

**STABILITY AND BIFURCATION IN A DELAYED
PREDATOR-PREY SYSTEM WITH STAGE STRUCTURE AND
FUNCTIONAL RESPONSE**

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ABSTRACT. In this paper, a delayed predator-prey system with stage structure and Holling type-II functional response is investigated. The local stability of a positive equilibrium and the existence of Hopf bifurcations are established. By using the normal form theory and center manifold reduction, explicit formulae determining the stability, direction of the bifurcating periodic solutions are derived. Finally, numerical simulations are carried out to illustrate the theoretical results.

1. INTRODUCTION

In the natural world, almost all animals have the stage structure of immature and mature. And the vital rates (rates of survival, development and reproduction and so on) are often quite different in these two stage. Hence, it is of ecological importance to investigate the effects of such a subdivision on the interaction of species. Chen [1] introduced the following stage-structured single-species population model without time delay

$$\begin{aligned}\dot{N}_i(t) &= B(t) - D_i(t) - W(t), \\ \dot{N}_m(t) &= \alpha W(t) - D_m(t),\end{aligned}\tag{1.1}$$

where $N_i(t)$ and $N_m(t)$ denote the immature and mature population densities at time t ; $B(t)$ is the birth rate of the immature population at time t ; $D_i(t)$ and $D_m(t)$ are the death rates of the immature and mature at time t ; $W(t)$ represents the transformation rate of the immature into the mature; α is the probability of the successful transformation of the immature into the mature. If the birth rate of model (1.1) obeys the Malthus rule, i.e., $B(t) = aN_m$; and the death rates of the immature and mature populations are logistic; i.e.,

$$D_i(t) = r_i N_i(t) + b_i N_i^2(t), \quad D_m(t) = r_m N_m(t) + b_m N_m^2(t),$$

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and the transformation rate of the immature into mature is proportional the immature population, i.e., $W(t) = bN_i(t)$. Then we rewrite model (1.1) as

$$\begin{aligned}\dot{N}_i(t) &= aN_m - r_i N_i(t) - b_i N_i^2(t) - bN_i(t), \\ \dot{N}_m(t) &= bN_i(t) - r_m N_m(t) - b_m N_m^2(t).\end{aligned}\tag{1.2}$$

Based on the idea above, many authors studied different kinds of stage-structured models and a significant body of work has been carried out (see, for example, [2, 3, 4, 5, 8, 10, 9, 12]).

Xu and Ma [11] considered the following model, where prey population have stage structure and immature individuals are consumed by their predator

$$\begin{aligned}\dot{x}_1(t) &= ax_2 - r_1 x_1(t) - a_{11} x_1^2(t) - bx_1(t) - a_1 x_1(t)y(t), \\ \dot{x}_2(t) &= bx_1(t) - r_2 x_2(t), \\ \dot{y}(t) &= a_2 x_1(t - \tau)y(t - \tau) - ry(t) - \beta y^2(t),\end{aligned}\tag{1.3}$$

where $a > 0$ is the birth rate of immature population; $r_1 > 0$ is the death rate of the immature population; $a_{11} > 0$ is the intra-specific competition rate of the immature population; $b > 0$ is the transformation rate from the immature individuals to mature individuals; $a_1 > 0$ is the capturing rate of the predator population; $r_2 > 0$ is the death rate of the mature population; a_2/a_1 is the conversion rate of nutrients into the reproduction of the predator; $r > 0$ is the death rate of the predator; $\beta > 0$ is the intra-specific competition rate of the predator, $\tau \geq 0$ is a constant delay due to the gestation of the predator. In [11], the global stability of the positive equilibrium and the two boundary equilibria of the model (1.3) is discussed.

In system (1.3), the capture ability of the predator population is proportional the number of prey population. That is to say if the number of prey population is large, then predator will capture more prey in unit time. Obviously, this is reasonless. The predator always have a handling time. In 1965, Holling proposed three types of functional response, proved that the functional response plays an important role in predator-prey systems. Based on the work developed in [11], in the present paper, we are concerned with the effect of functional response on the dynamics of a predator-prey model. To this end, we consider the following delay differential equations

$$\begin{aligned}\dot{x}_1(t) &= ax_2 - r_1 x_1(t) - a_{11} x_1^2(t) - bx_1(t) - \frac{a_1 x_1(t)y(t)}{1 + mx_1(t)}, \\ \dot{x}_2(t) &= bx_1(t) - r_2 x_2(t), \\ \dot{y}(t) &= \frac{a_2 x_1(t - \tau)y(t - \tau)}{1 + mx_1(t - \tau)} - ry(t),\end{aligned}\tag{1.4}$$

where the positive $a, r_1, a_{11}, b, r_2, r, a_1, a_2$ are meanings to same as system (1.3); the parameter m stands for half capturing saturation; $\frac{x_1(t)}{1 + mx_1(t)}$ is Holling type-II functional response, which reflects the capture ability of predator. In the system (1.4) we ignore the intra-specific competition rate of the predator population.

The initial conditions for system (1.4) take the form

$$\begin{aligned}x_1(\theta) &= \phi_1(\theta), \quad x_2(\theta) = \phi_2(\theta), \quad y(\theta) = \psi(\theta), \\ \phi_1(\theta) &\geq 0, \quad \phi_2(\theta) \geq 0, \quad \psi(\theta) \geq 0, \quad \theta \in [-\tau, 0], \\ \phi_1(0) &> 0, \quad \phi_2(0) > 0, \quad \psi(0) > 0,\end{aligned}\tag{1.5}$$

where $(\phi_1(\theta), \phi_2(\theta), \psi(\theta)) \in C([-\tau, 0], \mathbb{R}_{+0}^3)$, the Banach space of continuous functions mapping the interval $[-\tau, 0]$ into \mathbb{R}_{+0}^3 , where $\mathbb{R}_{+0}^3 = \{(x_1, x_2, x_3) : x_i \geq 0, i = 1, 2, 3\}$.

This paper is organized as follows. In Section 2, we discuss the local stability of a positive equilibrium and the existence of Hopf bifurcations of system (1.4). In Section 3, we study the stability of the bifurcating periodic solutions and the direction of the Hopf bifurcation in system (1.4) by using the normal form theory and center manifold reduction. Finally, some numerical examples are given to illustrate the results above.

