptotically stable when $d > e^*g(0)$.

(ii) In what follows, we assume $d < e^*g(0)$. To obtain that system (2.1) is uniformly persistent, we will apply Theorem 4.6 in [10] and Theorem A.2 in [8]. Let

$$X_1 = \{\varphi = (\varphi_1, \varphi_2) : \varphi \in X, \varphi_i \neq 0, \forall i = 1, 2\},$$

and $\Phi(t) : X \rightarrow X, t \geq 0$, be the solution semiflow generated by system (2.1); that is, $\Phi(t)\varphi = u_t(\varphi)$. Denote $X_2 = X \setminus X_1$. Then, for all nonzero $\varphi \in X_2, \Phi(t)\varphi \in X_1$ holds for $t > 0$.

In the following, we want to show that $\Phi(t)$ is point dissipative in X [2]. Let $u_m = \max\{\bar{u}, \tilde{u}\}, L \geq u_m$, and $u(t) = u_1(t) + u_2(t)$. Then, by our assumption (H), we have

$$\begin{aligned} \dot{u}(t) &= -du + e^*(b(u_1(t-r)) + b(u_2(t-r))) \\ &\leq -e^*g(\bar{u})u + 2Le^*g(L), \quad \text{for } u_i(t-r) \geq L. \end{aligned}$$

Note that the ordinary differential equation $\dot{u} = -e^*g(\bar{u})u + 2Le^*g(L)$ has a globally asymptotically stable equilibrium $2Lg(L)/g(\bar{u})$. By the standard comparison theorem, each solution of system (2.1) is ultimately bounded. Hence, $\Phi(t)$ is point dissipative in X .

Claim. *There exists small $\delta_1 > 0$ such that the solution semiflow $\Phi(t)$ satisfies $\limsup_{t \rightarrow \infty} \|\Phi(t)\varphi\| \geq \delta_1, \forall \varphi \in X_1$.*

We use an argument similar to [12, Claim 1]. Choose $0 < \delta_1 < \min\{\bar{u}, \tilde{u}\}$. Suppose that, by contradiction, $\limsup_{t \rightarrow \infty} \|\Phi(t)\varphi\| < \delta_1$ for some $\varphi \in X_1$. Then there exists $T > 0$ such that $\|\Phi(t)\varphi\| < \delta_1, \forall t \geq T$. Let $u(t) = u_1(t) + u_2(t)$, where $(u_1(t), u_2(t)) = (\Phi(t)\varphi)(0), t \geq 0$. By the monotonicity of $g(u)$, we have

$$\begin{aligned} \dot{u}(t) &= \dot{u}_1(t) + \dot{u}_2(t) = -du + e^*(b(u_1(t-r)) + b(u_2(t-r))) \\ &= -e^*g(\bar{u})u + e^*(u_1(t-r)g(u_1(t-r)) + u_2(t-r)g(u_2(t-r))) \\ &\geq -e^*g(\bar{u})u + e^*g(\delta_1)u(t-r), \quad \text{for } t \geq T. \end{aligned}$$

Clearly, the linear delayed differential equation

$$\dot{x}(t) = -e^*g(\bar{u})x(t) + e^*g(\delta_1)x(t - r) \tag{2.2}$$

is cooperative and irreducible. By Smith [6, Corollary 5.5.2], the stability of zero for (2.2) is the same as that for the following ordinary differential equation (obtained by simply ignoring the delay in (2.2)).

$$\dot{x}(t) = e^*(g(\delta_1) - g(\bar{u}))x(t), \quad t \geq T.$$

So, the stability modulus s of (2.2) is positive since $g(\delta_1) > g(\bar{u})$. Hence, by Smith [6, Theorem 5.5.1], Eq. (2.2) has a solution of the form $x^*(t) = e^{st}x_0$ with $x_0 > 0$. Since solutions of system (2.1) are positive, we can choose a $k > 0$, such that $u(t) = u_1(t) + u_2(t) \geq kx^*(t)$ for $t \in [T - r, T]$. By the comparison theorem [6, Theorem 5.5.1], we have $u(t) \geq kx^*(t)$, for all $t \geq T$. Hence, $\lim_{t \rightarrow \infty} u(t) = \infty$, which contradicts the boundedness of $(u_1(t), u_2(t))$ on $[0, \infty)$.

From the above claim, it follows that $(0, 0)$ is an isolated invariant set in X , and is a weak repeller for X_1 . By Thieme [10, Theorem 4.6], X_2 is a uniform strong repeller for X_1 . That is, there is a $\delta_1 > 0$ such that $\liminf_{t \rightarrow \infty} \text{dist}(\Phi(t)\varphi, X_2) \geq \delta_1$ for all $\varphi \in X_1$. Then, by Smith and Zhao [8, Theorem A.2] with $Z = X$ and $e = (1, 1)$, there exists a $\delta > 0$ such that every solution $(u_1(t, \varphi), u_2(t, \varphi))$ of system (2.1) with $\varphi \in X_1$ satisfies $\liminf_{t \rightarrow \infty} u_i(t, \varphi) \geq \delta$.

In order to obtain the global stability for the positive equilibrium $u^* = (\bar{u}, \bar{u})$, we further assume that $g(\infty) < d\alpha$, and $\bar{u} \leq \tilde{u}$. Let I represent the order interval

$$[\hat{0}, \hat{u}] = \{\varphi(s) = (\varphi_1(s), \varphi_2(s)) : \varphi_i \in C([-r, 0], [0, \tilde{u}]), i = 1, 2\}.$$

Then, $(\bar{u}, \bar{u}) \in I$.

