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一类具分段常数变量的捕食-食饵系统的 Neimark-Sacker 分支

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摘要:讨论了具时滞与分段常数变量的捕食-食饵生态模型的稳定性及 Neimark-Sacker 分支;通过计算得到连续模型对应的差分 模型,基于特征值理论和 Schur-Cohn 判据得到正平衡态局部渐进稳定的充分条件;以食饵的内禀增长率为分支参数,运用分支 理论和中心流形定理分析了 Neimark-Sacker 分支的存在性与稳定性条件;通过举例和数值模拟验证了理论的正确性。 关键词:分段常数变量;时滞;稳定性;Neimark-Sacker 分支

Neimark-Sacker bifurcation behavior of predator-prey system with piecewise constant arguments

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Abstract: The dynamic relationship between prey and predator has long been and will continue to be a dominant theme in ecology because of its universality. The prey-predator interaction, one of the most fundamental interspecies interactions, was first described mathematically by Lotka and Volterra in two independent works, resulting in what are now called the Lotka-Volterra equations. A predator-prey model based on the logistic equation was initially proposed by Alfred J. Lotka in 1910 to describe autocatalytic reactions. He later developed this model and in 1925 arrived at the Lotka-Volterra equations that we know today. Almost at the same time (1926), Vito Volterra, an Italian mathematician, independently established the Lotka-Volterra model after analyzing statistical data of fish catches in the Adriatic. The Lotka-Volterra equation is one of the fundamental population models in theoretical biology. Since these early works, prey-predator interactions have been studied systematically. Much of this work has focused on models with continuous time delay as well as their stability, oscillations, Hopf bifurcations and limit cycles, but no attention has been paid to models with piecewise constant arguments and a time delay. In fact, because of environmental factors or predator characteristics, prey are often captured only during certain times of the season. In addition, there is a time delay before hunting because of predator maturation times in practical predatorprey systems. Therefore, it is more realistic to employ the functional response with piecewise constant arguments and a time delay in predator-prey models. In this paper, we discuss the stability and bifurcations of predator-prey systems with piecewise constant arguments and a time delay. First, a discrete model that can equivalently describe the dynamical behavior of the original differential model is deduced. Sufficient conditions for the local asymptotic stability of the steady state are achieved based on an analysis of the eigenvalues and Schur-Cohn criterion. Second, by choosing a parameter r, the

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intrinsic growth rate of prey, as the bifurcation parameter and using the bifurcation theory and center manifold, we find that the discrete model undergoes a Neimark-Sacker bifurcation at an exceptive value of r. The results show that 1) the stability of the predator-prey system is very complex when we consider piecewise constant arguments and a time delay; and 2) the positive equilibrium of the model switches from being stable to unstable as the intrinsic growth rate of prey increases beyond a critical value, at which point the unique supercritical Neimark-Sacker bifurcation will occur. Finally, computer simulations based on the system supported our main results and illustrated them intuitively. The numerical examples also justify the reasonableness of the conditions given in our paper for the loss of equilibrium. The parameters of the predatorprey model come from nature. However, we can still add to the model a feedback control factor and interference from outside to change the equilibrium, bifurcation point, or amplitude of the periodic solution. Study of our model and its ameliorated version can provide a theoretical basis for understanding ecology and protecting the environment.

Key Words: piecewise constant arguments; delay; stability; Neimark-Sacker bifurcation

种群生态学是迄今数学在生态学中应用最为广泛、发展最为成熟的生态学的分支。捕食-食饵系统是种 群生态学中生物种群相互之间的基本关系之一,是构成复杂食物链、食物网和生物化学网络结构的基石,从而 引起了广大数学工作者和生物学家的关注。祁君和苏志勇^[1]在经典的捕食-食饵系统中考虑到由于捕食效应 对食饵种群带来的正向调节作用后,提出了具有捕食正效应的捕食-食饵系统。从理论上说明了正向调节作 用对系统的影响,并就第一象限内平衡点存在时的相图解释了捕食正效应的作用。杨立和李维德^[2]利用概 率元胞自动机模型对空间隐式的、食饵具 Allee 效应的一类捕食-食饵模型进行模拟,发现随着相关参数的变 化,种群的空间扩散前沿由连续的扩散波逐渐转变为一种相互隔离的斑块向外扩散。Freedman 与 Wolkowicz 在 Rosenzweig-MacArthur 模型^[3]中选取第4 功能反应函数进行了全局范围内的分支情况的研究。经典的捕 食-食饵模型可以被表达成如下的非线性微分方程模型:

$$\begin{cases} \frac{\mathrm{d}x(t)}{\mathrm{d}t} = xf(x) - yg(x,y) \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} = y(-s + h(x,y)) \end{cases}$$