2. STABILITY AND HOPF BIFURCATIONS

In this section, we discuss the local stability of a positive equilibrium and the existence of Hopf bifurcations of system (1.4).

It is easy to show that if the following holds:

$$(H1) \quad a_2 - rm > 0, \quad \frac{ab}{r_2} - \frac{a_{11}r}{a_2 - rm} - r_1 - b > 0,$$

system (1.4) has a unique positive equilibrium $E^* = (x_1^*, x_2^*, y^*)$, where

$$x_1^* = \frac{r}{a_2 - rm}, \quad x_2^* = \frac{br}{r_2(a_2 - rm)}, \quad y^* = \frac{a_2}{a_1(a_2 - rm)} \left(\frac{ab}{r_2} - \frac{a_{11}r}{a_2 - rm} - r_1 - b \right).$$

Linearizing system (1.4) at E^* , we derive

$$\begin{aligned} \dot{x}_1(t) &= p_1x_1(t) + p_2x_2(t) + p_3y(t), \\ \dot{x}_2(t) &= p_4x_1(t) + p_5x_2(t), \\ \dot{y}(t) &= p_6x_1(t - \tau) + p_7y(t - \tau) + p_8y(t). \end{aligned} \tag{2.1}$$

where

$$\begin{aligned} p_1 &= -r_1 - b - 2a_{11}x_1^* - \frac{a_1y^*}{(1 + mx_1^*)^2}, & p_2 &= a, & p_3 &= -\frac{a_1r}{a_2}, \\ p_4 &= b, & p_5 &= -r_2, & p_6 &= \frac{a_2y^*}{(1 + mx_1^*)^2}, & p_7 &= r, & p_8 &= -r. \end{aligned}$$

The characteristic equation of system (2.1) takes the form

$$\lambda^3 + A\lambda^2 + B\lambda + C + (D\lambda^2 + E\lambda + F)e^{-\lambda\tau} = 0, \tag{2.2}$$

where

$$\begin{aligned} A &= -(p_1 + p_5 + p_8), & B &= p_1p_5 + p_1p_8 + p_5p_8 - p_2p_4, & C &= p_8(p_2p_4 - p_1p_5), \\ D &= -p_7, & E &= p_1p_7 + p_5p_7 - p_3p_6, & F &= p_2p_4p_7 + p_3p_5p_6 - p_1p_5p_7. \end{aligned}$$

If $i\omega (\omega > 0)$ is a root of (2.2), then

$$-i\omega^3 - A\omega^2 + Bi\omega + C + (-D\omega^2 + Ei\omega + F)e^{-i\omega\tau} = 0. \tag{2.3}$$

Separating the real and imaginary parts, we obtain

$$\begin{aligned} C - \omega^2 &= D\omega^2 \cos \omega\tau - E\omega \sin \omega\tau - F \cos \omega\tau, \\ -\omega^3 + B\omega &= -D\omega^2 \sin \omega\tau - E\omega \cos \omega\tau + F \sin \omega\tau. \end{aligned} \tag{2.4}$$

It follows from (2.4) that

$$\omega^6 + Q_1\omega^4 + Q_2\omega^2 + Q_3 = 0, \tag{2.5}$$

where

$$Q_1 = A^2 - 2B - D^2, \quad Q_2 = B^2 + 2DF - 2AC - E^2, \quad Q_3 = C^2 - F^2.$$

It is easy to show that

$$\begin{aligned} Q_1 &= A^2 - D^2 - 2B = p_1^2 + p_5^2 + 2p_2p_4 > 0, \\ Q_2 &= (p_1p_5 - p_2p_4)^2 + p_3p_6(2p_1p_7 - p_3p_6). \end{aligned}$$

Noting that if $Q_3 > 0$, we have $2(p_1p_5 - p_2p_4)p_7 > p_3p_5p_6$, it is easy to see $Q_2 > 0$. Hence, the stability of positive equilibrium E^* of system (1.4) is unchanged for all $\tau > 0$. When $\tau = 0$, by Routh-Hurwitz Criterion we obtain that all roots of (2.2) have negative real parts only if

$$(H2) \quad p_1p_3p_6 > (p_1 + p_5)(p_1p_5 - p_2p_4).$$

Therefore if (H2) holds, the positive equilibrium E^* of system (1.4) is local asymptotically stable for all $\tau > 0$; or else the positive equilibrium E^* of system (1.4) is unstable for all $\tau > 0$.

If $Q_3 < 0$, we know that (2.5) has only one unique positive root ω_0 . Define

$$\tau_j = \frac{1}{\omega_0} \left(\arccos \frac{(E - DA)\omega_0^4 + (CD + AF - BE)\omega_0^2 - FC}{D^2\omega_0^4 + (E^2 - 2FD)\omega_0^2 + F^2} + 2j\pi \right), \quad (2.6)$$

for $j = 0, 1, \dots$. Then (τ_j, ω_0) solves (2.3). This means that when $\tau = \tau_j$, Equation (2.2) has a pair of purely imaginary roots $\pm i\omega_0$.

Denote $\lambda = \lambda(\tau)$, from (2.2) we have

$$\left(\frac{d\lambda(\tau)}{d\tau} \right)^{-1} = -\frac{3\lambda^2 + 2A\lambda + B}{\lambda(\lambda^3 + A\lambda^2 + B\lambda + C)} + \frac{2D\lambda + E}{\lambda(D\lambda^2 + E\lambda + F)} - \frac{\tau}{\lambda},$$

which leads to

$$\begin{aligned} & \text{sign} \left\{ \text{Re} \left(\frac{d\lambda}{d\tau} \right)_{\tau=\tau_j} \right\} \\ &= \text{sign} \left\{ \text{Re} \left(\frac{d\lambda}{d\tau} \right)_{\tau=\tau_j}^{-1} \right\} \\ &= \text{sign} \left\{ 3\omega_0^4 + (2A^2 - 4B - 2D^2)\omega_0^2 + B^2 + 2DF - 2AC - E^2 \right\} \\ &= \text{sign} \left\{ 3\omega_0^4 + 2Q_1\omega_0^2 + Q_2 \right\}. \end{aligned} \quad (2.7)$$

Because $Q_1 > 0$, so if the following holds

$$(H3) \quad Q_2 > 0,$$

then $3\omega_0^4 + 2Q_1\omega_0^2 + Q_2 > 0$, $\text{sign} \left\{ \text{Re} \left(\frac{d\lambda}{d\tau} \right)_{\tau=\tau_j} \right\} > 0$. And system (2.1) undergoes a Hopf bifurcation.