First, we show that system (2.1) is cooperative and irreducible over I , and I is an invariant set for system (2.1). Denote the right side of system (2.1) by $g_i(u_1(t), u_2(t), u_1(t-r), u_2(t-r))$, $i = 1, 2$. Then $g_i(x_1, x_2, y_1, y_2)$ satisfies

$$\frac{\partial g_1}{\partial x_2} = \frac{\partial g_2}{\partial x_1} = D > 0$$

and

$$\frac{\partial(g_1, g_2)}{\partial(y_1, y_2)} = \begin{pmatrix} e^*(1 - r^*)b'(y_1) & e^*r^*b'(y_2) \\ e^*r^*b'(y_1) & e^*(1 - r^*)b'(y_2) \end{pmatrix},$$

which is a nonnegative matrix whenever $y_1, y_2 \in [0, \tilde{u}]$. Moreover, if $G_i(x_1, x_2) = g_i(x_1, x_2, x_1, x_2)$, then the Jacobian matrix

$$J = \frac{\partial(G_1, G_2)}{\partial(x_1, x_2)} = \begin{pmatrix} -d - D + e^*(1 - r^*)b'(x_1) & D + e^*r^*b'(x_2) \\ D + e^*r^*b'(x_1) & -d - D + e^*(1 - r^*)b'(x_2) \end{pmatrix}$$

is irreducible for $x_1, x_2 \in [0, \tilde{u}]$. Thus, system (2.1) is cooperative and irreducible on I .

Letting f_i denote the right sides of system (2.1), $i = 1, 2$, and if $\varphi = (\varphi_1, \varphi_2) \in I = [\hat{0}, \hat{u}]$, and $\varphi_1(0) = \tilde{u}$, then we have

$$\begin{aligned} f_1(\varphi) &= -d\varphi_1(0) + D(\varphi_2(0) - \varphi_1(0)) \\ &\quad + e^*(1 - r^*)b(\varphi_1(-r)) + e^*r^*b(\varphi_2(-r)) \\ &\leq -d\tilde{u} + e^*b(\tilde{u}) = -e^*\tilde{u}(g(\tilde{u}) - g(\tilde{u})) \leq 0. \end{aligned}$$

Similarly, if $\varphi = (\varphi_1, \varphi_2) \in I$, and $\varphi_2(0) = \tilde{u}$, then we also have $f_2(\varphi) \leq 0$. Hence, I is positively invariant for system (2.1) by Smith [6, Remark 5.2.1]. That is, for any $\varphi \in I$, the unique solution $(u_1(t, \varphi), u_2(t, \varphi))$ satisfies $0 \leq u_i(t, \varphi) \leq \tilde{u}$ for all $t \geq 0$. By the same argument, it is easy to check that the order interval $I_L = [\hat{0}, \hat{L}]$ is positively invariant for all $L \geq \tilde{u}$.

Next, we prove that there is a globally stable equilibrium in I . Let $f = (f_1, f_2)$ and $\hat{0}(s) = (0, 0)$ for $s \in [-r, 0]$, then the Fréchet derivative Df at $\hat{0}$ is given by

$$Df(\hat{0})\varphi = \int_{-r}^0 d\eta(s)\varphi(s),$$

where $\eta(s) = (\eta_{ij})$, and

$$\begin{aligned} \eta_{11}(s) = \eta_{22}(s) &= \begin{cases} 0, & s = -r, \\ e^*(1 - r^*)b'(0), & s \in (-r, 0), \\ -d - D + e^*(1 - r^*)b'(0), & s = 0, \end{cases} \\ \eta_{12}(s) = \eta_{21}(s) &= \begin{cases} 0, & s = -r, \\ e^*r^*b'(0), & s \in (-r, 0), \\ D + e^*r^*b'(0), & s = 0. \end{cases} \end{aligned}$$

Note that f_i is strictly sublinear, and the maximal eigenvalue λ_0 of the Jacobian matrix J at $(0, 0)$ is $\lambda_0 = -d + e^*g(0)$. Therefore, when $d < e^*g(0)$, system (2.1) satisfies all the conditions of [11, Theorem 3.2], and hence, system (2.1) admits a unique positive equilibrium $u^* = (\tilde{u}, \tilde{u})$ which is globally asymptotically stable in $I \setminus \{\hat{0}\}$.

It remains to prove the global attractivity of u^* in X . We claim that the omega limit set of each solution in X is contained in I . Indeed, for any given $\varphi \in X$, there exists $L \geq \tilde{u}$ such that $\varphi \in I_L$. Then $u_t(\varphi) \in I_L$ for all $t \geq 0$. Thus, the omega limit set $\omega(\varphi)$ of $u_t(\varphi)$ is nonempty, compact and invariant for system (2.1). Let $G = \{\psi(s) : \psi \in \omega(\varphi), s \in [-r, 0]\}$. Then, G is a compact subset of R_+^2 because of the compactness of $\omega(\varphi)$ and $[-r, 0]$. Define $L_0 = \inf\{L \geq 0 : G \subseteq [0, L]^2\}$. Then, there exist $\psi \in \omega(\varphi)$ and $s_0 \in [-r, 0]$ such that $\psi(s_0) = (\psi_1(s_0), \psi_2(s_0))$ satisfies either $\psi_1(s_0) = L_0$ or $\psi_2(s_0) = L_0$. Thus, $\xi_i(s) \leq \psi_1(s_0)$ or $\xi_i(s) \leq \psi_2(s_0)$ for all $\xi = (\xi_1, \xi_2) \in \omega(\varphi)$. Since $\omega(\varphi)$ is invariant, we can assume that $s_0 = 0$, and there exists $\zeta = (\zeta_1, \zeta_2) \in \omega(\varphi)$ such that $u_r(\zeta) = \psi$, i.e., $u_i(r + s, \zeta) = \psi_i(s)$, $s \in [-r, 0]$. Suppose $L_0 > \tilde{u}$. Then, if $\psi_1(0) = L_0$, we have

$$\begin{aligned} \dot{u}_1(r, \zeta) &= -d\psi_1(0) + D(\psi_2(0) - \psi_1(0)) \\ &\quad + e^*(1 - r^*)b(\psi_1(-r)) + e^*r^*b(\psi_2(-r)) \\ &\leq -e^*g(\tilde{u})L_0 + e^*b(\tilde{u}) \leq e^*(\tilde{u}g(\tilde{u}) - L_0g(\tilde{u})) < 0. \end{aligned}$$

This inequality implies that there exists some $t < r$ such that

$$u_1(t, \zeta) > u_1(r, \zeta) = \psi_1(0) = L_0,$$

which contradicts that $u_t(\zeta) \in \omega(\varphi) \subseteq I_{L_0}$. By the similar argument, if $\psi_2(0) = L_0$, then, we get the same contradiction. Thus, $L_0 \leq \bar{u}$, and $\omega(\varphi) \subset I$.