该类模型稳定性、Hopf 分支、极限环等问题被广泛的给予研究^[4-12],式中 x(t),y(t),分别表示 t 时刻捕食 者和食饵种群的数量,s 表示捕食者的自然死亡率,f(x) 表示食饵在无捕食者时的相对增长率,捕食者单位时 间内捕获食饵的数量用功能反应函数 g(x,y)表示。实际上,由于受到气候、周围环境和捕食者所固有的特性 等因素影响,捕食者对食饵的捕获只在一定时间段或整数时刻并且对食饵的捕获具有滞后效应,故可选择更 加符合实际的具分段常数变量功能反应函数: $g(x,y) = \frac{ra_2x(t)y([t-1])}{y(t)}$, $h(x,y) = b_1x([t]) - b_2y(t)$ 。本文 考虑食饵在无捕食者时按通常的 Logistic 方式增长, $f(x) = r(1-a_1x(t))$,则模型可描述为:

$$\begin{cases} \frac{\mathrm{d}x(t)}{\mathrm{d}t} = rx(t) \left[1 - a_1 x(t) - a_2 y(\left[t - 1 \right] \right) \right] \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} = y(t) \left[-s + b_1 x(\left[t \right]) - b_2 y(t) \right] \end{cases}$$
(1)

模型(1)满足初始条件:

$$x(0) = x_0 > 0y(s) = \varphi(s) \ge 0, \varphi(0) > 0, \varphi \in C([-1,0], R_+)$$
(2)

式中,r表示食饵的内禀增长率, a_1 表示食饵的环境容纳量, a_2 表示捕食系数, b_1 表示捕食效率常数,[t]表示 对变量 $t \in [0, +\infty)$ 取整。

1 正平衡态稳定性分析

由模型(1)可知 $b_1 > a_1 s$ 时,模型(1)存在惟一的正平衡态:

$$E(\bar{x}, \bar{y}) = E(\frac{b_2 + sa_2}{a_1b_2 + a_2b_1}, \frac{b_1 - sa_1}{a_1b_2 + a_2b_1})$$

定理1模型(1)满足初始条件(2)的解为正、全局存在且有界(∀t≥0)。 说明:对定理1运用反证法和比较原理即可得证,故将其证明略去。 当 n≤t<n+1时,模型(1)为:

$$\begin{cases} \frac{dx(t)}{dt} = rx(t) \left[1 - a_1 x(t) - a_2 y(n-1) \right] \\ \frac{dy(t)}{dt} = y(t) \left[-s + b_1 x(n) - b_2 y(t) \right] \end{cases}$$
(3)

对(3)由 n 到 t 积分并令 t→n+1,即得:

$$x(n+1) = \frac{x(n)}{\left[e^{-h} + \frac{ra_1}{h}x(n)(1 - e^{-h})\right]}$$
(4)

$$y(n+1) = \frac{y(n)}{\left[e^{-q} + \frac{b_2}{q}y(n)(1 - e^{-q})\right]}$$

其中: $h=r[1-a_2y(n-1)]$, $q=-s+b_1x(n)$,对(4)在平衡态 $E(\bar{x},\bar{y})$ 处 Taylor 展开,令:

$$x(n) = \psi(n) + \bar{x}$$

 $y(n) = \varphi(n) + \bar{y}$ (5)得(4)式的线性近似系统 $v(n+1) = Av(n) + Bv(n-1)$
 $v(n) = (\psi(n), \varphi(n))^{\mathrm{T}}$

$$A = \begin{pmatrix} P & 0 \\ -\frac{b_1}{b_2} (e^{-b_2 \bar{y}} - 1) & e^{-b_2 \bar{y}} \end{pmatrix}, B = \begin{pmatrix} 0 & \frac{a_2}{a_1} (P - 1) \\ 0 & 0 \end{pmatrix}, P = e^{-ra_1 \bar{x}}$$

则线性系统(5)的特征方程为 $\lambda^3 + \vartheta_1 \lambda^2 + \vartheta_2 \lambda + \vartheta_3 = 0$

其中

$$\vartheta_{1} = -(P + e^{-b_{2}\bar{y}}), \vartheta_{2} = e^{-b_{2}\bar{y}}P, \vartheta_{3} = \frac{a_{2}b_{1}}{a_{1}b_{2}}(e^{-b_{2}\bar{y}} - 1)(P - 1)$$

以下应用 Schur-Cohn 判据^[13]对模型(1)正平衡态稳定性进行分析,给出捕食者和食饵共存且数量保持 稳定的条件。

定理2模型(1)满足下列5种情况之一:

