KYUNGPOOK Math. J. 49(2009), 605-618

A Stage-Structured Predator-Prey System with Time Delay and Beddington-DeAngelis Functional Response

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Abstract. A stage-structured predator-prey system with time delay and Beddington-DeAngelis functional response is considered. By analyzing the corresponding characteristic equation, the local stability of a positive equilibrium is investigated. The existence of Hopf bifurcations is established. Formulae are derived to determine the direction of bifurcations and the stability of bifurcating periodic solutions by using the normal form theory and center manifold theorem. Numerical simulations are carried out to illustrate the theoretical results.

1. Introduction

The predator-prey system is very important in population modelling and has been studied by many authors (see, for example, [1], [2], [4], [7], [9]). A generic predator-prey model takes the form

$$\begin{cases} \dot{x} = xf(x) - yp(x), \\ \dot{y} = kyp(x) - yg(y), \end{cases} \tag{1.1}$$

* Corresponding author.
Received June 6, 2008; accepted December 11, 2008.
2000 Mathematics Subject Classification: 34K15, 92D25.
Key words and phrases: stability, Hopf bifurcation, predator-prey system, stage structure, time delay, Beddington-DeAngelis functional response.
This work was supported by the National Natural Science Foundation of China (No. 10671209), China Postdoctoral Science Foundation (No. 20060391010), and the Scientific Research Foundation for the Returned Overseas Chinese Scholars, State Education Ministry.

where $x(t)$ and $y(t)$ are the densities of prey and predator populations at time t, respectively. The function $f(x)$ represents the growth rate of the prey; $g(y)$ represents the death rate and intra-specific competition rate of the predator; $p(x)$ denotes the predator response function. The most popular functional responses used in the modelling of predator-prey systems are the Michaelis-Menten type $p(x) = x/(c+x)$ and ratio-dependent type $p(x) = x/(x+by)$. The Michaelis-Menten type does not account for the mutual competitions among predators [9], while the ratio-dependent type allows unrealistic positive growth rate of the predator at low densities [2], [7]. The Beddington-DeAngelis functional response $p(x) = x/(1+bx+cy)$ was introduced independently by Beddington [1] and DeAngelis [4] as a solution of the observed problems in the classical predator-prey theory. It has an extra term in the denominator which models mutual interference between predators and avoids the "low densities problem" of the ratio-dependent type functional response.

We note that in the models mentioned above, it is assumed that both the immature and the mature predators have the same ability to attack prey individuals. However, in the real world, almost all animals have stage structure of immature and mature, and only mature predators can attack prey and have reproductive ability. Stage-structured models have received great attention in recent years (see, for example, [11], [12]). In [11], Sun studied the following predator-prey model with Beddington-DeAngelis functional response

$$\begin{cases} \dot{x}(t) = rx(t) - ax^2(t) - \dfrac{a_1 x(t) y_2(t)}{1 + bx(t) + cy_2(t)}, \\ \dot{y_1}(t) = \dfrac{k a_1 x(t) y_2(t)}{1 + bx(t) + cy_2(t)} - (r_1 + d) y_1(t), \\ \dot{y_2}(t) = d y_1(t) - r_2 y_2(t), \end{cases} \tag{1.2}$$

where $x(t)$ is the density of the prey population at time t, $y_1(t)$ and $y_2(t)$ are the densities of the immature and mature predators at time t, respectively. The parameters a, a_1, b, c, d, k, r, r_1 and r_2 are positive constants, where a is the intra-specific competition rate of the prey, a_1 is the capturing rate of the predator, k is the conversion rate of nutrients into the reproduction of the predator, d is the rate of immature predator becoming mature predator, r represents the intrinsic growth rate of the prey, $r_1(r_2)$ is the death rate of the immature(mature) predator. In [11], Sun systematically studied system (1.2) and obtained conditions for the permanence of predator and the existence of periodic orbit.

It is generally recognized that some kinds of time delays are inevitable in population interactions and tend to be destabilizing in the sense that longer delays may destroy the stability of positive equilibria. Time delay due to the gestation is a common example, because generally the consumption of prey by the predator throughout its past history governs the present birth rate of the predator. Recently, great attention has been received and a large body of work has been carried out on the existence of Hopf bifurcations in delayed population models (see, for example, [8], [10] and references cited therein). The stability of positive equilibria and the existence and the direction of Hopf bifurcations were discussed respectively in the references mentioned above.

In this paper, we are concerned with the effect of time delay on the dynamics of system (1.2). To this aim, we consider the following delay differential equations

$$
\begin{cases} \dot{x}(t) = rx(t) - ax^2(t) - \dfrac{a_1 x(t) y_2(t)}{1 + bx(t) + cy_2(t)}, \\ \dot{y_1}(t) = \dfrac{ka_1 x(t-\tau) y_2(t-\tau)}{1 + bx(t-\tau) + cy_2(t-\tau)} - (r_1 + d) y_1(t), \\ \dot{y_2}(t) = dy_1(t) - r_2 y_2(t), \end{cases} \tag{1.3}
$$

where $\tau \geq 0$ is a constant representing a time delay due to the gestation of the predator.

