

A STAGE-STRUCTURED PREDATOR-PREY SYSTEM WITH
TIME DELAY AND HOLLING TYPE-III
FUNCTIONAL RESPONSE

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Abstract: A stage-structured predator-prey system with time delay and Holling type-III 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.

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1. Introduction

The predator-prey system is very important in population modelling and has been studied by many authors (see, for example, [1, 6, 7, 8, 9, 10]). A predator-

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prey model generally takes the form

$$\begin{cases} \dot{x} = xf(x) - p(x)y, \\ \dot{y} = kp(x)y - yg(y), \end{cases} \quad (1.1)$$

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. In 1965, Holling [4] used the following function

$$p(x) = \frac{mx^2}{a + x^2}$$

as one of the predator response functions (it is now known as a Holling type-III response function). In [1], Chen and Zhang studied system (1.1) with $f(x) = r - ax$, $g(y) = r_1$ and $p(x) = mx^2/(a + x^2)$. By the qualitative theory of ordinary differential equations, they studied the stability of positive equilibria and gave sufficient conditions for the existence, uniqueness and nonexistence of limit cycles.

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, [8, 9, 10]).

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 (see [5]). 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, [3, 5, 7] and references cited therein).

In this paper, we are concerned with the effects of stage-structure for the predator and time delay due to the gestation of the predator on the dynamics of a predator-prey model with Holling type-III functional response. To this aim, we consider the following delay differential equations

$$\begin{cases} \dot{x}(t) = rx(t) - ax^2(t) - \frac{a_1x^2(t)y_2(t)}{m^2 + x^2(t)}, \\ y_1(t) = \frac{a_2x^2(t - \tau)y_2(t - \tau)}{m^2 + x^2(t - \tau)} - r_1y_1(t) - dy_1(t), \\ y_2(t) = dy_1(t) - r_2y_2(t), \end{cases} \quad (1.2)$$

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 $a, a_1, a_2, d, r, r_1, r_2$ and m are positive constants, where a is the intra-specific competition rate of the prey, a_1 is the capturing rate of the predator, a_2/a_1 is the conversion rate of the predator by consuming prey, 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. $\tau \geq 0$ is a constant representing a time delay due to the gestation of the predator.

The initial conditions for system (1.2) take the form

$$\begin{aligned} x(\theta) = \phi_1(\theta) \geq 0, y_1(\theta) = \phi_2(\theta) \geq 0, y_2(\theta) = \phi_3(\theta) \geq 0, \theta \in [-\tau, 0), \\ \phi_i(0) > 0 (i = 1, 2, 3), (\phi_1(\theta), \phi_2(\theta), \phi_3(\theta)) \in C([-\tau, 0], R_{+0}^3), \end{aligned}$$

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

The organization of this paper is as follows. In the next section, by analyzing the associated characteristic equation, we investigate the local stability of a positive equilibrium of system (1.2). 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 the positive equilibrium and the existence of Hopf bifurcations for system (1.2) with time delay τ as a parameter.

Let

$$\tilde{x} = \frac{a}{r}x, \quad \tilde{y}_1 = \frac{aa_1}{a_2r}y_1, \quad \tilde{y}_2 = \frac{aa_1}{r^2}y_2, \quad \tilde{t} = rt,$$

then system (1.2) becomes

$$\begin{cases} \dot{\tilde{x}}(t) = \tilde{x}(t) - \tilde{x}^2(t) - \frac{\tilde{x}^2(t)\tilde{y}_2(t)}{n + \tilde{x}^2(t)}, \\ \dot{\tilde{y}}_1(t) = \frac{\tilde{x}^2(t-\tau)\tilde{y}_2(t-\tau)}{n + \tilde{x}^2(t-\tau)} - \beta\tilde{y}_1(t), \\ \dot{\tilde{y}}_2(t) = \alpha\tilde{y}_1(t) - \gamma\tilde{y}_2(t), \end{cases} \quad (2.1)$$

where $\alpha = a_2d/r^2 > 0$, $\beta = (r_1 + d)/r > 0$, $\gamma = r_2/r > 0$ and $n = m^2k^2 > 0$.