Applying [6, Theorem 11.1], we obtain the following results.

Theorem 2.1. *Let (H1) hold, and*

- (i) *If $Q_3 > 0$ and (H2) holds, then the positive equilibrium E^* of system (1.4) is local asymptotically stable for all $\tau > 0$; or else the positive equilibrium E^* of system (1.4) is unstable for all $\tau > 0$.*
- (ii) *If $Q_3 < 0$ and (H2), (H3) hold, the positive equilibrium E^* of system (1.4) is asymptotically stable for $\tau \in [0, \tau_0)$, and E^* is unstable for $\tau > \tau_0$; and the system (1.4) undergoes a Hopf Bifurcation at the positive equilibrium E^* when $\tau = \tau_j (j = 0, 1, \dots)$.*

Xu and Ma [11] obtained the following results:

(i) If

$$2a_2a_{11}\beta[ab - r_2(r_1 + b)] + a_1r_2r \\ + (a_{11}\beta - a_1a_2)a_2[ab - r_2(r_1 + b)] - a_{11}r_2r > 0,$$

the positive equilibrium E^* of system (1.3) is local asymptotically stable for all $\tau > 0$.

(ii) If

$$2a_2a_{11}\beta[ab - r_2(r_1 + b)] + a_1r_2r \\ + (a_{11}\beta - a_1a_2)a_2[ab - r_2(r_1 + b)] - a_{11}r_2r < 0,$$

the positive equilibrium E^* of system (1.3) is asymptotically stable for $\tau \in [0, \tau_0)$, and E^* is unstable for $\tau > \tau_0$.

In system (1.3), we let $\beta = 0$, then we know that if $3a_{11}rr_2 > a_2(ab - r_2(r_1 + b))$, the system (1.3) is local asymptotically stable for all $\tau > 0$; if $3a_{11}rr_2 < a_2(ab - r_2(r_1 + b))$, the system (1.3) is asymptotically stable for $\tau \in [0, \tau_0)$, and unstable for $\tau > \tau_0$.

If we let $m = 0$ in system (1.4), then $Q_3 > 0$ means that $3a_{11}rr_2 > a_2(ab - r_2(r_1 + b))$, same to the results of system (1.3). So we know that system (1.3)(when $\beta = 0$) is the special situation of system (1.4).

3. DIRECTION OF HOPF BIFURCATION

In this section, we derive explicit formulae to determine the properties of the Hopf bifurcation at critical values τ_j by using the normal form theory and center manifold reduction (see, for example, Hassard et al. [7]).

Without loss of generality, denote the critical values τ_j by $\tilde{\tau}$, and set $\tau = \tilde{\tau} + \mu$. Then $\mu = 0$ is a Hopf bifurcation value of system (1.4). Thus, we can work in the phase space $C = C([-\tilde{\tau}, 0], \mathbb{R}^3)$. Let

$$u_1(t) = x_1(t) - x_1^*, \quad u_2(t) = x_2(t) - x_2^*, \quad u_3(t) = y(t) - y^*.$$

Then system (1.4) is transformed into

$$\begin{aligned} \dot{u}_1(t) &= p_1u_1(t) + p_2u_2(t) + p_3u_3(t) + \sum_{i+j+l \geq 2} \frac{1}{i!j!l!} f_{ijl}^{(1)} u_1^i(t) u_2^j(t) u_3^l(t), \\ \dot{u}_2(t) &= p_4u_1(t) + p_5u_2(t), \\ \dot{u}_3(t) &= p_6u_1(t - \tau) + p_7u_3(t - \tau) + p_8u_3(t) \\ &+ \sum_{i+j+l \geq 2} \frac{1}{i!j!l!} f_{ijl}^{(3)} u_1^i(t - \tau) u_3^j(t - \tau) u_3^l(t), \end{aligned} \quad (3.1)$$

where

$$f_{ijl}^{(1)} = \frac{\partial^{i+j+l} f^{(1)}}{\partial x_1^i \partial x_2^j \partial y^l} \Big|_{(x_1^*, x_2^*, y^*)}, \quad f_{ijl}^{(3)} = \frac{\partial^{i+j+l} f^{(3)}}{\partial x_1^i(t - \tau) \partial y^j(t - \tau) \partial y^l} \Big|_{(x_1^*, y^*, y^*)},$$

for $i, j, l \geq 0$, and

$$\begin{aligned} f^{(1)} &= ax_2 - r_1x_1(t) - a_{11}x_1^2(t) - bx_1(t) - \frac{a_1x_1(t)y(t)}{1 + mx_1(t)}, \\ f^{(3)} &= \frac{a_2x_1(t - \tau)y(t - \tau)}{1 + mx_1(t - \tau)} - ry(t). \end{aligned}$$

We rewrite (3.1) as

$$\dot{u}(t) = L_\mu(u_t) + f(u_t, \mu), \quad (3.2)$$

where $u(t) = (u_1(t), u_2(t), u_3(t))^T \in \mathbb{R}^3$, $u_t(\theta) \in C$ is defined by $u_t(\theta) = u(t + \theta)$, and $L_\mu : C \rightarrow \mathbb{R}^3$, $f : R \times C \in \mathbb{R}^3$ are given by

$$L_\mu \phi = \begin{pmatrix} p_1 & p_2 & p_3 \\ p_4 & p_5 & 0 \\ 0 & 0 & p_8 \end{pmatrix} \phi(0) + \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ p_6 & 0 & p_7 \end{pmatrix} \phi(-\tau), \quad (3.3)$$

and

$$f(\phi, \mu) = \begin{pmatrix} \sum_{i+j+l \geq 2} \frac{1}{i!j!l!} f_{ijl}^{(1)} \phi_1^i(0) \phi_2^j(0) \phi_3^l(0) \\ 0 \\ \sum_{i+j+l \geq 2} \frac{1}{i!j!l!} f_{ijl}^{(3)} \phi_1^i(-\tau) \phi_3^j(-\tau) \phi_3^l(0) \end{pmatrix} \quad (3.4)$$

respectively. By Riesz representation theorem, there exists a function $\eta(\theta, \mu)$ of bounded variation for $\theta \in [-\tau, 0]$ such that

$$L_\mu \phi = \int_{-\bar{\tau}}^0 d\eta(\theta, 0) \phi(\theta) \quad \text{for } \phi \in C. \quad (3.5)$$