The initial conditions for system (1.3) take the form

$$
\begin{aligned} &x(\theta) = \phi_1(\theta) \geq 0, \ \ y_1(\theta) = \phi_2(\theta) \geq 0, \ \ y_2(\theta) = \phi_3(\theta) \geq 0, \ \ \theta \in [-\tau, 0), \\ &\phi_1(0) > 0, \ \ \phi_2(0) > 0, \ \ \phi_3(0) > 0, \ \ (\phi_1(\theta), \phi_2(\theta), \phi_3(\theta)) \in C([-\tau, 0], R^3_{+0}), \end{aligned}
$$

where $R^3_{+0} = \{(x_1, x_2, x_3) : x_i \geq 0, i = 1, 2, 3\}$.

The organization of this paper is as follows. In the next section, by choosing the time delay τ as a parameter and analyzing the associated characteristic equation of a linearized system, we investigate the linear stability of the positive equilibrium of system (1.3). In addition, we get sufficient conditions for the existence of Hopf bifurcations. In Section 3, we derive formulae to determine the direction of bifurcations and the stability of bifurcating periodic solutions by using the normal form theory and center manifold theorem. Numerical simulations are carried out in Section 4 to illustrate the theoretical results.

2. Local stability and Hopf bifurcations

In this section, we discuss the stability of a positive equilibrium and the existence of Hopf bifurcations for system (1.3) with time delay τ as a parameter.

Assume

$$
(\mathtt{H_1}) \qquad 0 < \frac{r_2(r_1 + d)}{dka_1 - br_2(r_1 + d)} < \frac{r}{a}.
$$

It is easy to check that system (1.3) has a positive equilibrium $E = (x_*, y_{1*}, y_{2*})$, where

$$
\begin{aligned} &x_* = M + N y_{1*}, \quad y_{1*} = \frac{-(r_1 + d - krN + 2kaMN) + \sqrt{\triangle}}{2kaN^2}, \quad y_{2*} = \frac{d}{r_2} y_{1*}, \\ &M = \frac{r_2(r_1 + d)}{dka_1 - br_2(r_1 + d)}, \quad N = \frac{cd(r_1 + d)}{dka_1 - br_2(r_1 + d)}, \\ &\triangle = (r_1 + d - krN + 2kaMN)^2 - 4ak^2 MN^2 (aM - r). \end{aligned}
$$

Let $\bar{x} = x - x_*$, $\bar{y}_1 = y_1 - y_{1*}$, $\bar{y}_2 = y_2 - y_{2*}$. Dropping the bars, system (1.3) becomes

(2.1)

$$\begin{cases} \dot{x}(t) = (r - 2ax_* - A)x(t) - By_2(t) - ax^2(t) + \dfrac{bAx^2(t) + cBy_2^2(t) - Cx(t)y_2(t)}{1 + bx_* + cy_{2*} + bx(t) + cy_2(t)}, \\ \dot{y}_1(t) = -\dfrac{kbAx^2(t-\tau) + kcBy_2^2(t-\tau) - kCx(t-\tau)y_2(t-\tau)}{1 + bx_* + cy_{2*} + bx(t-\tau) + cy_2(t-\tau)} \\ \qquad\quad -(r_1 + d)y_1(t) + kAx(t-\tau) + kBy_2(t-\tau), \\ \dot{y}_2(t) = dy_1(t) - r_2 y_2(t), \end{cases}$$

where

$$A = \frac{a_1 y_{2*}(1 + cy_{2*})}{(1 + bx_* + cy_{2*})^2},\ B = \frac{a_1 x_*(1 + bx_*)}{(1 + bx_* + cy_{2*})^2},\ C = \frac{a_1(1 + bx_* + cy_{2*} + 2bcx_* y_{2*})}{(1 + bx_* + cy_{2*})^2}.$$

The characteristic equation of system (2.1) at the origin is of the form

$$\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 + (q_1\lambda + q_0)e^{-\lambda\tau} = 0, \tag{2.2}$$

where

(2.3)

$$\begin{array}{ll} p_0 = r_2(r_1 + d)(2ax_* + A - r), & p_1 = r_2(r_1 + d) + (r_2 + r_1 + d)(2ax_* + A - r), \\ p_2 = r_2 + r_1 + d + 2ax_* + A - r, & q_0 = kdB(r - 2ax_*), \quad q_1 = -kdB. \end{array}$$

When $\tau = 0$, equation (2.2) becomes

$$\lambda^3 + p_2\lambda^2 + (p_1 + q_1)\lambda + p_0 + q_0 = 0, \tag{2.4}$$

Assume

(H_2) $0 < r - 2ax_* < A < 2(r - 2ax_*)$,

(H_3) $p_2(p_1 + q_1) > p_0 + q_0$.

This assumption implies that

$$p_2 > 0, \quad p_0 + q_0 > 0,$$
$$p_2(p_1 + q_1) - (p_0 + q_0) > 0.$$

By Hurwitz criterion, we know that all roots of equation (2.4) are negative.

When $\tau > 0$, noting that $i\omega(\omega > 0)$ is a root of (2.2) if and only if ω satisfies

$$\begin{cases} q_1\omega\cos\omega\tau - q_0\sin\omega\tau = \omega^3 - p_1\omega, \\ q_1\omega\sin\omega\tau + q_0\cos\omega\tau = p_2\omega^2 - p_0. \end{cases} \tag{2.5}$$

Squaring and adding equations in (2.5) gives

$$\omega^6 + h_2\omega^4 + h_1\omega^2 + h_0 = 0, \tag{2.6}$$

where

$$h_0 = p_0^2 - q_0^2, \quad h_1 = p_1^2 - q_1^2 - 2p_0p_2, \quad h_2 = p_2^2 - 2p_1.$$