If $\alpha - (n+1)\beta\gamma > 0$, system (2.1) has a positive equilibrium $E^* = (x_*, y_{1*}, y_{2*})$, where

$$x_* = \sqrt{\frac{n\beta\gamma}{\alpha - \beta\gamma}}, \quad y_{1*} = \frac{\gamma(n - nx_* + x_*^2 - x_*^3)}{\alpha x_*}, \quad y_{2*} = \frac{n - nx_* + x_*^2 - x_*^3}{x_*}.$$

Let $\bar{x} = \tilde{x} - x_*$, $\bar{y}_1 = \tilde{y}_1 - y_{1*}$, $\bar{y}_2 = \tilde{y}_2 - y_{2*}$. Dropping the bars, system (2.1) becomes

$$\begin{cases} \dot{x}(t) = -cx(t) - \frac{\beta\gamma}{\alpha}y_2(t) - x^2(t) - F(x(t), y_2(t)), \\ \dot{y}_1(t) = F(x(t-\tau), y_2(t-\tau)) - \beta y_1(t) \\ \quad + (1 + c - 2x_*)x(t-\tau) + \frac{\beta\gamma}{\alpha}y_2(t-\tau), \\ \dot{y}_2(t) = \alpha y_1(t) - \gamma y_2(t), \end{cases} \quad (2.2)$$

where

$$F(x, y) = \frac{x^2(c_2 - 2nx_*y_2x) + c_1nxy(2x_* + x)}{c_1^2(c_1 + 2x_*x + x^2)},$$

$$c = 2x_* + \frac{2nx_*y_{2*}}{c_1^2} - 1, \quad c_1 = n + x_*^2, \quad c_2 = ny_{2*}(n - 3x_*^2).$$

The characteristic equation of system (2.2) at the origin is of the form

$$\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0 + (q_1\lambda + q_0)e^{-\lambda\tau} = 0, \quad (2.3)$$

where

$$\begin{aligned} p_0 &= c\beta\gamma, & p_1 &= \beta\gamma + c(\beta + \gamma), & p_2 &= \beta + \gamma + c, \\ q_0 &= \beta\gamma(1 - 2x_*), & q_1 &= -\beta\gamma. \end{aligned} \quad (2.4)$$

When $\tau = 0$, equation (2.3) becomes

$$\lambda^3 + p_2\lambda^2 + (p_1 + q_1)\lambda + p_0 + q_0 = 0. \quad (2.5)$$

Assume

$$(H_1) \quad c(\beta + \gamma)(\beta + \gamma + c) - \beta\gamma(1 + c - 2x_*) > 0.$$

This assumption implies that

$$\begin{aligned} p_2 &= \beta + \gamma + c > 0, & p_0 + q_0 &= \beta\gamma(1 + c - 2x_*) = \frac{2nx_*y_{2*}}{c_1^2} > 0, \\ p_2(p_1 + q_1) - (p_0 + q_0) &= c(\beta + \gamma)(\beta + \gamma + c) - \beta\gamma(1 + c - 2x_*) > 0. \end{aligned}$$

By Hurwitz criterion, we know that all roots of equation (2.5) have negative real root.

When $\tau > 0$, noting that $i\omega(\omega > 0)$ is a root of (2.3) if and only if ω satisfies

$$\begin{cases} q_1\omega \cos \omega\tau - q_0 \sin \omega\tau = \omega^3 - p_1\omega \\ q_1\omega \sin \omega\tau + q_0 \cos \omega\tau = p_2\omega^2 - p_0. \end{cases} \quad (2.6)$$

