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Bifurcations in a Delayed Predator-prey Model*

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Abstract: In this paper, the dynamics of a delayed predator-prey model with ratio-dependent type functional response are considered. We show that the asymptotic behavior depends crucially on the time delay parameter. We are particularly interested in the study of the Hopf bifurcation problem to predict the occurrence of a limit cycle bifurcating from the positive equilibrium. By choosing the the delay as a bifurcation parameter, the length of delay which preserves the stability of the positive equilibrium is calculated(i. e., $0<\tau<\tau_+$). Some numerical simulation for justifying the analytical findings is also provided. Main conclusions are as follows: the positive equilibrium of the system is asymptotically stable for $\tau\in[0,\tau_0)$. The system undergoes a Hopf bifurcation at the positive equilibrium when $\tau=\tau_k^j$, $k=1,2,3,4$; $j=0,1,2,\cdots$, and the length of delay is τ_+.

Key words: predator-prey model; time delay; stability; Hopf bifurcation; periodic solution

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1 Introduction

Since the work of Volterra and Lotka in the mid-1920s, time delays were already incorporated into the mathematical models of population dynamics. For a long time, it has been recognized that delays have a very complicated impact on the dynamics of a system. In recent years, a lot of predator-prey (PP of short) models with time delays have been formulated and studied extensively by many researchers. A great many results on the dynamics of PP models have been obtained[1-10].

In 1969, Hassell and Varley's[11] introduced the following PP model with the Hassell-Varley(HV for short) type functional response:

$$\begin{cases}\dot{x}(t) = rx(t)\left(1-\dfrac{x(t)}{K}\right)-\dfrac{cxy}{my^{\gamma}+x}\\ \dot{y}_1(t) = y\left(-d+\dfrac{fx}{my^{\gamma}+x}\right),\gamma\in(0,1)\\ x(0)>0,\ y(0)>0\end{cases}\tag{1}$$

where x, y denote the population of preys and predators at time t, respectively. The constants r, K, c, m, d and f are positive constants that stand for the prey's intrinsic growth rate, carrying capacity, capturing rate, half-saturation constant, predator death rate, maximal predator growth rate, respectively. γ is called the HV constant. In detailis, on can see[11-12]. In the typical predator-prey interaction where predator do not form groups, so we can assume that $\gamma=1$ which leads to the so-called ratio-dependent system. Meanwhile, considering that the delay may occur in the competition among preys, in this paper, we consider a non-autonomous PP model with HV functional response and a delay in the prey specific growth term and HV functional response term as follows:

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$$\begin{cases}\dot{N}_1(t) = N_1(t)\left[a - bN_1(t-\tau) - \dfrac{cN_2(t-\tau)}{mN_2(t-\tau) + N_1(t-\tau)}\right] \\ \dot{N}_2(t) = N_2(t)\left[-d + \dfrac{rN_1(t-\tau)}{mN_2(t-\tau) + N_1(t-\tau)}\right]\end{cases} \tag{2}$$

where N_1, N_2 denot the population of preys and predators at time t, respectively. The meaning of all the constants are same as those in model(1). To obtain a deep and clear understanding of dynamics of predator-prey system with time delay, in this paper, we will investigate the Hopf bifurcation of system(2).

2 Stability of the positive equilibrium and local Hopf bifurcations

It is easy to see that system(2) has a unique positive equilibrium $E_0(N_1^*, N_2^*)$, where

$$N_1^* = \frac{amr - cr + cd}{bmr}, N_2^* = \frac{(r-d)(amr - cr + cd)}{bdm^2 r}$$

if the following condition

$$(\text{H1})\ amr - cr + cd > 0, r - d > 0$$

holds. Let $\overline{N}_1(t) = N_1(t) - N_1^*$, $\overline{N}_2(t) = N_2(t) - N_2^*$ and drop the bar for the simpli-fication of notations, then the linearization of Eq. (2) at $E_0(N_1^*, N_2^*)$ is