It is easy to see that $(0, 0)$ and (\bar{u}, \bar{u}) are two isolated invariant sets, and there is no cycle among them for $\Phi(t) : I \rightarrow I$. Clearly, $\omega(\varphi)$ is internally chain transitive for $\Phi(t) : I \rightarrow I$ (see [3, Lemma 2.1]). By the continuous version of [3, Theorem 3.2], we have $\omega(\varphi) = (0, 0)$ or (\bar{u}, \bar{u}) . By the uniform persistence of system (2.1), it follows that $\omega(\varphi) = (\bar{u}, \bar{u})$ for all nonzero $\varphi \in X$. Consequently, (\bar{u}, \bar{u}) is globally asymptotically stable for system (2.1) in $X \setminus \{\hat{0}\}$. This completes the proof. \square

If we take $g(u) = e^{-\beta u}$, i.e., $b(u) = ue^{-\beta u}$, where $\beta > 0$, then $b(u)$ satisfies our assumption. Moreover, $\bar{u} = -(1/\beta) \ln(d\alpha)$, and $\tilde{u} = 1/\beta$. Hence, $\bar{u} \leq \tilde{u}$ if $e^{-1} \leq d\alpha$. In addition, it is not difficult to see that system (2.1) admits a positive homogeneous equilibrium $u^* = (\bar{u}, \bar{u})$ when $d\alpha < 1$.

The following result, as a consequence of Theorem 2.1, shows how the death rates of the immature and the mature determine the long-term behavior of the species.

Corollary 2.1. *Let $b(u) = ue^{-\beta u}$. If $d\alpha > 1$, the trivial equilibrium is globally asymptotically stable for system (2.1). If $d\alpha < 1$, system (2.1) is uniformly persistent and admits a positive homogeneous equilibrium $u^* = (\bar{u}, \bar{u})$. If $e^{-1} \leq d\alpha < 1$, the positive equilibrium is globally asymptotically stable.*

3. Hopf bifurcation

In this section, we assume the birth function takes $b(u) = ue^{-\beta u}$ for some $\beta > 0$. Therefore, we can investigate Hopf bifurcations of system (2.1) considering the delay r as a bifurcating parameter. We follow the algorithm of Kazarinoff and Wan [4] to determine Hopf bifurcations.

In the last section, we have shown that system (2.1) has a positive homogeneous equilibrium $u^* = (\bar{u}, \bar{u})$ when $d\alpha < 1$. Its local stability can be determined by the roots of the following characteristic equation.

$$\begin{aligned} 0 &= \begin{vmatrix} \lambda + d + D - e^*(1 - r^*)b'(\bar{u})e^{-\lambda r} & -D - e^*r^*b'(\bar{u})e^{-\lambda r} \\ -D - e^*r^*b'(\bar{u})e^{-\lambda r} & \lambda + d + D - e^*(1 - r^*)b'(\bar{u})e^{-\lambda r} \end{vmatrix} \\ &= [\lambda + d + D - e^*(1 - r^*)b'(\bar{u})e^{-\lambda r}]^2 - [D + e^*r^*b'(\bar{u})e^{-\lambda r}]^2 \\ &= (\lambda + d - e^*b'(\bar{u})e^{-\lambda r})(\lambda + d + 2D - e^*(1 - 2r^*)b'(\bar{u})e^{-\lambda r}), \end{aligned}$$

which can be reduced to

$$\lambda + d - e^*b'(\bar{u})e^{-\lambda r} = 0 \tag{3.1}$$

and

$$\lambda + d + 2D - e^*(1 - 2r^*)b'(\bar{u})e^{-\lambda r} = 0, \tag{3.2}$$

where $b'(\bar{u}) = e^{-\beta\bar{u}} - \beta\bar{u}e^{-\beta\bar{u}} = d\alpha(1 + \ln(d\alpha))$.

Eqs. (3.1) and (3.2) are of the form

$$\lambda + \gamma_1 + \gamma_2 e^{-\lambda r} = 0.$$

We know that the above equation has negative real parts if and only if

$$\gamma_1 + 1 > 0, \quad \gamma_1 + \gamma_2 > 0, \quad \gamma_2 r < \xi \sin \xi - \gamma_1 r \cos \xi, \tag{3.3}$$

where ξ is a root of $\xi = -\gamma_1 r \tan \xi$, $0 < \xi < \pi$ if $\gamma_1 \neq 0$, and $\xi = \pi/2$ if $\gamma_1 = 0$ (see [1, Theorem A.5]).

Let $\xi = \xi(u) \in (\pi/2, \pi)$ be a function defined by $-\xi/ur = \tan \xi$. Define

$$r_0 = \frac{\xi(d) \sin(\xi(d)) - dr \cos(\xi(d))}{d(1 + \ln(d\alpha))},$$

$$r_1 = \frac{\xi(d + 2D) \sin(\xi(d + 2D)) - (d + 2D)r \cos(\xi(d + 2D))}{d(1 + \ln(d\alpha)(1 - 2r^*))}.$$

The monotonicity of ξ implies $0 < r_0 < r_1$. Applying result (3.3), if $0 < r < r_0$, then all zeros of Eqs. (3.1) and (3.2) have negative real parts. Thus $u^* = (\bar{u}, \bar{u})$ is locally asymptotically stable.