Squaring and adding equations in (2.6) gives

$$\omega^6 + h_2\omega^4 + h_1\omega^2 + h_0 = 0, \quad (2.7)$$

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 (2.7), if

$$(H_2) \quad 0 < c < 1 - 2x_*$$

holds, we have

$$\begin{aligned} h_0 &= -\beta^2\gamma^2(1 + c - 2x_*)(1 - c - 2x_*) < 0, \\ h_1 &= c^2(\beta^2 + \gamma^2) > 0, \quad h_2 = \beta^2 + \gamma^2 + c^2 > 0. \end{aligned} \quad (2.8)$$

Hence, equation (2.7) has only one positive real root ω_0 . Let

$$\tau_j = \frac{1}{\omega_0} \arcsin\left(\frac{(p_2q_1 - q_0)\omega_0^3 + (p_1q_0 - p_0q_1)\omega_0}{q_1^2\omega_0^2 + q_0^2}\right) + \frac{2\pi j}{\omega_0}, \quad (2.9)$$

then equation (2.3) has a pair of purely imaginary roots $\pm i\omega_0$ with $\tau = \tau_j (j = 0, 1, 2, \dots)$.

Lemma 2.1. *For equation (2.3), if (H_2) holds, then we have the following transversal condition*

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

Proof. Differentiating both sides of (2.3) with respect to τ yields

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

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

$$\left(\frac{d\lambda}{d\tau} \right)^{-1} = -\frac{3\lambda^2 + 2p_2\lambda + p_1}{\lambda(\lambda^3 + p_2\lambda^2 + p_1\lambda + p_0)} + \frac{q_1}{\lambda(q_1\lambda + q_0)} - \frac{\tau}{\lambda}.$$

It therefore follows that

$$\operatorname{Re} \left(\frac{d\lambda}{d\tau} \right)^{-1} \Big|_{\lambda=i\omega_0} = \frac{3\omega_0^4 + 2(p_2^2 - 2p_1)\omega_0^2 + p_1^2 - q_1^2 - 2p_0p_2}{q_1^2\omega_0^2 + q_0^2} > 0.$$

Therefore,

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

This completes the proof of Lemma 2.1. \square

From Lemma 2.1 and the results in [2], we have the following result.

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

(i) *when $\tau \in [0, \tau_0)$, all roots of equation (2.3) have strictly negative real parts;*

(ii) *when $\tau = \tau_0$, equation (2.3) has a pair of conjugate purely imaginary roots $\pm i\omega_0$, and all other roots have strictly negative real parts;*

(iii) *when $\tau > \tau_0$, equation (2.3) has at least a root with positive real part.*

Applying Lemma 2.2, we have the following result.

Theorem 2.1. *For system (2.2), if (H_1) and (H_2) 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) *$\tau = \tau_j (j = 0, 1, 2, \dots)$ are the values of Hopf bifurcations, where τ_j are defined by (2.9).*

3. Direction and Stability of Hopf Bifurcations

In the previous section, we obtain conditions under which a family of periodic solutions bifurcates from the positive equilibrium at the critical values $\tau_j (j = 0, 1, 2, \dots)$. 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 [3].

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 (2.2) can be written as

$$\begin{cases} \dot{x}(t) = [-cx(t) - \frac{\beta\gamma}{\alpha}y_2(t) - x^2(t) - F(x(t), y_2(t))](\tau_0 + \mu), \\ \dot{y}_1(t) = [F(x(t-1), y_2(t-1)) - \beta y_1(t) \\ \quad + (1 + c - 2x_*)x(t-1) + \frac{\beta\gamma}{\alpha}y_2(t-1)](\tau_0 + \mu), \\ \dot{y}_2(t) = [\alpha y_1(t) - \gamma y_2(t)](\tau_0 + \mu). \end{cases} \quad (3.1)$$

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

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

where

$$B_1 = (\tau_0 + \mu) \begin{pmatrix} -c & 0 & -\frac{\beta\gamma}{\alpha} \\ 0 & -\beta & 0 \\ 0 & \alpha & -\gamma \end{pmatrix},$$

$$B_2 = (\tau_0 + \mu) \begin{pmatrix} 0 & 0 & 0 \\ 1 + c - 2x_* & 0 & \frac{\beta\gamma}{\alpha} \\ 0 & 0 & 0 \end{pmatrix}.$$