$$\begin{cases}\dot{N}_1(t) = k_1 N_1(t) + k_2 N_1(t-\tau) + k_3 N_2(t-\tau) \\ \dot{N}_2(t) = l_1 N_2(t) + l_2 N_1(t-\tau) + l_3 N_2(t-\tau)\end{cases} \tag{3}$$

where

$$k_1 = a - bN_1^* - \frac{cN_2^*}{mN_2^* + N_1^*}, k_2 = \frac{cN_1^* N_2^*}{(mN_2^* + N_1^*)^2} - b_1 N_1^*, k_3 = \frac{cmN_1^* N_2^*}{(mN_2^* + N_1^*)^2} - \frac{cN_1^*}{mN_2^* + N_1^*}$$

$$l_1 = \frac{rN_1^*}{mN_2^* + N_1^*} - d, l_2 = \frac{rN_2^*}{mN_2^* + N_1^*} - \frac{rN_1^* N_2^*}{(mN_2^* + N_1^*)^2}, l_3 = -\frac{mN_2^*}{(mN_2^* + N_1^*)^2}$$

The characteristic equation of system(3) takes the form

$$\lambda^2 + p_1\lambda + p_2 + (q_1\lambda + q_2)e^{-\lambda\tau} + r_1 e^{-2\lambda\tau} = 0 \tag{4}$$

where

$$p_1 = -(k_1 + l_1), p_2 = k_1 l_1, q_1 = -(l_3 + k_2), q_2 = k_1 l_3 + k_2 l_1, r_1 = k_2 l_3 - l_2 k_3$$

Multiplying $e^{\lambda\tau}$ on both sides of (4), it is obvious to obtain

$$(\lambda^2 + p_1\lambda + p_2)e^{\lambda\tau} + (q_1\lambda + q) + r_1 e^{-\lambda\tau} = 0 \tag{5}$$

In the sequel, we will investigate the locations of the roots of the characteristic equation(4).

For $\tau = 0$, equation(5) becomes

$$\lambda^2 + (p_1 + q_1)\lambda + p_2 + q_2 + r_1 = 0 \tag{6}$$

It is easy to see that a set of necessary and sufficient conditions which all roots of (6) have a negative real part is given in the following form:

$$(\text{H2})\ p_1 + q_1 > 0, p_2 + q_2 + r_1 > 0$$

Let $\lambda = i\omega_0 > 0, \tau = \tau_0$, and substituting this into(5), for the sake of simplicity, denote ω_0 and τ_0 by ω, τ, respectively, separating the real and imaginary parts, we have

$$\begin{cases}(p_2 - \omega^2 + r_1)\cos\omega\tau - p_1\omega\sin\omega\tau = -q_2 \\ (p_2 - \omega^2 + r_1)\sin\omega\tau + p_1\omega\cos\omega\tau = -q_1\omega\end{cases} \tag{7}$$

By simple calculation, the following equations are obtained

$$\sin\omega\tau = \frac{p_1 q_2\omega - q_1\omega(p_2 - \omega^2 + r_1)}{(p_2 - \omega^2 + r_1)(p_2 - \omega^2 - r_1)} \tag{8}$$

$$\cos\omega\tau = -\frac{p_1 q_1\omega + q_2\omega(p_2 - \omega^2 - r_1)}{(p_2 - \omega^2 + r_1)(p_2 - \omega^2 - r_1)} \tag{9}$$

As is known to all that $\sin^2\omega\tau+\cos^2\omega\tau=1$, if the condition

$$(H3)\ p_1q_1\neq 0$$

holds, we have

$$\omega^4-\omega^3+v_2\omega^2+v_1\omega+v_0=0 \tag{10}$$

where

$$v_2=\frac{p_1(p_1q_1+q_2r_1-p_2q_2)+p_2q_2}{p_1q_1}, v_1=q_2+r_1, v_0=\frac{q_2r_1(p_2+r_1)+q_2r_1^2}{p_1q_1}$$

Let

$$l(\omega)=\omega^4-\omega^3+v_2\omega^2+v_1\omega+v_0 \tag{11}$$

Suppose

(H4) (10) has at least one positive real root.