For equation (2.6), if $(\mathtt{H}_2)$ holds, we have

$$\begin{aligned} &h_0 < (p_0+q_0)r_2(r_1+d)[A - 2(r - 2ax_*)] < 0,\\ &h_1 > [r_2^2 + (r_1+d)^2](2ax_* + A - r)^2 > 0,\\ &h_2 = r_2^2 + (r_1+d)^2 + (2ax_* + A - r)^2 > 0. \end{aligned} \tag{2.7}$$

Hence, the number of positive real roots is not more than one by Descartes'rule of signs. On the other hand, let $z = \omega^2$, $f(z) = z^3 + h_2z^2 + h_1z + h_0$, we have

$$\begin{aligned} &f(0) = h_0 < 0,\\ &\lim_{z\to+\infty} f(z) = +\infty \end{aligned}$$

Then, the equations (2.6) has at least one positive real root. Hence, the equations (2.6) has only one positive real root ω_0. Let

$$\tau_j = \frac{1}{\omega_0}\arcsin\left(\frac{(p_2q_1 - q_0)\omega_0^3 + (p_1q_0 - p_0q_1)\omega_0}{q_1^2\omega_0^2 + q_0^2}\right) + \frac{2\pi j}{\omega_0}, \quad j = 0, 1, 2, \cdots, \tag{2.8}$$

then equation (2.2) has a pair of purely imaginary roots $\pm\mathtt{i}\omega_0$ with $\tau = \tau_j$.

Lemma 2.1. *For equation* (2.2), *if* (H_2) *holds, then we have the following transversal condition*

$$Re\left(\left.\frac{\mathtt{d}\lambda}{\mathtt{d}\tau}\right|_{\lambda=\mathtt{i}\omega_0}\right) > 0.$$

Proof. Differentiating both sides of (2.2) with respect to τ yields

$$[3\lambda^2 + 2p_2\lambda + p_1 + (q_1 - q_1\tau\lambda - q_0\tau)e^{-\lambda\tau}]\frac{\mathtt{d}\lambda}{\mathtt{d}\tau} = \lambda(q_1\lambda + q_0)e^{-\lambda\tau}.$$

For convenience, we study $(\mathtt{d}\lambda/\mathtt{d}\tau)^{-1}$ instead of $\mathtt{d}\lambda/\mathtt{d}\tau$. We have

$$\begin{aligned} \left(\frac{\mathtt{d}\lambda}{\mathtt{d}\tau}\right)^{-1} &= \frac{3\lambda^2 + 2p_2\lambda + p_1 + q_1e^{-\lambda\tau}}{\lambda(q_1\lambda + q_0)e^{-\lambda\tau}} - \frac{\tau}{\lambda}\\ &= -\frac{3\lambda^2 + 2p_2\lambda + p_1}{\lambda(\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0)} + \frac{q_1}{\lambda(q_1\lambda + q_0)} - \frac{\tau}{\lambda}. \end{aligned}$$

Hence,

$$\begin{aligned}
\mathtt{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\Bigg|_{\lambda=\mathrm{i}\omega_0} &= \frac{3\omega_0^4+2(p_2^2-2p_1)\omega_0^2+p_1^2-2p_0p_2}{\omega_0^6+(p_2^2-2p_1)\omega_0^4+(p_1^2-2p_0p_2)\omega_0^2+p_0^2}-\frac{q_1^2}{q_1^2\omega_0^2+q_0^2}\\
&= \frac{3\omega_0^4+2(p_2^2-2p_1)\omega_0^2+p_1^2-q_1^2-2p_0p_2}{q_1^2\omega_0^2+q_0^2}\\
&= \frac{3\omega_0^4+2h_2\omega_0^2+h_1}{q_1^2\omega_0^2+q_0^2}\\
&> 0
\end{aligned}$$

Therefore,

$$\mathtt{sign}\left\{\mathtt{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)\Bigg|_{\lambda=\mathrm{i}\omega_0}\right\}=\mathtt{sign}\left\{\mathtt{Re}\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1}\Bigg|_{\lambda=\mathrm{i}\omega_0}\right\}>0.$$

This completes the proof of lemma 2.1. □

From Lemma 2.1 and the results in [3], we have the following result.

Lemma 2.2. *Assume* (H_1), (H_2) *and* (H_3) *hold, then*

(i) *when* $\tau \in [0, \tau_0)$, *all roots of equation* (2.2) *have strictly negative real parts.*

(ii) *when* $\tau = \tau_0$, *equation* (2.2) *has a pair of conjugate purely imaginary roots* $\pm\mathrm{i}\omega_0$, *and all other roots have strictly negative real parts.*

(iii) *when* $\tau > \tau_0$, *equation* (2.2) *has at least one root with positive real part.*

Applying lemma 2.2, we have the following result.

Theorem 2.1. *For system* (2.1), *if* (H_1), (H_2) *and* (H_3) *are satisfied, then*

(i) *when* $\tau \in [0, \tau_0)$, *the zero solution is asymptotically stable;*

(ii) *when* $\tau > \tau_0$, *the zero solution is unstable;*

(iii) $\tau = \tau_j (j = 0, 1, 2, \cdots)$ *are the values of* `Hopf` *bifurcations , where* τ_j *are defined by* (2.8).

3. Direction and stability of Hopf bifurcations

In the previous section, we obtained conditions under which a family of periodic solutions bifurcate from the positive equilibrium at the critical values $\tau_j (j = 0, 1, 2, \cdots)$. In this section, we study the direction of bifurcations and the stability of bifurcating periodic solutions. The method we used here is based on the normal form theory and center manifold theory introduced by Hassard et al. in [5].

