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BIFURCATION OF A PREDATOR-PREY SYSTEM WITH GENERATION DELAY AND HABITAT COMPLEXITY

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Abstract. In this paper, we study a delayed predator-prey system with Holling type IV functional response incorporating the effect of habitat complexity. The results show that there exist stability switches and Hopf bifurcation occurs while the delay crosses a set of critical values. The explicit formulas which determine the direction and stability of Hopf bifurcation are obtained by the normal form theory and the center manifold theorem.

1. Introduction

Let $x(t)$ and $y(t)$ denote densities of prey population and predators at time t, respectively. The classical Gause type predator-prey system is presented by the following form [14]

$$\begin{cases} \dot{x}(t) = xf(x,K) - q(x)y, \\ \dot{y}(t) = (eq(x) - d)y \end{cases} \tag{1.1}$$

in which the parameter e $(0 < e < 1)$ is the conversion efficiency, measuring the number of newly born predators for each captured prey. The parameter d is the per capita death rate of predators. The function $f(x, K)$ is continuous and differentiable, and denotes the growth rate of prey in absence of predator's predation which satisfies $f(o, K) = r > 0$, $f(K, K) = 0$ and $f'_x(x, K) < 0$ for $0 \le x \le K$ [17]. The function $q(x)$ denotes a general functional response and refers to changes in densities of prey attached by per predator per unit time, such as Holling type function, Ivlev-type response, Beddington-DeAngelis function, Hassell-Varley-type, Crowley-Martin function, Ratio-dependent response and Monod-Haldane function (see e.g., [2,7,11,15–17,21,22,24,27,28,31,32,35]).

In this paper, we will consider a predator-prey system with generalized Holling IV type functional response being denoted by $q(x) = \frac{\alpha x^n}{1+\alpha h\varphi(x)}$ (α is the attack coefficient and h is the handling time of predators required per

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prey) under a assumption that $n > 0$. The growth rate of prey without predators applies the Logistic type $f(x, K) = rx(1 - \frac{x}{K})$ in which r is the intrinsic per capita growth rate of prey population and K is the prey environmental carrying capacity. Based on the above assumptions, the system (1.1) can be represented by

$$\begin{cases} \dot{x}(t) = rx(1 - \dfrac{x}{K}) - \dfrac{\alpha x^n y}{1 + \alpha h x^n}, \\ \dot{y}(t) = \left(\dfrac{e\alpha x^n}{1 + \alpha h x^n} - d \right) y. \end{cases} \tag{1.2}$$

Habitat complexity which is defined as the morphological characteristics within a structure itself or the heterogeneity in the arrangement of objects in space is studied by many researchers [1, 4–6, 8, 12, 13, 19, 20, 26, 37]. We incorporate the effect of habitat complexity in the system (1.2) based on Kot's grounding work [25]. Habitat complexity is more likely to affect the attack coefficient α than the handling time for search, so the attack coefficient α has to be replaced by $\alpha(1 - c)$, where c $(0 < c < 1)$ is a dimension less parameter that measures the degree or strength of habitat complexity. Assuming that the complexity is homogeneous throughout habitat, then the total number of prey caught $V(x)$ is given by

$$\begin{cases} V(x) = \alpha(1 - c)T_s(x)x^n, \\ T_s(x) = T - hV(x), \end{cases} \tag{1.3}$$

where $T_s(x)$ is availably searching time. T is the total time and positive.

Solving $V(x)$, the response function of the system (1.2) which incorporates the effect of habitat complexity is presented by

$$q(x) = \frac{\alpha(1 - c)x^n}{1 + \alpha h(1 - c)x^n}.$$

Hence, the system (1.2) can be presented as follows with the effect of habitat complex

$$\begin{cases} \dot{x}(t) = rx\left(1 - \dfrac{x}{K}\right) - \dfrac{\alpha(1 - c)x^n y}{1 + \alpha h(1 - c)x^n}, \\ \dot{y}(t) = \left(\dfrac{e\alpha(1 - c)x^n}{1 + \alpha h(1 - c)x^n} - d \right) y. \end{cases} \tag{1.4}$$

Predator-prey models with time delay are much more realistic since delay occurs in almost every biological situation and is assumed to be one of reasons of regular fluctuations in population' densities [25, 27–37]. Therefore, in order to make predator-prey models biologically more realistic, incorporating the generation delay in the system (1.4) is interesting. Based on the above analysis, we obtain the following delay-induced predator-prey system with habitat complexity.

$$\begin{cases} \dot{x}(t) = rx\left(1 - \dfrac{x(t-\tau)}{K}\right) - \dfrac{\alpha(1-c)x^n y}{1+\alpha h(1-c)x^n}, \\ \dot{y}(t) = \left(\dfrac{e\alpha(1-c)x^n}{1+\alpha h(1-c)x^n} - d\right) y, \\ x(\xi) = \varphi(\xi) > 0,\ y(\xi) = \psi(\xi) > 0. \end{cases} \tag{1.5}$$

Based on the system (1.5), we will consider existence of Hopf bifurcation, direction and stability of Hopf bifurcation. Recently, a great deal of researches have been devoted to this topic [9,10,18,29,32,33,36], such as Bairagi and Jana proposed a delayed and Holling II type predator-prey model with the gestation delay and habitat complexity and considered Hopf bifurcation and its direction and stability [27] by the norm form theory and the center manifold theorem. However, the above cited researches focus on some certain functional response to consider Hopf bifurcation. Therefore, it is an important mathematical subject to study delay-induced predator-prey models with a generalized functional response.