If all the coefficients of system(2) are given, it is easy to use computer to calculate the roots of (10). Since $\lim_{\omega\to+\infty}l(\omega)=+\infty$, we can conclude that if $v_0<0$, then (10) has at least one positive real root.

Without loss of generality, we assume that (10) has four positive roots denoted by $\omega_1,\omega_2,\omega_3,\omega_4$, respectively. Then by(9), we have

$$\tau_k^j=\frac{1}{\omega_k}\left[\arccos\frac{p_1q_1\omega_k+q_2\omega_k(p_2-\omega_k^2-r_1)}{(p_2-\omega_k^2+r_1)(p_2-\omega_k^2-r_1)}+2j\pi\right](k=1,2,3,4;j=0,1,2,\cdots) \tag{12}$$

at which Eq. (5) has a pair of purely imaginary roots $\pm i\omega_k$. Let $\lambda(\tau)=\alpha(\tau)+i\omega(t)$ be the root of Eq. (5) such that $\alpha(\tau_k^j)=0, \omega(\tau_k^j)=\omega_k$. Due to functional differnetial equation theory, for every $\tau_k^j, k=1,2,3,4; j=0,1,2,\cdots$, there exists $\varepsilon>0$ such that $\lambda(\tau)$ is continuously differentiable in τ for $|\tau-\tau_k^j|<\varepsilon$. Substituting $\lambda(\tau)$ into the left hand side of (5) and taking derivative with respect to τ, we have

$$\left(\frac{d\lambda}{d\tau}\right)^{-1}=-\frac{(2\lambda+p_1)e^{\lambda\tau}+q_1}{\lambda[(\lambda^2+p_1\lambda+p_2)e^{\lambda\tau}-r_1e^{-\lambda\tau}]}-\frac{\tau}{\lambda}$$

which, together with (7), leads to

$$\text{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}_{\tau=\tau_k^j}=\left\{\frac{(p_1q_1^2-2q_2)\omega^2\cos\omega\tau-(2q_1^2\omega^2+p_1q_2)\omega\sin\omega\tau+q_1^2\omega^2}{q_1^2\omega^4+q_2^2\omega^2}\right\}_{\tau=\tau_k^j}$$

Let $M=q_1^2\omega_k^4+q_2^2\omega_k^2>0$. It follows from (8) and(9) that

$$M\text{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}_{\tau=\tau_k^j}=(p_1q_1^2-2q_2)\omega_k^2\cos\omega_k\tau-(2q_1^2\omega_k^2+p_1q_2)\omega_k\sin\omega_k\tau+q_1^2\omega_k^2=$$

$$\frac{\omega_k^3[(2q_2-p_1q_1^2)(p_1q_1+q_2(p_2-\omega_k^2-r_1))]}{(p_2-\omega_k^2+r_1)(p_2-\omega_k^2-r_1)}+\frac{\omega_k^2\{(2q_1^2\omega_k+p_1q_2)[q_1(p_2-\omega_k^2+r_1)-p_1q_2]\}+q_1^2\omega_k^2]}{(p_2-\omega_k^2+r_1)(p_2-\omega_k^2-r_1)}$$

Notice that

$$\text{sign}\left[\text{Re}\left(\frac{d\lambda}{d\tau}\right)\bigg|_{\tau=\tau_k^j}\right]=\text{sign}\left[\text{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\bigg|_{\tau=\tau_k^j}\right]$$

In order to give the main results in this paper, it is necessary to make the following assumptlions:

$$(H5)\ \text{Re}\left(\frac{d\lambda}{d\tau}\right)\bigg|_{\tau=\tau_k^j}\neq 0$$