And define

$$f(\mu, \varphi) = (\tau_0 + \mu) \begin{pmatrix} -\varphi_0^2(0) - F(\varphi_0(0), \varphi_2(0)) \\ F(\varphi_0(-1), \varphi_2(-1)) \\ 0 \end{pmatrix}.$$

By the Riesz Representation Theorem, there exists a matrix whose components are bounded variation functions $\eta(\theta, \mu) : [-1, 0] \rightarrow R^3$, 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

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

and

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

Hence equation (3.1) can be rewritten as

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

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

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

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

$$\langle \psi, \varphi \rangle = \bar{\psi}^T(0)\varphi(0) - \int_{\theta=-1}^0 \int_{\xi=0}^{\theta} \bar{\psi}^T(\xi - \theta) \mathbf{d}\eta(\theta)\varphi(\xi) d\xi,$$

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

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

$$\begin{aligned} q_2 &= \frac{\omega_0^2 - c\gamma - i(c + \gamma)\omega_0}{\beta\gamma}, & q_3 &= \frac{-\alpha(c + i\omega_0)}{\beta\gamma}, \\ q_2^* &= \frac{-c + i\omega_0}{2x_* - c - 1} e^{-i\tau_0\omega_0}, & q_3^* &= \frac{\omega_0^2 - \beta c + i(\beta - c)\omega_0}{\alpha(2x_* - c - 1)} e^{-i\tau_0\omega_0}, \\ D &= [1 + q_2\bar{q}_2^* + q_3\bar{q}_3^* + \tau_0((1 + c - 2x_*)\bar{q}_2^* + \frac{\beta\gamma}{\alpha}q_3\bar{q}_3^*)]^{-1}. \end{aligned}$$

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

$$z(t) = \langle q^*, U_t \rangle, \quad W(t, \theta) = U_t(\theta) - 2\text{Re}\{z(t)q(\theta)\}. \quad (3.7)$$

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

$$W(z, \bar{z}, \theta) = W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta)z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} + \dots. \quad (3.8)$$

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

$$\dot{z}(t) = i\tau_0\omega_0 z(t) + \bar{q}^*(0)f_0(z, \bar{z}), \quad (3.9)$$

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

$$g(z, \bar{z}) = g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + \dots. \quad (3.10)$$

By (3.7), we have

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

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

$$\begin{aligned} g_{20} &= 2\tau_0 D\left[-1 + \frac{(c_2 + 2c_1nx_*q_3)(\bar{q}_2^*e^{-2i\tau_0\omega_0} - 1)}{c_1^3}\right], \\ g_{11} &= \tau_0 D\left[-2 + \frac{2(\bar{q}_2^* - 1)(c_2 + c_1nx_*(q_3 + \bar{q}_3))}{c_1^3}\right], \\ g_{02} &= 2\tau_0 D\left[-1 + \frac{(c_2 + 2c_1nx_*\bar{q}_3)(\bar{q}_2^*e^{2i\tau_0\omega_0} - 1)}{c_1^3}\right], \\ g_{21} &= 2\tau_0 D\left[-(W_{20}^{(0)}(0) + 2W_{11}^{(0)}(0)) + \frac{1}{c_1^3}(-c_2(W_{20}^{(0)}(0) + W_{11}^{(0)}(0)) \right. \\ &\quad - c_1n(2q_3 + \bar{q}_3) - c_1nx_*(W_{20}^{(2)}(0) + 2W_{11}^{(2)}(0) + W_{20}^{(0)}(0)\bar{q}_3 \\ &\quad + 2W_{11}^{(0)}(0)q_3) + e^{i\tau_0\omega_0}(c_2W_{20}^{(0)}(-1) + c_1nx_*(W_{20}^{(2)}(-1) \\ &\quad + \bar{q}_3W_{20}^{(0)}(-1))) + e^{-i\tau_0\omega_0}(c_1n(2q_3 + \bar{q}_3) - 6x_*y_{2*} + 2c_1nx_* \\ &\quad (W_{11}^{(2)}(-1) + q_3W_{11}^{(0)}(-1)) + 2c_2W_{11}^{(0)}(-1)) + \frac{1}{c_1^4}(2x_* \\ &\quad (c_2 + 2c_1nq_3x_*) + 4x_*(c_2 + c_1nx_*(q_3 + \bar{q}_3)) \\ &\quad \left. - 2x_*\bar{q}_2^*(3c_2 + 2c_1nx_*(2q_3 + \bar{q}_3))e^{-i\tau_0\omega_0})\right]. \end{aligned} \tag{3.11}$$