The organization of this paper are as follows: In Section 2, all equilibrium points are obtained and influences of habitat complex on equilibrium densities of prey and predator are studied. In Section 3, we investigated local stability property of interior equilibrium point of the system (1.5) without time delay. In Section 4, the Hopf bifurcation around the positive equilibrium point is studied. Direction and stability of Hopf bifurcation are investigated in Section 5.

2. Existence of equilibria

By solving the following equations

$$\begin{cases} rx\left(1 - \dfrac{x}{K}\right) - \dfrac{\alpha(1-c)x^n y}{1+\alpha h(1-c)x^n} = 0, \\ \left(e\dfrac{\alpha(1-c)x^n}{1+\alpha h(1-c)x^n} - d\right) y = 0, \end{cases} \tag{2.1}$$

we can obtain all equilibrium points of the system (1.5): $E_0(0,0)$, $E_K(K,0)$, $\tilde{E}(\tilde{x},\tilde{y})$, where

$$\tilde{x} = \left(\frac{d}{\alpha(1-c)(e-dh)}\right)^{1/n};\ \tilde{y} = \frac{er\tilde{x}}{d}\left(1 - \frac{\tilde{x}}{K}\right).$$

By simple computation, the equilibrium point $\tilde{E}$ is positive and has its own ecological meanings if and only if

($H1$) $h < \frac{e}{d}$,
($H2$) $\alpha > \frac{d}{K^n(e-dh)}$,
($H3$) $0 < c < 1 - \frac{d}{\alpha K^n(e-dh)}$.

If $c > 1 - \frac{d}{\alpha K^n(e-dh)}$, $\alpha > \frac{d}{K^n(e-dh)}$ and $h < \frac{e}{d}$, the equilibrium point $\tilde{E}(\tilde{x}, \tilde{y})$ collapses with the point $E_K(K, 0)$.

Based on ecological meanings, if the effect of habitat complexity is less than the threshold value $1 - \frac{d}{\alpha K^n(e-dh)}$, then two interacting populations (prey and predators) coexist while the attack coefficient α is lager than the critical value $\frac{d}{K^n(e-dh)}$ and the handling time required per prey is less than $\frac{e}{d}$. Otherwise, prey population reaches its environmental carrying capacity and predators will extinct when the effect of habitat complexity is lager than the threshold value $1 - \frac{d}{\alpha K^n(e-dh)}$.

3. Stability

Clearly, the system (1.5) establishes biological well behaved nature in the invariant region $\Sigma = \{(x, y) \,|\, 0 < x < K,\ y > 0\}$. Based on ecological meanings, stress is given on stability of the positive equilibrium point. Hence, we will interested to investigate stability property of coexisting equilibrium point of the system (1.5).

Let $u_1(t) = x(t) - \tilde{x}$ and $u_2(t) = y(t) - \tilde{y}$, then the system (1.5) can be expressed as in the following matrix form after linearization

$$\dot{U}(t) = A_1 U(t) + A_2 U(t - \tau), \tag{3.1}$$

where

$$A_1 = \begin{pmatrix} a_{11}^1 & -\frac{d}{e} \\ e a_{21}^1 & 0 \end{pmatrix}$$

and

$$A_2 = \begin{pmatrix} -\frac{r\tilde{x}}{K} & 0 \\ 0 & 0 \end{pmatrix}$$

in which

$$a_{11}^1 = \frac{r(K-\tilde{x})(1 - n + \alpha h(1-c)\tilde{x}^n)}{K(1 + \alpha h(1-c)\tilde{x}^n)} = \frac{r(1-k)(e - n(e-dh))}{e},$$

$$a_{21}^1 = \frac{r(K-\tilde{x})}{K(1 + \alpha h(1-c)\tilde{x}^n)} = \frac{r(1-k)(e-dh)}{e} > 0,\ k = \frac{\tilde{x}}{K}.$$

Hence, the characteristic equation of the system (1.5) is given by

$$|A_1 + A_2 e^{-\lambda\tau} - \lambda I| = 0,$$

that is

$$\lambda^2 - a_{11}^1 \lambda + d a_{21}^1 + rke^{-\lambda\tau}\lambda = 0. \tag{3.2}$$

If there is no delay ($\tau = 0$), the corresponding characteristic equation is given by

$$\lambda^2 - (a_{11}^1 - rk)\lambda + d a_{21}^1 = 0. \tag{3.3}$$

Thus, solutions of the characteristic Eq. (3.3) are

$$\lambda_{1,2} = \frac{(a_{11}^1 - rk) \pm \sqrt{(a_{11}^1 - rk)^2 - 4da_{21}^1}}{2}. \tag{3.4}$$

Therefore, two eigenvalues have negative real parts when $a_{11}^1 - rk < 0$ by Routh-Hurwitz rule. That is the interior equilibrium point $\tilde{E}$ is locally asymptotically stable if $a_{11}^1 - rk < 0$.

$$\begin{aligned} & a_{11}^1 - rk < 0 \\ \Leftrightarrow\ & \frac{r(1-k)(e - n(e - dh))}{e} - rk < 0 \\ \Leftrightarrow\ & \frac{r}{e}[(1-k)(e - n(e - dh)) - ek] < 0 \\ \Leftrightarrow\ & e(1-2k) - n(1-k)(e - dh) < 0. \end{aligned} \tag{3.5}$$

Hence, three cases will be considered as followings

(1) If $(H4)$ $\frac{1}{2} \le k < 1$, then (3.5) is always true,
(2) If $(H5)$ $k < \frac{1}{2}$, then (3.5) is equal with $(H7)$ $n > \frac{e(1-2k)}{(1-k)(e-dh)}$,
(3) If $(H6)$ $k > 1$, then (3.5) is equal with $(H8)$ $n < \frac{e(1-2k)}{(1-k)(e-dh)}$.