Employing the results of Yang[13] and Hale[14], we have

Theorem 1 Let $\tau_k^j(k=1,2,3,4;j=0,1,2,\cdots)$ be defined by (12) and $\tau_0=\min\{\tau_k^j\}$. Suppose that $(H_1),(H_2),(H_3),(H_4),(H_5)$ hold, then the positive equilibrium $E_0(N_1^*,N_2^*)$ of system (2) is asymptotically stable for $\tau\in[0,\tau_0)$. System(2) undergoes a Hopf bifurcation at the positive equilibrium $E_0(N_1^*,N_2^*)$ when $\tau=\tau_k^j, k=1,2,3,4; j=0,1,2,\cdots$

3 Estimation of the length of delay to preserve stability

In the present section, we will obtain an estimation τ_+ for the length of the delay τ which preserves the stability of the positive equilibrium $E_0(N_1^*, N_2^*)$, i.e., $E_0(N_1^*, N_2^*)$ is asymptotically stable if $\tau < \tau_+$.

We consider system(3) in $C([-\tau, \infty), R^2)$ with the initial values

$$N_1(\xi) = \varphi_1(\xi),\ N_2(\xi) = \varphi_2(\xi), \varphi_i(0) \geqslant 0, i = 1,2, \xi \in [-\tau, 0]$$

Taking Laplace transform of system (3), we get

$$\begin{cases}(s - k_1)\tilde{N}_1 = k_2 e^{-s\tau} M_1(s) + k_2 e^{-s\tau}\tilde{N}_1 + k_3 e^{-s\tau} M_2(s) + k_3 e^{-s\tau}\tilde{N}_2 + \varphi_1(0) \\ (s - l_1)\tilde{N}_2 = l_2 e^{-s\tau} M_1(s) + l_2 e^{-s\tau}\tilde{N}_1 + l_3 e^{-s\tau} M_2(s) + l_3 e^{-s\tau}\tilde{N}_2 + \varphi_2(0)\end{cases} \tag{13}$$

where $\tilde{N}_1, \tilde{N}_2$ are the Laplace transform of $N_1(t), N_2(t)$, respectively, and $M_1(s) = \int_{-\tau}^{0} e^{-s\tau} N_1(t)\,dt$, $M_2(s) = \int_{-\tau}^{0} e^{-s\tau} N_2(t)\,dt$.

Solving (13) for $\tilde{N}_1$ leads to $\tilde{N}_1 = \dfrac{K(s,\tau)}{J(S)}$, where

$$K(s,\tau) = k_3 e^{-s\tau}[l_2 e^{-s\tau} M_1(s) + l_3 e^{-s\tau} M_2(s) + \varphi_2(0)] - l_3 e^{-s\tau}[k_2 e^{-s\tau} M_1(s) + k_3 e^{-s\tau} M_2(s) + \varphi_1(0)]$$

$$J(s) = (s - l_1 - l_2 e^{-s\tau}) k_3 e^{-s\tau} - (s - k_1 - k_2 e^{-s\tau}) l_3 e^{-s\tau}$$

Following along the lines of [15] and using the Nyquist criterion, we obtain that the conditions for local asymptotic stability of $E_0(N_1^*, N_2^*)$ are given by

$$\mathrm{Im}\ \{J(i\omega_0)\} > 0 \tag{14}$$

$$\mathrm{Re}\ \{J(i\omega_0)\} = 0 \tag{15}$$

where Im $\{J(i\omega_0)\}$ and Re $\{J(i\omega_0)\}$ are the imaginary part and real part of $J(i\omega_0)$, respectively and ω_0 is the small positive root of (15).

It follows from (14) and (15) that

$$q_2\omega_0 > (\omega_0^2 - r_1 - p_2)\sin\omega_0\tau - p_1\omega_0\cos\omega_0\tau \tag{16}$$

$$(p_2 - \omega_0^2 + r_1)\cos\omega_0\tau - p_1\omega\sin\omega_0\tau = -q_2 \tag{17}$$