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

$$\begin{aligned} \dot{W} &= \dot{U}_t - \dot{z}q - \dot{\bar{z}}\bar{q} \\ &= \begin{cases} AW - 2Re\{\bar{q}^*(0)F_0q(\theta)\}, & \theta \in [-1, 0) \\ AW - 2Re\{\bar{q}^*(0)F_0q(\theta)\} + F_0, & \theta = 0 \end{cases} \\ &\stackrel{\text{def}}{=} AW + H(z, \bar{z}, \theta), \end{aligned}$$

where

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

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

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

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

$$\begin{aligned} H(z, \bar{z}, \theta) &= -2Re\{\bar{q}^*(0)F_0q(\theta)\} = -g(z, \bar{z})q(\theta) - \bar{g}(z, \bar{z})\bar{q}(\theta) \\ &= -(g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + \dots)q(\theta) \\ &\quad - (\bar{g}_{20}\frac{\bar{z}^2}{2} + \bar{g}_{11}z\bar{z} + \bar{g}_{02}\frac{z^2}{2} + \dots)\bar{q}(\theta). \end{aligned}$$

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 $\dot{W}_{20}(\theta) = 2i\tau_0\omega_0 W_{20}(\theta) - H_{20}(\theta)$. Solving it, we have

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

Similarly, we get

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

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

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

and

$$\int_{-1}^0 d\eta(\theta)W_{11}(\theta) = -H_{11}(0). \quad (3.17)$$

By the definition of H , we have

$$H_{20}(0) = -g_{20}q(0) - \bar{g}_{02}\bar{q}(0) + \tau_0 A, \quad (3.18)$$

$$H_{11}(0) = -g_{11}q(0) - \bar{g}_{11}\bar{q}(0) + \tau_0 B, \quad (3.19)$$

where

$$A = \left(-2 - \frac{2(c_2 + 2c_1nx_*q_3)}{c_1^3}, \frac{2(c_2 + 2c_1nx_*q_3)e^{-2i\tau_0\omega_0}}{c_1^3}, 0 \right)^T,$$

$$B = \left(-2 - \frac{2(c_2 + c_1nx_*(q_3 + \bar{q}_3))}{c_1^3}, \frac{2(c_2 + c_1nx_*(q_3 + \bar{q}_3))}{c_1^3}, 0 \right)^T.$$

Substituting (3.14) into (3.18), we obtain

$$\begin{pmatrix} 2i\omega_0 + c & 0 & \frac{\beta\gamma}{\alpha} \\ (2x_* - c - 1)e^{-2i\tau_0\omega_0} & 2i\omega_0 + \beta & -\frac{\beta\gamma}{\alpha}e^{-2i\tau_0\omega_0} \\ 0 & -\alpha & 2i\omega_0 + \gamma \end{pmatrix} E = A.$$