Based on the above analysis, we can obtain the following results.

Theorem 3.1. *Assuming that* $(H1)$, $(H2)$, $(H3)$ *and* $(H4)$ *are satisfied, the interior equilibrium point* $\tilde{E}$ *of system* (1.5) *without delay is always a locally asymptotically stable node or focus.*

Theorem 3.2. *Assuming that* $(H1)$, $(H2)$, $(H3)$ *and* $(H5)$ *are satisfied, the interior equilibrium point* $\tilde{E}$ *of system* (1.5) *without delay is locally asymptotically stable when* $(H7)$ *is true. Moreover,*

(i) *if* $(a_{11}^1 - rk)^2 > 4da_{21}^1$, *it is a stable node,*
(ii) *if* $(a_{11}^1 - rk)^2 < 4da_{21}^1$, *it is a stable focus,*

Theorem 3.3. *Assuming that* $(H1)$, $(H2)$, $(H3)$ *and* $(H6)$ *are satisfied, the interior equilibrium point* $\tilde{E}$ *of system* (1.5) *without delay is locally asymptotically stable when* $(H8)$ *is true. Moreover,*

(i) *if* $(a_{11}^1 - rk)^2 > 4da_{21}^1$, *it is a stable node,*
(ii) *if* $(a_{11}^1 - rk)^2 < 4da_{21}^1$, *it is a stable focus,*

4. Hopf bifurcation

For the delay-induced system (1.5), the interior equilibrium $\tilde{E}$ will be asymptotically stable if all roots of the corresponding characteristic Eq. (3.3) have negative real parts. To determine the nature of stability, we require the sign of the real parts of the roots of Eq. (3.3). We start with assumption that $\tilde{E}$ is asymptotically stable in case of non-delayed system and then find conditions for which $\tilde{E}$ is still stable for all delays [3]. By Rouche's Theorem [23] and the continuity in τ, the transcendental Eq. (3.2) has roots with positive real parts if and only if it has purely imaginary roots. From these, we shall be able to find conditions for all eigenvalues to have negative real parts.

Let

$$\lambda(\tau) = \eta(\tau) + i\omega(\tau),$$

in which $\eta(\tau)$ and $\omega(\tau)$ are real.

As the positive equilibrium $\tilde{E}$ of the non-delayed system (1.5) is asymptotically stable, we have $\eta(0) < 0$. By continuity, if $\tau > 0$ is sufficiently small, we still have $\eta(\tau) < 0$ and the positive equilibrium $\tilde{E}$ is still asymptotically stable. The changes of stability will occur at some values of $\lambda(\tau)$ for which $\eta(\overline{\tau}) = 0$ and $\omega(\tau) \neq 0$, that is λ will be purely imaginary.

Let $\overline{\tau}$ be such that $\eta(\overline{\tau}) = 0$ and $\omega(\overline{\tau}) = \overline{\omega} \neq 0$. So that $\lambda = i\omega(\overline{\tau}) = i\overline{\omega}$. In this case, the steady state loses stability and eventually becomes unstable when $\eta(\tau)$ becomes positive. In other words, if such an $\omega(\overline{\tau})$ does not exist, i.e., if $\lambda(\tau)$ be not purely imaginary for any $\tau = \overline{\tau}$, then the positive equilibrium $\tilde{E}$ will always be stable.

Now, $i\omega(\overline{\tau})$ is a root of Eq. (3.2) if and only if

$$-(\overline{\omega})^2 + irk\overline{\omega}[\cos(\overline{\omega}\overline{\tau}) - i\sin(\overline{\omega}\overline{\tau})] - ia_{11}^1\overline{\omega} + da_{21}^1 = 0.$$

Separating the real and imaginary parts of both sides of the above equation, we have

$$-(\overline{\omega})^2 + rk\overline{\omega}\sin(\overline{\omega}\overline{\tau}) + da_{21}^1 = 0,$$
$$rk\overline{\omega}\cos(\overline{\omega}\overline{\tau}) - a_{11}^1\overline{\omega} = 0.$$

From the above two equations, it is obtained

$$(\overline{\omega})^4 + (a_{11}^1 - (rk)^2 - 2da_{21}^1)(\overline{\omega})^2 + (da_{21}^1)^2 = 0. \tag{4.1}$$

According to the above Eq. (4.1) and the theory of the second-degree polynomial equation, two following cases are considered

(1) If $a_{11}^1 - (\frac{r\tilde{x}}{K})^2 - 2da_{21}^1 < 0$ and $(a_{11}^1 - (\frac{r\tilde{x}}{K})^2 - 2da_{21}^1)^2 - 4(da_{21}^1)^2 > 0$, then Eq. (12) has two positive roots with respect to $\overline{\omega}$, denoting as $\overline{\omega}_\pm$, the corresponding $\overline{\tau}_j^\pm$, where

$$\overline{\omega}_\pm = [\frac{-(a_{11}^1 - (\frac{r\tilde{x}}{K})^2 - 2da_{21}^1) \pm \sqrt{(a_{11}^1 - (\frac{r\tilde{x}}{K})^2 - 2da_{21}^1)^2 - 4(da_{21}^1)^2}}{2}]^{1/2}, \tag{4.2}$$

and

$$\overline{\tau}_j^\pm = \frac{1}{\overline{\omega}_\pm}\cos(\frac{Ka_{11}^1}{\tilde{x}}) + \frac{2\pi j}{\overline{\omega}_\pm},\ j = 0, 1, 2, \ldots. \tag{4.3}$$