In fact, we can choose

$$\eta(\theta, \mu) = \begin{pmatrix} p_1 & p_2 & p_3 \\ p_4 & p_5 & 0 \\ 0 & 0 & p_8 \end{pmatrix} \delta(\theta) - \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ p_6 & 0 & p_7 \end{pmatrix} \delta(\theta + \tau), \quad (3.6)$$

where δ is the Dirac delta function. For $\phi \in C^1([-\tau, 0], \mathbb{R}^3)$, define

$$A(\mu)\phi = \begin{cases} \frac{d\phi(\theta)}{d\theta}, & \theta \in [-\tau, 0), \\ \int_{-\bar{\tau}}^0 d\eta(\mu, s) \phi(s), & \theta = 0. \end{cases}$$

and

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

Then system (3.2) is equivalent to

$$\dot{u}_t = A(\mu)u_t + R(\mu)u_t. \quad (3.7)$$

For $\psi \in C^1([0, \tau], (\mathbb{R}^2)^*)$, define

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

and a bilinear inner product

$$\langle \psi(s), \phi(\theta) \rangle = \bar{\psi}(0) \phi(0) - \int_{-\bar{\tau}}^0 \int_{\xi=0}^\theta \bar{\psi}(\xi - \theta) d\eta(\theta) \phi(\xi) d\xi, \quad (3.8)$$

where $\eta(\theta) = \eta(\theta, 0)$. Then $A(0)$ and A^* are adjoint operators. By discussions in Section 2 and foregoing assumption, we know that $\pm i\omega_0$ are eigenvalues of $A(0)$. Thus, they are also eigenvalues of A^* . We first need to compute the eigenvector of $A(0)$ and A^* corresponding to $i\omega_0$ and $-i\omega_0$, respectively.

Suppose that $q(\theta) = (1, \alpha, \beta)^T e^{i\omega_0\theta}$ is the eigenvector of $A(0)$ corresponding to $i\omega_0$. Then $A(0)q(\theta) = i\omega_0q(\theta)$. It follows from the definition of $A(0)$, (3.5) and (3.6) that

$$\begin{pmatrix} p_1 - i\omega_0 & p_2 & p_3 \\ p_4 & p_5 - i\omega_0 & 0 \\ p_6 e^{-i\omega_0\tau} & 0 & p_8 + p_7 e^{-i\omega_0\tau} - i\omega_0 \end{pmatrix} q(0) = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}.$$

We therefore derive that

$$q(0) = (1, \alpha, \beta)^T = \left(1, -\frac{p_4}{p_5 - i\omega_0}, -\frac{p_6 e^{-i\omega_0\tau}}{p_8 + p_7 e^{-i\omega_0\tau} - i\omega_0}\right)^T.$$

On the other hand, suppose that $q^*(s) = D(1, \alpha^*, \beta^*) e^{i\omega_0 s}$ is the eigenvector of A^* corresponding to $-i\omega_0$. From the definition of A^* , (3.5) and (3.6) we have

$$\begin{pmatrix} p_1 + i\omega_0 & p_2 & p_3 \\ p_4 & p_5 + i\omega_0 & 0 \\ p_6 e^{i\omega_0\tau} & 0 & p_8 + p_7 e^{i\omega_0\tau} + i\omega_0 \end{pmatrix}^T (q^*(0))^T = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix},$$

then

$$q^*(0) = D(1, \alpha^*, \beta^*) = D\left(1, -\frac{p_2}{p_5 + i\omega_0}, -\frac{p_3}{p_8 + p_7 e^{i\omega_0\tau} + i\omega_0}\right).$$

To assure that $\langle q^*(s), q(\theta) \rangle = 1$, we need to determine the value of D . From (3.8), we can choose

$$D = \frac{1}{1 + \bar{\alpha}\alpha^* + \bar{\beta}\beta^* + (p_6\beta^* + p_7\bar{\beta}\beta^*)\tau e^{i\omega_0\tau}}.$$

In the remainder of this section, we use the same notations as in Hassard et al. [7]. We first compute the coordinates to describe the center manifold \mathbf{C}_0 at $\mu = 0$. Let u_t be the solution of (3.2) with $\mu = 0$. Define

$$z(t) = \langle q^*, u_t \rangle, \quad W(t, \theta) = u_t(\theta) - 2 \operatorname{Re}\{z(t)q(\theta)\}. \tag{3.9}$$

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

$$W(t, \theta) = W(z(t), \bar{z}(t), \theta) = W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + \dots,$$

z and \bar{z} are local coordinates for center manifold \mathbf{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 $u_t \in \mathbf{C}_0$ of (3.2), since $\mu = 0$, we have

$$\begin{aligned} \dot{z} &= \langle q^*, \dot{u}_t \rangle = \langle q^*, A(\mu)u_t \rangle + \langle q^*, R(\mu)u_t \rangle \\ &= i\omega_0 z + \langle \bar{q}^*(\theta), f(0, W(z, \bar{z}, \theta) + 2 \operatorname{Re}\{zq(\theta)\}) \rangle \\ &= i\omega_0 z + \bar{q}^*(\theta) f(0, W(z, \bar{z}, \theta) + 2 \operatorname{Re}\{zq(\theta)\}) \\ &= i\omega_0 z + \bar{q}^*(0) f(0, W(z, \bar{z}, 0) + 2 \operatorname{Re}\{zq(0)\}) \\ &:= i\omega_0 z + \bar{q}^*(0) f_0(z, \bar{z}). \end{aligned} \tag{3.10}$$

We rewrite (3.10) as $\dot{z} = i\omega_0 z + g(z, \bar{z})$, with

$$g(z, \bar{z}) = \bar{q}^*(0) f_0(z, \bar{z}) = g_{20} \frac{z^2}{2} + g_{11} z\bar{z} + g_{02} \frac{\bar{z}^2}{2} + g_{21} \frac{z^2 \bar{z}}{2} + \dots \tag{3.11}$$