Regarding the time delay r as a bifurcation parameter, we now check the usual Hopf bifurcation assumptions at $r = r_0$ (see e.g. [4]). When $r = r_0$, Eq. (3.1) has simple roots

$$\pm \omega_0 i = \pm \sqrt{d^2(1 + \ln(d\alpha))^2 - d^2} i, \quad \omega_0 > 0$$

and the other roots of (3.1) and the roots of Eq. (3.2) have negative real parts. Let $\lambda(r)$ be the root of (3.1) with $\lambda(r_0) = \omega_0 i$. Differentiating both sides of (3.1) with respect to r , we then obtain

$$\text{Re}\{\lambda'(r_0)\} = \frac{\omega_0^2}{(1 + r_0 d)^2 + (r_0 \omega_0)^2} > 0.$$

Consequently, we have the following result.

Theorem 3.1. *When the delay r crosses r_0 either from left or from right, and if $d\alpha < 1$, then the homogenous equilibrium u^* undergoes a Hopf bifurcation.*

In order to determine the stability of the bifurcated periodic solutions and the bifurcating direction, we proceed with four steps.

Step 1: Change system (2.1) into $\dot{X}(t) = \int_{-1}^0 d\eta(\theta, \mu) X(t + \theta) + F(X(t - 1))$ by certain transformations.

By the transformation $x(t) = u_1(rt) - \bar{u}$, $y(t) = u_2(rt) - \bar{u}$, we can change system (2.1) into

$$\begin{cases} \frac{dx(t)}{dt} = r[-dx(t) + D(y(t) - x(t)) + e^*(1 - r^*)B(x(t - 1)) + e^*r^*B(y(t - 1))], \\ \frac{dy(t)}{dt} = r[-dy(t) + D(x(t) - y(t)) + e^*r^*B(x(t - 1)) + e^*(1 - r^*)B(y(t - 1))], \end{cases} \tag{3.4}$$

where

$$B(u) = b_1u + \frac{1}{2}b_2u^2 + \frac{1}{6}b_3u^3 + O(u^4),$$

and

$$b_1 = b'(u^*) = d\alpha(1 + \ln(d\alpha)),$$

$$b_2 = b''(u^*) = -\beta d\alpha(2 + \ln(d\alpha)),$$

$$b_3 = b'''(u^*) = \beta^2 d\alpha(3 + \ln(d\alpha)).$$

Let $r = r_0 + \mu$, and rewrite system (3.4) as a system for $X(t) = (x(t), y(t))^T$

$$\dot{X}(t) = \int_{-1}^0 d\eta(\theta, \mu)X(t + \theta) + F(X(t - 1)), \tag{3.5}$$

where θ is the integration variable, $F(X(t - 1)) = (F_1, F_2)^T$, $\eta(\theta, \mu) = (\eta_{i,j}(\theta, \mu))$, and

$$\eta_{1,1}(\theta, \mu) = \eta_{2,2}(\theta, \mu) = \begin{cases} 0, & \theta = -1, \\ (\mu + r_0)e^*(1 - r^*)b_1, & \theta \in (-1, 0), \\ (\mu + r_0)(-d - D + e^*(1 - r^*)b_1), & \theta = 0, \end{cases}$$

$$\eta_{1,2}(\theta, \mu) = \eta_{2,1}(\theta, \mu) = \begin{cases} 0, & \theta = -1, \\ (\mu + r_0)e^*r^*b_1, & \theta \in (-1, 0), \\ (\mu + r_0)(D + e^*r^*b_1), & \theta = 0, \end{cases}$$

$$F_1 = (\mu + r_0)[e^*(1 - r^*)(\frac{1}{2}b_2x^2(t - 1) + \frac{1}{6}b_3x^3(t - 1)) + e^*r^*(\frac{1}{2}b_2y^2(t - 1) + \frac{1}{6}b_3y^3(t - 1))] + \dots,$$

$$F_2 = (\mu + r_0)[e^*r^*(\frac{1}{2}b_2x^2(t - 1) + \frac{1}{6}b_3x^3(t - 1)) + e^*(1 - r^*)(\frac{1}{2}b_2y^2(t - 1) + \frac{1}{6}b_3y^3(t - 1))] + \dots.$$

The eigenvalues for system (3.5) are given by

$$\lambda + d(\mu + r_0) - e^*b_1(\mu + r_0)e^{-\lambda} = 0 \tag{3.6}$$

and

$$\lambda + (d + 2D)(\mu + r_0) - e^*b_1(1 - 2r^*)(\mu + r_0)e^{-\lambda} = 0. \tag{3.7}$$

Therefore, at $\mu = 0$, system (3.5) has eigenvalues $\pm\omega_0r_0i$, and all other eigenvalues have negative real parts.

Step 2: Compute the eigenvectors $q(\theta)$ and $q^*(s)$ for the operator A and the adjoint operator A^* corresponding to ω_0r_0i , and $-\omega_0r_0i$, respectively, where operators A and A^* are

defined by

$$A\varphi(\theta) = \begin{cases} \frac{d\varphi}{d\theta}, & -1 \leq \theta < 0, \\ \int_{-1}^0 d\eta(s, 0)\varphi(s), & \theta = 0, \end{cases} \quad \forall \varphi(\theta) \in C([-1, 0], \mathbb{R}^2),$$

$$A^*\psi(s) = \begin{cases} -\frac{d\psi}{ds}, & 0 \leq s < 1, \\ \int_{-1}^0 d\eta^T(s, 0)\psi(-s), & s = 0, \end{cases} \quad \forall \psi(s) \in C([0, 1], \mathbb{R}^2).$$