From (16), we obtain

$$q_2\omega_0 > |\omega_0^2 - r_1 - p_2| + |p_1|\omega_0 \tag{18}$$

Then

$$\omega_0^2 - (q_2 - |p_1|)\omega_0 - |r_1 + p_2| < 0 \tag{19}$$

which leads to $\omega_0 \leqslant \omega_+$, where $\omega_+ = \dfrac{q_2 - |p_1| + \sqrt{(q_2 - |p_1|)^2 + 4|r_1 + p_2|}}{2}$. By (17), we have

$$(p_2 - \omega_0^2 + r_1)(\cos\omega_0\tau - 1) - p_1\omega\sin\omega_0\tau = \omega_0^2 - p_2 - r_1 - q_2 \tag{20}$$

Since $(p_2 - \omega_0^2 + r_1)(\cos\omega_0\tau - 1) \leqslant \dfrac{1}{2}|p_2 - \omega_0^2 + r_1|\omega_+^2\tau^2$ and $-p_1\omega\sin\omega_0\tau \leqslant |p_1|\omega_+^2\tau$, we obtain from (20) that $L_1\tau^2 + L_2\tau \leqslant L_3$, where $L_1 = \dfrac{1}{2}|p - 2 - \omega_0^2 + r_1|\omega_+^2$, $L_2 = |p_1|\omega_+^2$, $L_3 = \omega_0^2 - p_2 - r_1 - q_2$. It is easy to see that if $\tau < \tau_+ = \dfrac{-L_2 + \sqrt{L_2^2 + 4L_1L_3}}{2L_1}$, the stability of $E_0(N_1^*, N_2^*)$ of system (2) is preserved.

4 Numerical examples

In this section, we give some numerical simulations of a special version of system (2) with ratio-dependent type functional response to verify the analytical predictions obtained in Section 2. Let us consider the following system:

$$\begin{cases} N_1(t) = N_1(t)\left[1 - 2N_1(t-\tau) - \dfrac{0.3\,N_2(t-\tau)}{0.5\,N_2(t-\tau) + N_1(t-\tau)}\right] \\ N_2(t) = N_2(t)\left[-0.8 + \dfrac{2N_1(t-\tau)}{0.5N_2(t-\tau) + N_1(t-\tau)}\right] \end{cases} \tag{21}$$

which has a positive equilibrium $E_0(0.32, 0.96)$ and satisfies the conditions indicated in Theorem 1. When $\tau = 0$, the positive equilibrium $E_0(0.32, 0.96)$ is asymp-totically stable. The positive equilibrium $E_0(0.32, 0.96)$ is stable when $\tau < \tau_0 \approx 1.94$ as is illustrated by the computer simulations (see Fig. 1). When τ passes through the critical value τ_0, the positive equilibrium loses its stability and a Hopf bifurcation occurs, i. e., a family of periodic solutions bifurcate from the positive equilibrium $E_0(0.32, 0.96)$ (see Fig. 2).

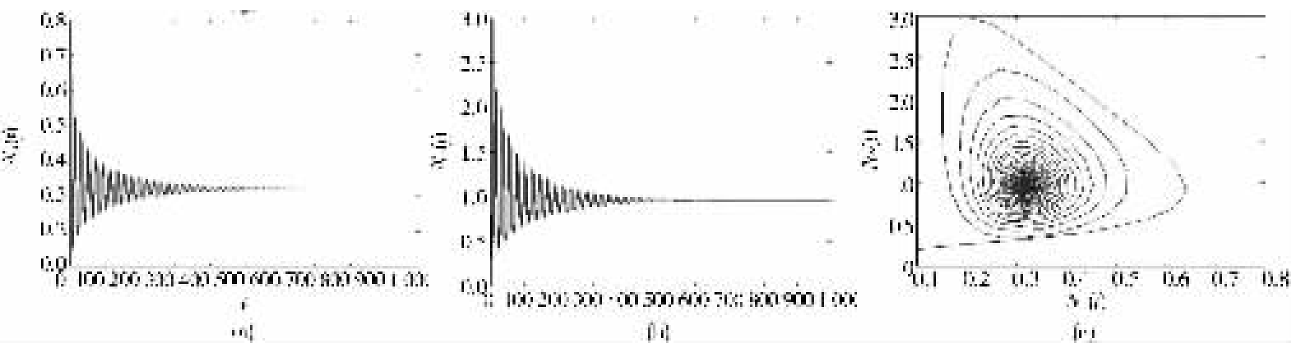

Fig. 1　Behavior and phase portrait of system (21) with $\tau = 1.9 < \tau_0 \approx 1.94$. The positive equilibrium $E_0(0.32, 0.96)$ is asymptotically stable. The initial value is (0.1, 0.2)