Noting that $u_t(\theta) = (u_{1t}(\theta), u_{2t}(\theta), u_{3t}(\theta)) = W(t, \theta) + zq(\theta) + \bar{z}\bar{q}(\theta)$ and $q(\theta) = (1, \alpha, \beta)^T e^{i\omega_0\theta}$, we have

$$\begin{aligned} u_{1t}(0) &= z + \bar{z} + W_{20}^{(1)}(0) \frac{z^2}{2} + W_{11}^{(1)}(0) z\bar{z} + W_{02}^{(1)}(0) \frac{\bar{z}^2}{2} + \dots, \\ u_{2t}(0) &= \alpha z + \bar{\alpha}\bar{z} + W_{20}^{(2)}(0) \frac{z^2}{2} + W_{11}^{(2)}(0) z\bar{z} + W_{02}^{(2)}(0) \frac{\bar{z}^2}{2} + \dots, \\ u_{3t}(0) &= \beta z + \bar{\beta}\bar{z} + W_{20}^{(3)}(0) \frac{z^2}{2} + W_{11}^{(3)}(0) z\bar{z} + W_{02}^{(3)}(0) \frac{\bar{z}^2}{2} + \dots, \\ u_{1t}(-\tilde{\tau}) &= e^{-i\omega_0\tilde{\tau}} z + e^{i\omega_0\tilde{\tau}} \bar{z} + W_{20}^{(1)}(-\tilde{\tau}) \frac{z^2}{2} + W_{11}^{(1)}(-\tilde{\tau}) z\bar{z} + W_{02}^{(1)}(-\tilde{\tau}) \frac{\bar{z}^2}{2} + \dots, \\ u_{3t}(-\tilde{\tau}) &= \beta e^{-i\omega_0\tilde{\tau}} z + \bar{\beta} e^{i\omega_0\tilde{\tau}} \bar{z} + W_{20}^{(3)}(-\tilde{\tau}) \frac{z^2}{2} + W_{11}^{(3)}(-\tilde{\tau}) z\bar{z} + W_{02}^{(3)}(-\tilde{\tau}) \frac{\bar{z}^2}{2} + \dots \end{aligned}$$

Thus, it follows from (3.4) and (3.11) that

$$\begin{aligned} g(z, \bar{z}) &= \bar{q}^*(0) f_0(z, \bar{z}) \\ &= \bar{D}(1, \bar{\alpha}^*, \bar{\beta}^*) \begin{pmatrix} \sum_{i+j+l \geq 2} \frac{1}{i!j!l!} f_{ijl}^{(1)} u_{1t}^i(0) u_{2t}^j(0) u_{3t}^l(0) \\ 0 \\ \sum_{i+j+l \geq 2} \frac{1}{i!j!l!} f_{ijl}^{(3)} u_{1t}^i(-\tilde{\tau}) u_{3t}^j(-\tilde{\tau}) u_{3t}^l(0) \end{pmatrix} \\ &= \bar{D} \left\{ z^2 \left(\frac{1}{2} f_{200}^{(1)} + f_{101}^{(1)} \beta \right) + \bar{\beta}^* z^2 \left(\frac{1}{2} f_{200}^{(3)} e^{-2i\omega_0\tilde{\tau}} + f_{110}^{(3)} \beta e^{-2i\omega_0\tilde{\tau}} \right) \right. \\ &\quad + z\bar{z} \left(f_{200}^{(1)} + 2f_{101}^{(1)} \operatorname{Re}\{\beta\} \right) + \bar{\beta}^* z\bar{z} \left(f_{200}^{(3)} + 2f_{110}^{(3)} \operatorname{Re}\{\beta\} \right) \\ &\quad + z^2 \left(\frac{1}{2} f_{200}^{(1)} + f_{101}^{(1)} \bar{\beta} \right) + \bar{\beta}^* z^2 \left(\frac{1}{2} f_{200}^{(3)} e^{2i\omega_0\tilde{\tau}} + f_{110}^{(3)} \bar{\beta} e^{2i\omega_0\tilde{\tau}} \right) \\ &\quad + z^2 \bar{z} \left(\frac{1}{2} f_{300}^{(1)} + \frac{1}{2} f_{201}^{(1)} (\bar{\beta} + 2\beta) + \frac{1}{2} f_{200}^{(1)} (W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)) \right. \\ &\quad + f_{101}^{(1)} (W_{11}^{(3)}(0) + \frac{1}{2} W_{20}^{(1)}(0) \bar{\alpha} + \frac{1}{2} W_{20}^{(3)}(0) + W_{11}^{(1)}(0) \beta) \\ &\quad + \bar{\beta}^* z^2 \bar{z} \left(\frac{1}{2} f_{300}^{(3)} e^{-i\omega_0\tilde{\tau}} + \frac{1}{2} f_{210}^{(3)} (2\beta e^{-i\omega_0\tilde{\tau}} + \bar{\beta} e^{-i\omega_0\tilde{\tau}}) \right. \\ &\quad + f_{110}^{(3)} \left(\frac{1}{2} W_{20}^{(1)}(-\tilde{\tau}) \bar{\beta} e^{i\omega_0\tilde{\tau}} + \frac{1}{2} W_{20}^{(3)}(-\tilde{\tau}) e^{i\omega_0\tilde{\tau}} \right. \\ &\quad \left. \left. + W_{11}^{(1)}(-\tilde{\tau}) \beta e^{-i\omega_0\tilde{\tau}} + W_{11}^{(3)}(-\tilde{\tau}) e^{-i\omega_0\tilde{\tau}} \right) + \dots \right\}. \end{aligned}$$