Now, we re-scale the time by $t = s\tau$, $\hat{x}(s) = x(s\tau)$, $\hat{y}_1(s) = y_1(s\tau)$, $\hat{y}_2(s) = y_2(s\tau)$, $\tau = \tau_0 + \mu$, $\mu \in R$, and still denoting by $x(t) = \hat{x}(s)$, $y_1(t) = \hat{y}_1(s)$, $y_2(t) = \hat{y}_2(s)$, then system (2.1) can be written as

$$\tag{3.1} \begin{cases} \dot{x}(t) = (\tau_0+\mu)[(r-2ax_*-A)x(t) - By_2(t) - ax^2(t) \\ \qquad + \dfrac{bAx^2(t) + cBy_2^2(t) - Cx(t)y_2(t)}{1+bx_*+cy_{2*}+bx(t)+cy_2(t)}], \\ \dot{y}_1(t) = (\tau_0+\mu)[-\dfrac{kbAx^2(t-1) + kcBy_2^2(t-1) - kCx(t-1)y_2(t-1)}{1+bx_*+cy_{2*}+bx(t-1)+cy_2(t-1)} \\ \qquad -(r_1+d)y_1(t) + kAx(t-1) + kBy_2(t-1)], \\ \dot{y}_2(t) = (\tau_0+\mu)[dy_1(t) - r_2y_2(t)]. \end{cases}$$

For $\varphi = (\varphi_0, \varphi_1, \varphi_2)^T \in C[-1,0] = C([-1,0], R^3)$, define a family of operators

$$\tag{3.2} L_\mu\varphi = B_1\varphi(0) + B_2\varphi(-1)\ ,$$

where

$$B_1 = (\tau_0+\mu)\begin{pmatrix} r-2ax_*-A & 0 & -B \\ 0 & -(r_1+d) & 0 \\ 0 & d & -r_2 \end{pmatrix}, \quad B_2 = (\tau_0+\mu)\begin{pmatrix} 0 & 0 & 0 \\ kA & 0 & kB \\ 0 & 0 & 0 \end{pmatrix}.$$

And define

$$f(\mu,\varphi) = (\tau_0+\mu)\begin{pmatrix} -a\varphi_0^2(0) + \dfrac{bA\varphi_0^2(0) + cB\varphi_2^2(0) - C\varphi_0(0)\varphi_2(0)}{1+bx_*+cy_{2*}+b\varphi_0(0)+c\varphi_2(0)} \\ -\dfrac{kbA\varphi_0^2(-1) + kcB\varphi_2^2(-1)) - kC\varphi_0(-1)\varphi_2(-1)}{1+bx_*+cy_{2*}+b\varphi_0(-1)+c\varphi_2(-1)} \\ 0 \end{pmatrix}.$$

By the Riesz representation theorem, there exists a matrix whose components are bounded variation functions $\eta(\theta,\mu) : [-1,0] \to R^3$, such that $L_\mu\varphi = \int_{-1}^0 d\eta(\theta,\mu)\varphi(\theta)$. In fact, we can choose

$$\eta(\theta,\mu) = \begin{cases} 0, & \theta = -1, \\ B_2, & \theta \in (-1,0), \\ B_1 + B_2, & \theta = 0. \end{cases}$$

For $\varphi = (\varphi_0, \varphi_1, \varphi_2)^T \in C^1[-1,0]$, define

$$\tag{3.3} A(\mu)\varphi = \begin{cases} \dfrac{\mathrm{d}\varphi(\theta)}{\mathrm{d}\theta}\ , & \theta \in [-1,0), \\ \int_{-1}^0 \mathrm{d}\eta(s,\mu)\varphi(s)\ , & \theta = 0, \end{cases}$$

and

$$\tag{3.4} R(\mu)\varphi = \begin{cases} 0\ , & \theta \in [-1,0), \\ f(\mu,\varphi)\ , & \theta = 0. \end{cases}$$

Hence, equation (3.1) can be rewritten as

$$\dot{U}_t = A(\mu)U_t + R(\mu)U_t \ , \tag{3.5}$$

where $U = (x, y_1, y_2)^{\mathtt{T}}$. For $\psi \in C^1[0,1]$, define

$$A^*\psi(s) = \begin{cases} -\dfrac{\mathtt{d}\psi(s)}{\mathtt{d}s}, & s \in [-1,0), \\ \int_{-1}^{0} \mathtt{d}\eta^T(t,0)\psi(-t), & s = 0. \end{cases} \tag{3.6}$$

For $\varphi \in C([-1,0]\ ,C^3)$ and $\psi \in C([0,1]\ ,(C^3)^*)$, define a bilinear inner product

$$< \psi, \varphi >= \overline{\psi}^{\mathtt{T}}(0)\varphi(0) - \int_{\theta=-1}^{0} \int_{\xi=0}^{\theta} \overline{\psi}^{\mathtt{T}}(\xi-\theta)\mathtt{d}\eta(\theta)\varphi(\xi)d\xi \ ,$$

where $\eta(\theta) = \eta(\theta, 0)$. Then, $A = A(0)$ and A^* are adjoint operators. By discussion in Section 2 and transformation $t = s\tau$, we know that $\pm \mathtt{i}\tau_0\omega_0$ are eigenvalues of A. Thus, they are also eigenvalues of A^*. Direct computation yields the following result.