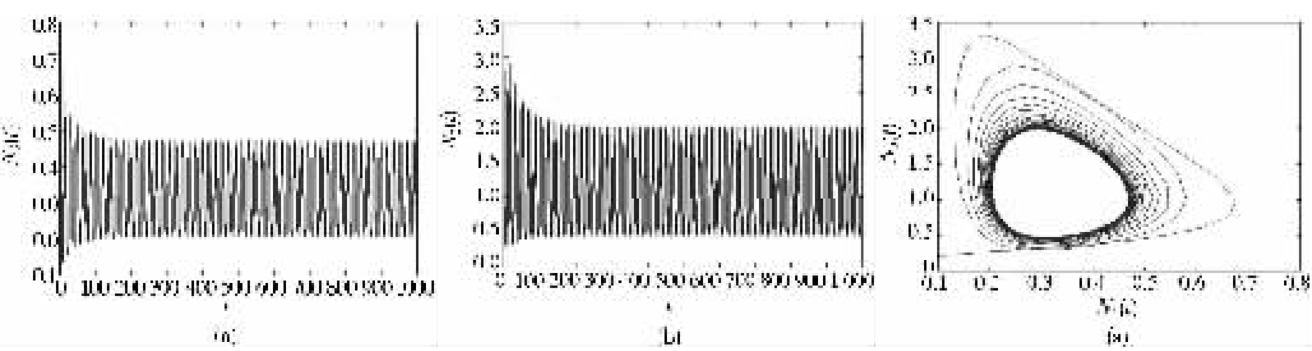

Fig. 2　Behavior and phase portrait of system (21) with $\tau = 2 > \tau_0 \approx 1.94$. Hopf bifurcation occurs from the positive equilibrium $E_0(0.32, 0.96)$. The initial value is (0.1, 0.2)

5 Conclusions

In this paper, we have investigated local stability of the positive equilibrium $E_0(N_1^*, N_2^*)$ and local Hopf bifurcation in a predator-prey model with time delay. We have showed that if the conditions (H1), (H2), (H3), (H4), (H5) hold, the positive equilibrium $E_0(N_1^*, N_2^*)$ of system (2) is asymptotically stable for all $\tau \in [0, \tau_0)$. As the delay τ increases, the positive equilibrium loses its stability and a sequence of Hopf bifurcations occur at the positive equilibrium $E_0(N_1^*, N_2^*)$, i. e., a family of periodic orbits bifurcates from the the positive equilibrium $E_0(N_1^*, N_2^*)$. Meanwhile, the length of delay preserving the stability of the positive equilibrium $E_0(N_1^*, N_2^*)$ is estimated, i. e., the length of delay is τ_+. Numerical simulations have also been demonstrated the validity of our theoretical analysis.

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具有时滞的食饵-捕食者模型的分支问题

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摘要:研究一类具有时滞和比率依赖型功能反应函数的食饵-捕食者模型的动力学行为,分析表明系统的渐近稳定关键依赖于时滞。通过选择时滞作为参数,分析了系统从正平衡点处产生极限环的Hopf分支问题,同时得到了系统正平衡点稳定的时滞范围为$0<\tau<\tau_+$,给出数值模拟验证了作者所得结果的正确性。最后给出本文的主要结论:当$\tau\in[0,\tau_0)$时,系统(2)的平衡点是渐近稳定的,当$\tau=\tau_k^j$, $k=1,2,3,4$;$j=0,1,2,\cdots$时,系统(2)在平衡点附近产生Hopf分支,时滞长度为τ_+。

关键词:食饵-捕食者模型;时滞;稳定性;Hopf分支;周期解

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