(2) If $a_{11}^1 - (\frac{r\tilde{x}}{K})^2 - 2da_{21}^1 < 0$ and $(a_{11}^1 - (\frac{r\tilde{x}}{K})^2 - 2da_{21}^1)^2 - 4(da_{21}^1)^2 = 0$, then Eq. (12) has one positive root with respect to $\overline{\omega}$, denoting as $\overline{\omega}_+$,

the corresponding $\overline{\tau}_j^+$, where

$$\overline{\omega}_+ = (\frac{-(a_{11}^1 - (\frac{r\tilde{x}}{K})^2 - 2da_{21}^1)}{2})^{1/2}, \tag{4.4}$$

and

$$\overline{\tau}_j^+ = \frac{1}{\overline{\omega}_+}\cos(\frac{Ka_{11}^1}{\tilde{x}}) + \frac{2\pi j}{\overline{\omega}_+},\ j = 0, 1, 2, \ldots. \tag{4.5}$$

Next, we shall verify the transversally condition

$$\frac{d}{d\tau}(Re\lambda(\tau)) \mid (\tau = \overline{\tau}) \neq 0.$$

Differentiating Eq. (3.2) with respect to τ, we obtain

$$2\lambda\frac{d\lambda}{d\tau} - a_{11}^1\frac{d\lambda}{d\tau} + rke^{-\lambda\tau}\frac{d\lambda}{d\tau} + rke^{-\lambda\tau}(-\lambda - \frac{d\lambda}{d\tau}) = 0.$$

This gives

$$(\frac{d\lambda}{d\tau})^{-1} = \frac{(2\lambda - a_{11}^1)e^{\lambda\tau} + rk}{rk\lambda^2} - \frac{\tau}{\lambda}.$$

Hence,

$$\begin{aligned} (\frac{dRe(\lambda)}{d\tau})^{-1}|_{\tau=\overline{\tau}^{\pm}} &= \frac{-2\overline{\omega}\sin(\overline{\omega\tau}) - a_{11}^1)\sin(\overline{\omega\tau})}{-rk\overline{\omega}^2} \\ &= \frac{\pm\sqrt{(a_{11}^1 - (rk)^2 - 2da_{21}^1)^2 - 4(da_{21}^1)^2}}{-rk\overline{\omega}^2} \neq 0. \end{aligned} \tag{4.6}$$

By continuity, the real part of $\eta(\tau)$ becomes positive when $\tau > \overline{\tau}^{\pm}$ and the steady state becomes unstable. Moreover, a Hopf bifurcation occurs when τ passes through the critical value $\overline{\tau}^{\pm}$. Therefore, we can obtain following theorem.

Theorem 4.1. *Supposing* $(H1)$, $(H2)$, $(H3)$ *and* $(H4)$, *or* $(H5)$ *and* $(H7)$, *or* $(H6)$ *and* $(H8)$ *are satisfied respectively, we obtain that*

(i) *If* $a_{11}^1 - (rk)^2 - 2da_{21}^1 < 0$ *and* $(a_{11}^1 - (rk)^2 - 2da_{21}^1)^2 - 4(da_{21}^1)^2 = 0$, *then the positive equilibrium* $\tilde{E}$ *is locally asymptotically stable for* $\tau < \overline{\tau}^+$ *and unstable for* $\tau > \overline{\tau}^+$. *A Hopf bifurcation occurs as* τ *passes through the threshold value* $\overline{\tau}^+$, *where* $\overline{\tau}^+ = \frac{1}{\overline{\omega}_+}\cos(\frac{a_{11}^1}{rk})$ *and* $\overline{\omega}_+ = [\frac{-(a_{11}^1-(rk)^2-2da_{21}^1)}{2}]^{1/2}$,

(ii) *If* $a_{11}^1 - (rk)^2 - 2da_{21}^1 < 0$ *and* $(a_{11}^1 - (rk)^2 - 2da_{21}^1)^2 - 4(da_{21}^1)^2 > 0$, *then there is a positive integer* T, *such that the positive equilibrium* $\tilde{E}$ *switches* T *times from stability to instability to stability, that is, the positive equilibrium* $\tilde{E}$ *is asymptotically stable when*

$$\tau \in [0, \overline{\tau}_0^+) \cup (\overline{\tau}_0^-, \overline{\tau}_1^+) \cup \cdots \cup (\overline{\tau}_{T-1}^-, \overline{\tau}_T^+)$$

and unstable when

$$\tau \in (\overline{\tau}_0^+, \overline{\tau}_0^-) \cup (\overline{\tau}_1^+, \overline{\tau}_1^-) \cup \cdots \cup (\overline{\tau}_{T-1}^+, \overline{\tau}_{T-1}^-) \cup (\overline{\tau}_T^+, \infty),$$

where $\overline{\tau}^{\pm}=\frac{1}{\overline{\omega}_{\pm}}\cos(\frac{a_{11}^1}{rk})$ *and*

$$\overline{\omega}_{\pm}=[\frac{-(a_{11}^1-(rk)^2-2da_{21}^1)\pm\sqrt{(a_{11}^1-(rk)^2-2da_{21}^1)^2-4(da_{21}^1)^2}}{2}]^{1/2}.$$

5. Direction and stability of Hopf bifurcation

In the previous section, we obtain the conditions under which a family of periodic solutions bifurcating from the positive equilibrium $\tilde{E}$ at the threshold $\tau=\overline{\tau}_j^{\pm}$ $(j=0,1,2,\ldots)$. It will be interesting to determine the direction, stability and period of the bifurcating periodic solutions. Following the ideas of Hassard et al. [18], we will derive explicit formulas for determining the properties of the Hopf bifurcation at the threshold value of $\tau=\overline{\tau}_j^{\pm}$ $(j=0,1,2,\ldots)$ by using the normal form concept and the center manifold theory. Throughout this section, we always assume that the system (1.5) undergoes Hopf bifurcation at the positive equilibrium $\tilde{E}$ for $\tau=\overline{\tau}_j^{\pm}$ $(j=0,1,2,\ldots)$; and then $\pm i\overline{\omega}_{\pm}$ is the corresponding purely imaginary roots of the characteristic equation.