Lemma 3.1. *$q(\theta) = (1, q_2, q_3)^{\mathtt{T}} e^{\mathtt{i}\tau_0\omega_0\theta}$ and $q^*(s) = \bar{D}(1, q_2^*, q_3^*)^{\mathtt{T}} e^{\mathtt{i}\tau_0\omega_0 s}$ are eigenvectors of A and A^* corresponding to $\mathtt{i}\tau_0\omega_0$ and $-\mathtt{i}\tau_0\omega_0$, respectively, and $< q^*(\theta), q(\theta) >= 1$, $< q^*(\theta), \overline{q}(\theta) >= 0$, where*

$$\begin{aligned} q_2 &= \frac{\omega_0^2 + r_2(r - 2ax_* - A) + \mathtt{i}(r - 2ax_* - A - r_2)\omega_0}{Bd}, \\ q_3 &= \frac{r - 2ax_* - A - \mathtt{i}\omega_0}{\beta\gamma}, \\ q_2^* &= \frac{2ax_* + A - r - \mathtt{i}\omega_0}{kA} e^{-\mathtt{i}\tau_0\omega_0}, \\ q_3^* &= \frac{-\omega_0^2 + (r_1 + d)(2ax_* + A - r) - \mathtt{i}(2ax_* + A - r + r_1 + d)\omega_0}{kdA} e^{-\mathtt{i}\tau_0\omega_0}, \\ D &= [1 + q_2\bar{q}_2^* + q_3\bar{q}_3^* + \tau_0(kA\bar{q}_2^* + kBq_3\bar{q}_3{}^*)]^{-1}. \end{aligned}$$

Now we compute the coordinates to describe the center manifold C_0 at $\mu = 0$. Let U_t be the solution of equation (3.5) when $\mu = 0$, and define

$$z(t) =< q^*, U_t >, \quad W(t,\theta) = U_t(\theta) - 2Re\{z(t)q(\theta)\}. \tag{3.7}$$

On the center manifold C_0, we have $W(t,\theta) = W(z(t), \bar{z}(t), \theta)$, where

$$W(z, \overline{z}, \theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\overline{z} + W_{02}(\theta)\frac{\overline{z}^2}{2} + \cdots . \tag{3.8}$$

z and $\bar{z}$ are local coordinates for center manifold C_0 in the direction of q^* and $\bar{q}^*$. Note that W is real if U_t is real, we consider only real solutions. For the solution $U_t \in C_0$, since $\mu = 0$, then

$$\dot{z}(t) = \mathtt{i}\tau_0\omega_0 z(t) + \overline{q}^*(0) f_0(z, \overline{z}). \tag{3.9}$$

We rewrite this equation as $\dot{z}(t) = \mathtt{i}\tau_0\omega_0 z(t) + g(z, \overline{z})$ with

$$g(z, \overline{z}) = g_{20}\frac{z^2}{2} + g_{11}z\overline{z} + g_{02}\frac{\overline{z}^2}{2} + g_{21}\frac{z^2\overline{z}}{2} + \cdots . \tag{3.10}$$

By (3.7), we have

$$\begin{aligned} U_t(\theta) &= W(z, \bar{z}, \theta) + zq(\theta) + \bar{z}\bar{q}(\theta) \\ &= \begin{pmatrix} W^{(0)}(z, \bar{z}, \theta) \\ W^{(1)}(z, \bar{z}, \theta) \\ W^{(2)}(z, \bar{z}, \theta) \end{pmatrix} + z \begin{pmatrix} 1 \\ q_2 \\ q_3 \end{pmatrix} e^{\mathtt{i}\tau_0\omega_0\theta} + \bar{z} \begin{pmatrix} 1 \\ \bar{q}_2 \\ \bar{q}_3 \end{pmatrix} e^{-\mathtt{i}\tau_0\omega_0\theta}. \end{aligned}$$

Hence,

$$g(z, \bar{z}) \;=\; \bar{q}^*(0) f_0(z, \bar{z}) = \bar{q}^*(0) f(0, U_t)$$

Substitute $U_t(\theta)$ into above and comparing the coefficients with (3.10), we get (3.11)