Comparing the coefficients in (3.11), we get

$$\begin{aligned} g_{20} &= \bar{D} \left(f_{200}^{(1)} + 2f_{101}^{(1)} \beta + \bar{\beta}^* \left(f_{200}^{(3)} e^{-2i\omega_0\tilde{\tau}} + 2f_{110}^{(3)} \beta e^{-2i\omega_0\tilde{\tau}} \right) \right), \\ g_{11} &= \bar{D} \left(f_{200}^{(1)} + 2f_{101}^{(1)} \operatorname{Re}\{\beta\} + \bar{\beta}^* \left(f_{200}^{(3)} + 2f_{110}^{(3)} \operatorname{Re}\{\beta\} \right) \right), \\ g_{02} &= \bar{D} \left(f_{200}^{(1)} + 2f_{101}^{(1)} \bar{\beta} + \bar{\beta}^* \left(f_{200}^{(3)} e^{2i\omega_0\tilde{\tau}} + 2f_{110}^{(3)} \bar{\beta} e^{2i\omega_0\tilde{\tau}} \right) \right), \end{aligned}$$

$$\begin{aligned}
 g_{21} = & \bar{D} \left(f_{300}^{(1)} + f_{201}^{(1)}(\bar{\beta} + 2\beta) + f_{200}^{(1)}(W_{20}^{(1)}(0) + 2W_{11}^{(1)}(0)) \right. \\
 & + f_{101}^{(1)}(2W_{11}^{(3)}(0) + W_{20}^{(1)}(0))\bar{\alpha} + W_{20}^{(3)}(0) + 2W_{11}^{(1)}(0)\beta \\
 & + \bar{\beta}^* \left(f_{300}^{(3)}e^{-i\omega_0\bar{\tau}} + f_{210}^{(3)}(2\beta e^{-i\omega_0\bar{\tau}} + \bar{\beta}e^{-i\omega_0\bar{\tau}}) \right. \\
 & + f_{110}^{(3)}(W_{20}^{(1)}(-\bar{\tau})\bar{\beta}e^{i\omega_0\bar{\tau}} + W_{20}^{(3)}(-\bar{\tau})e^{i\omega_0\bar{\tau}} \\
 & \left. \left. + 2W_{11}^{(1)}(-\bar{\tau})\beta e^{-i\omega_0\bar{\tau}} + 2W_{11}^{(3)}(-\bar{\tau})e^{-i\omega_0\bar{\tau}}) \right) \right). \tag{3.12}
 \end{aligned}$$

We now compute $W_{20}(\theta)$ and $W_{11}(\theta)$. It follows from (3.7) and (3.9) that

$$\begin{aligned}
 \dot{W} &= \dot{u}_t - \dot{z}q - \dot{\bar{z}}\bar{q} \\
 &= \begin{cases} AW - 2\operatorname{Re}\{\bar{q}^*(0)f_0q(\theta)\}, & \theta \in (0, \bar{\tau}], \\ AW - 2\operatorname{Re}\{\bar{q}^*(0)f_0q(0)\} + f_0, & \theta = 0, \end{cases} \quad := AW + H(z, \bar{z}, \theta), \tag{3.13}
 \end{aligned}$$

where

$$H(z, \bar{z}, \theta) = H_{20}(\theta)\frac{z^2}{2} + H_{11}(\theta)z\bar{z} + H_{02}(\theta)\frac{\bar{z}^2}{2} + \dots \tag{3.14}$$

On the other hand, on \mathbf{C}_0 near the origin

$$\dot{W} = W_z\dot{z} + W_{\bar{z}}\dot{\bar{z}}. \tag{3.15}$$

We derive from (3.13)-(3.15) that

$$(A - 2i\omega_0)W_{20}(\theta) = -H_{20}(\theta), \quad AW_{11}(\theta) = -H_{11}(\theta), \dots \tag{3.16}$$

It follows from (3.11) and (3.13) that for $\theta \in [-\bar{\tau}, 0)$,

$$H(z, \bar{z}, \theta) = -\bar{q}^*(0)f_0q(\theta) - q^*(0)\bar{f}_0\bar{q}(\theta) = -gq(\theta) - \bar{g}\bar{q}(\theta). \tag{3.17}$$

Comparing the coefficients in (3.14) gives that for $\theta \in [-\bar{\tau}, 0)$,

$$H_{20}(\theta) = -g_{20}q(\theta) - \bar{g}_{02}\bar{q}(\theta), \tag{3.18}$$

$$H_{11}(\theta) = -g_{11}q(\theta) - \bar{g}_{11}\bar{q}(\theta). \tag{3.19}$$

We derive from (3.16), (3.18) and the definition of A that

$$\dot{W}_{20}(\theta) = 2i\omega_0W_{20}(\theta) + g_{20}q(\theta) + \bar{g}_{02}\bar{q}(\theta).$$

Noting that $q(\theta) = q(0)e^{i\omega_0\theta}$, it follows that

$$W_{20}(\theta) = \frac{ig_{20}}{\omega_0}q(0)e^{i\omega_0\theta} + \frac{i\bar{g}_{02}}{3\omega_0}\bar{q}(0)e^{-i\omega_0\theta} + E_1e^{2i\omega_0\theta}, \tag{3.20}$$

where $E_1 = (E_1^{(1)}, E_1^{(2)}, E_1^{(3)}) \in \mathbb{R}^3$ is a constant vector. Similarly, from (3.16) and (3.19), we obtain

$$W_{11}(\theta) = -\frac{ig_{11}}{\omega_0}q(0)e^{i\omega_0\theta} + \frac{i\bar{g}_{11}}{\omega_0}\bar{q}(0)e^{-i\omega_0\theta} + E_2, \tag{3.21}$$

where $E_2 = (E_2^{(1)}, E_2^{(2)}, E_2^{(3)}) \in \mathbb{R}^3$ is also a constant vector.

In what follows, we seek appropriate E_1 and E_2 . From the definition of A and (3.16), we obtain

$$\int_{-\bar{\tau}}^0 d\eta(\theta)W_{20}(\theta) = 2i\omega_0 W_{20}(0) - H_{20}(0), \quad (3.22)$$

$$\int_{-\bar{\tau}}^0 d\eta(\theta)W_{11}(\theta) = -H_{11}(0), \quad (3.23)$$

where $\eta(\theta) = \eta(0, \theta)$. From (3.13), it follows that

$$H_{20}(0) = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + \begin{pmatrix} f_{200}^{(1)} + 2f_{101}^{(1)}\beta \\ 0 \\ f_{200}^{(3)}e^{-2i\omega_0\bar{\tau}} + 2f_{110}^{(3)}\beta e^{-2i\omega_0\bar{\tau}} \end{pmatrix}, \quad (3.24)$$

$$H_{11}(0) = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + \begin{pmatrix} f_{200}^{(1)} + 2f_{101}^{(1)}\operatorname{Re}\{\beta\} \\ 0 \\ f_{200}^{(3)} + 2f_{110}^{(3)}\operatorname{Re}\{\beta\} \end{pmatrix}. \quad (3.25)$$