Let $u_1(t)=x(\overline{\tau}t)-\tilde{x}$, $u_2(t)=y(\overline{\tau}t)-\tilde{y}$ and $\tau=\overline{\tau}+\mu$, $\mu\in R$. Thus $\mu=0$ is Hopf bifurcation value of system (1.5) and it can be written as

$$\begin{cases}\dot{u_1}(t)=\tau r(u_1+\tilde{x})\left(1-\dfrac{u_1(t-\tau)+\tilde{x}}{K}\right)-\dfrac{\alpha(1-c)(u_1+\tilde{x})^n(u_2+\tilde{y})}{1+\alpha h(1-c)(u_1+\tilde{x})^n},\\ \dot{u_2}(t)=\tau(u_2+\tilde{y})\left(e\dfrac{\alpha(1-c)(u_1+\tilde{x})^n}{1+\alpha h(1-c)(u_1+\tilde{x})^n}-d\right).\end{cases}\tag{5.1}$$

Thus, we can work in the fixed phase space $C=C([-1,0],R^2)$, which does not depend on the delay τ.

For $\phi=(\phi_1,\phi_2)\in C$, let

$$L_\mu(\phi)=\tau A_1(\phi_1(0),\phi_2(0))^T+\tau A_2(\phi_1(-1),\phi_2(-1))^T,\tag{5.2}$$

and

$$f(\mu,\phi)=\tau\begin{pmatrix}-\frac{r}{K}\phi_1(0)\phi_1(-1)-\frac{\alpha(1-c)(\phi_1(0))^n\phi_2(0)}{1+\alpha h(1-c)(\phi_1(0))^n}\\ \frac{e\alpha(1-c)(\phi_1(0))^n\phi_2(0)}{1+\alpha h(1-c)(\phi_1(0))^n}\end{pmatrix}.$$

By the Riese representation theorem, there exists a matrix whose components are bounded variation functions $\eta(\theta,\mu)$ in $\theta\in[-1,0]$ such that

$$L_\mu(\phi)=\int_{-1}^0 d\eta(\theta,\mu)\phi(\theta),\ \phi\in C.\tag{5.3}$$

Where the bounded variation functions $\eta(\theta,\mu)$ can be chosen as

$$\eta(\theta,\mu)=\tau A_1\delta(\theta)-\tau A_2\delta(\theta+1).\tag{5.4}$$

in which $\delta(\theta)$ is the Dirac delta function. For $\phi\in C^1([-1,0],R^2)$, defining

$$A(\mu)\phi=\begin{cases}\dfrac{d\phi(\theta)}{d\theta},\ \theta\in[-1,0),\\ \int_{-1}^0 d\eta(\theta,\mu)\phi(\theta),\ \theta=0,\end{cases}\tag{5.5}$$

and

$$R(\mu)\phi = \begin{cases} 0,\ \theta \in [-1, 0), \\ f(\mu, \theta),\ \theta = 0. \end{cases} \tag{5.6}$$

Then the system (5.1) is equivalent to

$$\dot{u}_t = A(\mu)u_t + R(\mu)u_t. \tag{5.7}$$

For $\psi \in C^1([0, 1], (R2)^*)$, defining

$$A^*\psi(s) = \begin{cases} -\dfrac{d\psi(s)}{ds},\ s \in (0, 1], \\ \int_{-1}^{0} d\eta^T(t, 0)\phi(-t),\ \theta = 0, \end{cases} \tag{5.8}$$

and a bilinear inner product

$$\langle\psi(s), \phi(\theta)\rangle = \overline{\psi}(0)\phi(0) - \int_{-1}^{0}\int_{\theta}^{\xi=0} \overline{\psi}(\xi - \theta)d\eta(\theta, 0)\phi(\theta). \tag{5.9}$$

Then $A(0)$ and A^* are adjoint operators. In addition, from Section 4 we know that $\pm i\overline{\omega}\overline{\tau}$ are eigenvalues of $A(0)$. Thus, they are also eigenvalues of A^*. Let $q(\theta)$ is the eigenvector of $A(0)$ corresponding to $i\overline{\omega}\overline{\tau}$ and $q^*(s)$ is the eigenvector of A^* corresponding to $-i\overline{\omega}\overline{\tau}$. Then it is not difficult to show that

$$q(\theta) = (1, \beta)^T = (1, \frac{-ie\overline{\omega} + ea^1_{11} - erke^{-i\overline{\omega}\overline{\tau}}}{d})^T e^{i\overline{\omega}\overline{\tau}\theta}, \tag{5.10}$$

and

$$q^*(s) = D(\beta^*, 1) = D(\frac{ie\overline{\omega}}{d}, 1)^T e^{i\overline{\omega}\overline{\tau}s}. \tag{5.11}$$