$$\begin{aligned}
g_{20} &= 2\tau_0 D[-a + \frac{(bA + cBq_3^2 - Cq_3)(1 - k\bar{q}_2^* e^{-2\mathtt{i}\tau_0\omega_0})}{1 + bx_* + cy_{2*}}], \\
g_{11} &= \tau_0 D[-2a + \frac{(1 - k\bar{q}_2^*)(-C(q_3 + \bar{q}_3) + 2bA + 2cBq_3\bar{q}_3)}{1 + bx_* + cy_{2*}}], \\
g_{02} &= 2\tau_0 D[-a + \frac{(bA + cB\bar{q}_3^2 - C\bar{q}_3)(1 - k\bar{q}_2^* e^{2\mathtt{i}\tau_0\omega_0})}{1 + bx_* + cy_{2*}}], \\
g_{21} &= 2\tau_0 D[-a(W_{20}^{(0)}(0) + 2W_{11}^{(0)}(0)) + \frac{1}{1 + bx_* + cy_{2*}}(-C(W_{11}^{(2)}(0) + q_3 W_{11}^{(0)}(0)) \\
&\quad -\frac{1}{2}C(W_{20}^{(2)}(0) + W_{20}^{(0)}(0)\bar{q}_3) + cB(\bar{q}_3 W_{20}^{(2)}(0) + 2q_3 W_{11}^{(2)}(0)) \\
&\quad +bA(W_{20}^{(0)}(0) + 2W_{11}^{(0)}(0)) - \bar{q}_2^*(-kCe^{-\mathtt{i}\tau_0\omega_0}(W_{11}^{(2)}(-1) + W_{11}^{(0)}(-1)) \\
&\quad -\frac{1}{2}kCe^{\mathtt{i}\tau_0\omega_0}(W_{20}^{(2)}(-1) + W_{20}^{(0)}(-1)\bar{q}_3) + kcB(\bar{q}_3 W_{20}^{(2)}(0)e^{\mathtt{i}\tau_0\omega_0} \\
&\quad +2q_3 W_{11}^{(2)}(-1)e^{-\mathtt{i}\tau_0\omega_0}) + kbA(W_{20}^{(0)}(-1)e^{\mathtt{i}\tau_0\omega_0} + 2W_{11}^{(0)}(-1)e^{-\mathtt{i}\tau_0\omega_0}))) \\
&\quad +\frac{1}{(1 + bx_* + cy_{2*})^2}((b + cq_3)(-C(q_3 + \bar{q}_3) + 2bA + 2cBq_3\bar{q}_3)(k\bar{q}_2^* e^{-\mathtt{i}\tau_0\omega_0} \\
&\quad\; -1) + k\bar{q}_2^* e^{-\mathtt{i}\tau_0\omega_0}(b + cq_3)(bA + cBq_3^2 - kCq_3))].
\end{aligned}$$

Now we compute $W_{20}(\theta)$ and $W_{11}(\theta)$. From (3.5) and (3.7), we have

$$\begin{aligned}\dot{W} &= \dot{U}_t - \dot{z}q - \dot{\bar{z}}\bar{q} \\ &= \begin{cases} AW - 2Re\{\bar{q}^*(0)F_0 q(\theta)\}, & \theta \in [-1,0) \\ AW - 2Re\{\bar{q}^*(0)F_0 q(\theta)\} + F_0, & \theta = 0 \end{cases} \\ &\overset{\text{def}}{=} AW + H(z,\bar{z},\theta),\end{aligned}$$

where

$$H(z,\bar{z},\theta) = h_{20}(\theta)\frac{z^2}{2} + h_{11}(\theta)z\bar{z} + h_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots . \tag{3.12}$$

For $\theta \in [-1,0)$, we can get

$$(A - 2\mathtt{i}\tau_0\omega_0)W_{20}(\theta) = -h_{20}(\theta)\ , \quad AW_{11}(\theta) = -h_{11}(\theta). \tag{3.13}$$

From (3.12), we know that for $\theta \in [-1,0)$,

$$\begin{aligned} & H(z,\bar{z},\theta) \\ = & -2Re\{\bar{q}^*(0)F_0 q(\theta)\} \\ = & -g(z,\bar{z})q(\theta) - \bar{g}(z,\bar{z})\bar{q}(\theta) \\ = & -(g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + \cdots)q(\theta) - (\bar{g}_{20}\frac{\bar{z}^2}{2} + \bar{g}_{11}z\bar{z} + \bar{g}_{02}\frac{z^2}{2} + \cdots)\bar{q}(\theta).\end{aligned}$$

Comparing the coefficients with (3.12), we can obtain

$$h_{20}(\theta) = -g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta), \quad h_{11}(\theta) = -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta).$$

On the other hand, by (3.13), we get $\dot{W}_{20}(\theta) = 2\mathtt{i}\tau_0\omega_0 W_{20}(\theta) - h_{20}(\theta)$. Solving it, we have

$$W_{20}(\theta) = \frac{\mathtt{i}g_{20}}{\tau_0\omega_0}q(0)e^{\mathtt{i}\tau_0\omega_0\theta} + \frac{\mathtt{i}\bar{g}_{02}}{3\tau_0\omega_0}\bar{q}(0)e^{-\mathtt{i}\tau_0\omega_0\theta} + Ee^{2\mathtt{i}\tau_0\omega_0\theta}. \tag{3.14}$$

Similarly, we can get

$$W_{11}(\theta) = -\frac{\mathtt{i}g_{11}}{\tau_0\omega_0}q(0)e^{\mathtt{i}\tau_0\omega_0\theta} + \frac{\mathtt{i}\bar{g}_{11}}{\tau_0\omega_0}\bar{q}(0)e^{-\mathtt{i}\tau_0\omega_0\theta} + F. \tag{3.15}$$

In what follows, we seek appropriate E and F. The definition of A and (3.13) imply that

$$\int_{-1}^{0} \mathtt{d}\eta(\theta)W_{20}(\theta) = 2\mathtt{i}\tau_0\omega_0 W_{20}(0) - h_{20}(0) \tag{3.16}$$

and

$$\int_{-1}^{0} \mathtt{d}\eta(\theta)W_{11}(\theta) = -h_{11}(0). \tag{3.17}$$

By the definition of $H(z,\bar{z},\theta)$ in (3.12), we have

$$h_{20}(0) = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + \tau_0 H_1, \tag{3.18}$$

$$h_{11}(0) = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + \tau_0 H_2, \tag{3.19}$$

where

$$H_1 = \left(-2a + \frac{2(bA + cBq_3^2 - Cq_3)}{1 + bx_* + cy_{2*}}, -\frac{2k(bA + cBq_3^2 - Cq_3)e^{-2\mathtt{i}\tau_0\omega_0})}{1 + bx_* + cy_{2*}}, 0\right)^{\mathtt{T}},$$
$$H_2 = \left(-2a - \frac{C(q_3 + \bar{q}_3) - 2bA - 2cBq_3\bar{q}_3}{1 + bx_* + cy_{2*}}, \frac{kC(q_3 + \bar{q}_3) - 2bkA - 2ckBq_3\bar{q}_3}{1 + bx_* + cy_{2*}}, 0\right)^{\mathtt{T}}.$$