Substituting (3.20) and (3.24) into (3.22) and noticing that

$$\begin{aligned} \left(i\omega_0 I - \int_{-\bar{\tau}}^0 e^{i\omega_0\theta} d\eta(\theta)\right)q(0) &= 0, \\ \left(-i\omega_0 I - \int_{-\bar{\tau}}^0 e^{-i\omega_0\theta} d\eta(\theta)\right)\bar{q}(0) &= 0, \end{aligned}$$

we obtain

$$\left(2i\omega_0 I - \int_{-\bar{\tau}}^0 e^{2i\omega_0\theta} d\eta(\theta)\right)E_1 = \begin{pmatrix} f_{200}^{(1)} + 2f_{101}^{(1)}\beta \\ 0 \\ f_{200}^{(3)}e^{-2i\omega_0\bar{\tau}} + 2f_{110}^{(3)}\beta e^{-2i\omega_0\bar{\tau}} \end{pmatrix},$$

which leads to

$$\begin{aligned} &\begin{pmatrix} 2i\omega_0 - p_1 & -p_2 & -p_3 \\ -p_4 & 2i\omega_0 - p_5 & 0 \\ -p_6 e^{-2i\omega_0\bar{\tau}} & 0 & 2i\omega_0 - p_8 - p_7 e^{-2i\omega_0\bar{\tau}} \end{pmatrix} E_1 \\ &= \begin{pmatrix} f_{200}^{(1)} + 2f_{101}^{(1)}\beta \\ 0 \\ f_{200}^{(3)}e^{-2i\omega_0\bar{\tau}} + 2f_{110}^{(3)}\beta e^{-2i\omega_0\bar{\tau}} \end{pmatrix}. \end{aligned}$$

It follows that

$$E_1^{(1)} = \frac{1}{A} \det \begin{pmatrix} f_{200}^{(1)} + 2f_{101}^{(1)}\beta & -p_2 & -p_3 \\ 0 & 2i\omega_0 - p_5 & 0 \\ f_{200}^{(3)}e^{-2i\omega_0\bar{\tau}} + 2f_{110}^{(3)}\beta e^{-2i\omega_0\bar{\tau}} & 0 & 2i\omega_0 - p_8 - p_7 e^{-2i\omega_0\bar{\tau}} \end{pmatrix},$$

$$E_1^{(2)} = \frac{1}{A} \det \begin{pmatrix} 2i\omega_0 - p_1 & f_{200}^{(1)} + 2f_{101}^{(1)}\beta & -p_3 \\ -p_4 & 0 & 0 \\ -p_6 e^{-2i\omega_0\bar{\tau}} & f_{200}^{(3)}e^{-2i\omega_0\bar{\tau}} + 2f_{110}^{(3)}\beta e^{-2i\omega_0\bar{\tau}} & 2i\omega_0 - p_8 - p_7 e^{-2i\omega_0\bar{\tau}} \end{pmatrix},$$

$$E_1^{(3)} = \frac{1}{A} \det \begin{pmatrix} 2i\omega_0 - p_1 & -p_2 & f_{200}^{(1)} + 2f_{101}^{(1)}\beta \\ -p_4 & 2i\omega_0 - p_5 & 0 \\ -p_6 e^{-2i\omega_0\tilde{\tau}} & 0 & f_{200}^{(3)} e^{-2i\omega_0\tilde{\tau}} + 2f_{110}^{(3)}\beta e^{-2i\omega_0\tilde{\tau}} \end{pmatrix}.$$

where

$$A = \det \begin{pmatrix} 2i\omega_0 - p_1 & -p_2 & -p_3 \\ -p_4 & 2i\omega_0 - p_5 & 0 \\ -p_6 e^{-2i\omega_0\tilde{\tau}} & 0 & 2i\omega_0 - p_8 - p_7 e^{-2i\omega_0\tilde{\tau}} \end{pmatrix}.$$

Similarly, we can get

$$\begin{pmatrix} -p_1 & -p_2 & -p_3 \\ -p_4 & -p_5 & 0 \\ -p_6 & 0 & 0 \end{pmatrix} E_2 = \begin{pmatrix} f_{200}^{(1)} + 2f_{101}^{(1)} \operatorname{Re}\{\beta\} \\ 0 \\ f_{200}^{(3)} + 2f_{110}^{(3)} \operatorname{Re}\{\beta\} \end{pmatrix},$$

and hence,

$$E_2^{(1)} = \frac{f_{200}^{(3)} + 2f_{110}^{(3)} \operatorname{Re}\{\beta\}}{p_6}, \quad E_2^{(2)} = \frac{p_4(f_{200}^{(3)} + 2f_{110}^{(3)} \operatorname{Re}\{\beta\})}{p_5 p_6},$$

$$E_2^{(3)} = \frac{1}{p_3 p_5 p_6} \det \begin{pmatrix} -p_1 & -p_2 & f_{200}^{(1)} + 2f_{101}^{(1)} \operatorname{Re}\{\beta\} \\ -p_4 & -p_5 & 0 \\ -p_6 & 0 & f_{200}^{(3)} + 2f_{110}^{(3)} \operatorname{Re}\{\beta\} \end{pmatrix}.$$

Thus, we can determine $W_{20}(\theta)$ and $W_{11}(\theta)$ from (3.20) and (3.21). Furthermore, we can determine g_{21} . Therefore, each g_{ij} in (3.12) is determined by the parameters and delay in system (3.1). Thus, we can compute the following values:

$$c_1(0) = \frac{i}{2\omega_0} \left(g_{11}g_{20} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3} \right) + \frac{g_{21}}{2},$$

$$\mu_2 = -\frac{\operatorname{Re}\{c_1(0)\}}{\operatorname{Re}\{\lambda'(\tilde{\tau})\}}, \quad \beta_2 = 2 \operatorname{Re}\{c_1(0)\}, \quad (3.26)$$

$$T_2 = -\frac{\operatorname{Im}\{c_1(0)\} + \mu_2 \operatorname{Im}\{\lambda'(\tilde{\tau})\}}{\omega_0},$$

which determine the quantities of bifurcating periodic solutions in the center manifold at the critical value $\tilde{\tau}$, 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); β_2 determines the stability of the bifurcating periodic solutions: the bifurcating periodic solutions 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 $T_2 > 0$ ($T_2 < 0$).