It is easy to see that $q(\theta)$ and $q^*(s)$ satisfy

$$\frac{dq(\theta)}{d\theta} = i\omega_0 r_0 q(\theta), \quad \frac{dq^*(s)}{ds} = -i\omega_0 r_0 q^*(s),$$

$$\int_{-1}^0 d\eta(s, 0)q(s) = i\omega_0 r_0 q(0), \quad \int_{-1}^0 d\eta^T(s, 0)q^*(-s) = -i\omega_0 r_0 q^*(0).$$

At the same time, we require that $\langle q^*, q \rangle = 1$. By the definition of the inner product $\langle \cdot, \cdot \rangle$ (see [4]), we have

$$\begin{aligned} \langle q^*, q \rangle &= \bar{q}^*(0) \cdot q(0) - \int_{-1}^0 \int_{\xi=0}^\theta (\bar{q}^*(\xi - \theta))^T d\eta(\theta, 0)q(\xi) d\xi \\ &= \bar{q}^*(0)q(0) - e^{-\omega_0 r_0 i} (\bar{q}^*(0))^T \eta(-1, 0)q(0), \end{aligned}$$

where \bar{q}^* denotes the conjugate of q^* . Therefore, we can obtain $q(\theta) = q(0)e^{\omega_0 r_0 \theta i}$ and $q^*(s) = q^*(0)e^{\omega_0 r_0 s i}$, and choose $q(0)$ and $\bar{q}^*(0)$ as follows:

$$q_{01} = 1,$$

$$q_{02} = \frac{i\omega_0 r_0 - A_1 + B_1 e^{-i\omega_0 r_0}}{A_2 - B_2 e^{-i\omega_0 r_0}},$$

$$q_{01}^* = \frac{\xi_0^2}{(1 - B_1 e^{-ir_0\omega})(\xi_0^2 + \xi_1^2) - 2B_2(A_1 - B_2 e^{-i\omega_0 r_0} - ir_0\omega)\xi_0},$$

$$q_{02}^* = \frac{\xi_0 e^{-i\omega_0 r_0} (i\omega_0 r_0 - A_1 + B_1 e^{-i\omega_0 r_0})}{(1 - B_1 e^{-ir_0\omega})(\xi_0^2 + \xi_1^2) - 2B_2(A_1 - B_2 e^{-i\omega_0 r_0} - ir_0\omega)\xi_0},$$

where q_{0i} and q_{0i}^* ($i = 1, 2$) are the i th components of $q(0)$ and the conjugate $\bar{q}^*(0)$ of $q^*(0)$, respectively, and

$$A_1 = -r_0(d + D), \quad A_2 = r_0 D, \quad B_1 = -r_0 e^*(1 - r^*)b_1, \quad B_2 = -r_0 e^* r^* b_1,$$

$$\xi_0 = B_2 - A_2 e^{ir_0\omega_0}, \quad \xi_1 = B_1 - e^{i\omega_0 r_0} (A_1 - ir_0\omega_0).$$

Step 3: Reduce system (3.5) to an ordinary differential equation for a single complex variable z , and expand it in powers of z and \bar{z} .

Let $z = \langle q^*, X_t \rangle$, $w(z, \bar{z}, \theta) = X_t(\theta) - 2 \operatorname{Re}\{z(t)q(\theta)\}$. Then, system (3.5) can be reduced to an ordinary differential equation for z . At $\mu = 0$, this equation is

$$\dot{z}(t) = \omega_0 r_0 i z(t) + \bar{q}^*(0) \cdot F_0,$$

where $F_0 = (F_1, F_2)^T = F(w(z, \bar{z}, \theta) + zq(\theta) + \bar{z}\bar{q}(\theta))$. In the followings, we expand \dot{z} in powers of z and \bar{z} . Let

$$w(z, \bar{z}, \theta) = \frac{1}{2}w_{20}(\theta)z^2 + w_{11}(\theta)z\bar{z} + \frac{1}{2}w_{02}(\theta)\bar{z}^2 + \dots,$$

where $w_{i,j}(\theta) = (w_{i,j}^{(1)}(\theta), w_{i,j}^{(2)}(\theta))^T \in C([-1, 0], \mathcal{C}^2)$, $i, j = 0, 1, 2$. Then, F_0 can be expanded as follows:

$$F_1 = F_{1,20}z^2 + F_{1,11}z\bar{z} + F_{1,02}\bar{z}^2 + F_{1,21}z^2\bar{z} + \dots,$$

$$F_2 = F_{2,20}z^2 + F_{2,11}z\bar{z} + F_{2,02}\bar{z}^2 + F_{2,21}z^2\bar{z} + \dots,$$

where

$$F_{1,20} = -\frac{b_2}{2b_1}(B_1q_1^2(-1) + B_2q_2^2(-1)),$$

$$F_{1,11} = -\frac{b_2}{b_1}(B_1q_1(-1)\bar{q}_1(-1) + B_2q_2(-1)\bar{q}_2(-1)),$$

$$F_{1,02} = -\frac{b_2}{2b_1}(B_1\bar{q}_1^2(-1) + B_2\bar{q}_2^2(-1)) = \bar{F}_{1,20},$$

$$\begin{aligned} F_{1,21} = & -\frac{b_2}{2b_1}B_1(w_{20}^{(1)}(-1)\bar{q}_1(-1) + 2w_{11}^{(1)}(-1)q_1(-1)) \\ & -\frac{b_3}{2b_1}B_1q_1^2(-1)\bar{q}_1(-1) - \frac{b_2}{2b_1}B_2(w_{20}^{(2)}(-1)\bar{q}_2(-1) \\ & + 2w_{11}^{(2)}(-1)q_2(-1)) - \frac{b_3}{2b_1}B_2q_2^2(-1)\bar{q}_2(-1), \end{aligned}$$

$$F_{2,20} = -\frac{b_2}{2b_1}(B_2q_1^2(-1) + B_1q_2^2(-1)),$$

$$F_{2,11} = -\frac{b_2}{b_1}(B_2q_1(-1)\bar{q}_1(-1) + B_1q_2(-1)\bar{q}_2(-1)),$$