Since

$$\begin{aligned}
\langle q^*(s), q(\theta)\rangle &= \overline{D}\overline{q^*}(0)q(0) - \int_{-1}^{0}\int_{\theta}^{\xi=0} \overline{q^*}(\xi - \theta)d\eta(\theta, 0)q(\theta) \\
&= \overline{D}\{(\overline{\beta^*}, 1)(1, \beta)^T\} \\
&\quad - \overline{D}\left\{\int_{-1}^{0}\int_{\theta}^{\xi=0} (\overline{\beta^*}, 1)e^{-i\overline{\omega}\overline{\tau}(\xi-\theta)}d\eta(\theta, 0)(1, \beta)^T e^{-i\overline{\omega}\overline{\tau}\xi}\right\} \\
&= \overline{D}\{\overline{\beta^*} + \beta\} - \overline{D}\left\{\int_{-1}^{0} (\overline{\beta^*}, 1)\theta e^{i\overline{\omega}\overline{\tau}\theta}d\eta(\theta, 0)(1, \beta)^T\right\} \\
&= \overline{D}\{\overline{\beta^*} + \beta + rk\overline{\beta^*}\overline{\tau}\} \\
&= \overline{D}\left\{\frac{2ie\overline{\omega} - ierk\overline{\tau} - erke^{i\overline{\omega}\overline{\tau}} + ea^1_{11}}{d}\right\},
\end{aligned} \tag{5.12}$$

we may chose $\overline{D}$ as

$$\overline{D} = \frac{d}{2ie\overline{\omega} - ierk\overline{\tau} - erke^{i\overline{\omega}\overline{\tau}} + ea^1_{11}}, \tag{5.13}$$

which assures that

$$\langle q^*(s), q(\theta)\rangle = 1.$$

Using the same notations as in Hassard et al. [18] to consider properties of the bifurcating solutions at the positive equilibrium $\tilde{E}(\tilde{x}, \tilde{y})$. Thus we first compute coordinates to describe the center manifold $\mathbf{C}_0$ at $\mu = 0$. Let μ_t be the solution of Eqs. (5.1) when $\mu = 0$. Defining

$$z(t) = \langle q^*, \mu_t\rangle,\ W(t,\theta) = \mu_t(\theta) - 2Re(z(t)q(\theta)). \tag{5.14}$$

On the center manifold $\mathbf{C}_0$, we have

$$W(t,\theta) = W(z(t), \overline{z}(t), \theta),$$

in which

$$W(z(t),\overline{z}(t),\theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\overline{z} + W_{02}(\theta)\frac{\overline{z}^2}{2} + W_{30}(\theta)\frac{z^3}{6} + \cdots, \tag{5.15}$$

z and $\overline{z}$ are local coordinates for center manifold $\mathbf{C}_0$ in the direction of q^* and $\overline{q}^*$. Noting that W is real if μ_t is real. We consider only real solutions. For solution $\mu_t \in \mathbf{C}_0$ of Eqs. (5.1), since $\mu = 0$, then we have

$$\begin{aligned} \dot{z}(t) &= \langle q^*, \dot{u}_t\rangle \\ &= \langle q^*, A(0)u_t + R(0)u_t\rangle \\ &= \langle A^*(q^*), u_t\rangle + \langle q^*, R(0)u_t\rangle \\ &= i\overline{\omega}z(t) + \overline{q}^*(0)f(0, W(z(t),\overline{z}(t),\theta) + 2Re(zq(\theta))) \\ &\doteq i\overline{\omega}z(t) + \overline{q}^*(0)f_0, \end{aligned} \tag{5.16}$$

that is

$$\dot{z}(t) = i\overline{\omega}z(t) + g(z,\overline{z}), \tag{5.17}$$

in which

$$g(z,\overline{z}) = g_{20}(\theta)\frac{z^2}{2} + g_{11}(\theta)z\overline{z} + g_{02}(\theta)\frac{\overline{z}^2}{2} + g_{21}(\theta)\frac{z^2\overline{z}}{2} + \cdots. \tag{5.18}$$

Then it follows from Eq. (5.14) that

$$\begin{aligned} u_t(\theta) &= W(t,0) + 2Re(z(t)q(\theta)) \\ &= W(t,0) + z(t)q(\theta) + \overline{z}(t)\overline{q}(\theta) \\ &= W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\overline{z} + W_{02}(\theta)\frac{\overline{z}^2}{2} + (1,\beta)^T e^{i\overline{\omega}\tau\theta}z \\ &\quad + (1,\overline{\beta})^T e^{-i\overline{\omega}\tau\theta}\overline{z} + \cdots. \end{aligned} \tag{5.19}$$

From Eq. (5.19), we obtain that

$$\begin{aligned} u_1(t,0) &= z + \overline{z} + W^{(1)}(t,0), \\ u_2(t,0) &= z\beta + \overline{z}\overline{\beta} + W^{(2)}(t,0), \\ u_1(t-\tau) &= ze^{-i\overline{\omega}\tau} + \overline{z}e^{i\overline{\omega}\tau} + W^{(1)}(t,-\tau). \end{aligned} \tag{5.20}$$

Again, it follows together with Eq. (5.16) that

$$
\begin{aligned}
g(z,\overline{z}) &= \overline{q}^*(0)f_0(z,\overline{z}) \\
&= \overline{\tau}\ \overline{q}^*(0)\begin{pmatrix} -\dfrac{r\tilde{x}}{K}u_1(t)u_1(t-\tau)-\dfrac{d}{e}u_1(t))u_2(t) \\ du_1(t))u_2(t)\end{pmatrix}.
\end{aligned} \tag{5.21}
$$