Substituting (3.14) into (3.18), we obtain

$$\begin{pmatrix} 2\mathtt{i}\omega_0 + 2ax_* + A - r & 0 & B \\ -kAe^{-2\mathtt{i}\tau_0\omega_0} & 2\mathtt{i}\omega_0 + r_1 + d & -kBe^{-2\mathtt{i}\tau_0\omega_0} \\ 0 & -d & 2\mathtt{i}\omega_0 + r_2 \end{pmatrix} E = H_1$$

Hence, we have $E = \dfrac{1}{\triangle_1}\left(\triangle_1^1, \triangle_1^2, \triangle_1^3\right)^{\mathtt{T}}$, where

$$\begin{aligned}
\triangle_1 &= (2\mathtt{i}\omega_0 + r_2)(2\mathtt{i}\omega_0 + r_1 + d)(2\mathtt{i}\omega_0 + 2ax_* + A - r) \\
&\quad + kdB(r - 2ax_* - 2\mathtt{i}\omega_0)e^{-2\mathtt{i}\tau_0\omega_0}, \\
\triangle_1^1 &= (2\mathtt{i}\omega_0 + r_2)(2\mathtt{i}\omega_0 + r_1 + d)(-2a + \frac{2(bA + cBq_3^2 - Cq_3)}{1 + bx_* + cy_{2*}}) \\
&\quad + \frac{2kdB(bA + cBq_3^2 - Cq_3)}{1 + bx_* + cy_{2*}}(1 - e^{-2\mathtt{i}\tau_0\omega_0}) + 2akdBe^{-2\mathtt{i}\tau_0\omega_0}, \\
\triangle_1^2 &= (2\mathtt{i}\omega_0 + r_2)(2\mathtt{i}\omega_0 + 2ax_* + A - r)(-\frac{2k(bA + cBq_3^2 - Cq_3)}{1 + bx_* + cy_{2*}}e^{-2\mathtt{i}\tau_0\omega_0}) \\
&\quad + kA(2\mathtt{i}\omega_0 + r_2)(-2a + \frac{2(bA + cBq_3^2 - Cq_3)}{1 + bx_* + cy_{2*}})e^{-2\mathtt{i}\tau_0\omega_0}, \\
\triangle_1^3 &= kdA(-2a + \frac{2(bA + cBq_3^2 - Cq_3)}{1 + bx_* + cy_{2*}})e^{-2\mathtt{i}\tau_0\omega_0} - (2\mathtt{i}\omega_0 + 2ax_* + A - r) \\
&\quad \frac{2kd(bA + cBq_3^2 - Cq_3)}{1 + bx_* + cy_{2*}}e^{-2\mathtt{i}\tau_0\omega_0}.
\end{aligned}$$

Similarly, substituting (3.15) into (3.19), we can get $F = \frac{1}{\triangle_2}\left(\triangle_2^1, \triangle_2^2, \triangle_2^3\right)^{\mathtt{T}}$, where

$$\begin{aligned}
\triangle_2 &= r_2(r_1+d)(r-2ax_*-A) - kdB(r-2ax_*),\\
\triangle_2^1 &= 2akdB - r_2(r_1+d)(2a + \frac{C(q_3+\bar{q}_3) - 2bA - 2cBq_3\bar{q}_3}{1+bx_*+cy_{2*}}),\\
\triangle_2^2 &= kr_2(2ax_*-r)\frac{C(q_3+\bar{q}_3) - 2bA - 2cBq_3\bar{q}_3}{1+bx_*+cy_{2*}} - 2kaAr_2,\\
\triangle_2^3 &= -2adkA - kd(r-2ax_*)\frac{C(q_3+\bar{q}_3) - 2bA - 2cBq_3\bar{q}_3}{1+bx_*+cy_{2*}}.
\end{aligned}$$

Based on the analysis above, we see that g_{ij} in (3.11) is determined by the parameters and the time delay in (2.1). Thus, we can compute the following quantities,

$$\begin{aligned}
C_1(0) &= \frac{\mathtt{i}}{2\tau_0\omega_0}(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2) + \frac{g_{21}}{2},\\
\mu_2 &= -\frac{ReC_1(0)}{Re\lambda'(\tau_0)},\\
t_2 &= -\frac{ImC_1(0) + \mu_2 Im\lambda'(\tau_0)}{\tau_0\omega_0},\\
\beta_2 &= 2ReC_1(0).
\end{aligned} \tag{3.20}$$

From the expression of $C_1(0)$ in (3.20), it is easy to get the values of μ_2, β_2 and t_2. On the other hand, we know that μ_2 determines the direction of the `Hopf` bifurcation: if $\mu_2 > 0(< 0)$, then the Hopf bifurcation is supercritical(subcritical) and the bifurcating periodic solutions exist for $\tau > \tau_0(< \tau_0)$; β_2 determines the stability of the bifurcating periodic solutions: if $\beta_2 < 0(> 0)$ the bifurcating periodic solutions are stable(unstable); and t_2 determines the period of the bifurcating periodic solutions: the period increase(decrease) if $t_2 > 0(< 0)$.