$$F_{2,02} = -\frac{b_2}{2b_1}(B_2\bar{q}_1^2(-1) + B_1\bar{q}_2^2(-1)) = \bar{F}_{2,20},$$

$$\begin{aligned} F_{2,21} = & -\frac{b_2}{2b_1}B_2(w_{20}^{(1)}(-1)\bar{q}_1(-1) + 2w_{11}^{(1)}(-1)q_1(-1)) \\ & -\frac{b_3}{2b_1}B_2q_1^2(-1)\bar{q}_1(-1) - \frac{b_2}{2b_1}B_1(w_{20}^{(2)}(-1)\bar{q}_2(-1) \\ & + 2w_{11}^{(2)}(-1)q_2(-1)) - \frac{b_3}{2b_1}B_1q_2^2(-1)\bar{q}_2(-1), \end{aligned}$$

where $q_i(\theta)$ is the i th component of the eigenvector $q(\theta)$, $i = 1, 2$.

Thus, we obtain

$$\dot{z} = \omega_0 r_0 i z + \frac{1}{2} g_{20} z^2 + g_{11} z \bar{z} + \frac{1}{2} g_{02} \bar{z}^2 + \frac{1}{2} g_{21} z^2 \bar{z} + \dots,$$

where

$$g_{20} = q_{01}^* F_{1,20} + q_{02}^* F_{2,20},$$

$$g_{11} = q_{01}^* F_{1,11} + q_{02}^* F_{2,11},$$

$$g_{02} = q_{01}^* F_{1,02} + q_{02}^* F_{2,02},$$

$$g_{21} = q_{01}^* F_{1,21} + q_{02}^* F_{2,21}.$$

g_{21} is still unknown due to $w(z, \bar{z}, \theta)$.

Step 4: In order to get the coefficient g_{21} of $z^2 \bar{z}$, we must first work out $w(z, \bar{z}, \theta)$. Let

$$\begin{aligned} & \frac{1}{2} H_{20}(\theta) z^2 + H_{11}(\theta) z \bar{z} + \frac{1}{2} H_{02}(\theta) \bar{z}^2 + \dots \\ &= \begin{cases} -2 \operatorname{Re}\{\bar{q}^*(0) \cdot F_0 q(\theta)\}, & -1 \leq \theta < 0, \\ -2 \operatorname{Re}\{\bar{q}^*(0) \cdot F_0 q(0)\} + F_0, & \theta = 0. \end{cases} \end{aligned}$$

Comparing the coefficients of all powers of z and \bar{z} , we can compute $H_{20}(\theta)$ and $H_{11}(\theta)$ as follows:

$$\begin{aligned} H_{20}(\theta) &= \begin{cases} -2(q_{01}^* F_{1,20} + q_{02}^* F_{2,20})q(\theta) \\ \quad - 2(\bar{q}_{01}^* \bar{F}_{1,02} + \bar{q}_{02}^* \bar{F}_{2,02})\bar{q}(\theta), & -1 \leq \theta < 0, \\ -2(q_{01}^* F_{1,20} + q_{02}^* F_{2,20})q(0) \\ \quad - 2(\bar{q}_{01}^* \bar{F}_{1,02} + \bar{q}_{02}^* \bar{F}_{2,02})\bar{q}(0) + h_{20}, & \theta = 0, \end{cases} \\ H_{11}(\theta) &= \begin{cases} -(q_{01}^* F_{1,11} + q_{02}^* F_{2,11})q(\theta) \\ \quad - (\bar{q}_{01}^* \bar{F}_{1,11} + \bar{q}_{02}^* \bar{F}_{2,11})\bar{q}(\theta), & -1 \leq \theta < 0, \\ -(q_{01}^* F_{1,11} + q_{02}^* F_{2,11})q(0) \\ \quad - (\bar{q}_{01}^* \bar{F}_{1,11} + \bar{q}_{02}^* \bar{F}_{2,11})\bar{q}(0) + h_{11}, & \theta = 0, \end{cases} \end{aligned}$$

where $h_{20} = (F_{1,20}, F_{2,20})^T$, $h_{11} = (F_{1,11}, F_{2,11})^T$.

By the algorithm in [4, Section 2], we have

$$\begin{aligned} (2i\omega_0 r_0 - A)w_{20}(\theta) &= H_{20}(\theta), \\ -Aw_{11}(\theta) &= H_{11}(\theta) \end{aligned} \tag{3.8}$$

Let

$$\begin{aligned} w_{20}(\theta) &= c_1 q(\theta) + c_2 \bar{q}(\theta) + E E e^{2i\omega_0 r_0 \theta}, \\ w_{11}(\theta) &= c_3 q(\theta) + c_4 \bar{q}(\theta) + F F. \end{aligned} \tag{3.9}$$

Substituting (3.9) into Eq. (3.8), we can determine w_{20} and w_{11} . The unknown coefficients are given by:

$$c_1 = -\frac{2}{\omega_0 r_0 i} (q_{01}^* F_{1,20} + q_{02}^* F_{2,20}),$$

$$c_2 = -\frac{2}{3\omega_0 r_0 i} (\bar{q}_{01}^* \bar{F}_{1,02} + \bar{q}_{02}^* F_{2,02}),$$

$$c_3 = \frac{1}{\omega_0 r_0 i} (q_{01}^* F_{1,11} + q_{02}^* F_{2,11}),$$

$$c_4 = -\frac{1}{\omega_0 r_0 i} (\bar{q}_{01}^* \bar{F}_{1,11} + \bar{q}_{02}^* \bar{F}_{2,11}),$$

$$\xi_E = -(A_2 - B_2 e^{-2ir_0\omega_0})^2 + (A_1 - B_1 e^{-2ir_0\omega_0} - 2ir_0\omega_0)^2,$$