Hence, we have $E = \frac{1}{\Delta_1} (\Delta_1^1, \Delta_1^2, \Delta_1^3)^T$, where

$$\Delta_1 = -4(\beta + \gamma + c)\omega_0^2 + \beta\gamma c + (-8\omega_0^3 + (2\beta\gamma + 2c\beta + 2c\gamma)\omega_0)i - \beta\gamma(2x_* - 1 + 2i\omega_0)e^{-2i\tau_0\omega_0},$$

$$\begin{aligned}
 \Delta_1^1 &= -2\left(1 + \frac{c_2 + 2c_1nx_*q_3}{c_1^3}\right)(-4\omega_0^2 + \beta\gamma + 2\omega_0(\beta + \gamma)\mathbf{i}) \\
 &\quad + 2\beta\gamma\left(1 + \frac{c_2 + 2c_1nx_*q_3}{c_1^3} - (c_2 + 2c_1nx_*q_3)\right)e^{-2i\tau_0\omega_0}, \\
 \Delta_1^2 &= 2(-4\omega_0^2 + c\gamma + 2(c + \gamma)\omega_0\mathbf{i})\frac{c_2 + 2c_1nx_*q_3}{c_1^3}e^{-2i\tau_0\omega_0} \\
 &\quad + 2(\gamma + 2\omega_0\mathbf{i})(2x_* - c - 1)\left(1 + \frac{c_2 + 2c_1nx_*q_3}{c_1^3}\right)e^{-2i\tau_0\omega_0}, \\
 \Delta_1^3 &= 2\alpha(2x_* - c - 1)\left(1 + \frac{c_2 + 2c_1nx_*q_3}{c_1^3}\right)e^{-2i\tau_0\omega_0} \\
 &\quad + 2\alpha(c + 2i\omega_0)\frac{c_2 + 2c_1nx_*q_3}{c_1^3}e^{-2i\tau_0\omega_0}.
 \end{aligned}$$

Similarly, substituting (3.15) into (3.19), we can get $F = \frac{1}{\Delta_2} (\Delta_2^1, \Delta_2^2, \Delta_2^3)^T$, where

$$\begin{aligned}
 \Delta_2 &= \beta\gamma(2x_* - c - 1), \\
 \Delta_2^1 &= -2\beta\gamma\frac{c_2 + c_1nx_*(q_3 + \bar{q}_3)}{c_1^3}, \\
 \Delta_2^2 &= 2\gamma(2x_* - 1)\frac{c_2 + c_1nx_*(q_3 + \bar{q}_3)}{c_1^3}, \\
 \Delta_2^3 &= 2\alpha(2x_* - 1)\left(1 + \frac{c_2 + c_1nx_*(q_3 + \bar{q}_3)}{c_1^3}\right).
 \end{aligned}$$

Based on the analysis above, we see that g_{ij} in (3.11) is determined by the parameters and the time delay in (2.2). Thus, we can compute the following quantities,

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

From the expression of $C_1(0)$ in (3.20), it is easy to get the values of μ_2, β_2, 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 $t_2 > 0 (< 0)$.

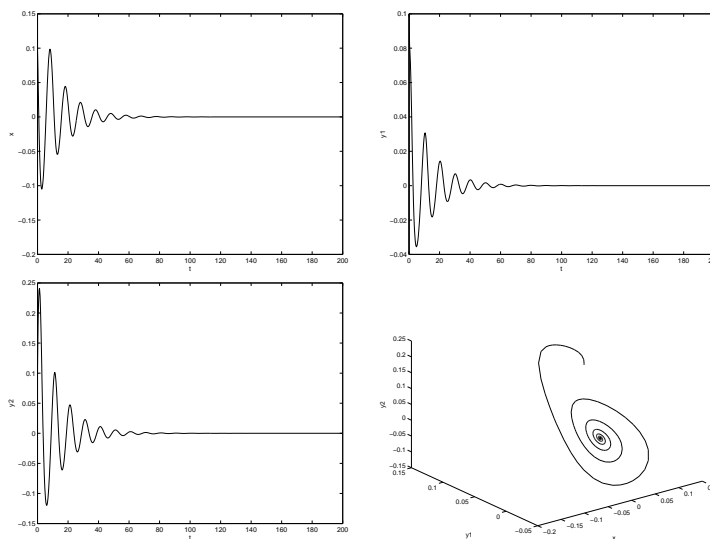


Figure 1: Behavior and phase portrait of system (2.2) with $\tau = 0.1$, the origin is stable