Hence, it is got with the form of $f(\mu,\phi)$

$$
\begin{aligned}
g(z,\overline{z}) &= \overline{\tau}\overline{D}\{\overline{\beta}^*(-rku_1(t)u_1(t-\tau)-\frac{d}{e}u_1(t)u_2(t))+du_1(t)u_2(t)\} \\
&= \overline{\tau}\overline{D}\{\overline{\beta}^*(-rk(z+\overline{z}+W^{(1)}(t,0))(ze^{-i\overline{\omega}\tau}+\overline{z}e^{i\overline{\omega}\tau}+W^{(1)}(t,-\tau))) \\
&\quad -\overline{\beta}^*\frac{d}{e}(z+\overline{z}+W^{(1)}(t,0))(z\beta+\overline{z}\overline{\beta}+W^{(2)}(t,0))) \\
&\quad +d(z+\overline{z}+W^{(1)}(t,0))(z\beta+\overline{z}\overline{\beta}+W^{(2)}(t,0))\} \\
&= \overline{\tau}\overline{D}\{-rk\overline{\beta}^*(z^2e^{-i\overline{\omega}\tau}+z\overline{z}e^{i\overline{\omega}\tau}+z\overline{z}e^{-i\overline{\omega}\tau}+\overline{z}^2e^{i\overline{\omega}\tau}+z^2\overline{z}W_{11}^{(1)}(0) \\
&\quad +\frac{z^2\overline{z}}{2}W_{11}^{(1)}(0)+z^2\overline{z}W_{11}^{(1)}(-\overline{\tau})+\frac{z^2\overline{z}}{2}W_{20}^{(1)}(-\overline{\tau})) \\
&\quad +\frac{d}{e}(e-\overline{\beta}^*)(z^2\beta+z\overline{z}\overline{\beta}+z\overline{z}\beta+\overline{z}^2\overline{\beta}+z^2\overline{z}W_{11}^{(2)}(0)+\frac{z^2\overline{z}}{2}W_{20}^{(2)}(0) \\
&\quad +z^2\overline{z}\beta W_{11}^{(1)}(0)+\frac{z^2\overline{z}}{2}\overline{\beta}W_{20}^{(1)}(0)\}+\cdots.
\end{aligned} \tag{5.22}
$$

Comparing coefficients with Eq. (5.15), we obtain that

$$
\begin{aligned}
g_{20} &= 2\overline{\tau}\overline{D}[-rk\overline{\beta}^*e^{-i\overline{\omega}\tau}+p(e-\overline{\beta}^*)\beta], \\
g_{11} &= \overline{\tau}\overline{D}[-rk\overline{\beta}^*(e^{i\overline{\omega}\tau}+e^{-i\overline{\omega}\tau})+\frac{d}{e}(e-\overline{\beta}^*)(\beta+\overline{\beta})], \\
g_{02} &= 2\overline{\tau}\overline{D}[-rk\overline{\beta}^*e^{i\overline{\omega}\tau}+\frac{d}{e}(e-\overline{\beta}^*)\overline{\beta}], \\
g_{21} &= \overline{\tau}\overline{D}[-rk\overline{\beta}^*(2W_{11}^{(1)}(0)+W_{11}^{(1)}(0)+2W_{11}^{(1)}(-\overline{\tau})+W_{20}^{(1)}(-\overline{\tau})) \\
&\qquad +\frac{d}{e}(e-\overline{\beta}^*)(2W_{11}^{(2)}(0)+W_{20}^{(2)}(0)+2\beta W_{11}^{(1)}(0)+\overline{\beta}W_{20}^{(1)}(0)].
\end{aligned} \tag{5.23}
$$

Since there are $W_{20}(\theta)$ and $W_{11}(\theta)$ in g_{21}, we still need to compute them. From Eq. (5.7) and Eq. (5.14), we have

$$
\begin{aligned}
\dot{W} = \dot{u}_t-\dot{z}q-\dot{\overline{z}}\overline{q} &= \begin{cases} AW-2Re(\overline{q}^*(0)f_0q(\theta)), \ \theta\in[-1,0) \\ AW-2Re(\overline{q}^*(0)f_0q(0))+f_0, \ \theta=0 \end{cases} \\
&\doteq AW+H(z,\overline{z},\theta)
\end{aligned} \tag{5.24}
$$

in which

$$
H(z,\overline{z},\theta) = H_{20}(\theta)\frac{z^2}{2}+H_{11}(\theta)z\overline{z}+H_{02}(\theta)\frac{\overline{z}^2}{2}+\cdots. \tag{5.25}
$$

Substituting the corresponding series into Eqs. (5.24) and comparing the coefficients, we obtain

$$(A-2i\varpi)W_{20}(\theta)=-H_{20}(\theta),\ AW_{11}(\theta)=-H_{11}(\theta). \tag{5.26}$$

From Eqs. (5.24), we know that for $\theta\in[-1,0)$,

$$H(z,\overline{z},\theta)=-\overline{q}^{*}(0)f_0q(\theta)-q^{*}(0)\overline{f}_0\overline{q}(\theta)=-g(z,\overline{z})q(\theta)-\overline{g}(z,\overline{z})\overline{q}(\theta). \tag{5.27}$$

Comparing coefficients with Eq. (5.25) gives that

$$H_{20}(\theta)=-g_{20}q(\theta)-\overline{g}_{02}\overline{q}(\theta),\ H_{11}(\theta)=-g_{11}q(\theta)-\overline{g}_{11}\overline{q}(\theta). \tag{5.28}$$

From the first equations of Eqs. (5.26) and Eqs. (5.28), we get

$$\dot{W}_{20}(\theta)=2i\varpi W_{20}(\theta)+g_{20}q(\theta)+\overline{g}_{02}\overline{q}(\theta). \tag{5.29}$$