$$\xi_F = A_1^2 - A_2^2 - 2A_1 B_1 + B_1^2 + 2A_2 B_2 - B_2^2,$$

$$\begin{aligned} EE_1 = & (-A_1 + B_1 e^{-2ir_0\omega_0} + 2ir_0\omega_0)(F_{1,20} + A_1 c_1 q_{01} - B_1 c_1 q_{01} e^{-ir_0\omega_0} \\ & + A_2 c_1 q_{02} - B_2 c_1 q_{02} e^{-ir_0\omega_0} + 2F_{1,20} q_{01} q_{01}^* + 2F_{2,20} q_{01} q_{02}^* \\ & - 2ic_1 q_{01} r_0 \omega_0 + c_2(A_2 - B_2 e^{ir_0\omega_0}) \bar{q}_{02} + \bar{q}_{01}(c_2(A_1 - B_1 e^{ir_0\omega_0} \\ & - 2ir_0\omega_0) + 2\bar{F}_{1,02} \bar{q}_{01}^* + 2\bar{F}_{2,02} \bar{q}_{02}^*)) + (A_2 - B_2 e^{-2ir_0\omega_0})(F_{2,20} \\ & + A_2 c_1 q_{01} - B_2 c_1 q_{01} e^{-ir_0\omega_0} + A_1 c_1 q_{02} - B_1 c_1 q_{02} e^{-ir_0\omega_0} \\ & + 2F_{1,20} q_{02} q_{01}^* + 2F_{2,20} q_{02} q_{02}^* - 2ic_1 q_{02} r_0 \omega_0 + c_2(A_2 - B_2 e^{ir_0\omega_0}) \bar{q}_{01} \\ & + \bar{q}_{02}(c_2(A_1 - B_1 e^{ir_0\omega_0} - 2ir_0\omega_0) + 2\bar{F}_{1,02} \bar{q}_{01}^* + 2\bar{F}_{2,02} \bar{q}_{02}^*)), \end{aligned}$$

$$\begin{aligned} EE_2 = & (A_2 - B_2 e^{-2ir_0\omega_0})(F_{1,20} + A_1 c_1 q_{01} - B_1 c_1 q_{01} e^{-ir_0\omega_0} \\ & + A_2 c_1 q_{02} - B_2 c_1 q_{02} e^{-ir_0\omega_0} \\ & + 2F_{1,20} q_{01} q_{01}^* + 2F_{2,20} q_{01} q_{02}^* - 2ic_1 q_{01} r_0 \omega_0 \\ & + c_2(A_2 - B_2 e^{ir_0\omega_0}) \bar{q}_{02} + \bar{q}_{01}(c_2(A_1 - B_1 e^{ir_0\omega_0} - 2ir_0\omega_0) \\ & + 2\bar{F}_{1,02} \bar{q}_{01}^* + 2\bar{F}_{2,02} \bar{q}_{02}^*)) + (-A_1 + B_1 e^{-2ir_0\omega_0} \\ & + 2ir_0\omega_0)(F_{2,20} + A_2 c_1 q_{01} - B_2 c_1 q_{01} e^{-ir_0\omega_0} \\ & + A_1 c_1 q_{02} - B_1 c_1 q_{02} e^{-ir_0\omega_0} + 2F_{1,20} q_{02} q_{01}^* \\ & + 2F_{2,20} q_{02} q_{02}^* - 2ic_1 q_{02} r_0 \omega_0 + c_2(A_2 - B_2 e^{ir_0\omega_0}) \bar{q}_{01} \\ & + \bar{q}_{02}(c_2(A_1 - B_1 e^{ir_0\omega_0} - 2ir_0\omega_0) + 2\bar{F}_{1,02} \bar{q}_{01}^* + 2\bar{F}_{2,02} \bar{q}_{02}^*)), \end{aligned}$$

$$\begin{aligned} FF_1 = & (-A_1 + B_1)(F_{1,11} + A_2 c_3 q_{02} - c_3(B_1 q_{01} + B_2 q_{02}) e^{-ir_0\omega_0} + q_{01}(A_1 c_3 \\ & - F_{1,11} q_{01}^* - F_{2,11} q_{02}^*) + A_2 c_4 \bar{q}_{02} - c_4 e^{ir_0\omega_0}(B_1 \bar{q}_{01} + B_2 \bar{q}_{02}) \\ & + \bar{q}_{01}(A_1 c_4 - \bar{F}_{1,11} \bar{q}_{01}^* - \bar{F}_{2,11} \bar{q}_{02}^*)) \\ & + (A_2 - B_2)(F_{2,11} + A_2 c_3 q_{01} - c_3(B_2 q_{01} \\ & + B_1 q_{02}) e^{-ir_0\omega_0} + q_{02}(A_1 c_3 - F_{1,11} q_{01}^* \\ & - F_{2,11} q_{02}^*) + A_2 c_4 \bar{q}_{01} - c_4 e^{ir_0\omega_0}(B_2 \bar{q}_{01} \\ & + B_1 \bar{q}_{02}) + \bar{q}_{02}(A_1 c_4 - \bar{F}_{1,11} \bar{q}_{01}^* - \bar{F}_{2,11} \bar{q}_{02}^*)), \end{aligned}$$

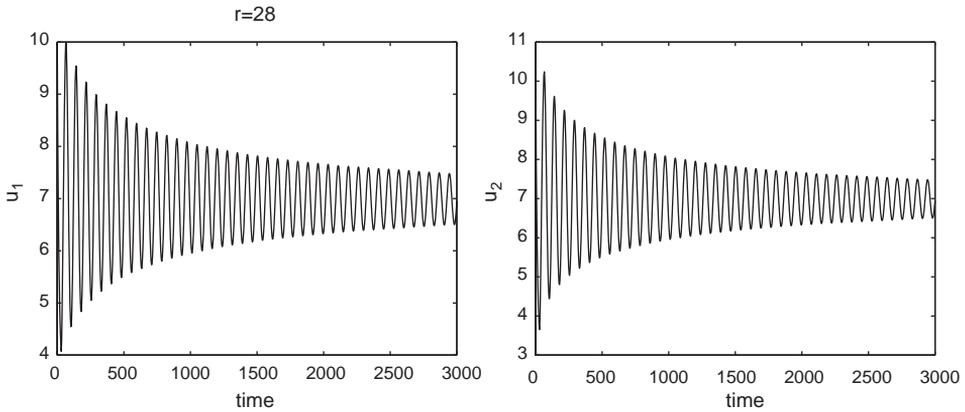


Fig. 1. The solution of system (2.1) with initial values: $(u_1(t), u_2(t)) = (10, 11)$ for $t \in [-r, 0]$, and $r = 28$.