4. NUMERICAL EXAMPLES

In this section, we give some examples to illustrate the results above.

Example 4.1. In system (1.4), we let $a = 4, a_1 = a_2 = 2, a_{11} = 3, b = 3, r = r_1 = r_2 = 1, m = 1$, then system (1.4) has a positive equilibrium $E^* = (1, 3, 5)$. It is easy to show that $\omega_0 = 0.2371, \tau_0 = 2.4144$. By Theorem 2.1, we see that the positive equilibrium E^* is stable when $\tau < \tau_0$ (see, Fig. 1); when $\tau > \tau_0$ E^* is unstable (see, Fig. 2); and system (1.4) undergoes a Hopf bifurcation at τ_j . When $\tau = \tau_0$, $c_1(0) = -0.0710 - 0.2882i$. It follows from (3.26) that $\mu_2 > 0$ and $\beta_2 < 0$. Therefore, the Hopf bifurcation of system (1.4) is supercritical, and the bifurcating periodic solutions are stable.

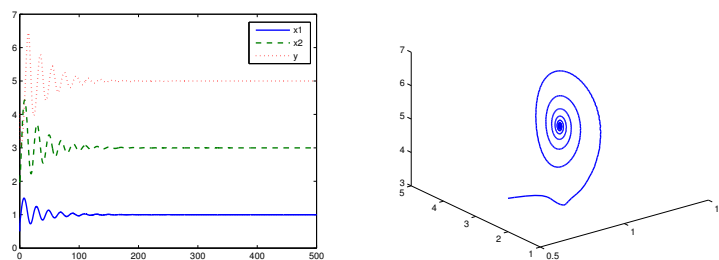


FIGURE 1. When $\tau = 1 < \tau_0$, the positive equilibrium E^* of system (1.4) is asymptotically stable. The initial value is $(0.5, 2, 4)$.

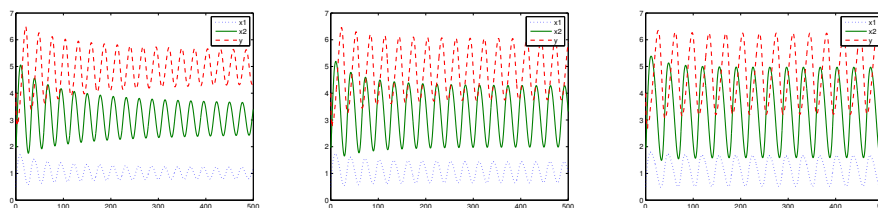


FIGURE 2. When $\tau = 2.5, 3, 4 > \tau_0$, bifurcating periodic solutions from E^* occur. The initial value is $(0.5, 2, 4)$.

Example 4.2. We consider the responding system without functional response. In system (1.3), we let $a = 4, a_1 = a_2 = 2, a_{11} = 3, b = 3, r = r_1 = r_2 = 1, \beta = 0$. It is easy to show that $E^* = (0.5, 1.5, 3.25)$, $\omega_0 = 0.3722, \tau_0 = 2.5160$. We know that the positive equilibrium E^* of system (1.3) is stable when $\tau < \tau_0$ (see, Fig. 3); when $\tau > \tau_0$, E^* is unstable (see, Fig. 4), and system (1.3) undergoes a Hopf bifurcation at τ_j .

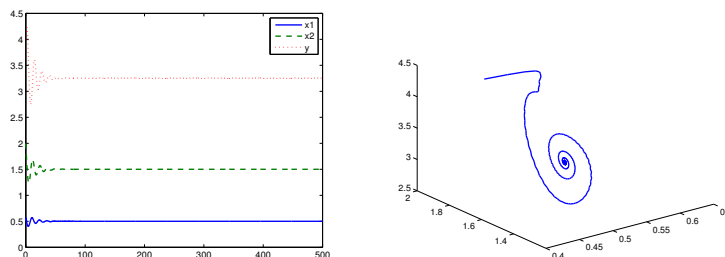


FIGURE 3. When $\tau = 1 < \tau_0$, the positive equilibrium E^* of system (1.3) is asymptotically stable. The initial value is $(0.5, 2, 4)$.

Discussion. In this article, we considered a delayed predator-prey system with stage structure and Holling type-II functional response. The conditions of the local

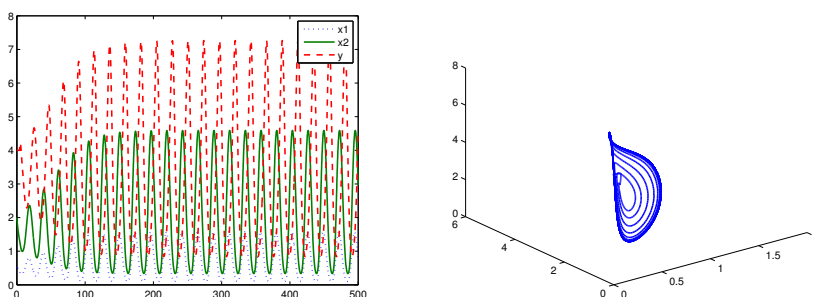


FIGURE 4. When $\tau = 4 > \tau_0$, bifurcating periodic solutions from E^* occur. The initial value is $(0.5, 2, 4)$.

stability of system (1.4) are obtained, and the direction of the bifurcating periodic solutions are derived. From Theorem 2.1, we know that when $Q_3 > 0$ the delay is harmless, and the local stability of system (1.4) doesn't change; when $Q_3 < 0$, system (1.4) will lose stability and a Hopf bifurcation can occur as the delay τ increases. From fig 2, we can see that the bifurcating periodic solutions of system (1.4) are different. The oscillatory extent of the bifurcating periodic solution of system (1.4) becomes more and more large as the delay τ increases.

From the figs, we known that the rapidity of convergence to equilibrium of system (1.4) is slower than corresponding system without functional response. Furthermore, the value of τ_0 obtained for the model (1.4) is smaller than the corresponding value for a similar model without functional response. At the same time stage-structured system with time delay and functional response has a similar asymptotic behavior to that in the delayed system without functional response.

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