Noting that $q(\theta)=q(0)e^{i\varpi\tau\theta}$, hence

$$W_{20}(\theta)=\frac{ig_{20}}{\varpi}q(0)e^{i\varpi\theta}+\frac{i\overline{g}_{02}}{3\varpi}\overline{q}(0)e^{-i\varpi\theta}+E_1e^{2i\varpi\theta}. \tag{5.30}$$

Similarly, from the second equations of Eqs. (5.26) and Eqs. (5.28), we obtain

$$\dot{W}_{11}(\theta)=g_{11}q(\theta)+\overline{g}_{11}\overline{q}(\theta), \tag{5.31}$$

and

$$W_{11}(\theta)=-\frac{ig_{11}}{\varpi}q(0)e^{i\varpi\theta}+\frac{i\overline{g}_{11}}{\varpi}\overline{q}(0)e^{-i\varpi\theta}+E_2. \tag{5.32}$$

Next, we will select appropriate E_1 and E_2, respectively. It follows from the definition of A and Eq. (5.26) that

$$\begin{aligned}&\int_{-1}^{0}d\eta(0,\theta)W_{20}(\theta)=2i\varpi W_{20}(0)-H_{20}(0),\\&\int_{-1}^{0}d\eta(0,\theta)W_{11}(\theta)=-H_{11}(0).\end{aligned} \tag{5.33}$$

From Eqs. (5.24), we have

$$\begin{aligned}H_{20}(0)&=-g_{20}(0)q(0)-\overline{g}_{02}(0)\overline{q}(0)+M_1,\\H_{11}(0)&=-g_{11}(0)q(0)-\overline{g}_{11}(0)\overline{q}(0)+M_2,\end{aligned} \tag{5.34}$$

in which

$$M_1=\overline{\tau}\begin{pmatrix}-2rke^{-i\varpi\tau}-\dfrac{2\alpha(1-c)\beta}{1+\alpha h(1-c)}\\ \dfrac{2e\alpha(1-c)\beta}{1+\alpha h(1-c)}\end{pmatrix},$$

and

$$M_2=\overline{\tau}\begin{pmatrix}-2rkRe(e^{-i\varpi\tau})-\dfrac{2\alpha(1-c)Re(\beta)}{1+\alpha h(1-c)}\\ \dfrac{2e\alpha(1-c)Re(\beta)}{1+\alpha h(1-c)}\end{pmatrix}.$$

Substituting Eq. (5.30) and the first equation of Eqs. (5.33) into the first equation of Eqs. (5.34), we obtain

(5.35) $$N_1E_1 = M_1,$$

in which

$$N_1 = \begin{pmatrix} 2i\overline{\omega} - \frac{r\tilde{x}}{K}e^{-2i\overline{\omega}\overline{\tau}} + a^1_{11} & -\frac{d}{e} \\ ea^1_{21} & 2\overline{\omega}i \end{pmatrix}.$$

Similarly, substituting Eq. (5.30) and the second equation of Eqs. (5.33) into the second equation of Eqs. (5.34), we get

(5.36) $$N_2E_2 = M_2,$$

in which

$$N_2 = \begin{pmatrix} -rke^{-2i\overline{\omega}\overline{\tau}} + a^1_{11} & -\frac{d}{e} \\ ea^1_{21} & 0 \end{pmatrix}.$$

It follows from Eq. (5.30), Eq. (5.34), Eq. (5.35), and Eq. (5.36) that g_{21} can be expressed. Thus, we can compute the following values

(5.37)
$$\begin{aligned} c_1(0) &= \frac{i}{\overline{\omega}\overline{\tau}}(g_{11}g_{20} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2) + \frac{1}{2}g_{21}, \\ \mu_2 &= -\frac{Re(c_1(0))}{Re(\lambda_0'(\overline{\tau}))}, \\ \beta_2 &= 2Re(c_1(0)), \\ T_2 &= -\frac{Im(c_1(0)) + \mu_2 Im(\lambda_0'(\overline{\tau}))}{\overline{\omega}}, \end{aligned}$$

which determine quantities of the bifurcating periodic solutions at the critical value $\overline{\tau}$, i.e., μ_2 determines the direction of the Hopf bifurcation: if $\mu_2 > 0$ ($\mu_2 < 0$), then the Hopf bifurcation is supercritical (subcritical) and the bifurcating periodic solutions exist for $\tau > \overline{\tau}$ ($\tau < \overline{\tau}$); β_2 determines the stability of the bifurcating periodic solutions: the bi- furcating periodic solutions in the center manifold are stable (unstable) if $\beta_2 < 0$ ($\beta_2 > 0$); and T_2 determines the period of the bifurcating periodic solutions: the period increase (decrease) if $T_2 > 0$ ($T_2 < 0$). Further, it follows from Eq. (4.6) and Eqs. (5.37), the following results about the direction of the Hopf bifurcations hold.

Theorem 5.1. *Suppose that* $e(1-2k) - n(1-k)(e-dh) < 0$ *and* $(a^1_{11} - rk)^2 - 4da^1_{21} \neq 0$. *The Hopf bifurcations of the system* (1.5) *at the positive equilibrium point* $\tilde{E}(\tilde{x}, \tilde{y})$ *and* $\tau = \tau_j^+$ *are supercritical* (*respectively subcritical*) *if* $Re(c_1(0)) < 0$ (*respectively* $Re(c_1(0)) > 0$). *However,the directions of the Hopf bifurcations system* (5) *at the positive equilibrium point* $\tilde{E}(\tilde{x}, \tilde{y})$ *and*$\tau = \tau_j^-$ *is* $\tau < \tau_j^-$ (*respectively* $\tau > \tau_j^-$) *if* $Re(c_1(0)) < 0$ (*respectively* $Re(c_1(0)) > 0$).

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