4. Computer simulations

To illustrate the theoretical results, let us give some numerical simulations in this section. For system (2.1), we choose $a = 1/2$, $a_1 = 2$, $b = 1/2$, $c = 1/4$, $d = 1/8$, $k = 1$, $r = 2$, $r_1 = 1/2$ and $r_2 = 1/4$. From the formulae in Section 3 and by direct computation, we obtain

$$\tau_0 \approx 0.7323,$$
$$C_1(0) \approx -1.0214 + 0.1165\mathtt{i}.$$

By $Re\lambda'(\tau_0) > 0$ and the above results, we know $\mu_2 > 0$. This indicates that it is a supercritical Hopf bifurcation. Numerical simulations are presented in Figs. 1 and 2.

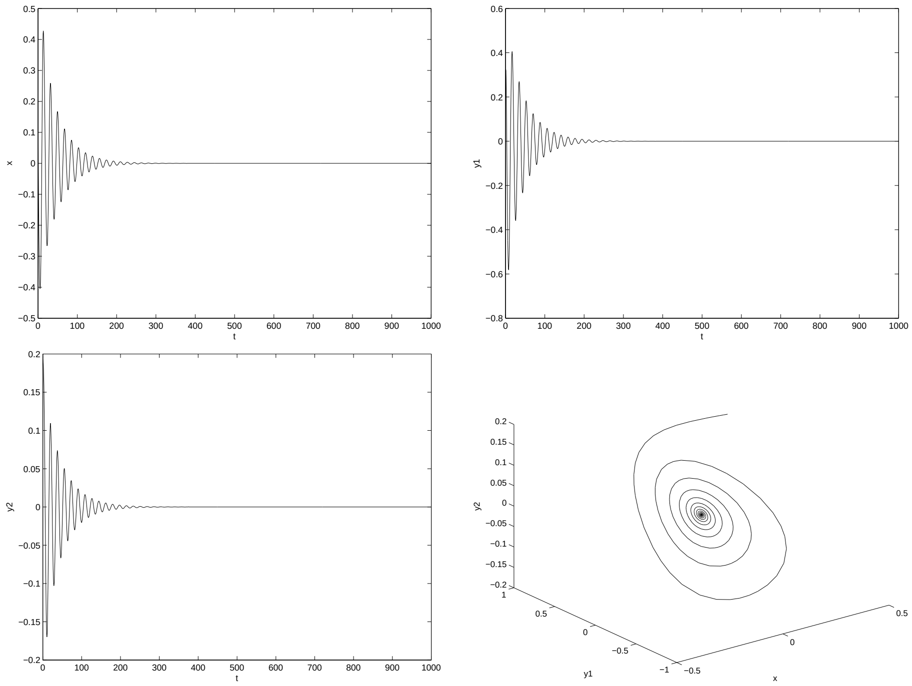

Figure 1: Behavior and phase portrait of system (2.1) with $\tau = 0.1$, the origin is stable.

From Fig. 1, it is clear that the origin is asymptotically stable with $\tau = 0.1 < \tau_0$. When τ varies and passes through τ_0, the origin losses its stability and a periodic solution bifurcates from the origin for $\tau = 0.8 > \tau_0$ (see Fig. 2).

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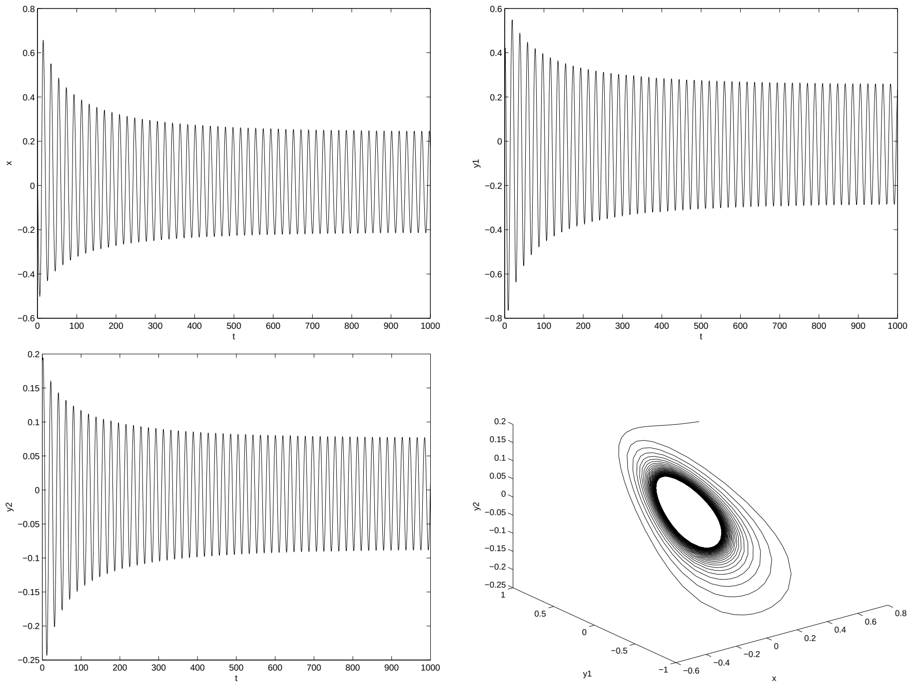

Figure 2: Behavior and phase portrait of system (2.1) with $\tau = 0.8$, the origin losses its stability and Hopf bifurcation occurs.

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