(1) 当
$$M_3 > 1, M_4 < 0, \Delta > 0$$
时, max $(P_1, \frac{M_3 - 1}{M_3}) < P < 1$;
(2)当 $M_3 = 1$ 时, $P_5 < P < 1$;
(3)当 $M_3 < 1$ 且 $\Delta < 0$ 或 $M_4 < 0, M_5 < 0, \Delta > 0$ 或 $M_4 > 0, M_5 < 0, \Delta > 0, 2M_3 + \frac{a_1b_2}{a_2b_1}(1 - M_3)M_3 < 1$ 时, $0 < P < 1$;
(4)当 $M_3 < 1, M_4 > 0, M_5 < 0, \Delta > 0, 2M_3 + \frac{a_1b_2}{a_2b_1}(1 - M_3)M_3 > 1$ 时, $0 < P < P_2$ 或 $P_1 < P < 1$;
(5)当 $M_3 < 1, M_5 > 0, \Delta > 0$ 时, $P_1 < P < 1$;
则正平衡态 $E(\bar{x}, \bar{y})$ 局部渐近稳定。

(6)

$$M_1 = \frac{a_2 b_1}{a_1 b_2} (1 - e^{-b_2 \bar{y}}) + e^{-b_2 \bar{y}} + 1, M_2 = \frac{a_2 b_1}{a_1 b_2} (1 - e^{-b_2 \bar{y}}) - e^{-b_2 \bar{y}} - 1$$

其中:

$$M_{3} = \frac{a_{2}b_{1}}{a_{1}b_{2}} (1 - e^{-b_{2}\bar{y}}), M_{4} = e^{-b_{2}\bar{y}} + M_{3} - e^{-b_{2}\bar{y}} M_{3} - 2M_{3}^{2}, M_{5} = e^{-b_{2}\bar{y}} M_{3} + M_{3}^{2} - 1$$

$$\Delta = M_4^2 - 4(M_3^2 - M_3)M_5, P_1 = \frac{-M_4 - \sqrt{\Delta}}{2(M_3^2 - M_3)}, P_2 = \frac{-M_4 + \sqrt{\Delta}}{2(M_3^2 - M_3)}$$

证明 由 $P = e^{-ra_1 \hat{x}}$ 知 0 < P < 1,根据文献^[13],模型(1)满足如下 3 个条件: (H₁) | $\vartheta_1 + \vartheta_3 | < \vartheta_2 + 1$;(H₂) | $\vartheta_3 | < 1$;(H₃) | $\vartheta_2 - \vartheta_1 \vartheta_3 | < |1 - \vartheta_3|^2$ |

1

则正平衡态
$$E(\bar{x},\bar{y})$$
 局部渐近稳定

首先考虑条件(H₁) (H₁)⇔
$$\left| -(P+e^{-b_{2}\bar{y}}) + \frac{a_{2}b_{1}}{a_{1}b_{2}}(e^{-b_{2}\bar{y}}-1)(P-1) \right| < Pe^{-b_{2}\bar{y}} + 1 ⇔ M_{1}P > M_{2}$$

$$\mathbb{E}\left[\frac{a_{2}b_{1}}{a_{1}b_{2}}(1-e^{-b_{2}\bar{y}}) - e^{-b_{2}\bar{y}} + 1\right]P < \frac{a_{2}b_{1}}{a_{1}b_{2}}(1-e^{-b_{2}\bar{y}}) - e^{-b_{2}\bar{y}} + 1 \ \$\$\$\$\$\$\$\$\$\$\$\$Typ Typ Ts, \$\$(i) \\$\]
(i) \\$\] $M_{2} < 0 \ B, 0 < P < 1; (ii) \\$\] $M_{2} > 0 \ B, \frac{M_{2}}{M_{1}} < P < 1_{\circ}$$$$

其次考虑条件(H₂) 由 $\vartheta_3 > 0$ 知(H₂) ⇔ $\frac{a_2 b_1}{a_1 b_2} (1 - e^{-b_2 y}) (1 - P) < 1$ 等价于如下条件(iii) 或(iv):(iii) 当

 $M_3 \le 1$ 时,0<P<1;(iv) 当 $M_3 > 1$ 时, $\frac{M_3 - 1}{M_3} < P < 1_{\circ}$

最后考虑条件(H₃) 由 $\vartheta_1 < 0, \vartheta_2 > 0, \vartheta_3 > 0$ 知(H₂)和(H₃)⇔($M_3^2 - M_3$) $P^2 + M_4 P + M_5 < 0$ 等价于如下条件 (v)或(vi):