4. Computer Simulations

To illustrate the analytical results, let us give some numerical simulations in this section. For system (2.2), we choose $\alpha = 4$, $\beta = 2$, $\gamma = 1$ and $n = 0.1$. From the formulae in Section 3 and by direct computation, we obtain

$$\begin{aligned}\tau_0 &\approx 2.9440, \\ C_1(0) &\approx -0.0254 + 1.3185i.\end{aligned}$$

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

From Figure 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 loses its stability and a periodic solution bifurcates from the origin for $\tau = 4 > \tau_0$ (see Figure 2).

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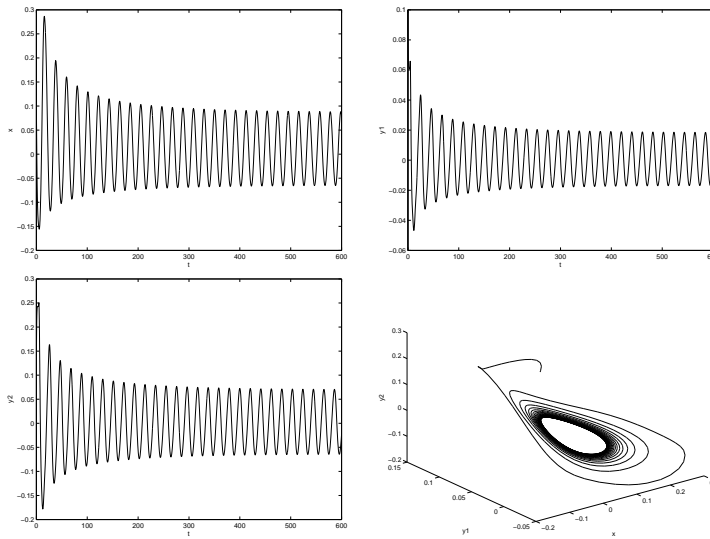


Figure 2: Behavior and phase portrait of system (2.2) with $\tau = 4$, the origin loses its stability and Hopf bifurcation occurs

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References

- [1] J.P. Chen, H.D. Zhang, The qualitative analysis of two species predator-prey model with Holling type-III functional response, *Appl. Math. and Mech.*, **7**, No. 1 (1986), 73-80, In Chinese.
- [2] K. Cooke, Z. Grossman, Discrete delay, distributed delay and stability switches, *J. Math. Anal. Appl.*, **86** (1982), 592-627.
- [3] B. Hassard, N. Kazarinoff, Y.H. Wan, *Theory and Applications of Hopf Bifurcation*, London Math Soc. Lect. Notes, Series, **41**, Cambridge Univ. Press, Cambridge (1981).
- [4] C. S. Holling, The functional response of predators to prey density and its role in mimicry and population regulation, *Mem. Entomolog. Soc. Can.*, **45** (1965), 3-60.
- [5] Y. Kuang, *Delay Differential Equations with Applications in Population Dynamics*, Academic Press, New York (1993).

- [6] S. Ruan, D. Xiao, Global analysis in a predator-prey system with non-monotonic functional response, *SIAM J. Appl. Math.*, **61**, No. 4 (2001), 1445-1472.
- [7] C. Sun, M. Han, Y. Lin, Analysis of stability and Hopf bifurcation for a delayed logistic equation, *Chaos, Solitons and Fractals*, **31** (2007), 672-682.
- [8] W. Wang, L. Chen, A predator-prey system with stage-structure for predator, *Comput. Math. Appl.*, **33** (1997), 83-91.
- [9] Y. Xiao, L. Chen, Global stability of a predator-prey system with stage structure for the predator, *Acta Math. Sinica*, **19** (2003), 1-11.
- [10] R. Xu, Z. Ma, The effect of stage-structure on the permanence of a predator-prey system with time delay, *Appl. Math. Comput.*, **189** (2007), 1164-1177.