$$\begin{aligned}
 FF_2 = & (A_2 - B_2)(F_{1,11} + A_2c_3q_{02} - c_3(B_1q_{01} + B_2q_{02})e^{-ir_0\omega_0} \\
 & + q_{01}(A_1c_3 - F_{1,11}q_{01}^* - F_{2,11}q_{02}^*) + A_2c_4\bar{q}_{02} - c_4e^{ir_0\omega_0}(B_1\bar{q}_{01} \\
 & + B_2\bar{q}_{02}) + \bar{q}_{01}(A_1c_4 - \bar{F}_{1,11}\bar{q}_{01}^* - \bar{F}_{2,11}\bar{q}_{02}^*)) \\
 & + (-A_1 + B_1)(F_{2,11} + A_2c_3q_{01} - c_3(B_2q_{01} \\
 & + B_1q_{02})e^{-ir_0\omega_0} + q_{02}(A_1c_3 - F_{1,11}q_{01}^* \\
 & - F_{2,11}q_{02}^*) + A_2c_4\bar{q}_{01} - c_4e^{ir_0\omega_0}(B_2\bar{q}_{01} \\
 & + B_1\bar{q}_{02}) + \bar{q}_{02}(A_1c_4 - \bar{F}_{1,11}\bar{q}_{01}^* - \bar{F}_{2,11}\bar{q}_{02}^*)),
 \end{aligned}$$

where EE_i and FF_i are the i th components of EE and FF , respectively. Thus, we can compute g_{21} by $g_{21} = q_{01}^*F_{1,21} + q_{02}^*F_{2,21}$.

Define

$$\sigma = -\text{Re} \left(\frac{i}{2\omega_0 r_0} (g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2) + \frac{1}{2}g_{21} \right).$$

Then, by the theory in [4], we can determine the type of Hopf bifurcation according to the sign of σ .

Theorem 3.2. *Let $d\alpha < 1$. If $\sigma > 0$, a supercritical Hopf bifurcation occurs at $r = r_0$, which means that system (2.1) has a stable periodic solution near u^* for r near r_0 and $r > r_0$. If $\sigma < 0$, a subcritical Hopf bifurcation occurs at $r = r_0$, which implies that system (2.1) has an unstable periodic solution near u^* for r near r_0 and $r < r_0$.*

From Theorems 3.1 and 3.2, it follows that the maturation age r of a species may lead to oscillatory behaviors of the mature populations. When the maturation age r crosses r_0 from left ($\sigma > 0$), the mature populations in the two patches will periodically oscillate near u^* , while the populations will be stabilized at u^* when r crosses r_0 from right ($\sigma < 0$).

In order to check our computation for Theorem 3.2, we perform some numerical simulations. Let $d = 0.08$, $D = 0.01$, $e^* = 0.9$, $r^* = 0.1$, $\beta = \frac{1}{2} \ln 2$. We then have $d\alpha = 0.08889$.

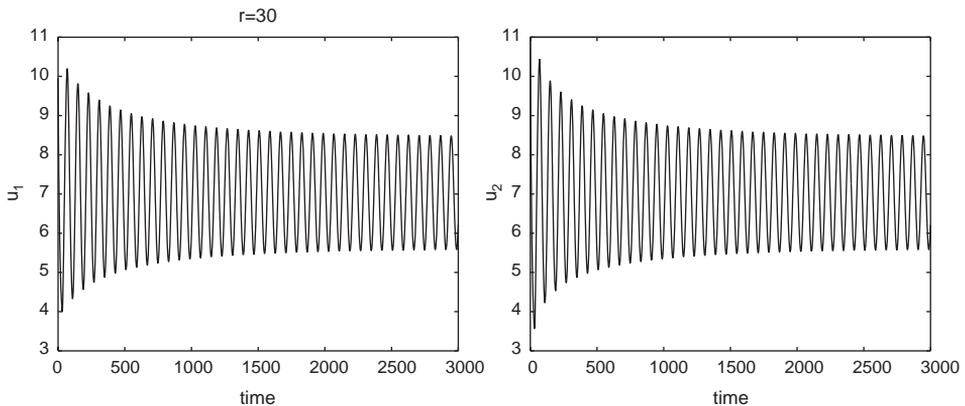


Fig. 2. The solution with the same parameters as those in Fig. 1 except $r = 30$.

By Corollary 2.1, system (2.1) is uniformly persistent. Further computation shows that

$$\begin{aligned} r_0 &= 29.15, & g_{20} &= 0.0237 + 0.03423i, & g_{02} &= -0.02435 - 0.03378i, \\ g_{11} &= 0.068 - 0.048i, & g_{21} &= -0.0254 - 0.00465i, & \sigma &= 0.01296. \end{aligned}$$

By Theorem 3.2, system (2.1) has some stable periodic oscillations near $u^* = (\bar{u}, \bar{u})$ for $r > r_0 = 29.15$. We simulate the solutions of system (2.1) while $r < r_0$ and $r > r_0$. The solutions in Figs. 1 and 2 have the same parameter values except for the values of r . For $r = 28$, Fig. 1 shows the solution will eventually converge to a positive homogeneous equilibrium, while, for $r = 30$, the solution shown in Fig. 2 converges to a stable periodic oscillation. These results coincide with our theoretical predictions.

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