(v) 当 $M_3>1$ 时,知 $M_5>0$,若 $\Delta<0$ 或 $\Delta>0, M_4>0$ (此时 $P_i<0(i=1,2)$),则其交集为空集;若 $\Delta>0, M_4<0$, 知 $P_i>0(i=1,2), P_1<P<P_2$,设函数

 $f(x) = (M_3^2 - M_3)P^2 + M_4P + M_5, \text{ if } f(1) = M_3^2 - M_3 + M_4 + M_5 = e^{-b_2 y} - 1 < 0 \text{ } \text{ } \text{ } P_1 < 1 < P_2, \text{ } \text{ } \text{ } P_1 < P < 1$

(vi) 当 $M_3 = 1$ 时,知 $M_2 = -e^{-b_2 \bar{y}}, M_4 = -1, M_5 = e^{-b_2 \bar{y}}, 则 M_5 < P_{\odot}$

(vii) 当 $M_3 < 1$ 时,知 $M_3^2 - M_3 < 0$,若 $\Delta < 0$ 时,0<P<1;若 $\Delta > 0$, $M_4 < 0$, $M_5 < 0$,则当 $P_i < 0$ (i=1,2)时,0<P<1; 若 $\Delta > 0$, $M_4 > 0$, $M_5 > 0$ 或 $\Delta > 0$, $M_4 < 0$, $M_5 > 0$ 时,知 $P_1 > 0$, $P_2 < 0$,由f(1) < 0得 $P_1 < 1$,则 $P_1 < P < 1$;若 $\Delta > 0$, $M_4 > 0$, $M_5 < 0$,

由
$$f(1) < 0$$
 知 $1 < P_2 < P_1$ 或 $0 < P_2 < P_1 < 1$,若 $2M_3 + \frac{a_1b_2}{a_2b_1}(1-M_3)M_3 < 1$,

$$\mathbb{M}f'(1) = -(M_3 - e^{-b_2\bar{y}} + e^{-b_2\bar{y}}M_3) = -[2M_3 + (1 - e^{-b_2\bar{y}}) - (1 - e^{-b_2\bar{y}})M_3 - 1] = -[2M_3 + \frac{a_1b_2}{a_2b_1}(1 - M_3)M_3 - 1] > 0, \pm \mathbb{M}$$

知 1< P_2 < P_1 ,故 0<P<1.若 2 M_3 + $\frac{a_1b_2}{a_2b_1}$ (1- M_3) M_3 >1,则f(1)<0,

由此知 0<*P*₂<*P*₁<1,故 0<*P*<*P*₂ 或 *P*₁<*P*<1。综合上述讨论与计算,由(i)、(iv)、(v)或(ii)、(iv)、(v)取 交集可得定理中(1)的结论,由(i)、(iii)、(vi)取交集可得定理中(2)的结论,由(i)、(iii)、(vii)取交集可得定 理中(3)、(4)、(5)的结论,证毕。

2 Neimark-Sacker 分支分析

本节以 r 作为分支参数,分别讨论模型(1)的 Neimark-sacker 分支存在性及其分支方向与稳定性。因情况(2)不会产生分支(分支临界值 r₀ 趋于零或无穷大),故下文对定理 2 中(1)的情况给出产生分支的条件,

情况(3)的分支条件可同理给出。

定理3设(1)中的参数满足 $M_3>1, M_4<0, \Delta>0, 则当\max(P_1, \frac{M_3-1}{M_3}) < P<1$ 时,(1)的正平衡态 $E(\bar{x}, \bar{y})$ 局 部渐近稳定;当 $P=\max(P_1, \frac{M_3-1}{M_3})$ 时,(6)存在一对位于单位圆环上共轭的特征根,且不存在 $\lambda=\pm 1$ 的根;当 $P > \max(P_1, \frac{M_3-1}{M_2})$ 时,(1)的正平衡态 $E(\bar{x}, \bar{y})$ 不稳定,则(1)产生 Neimark-sacker 分支。 证明:由定理2可知,当 $M_3>1, M_4<0, \Delta>0$ 时,若 $\max(P_1, \frac{M_3-1}{M_2}) < P < 1, 则(1) 正平衡态 E(x, y) 局部渐近$ 稳定;当 $P=\max(P_1, \frac{M_3-1}{M_3})$ 时,假设 $\lambda_{1,2}=e^{\pm i\theta_1}$ 是特征方程(6)的一对共轭纯虚根,则有 $\begin{cases} \cos 3\theta_1 + \vartheta_1 \cos 2\theta_1 + \vartheta_2 \cos \theta_1 + \vartheta_3 = 0\\ \sin 3\theta_1 + \vartheta_1 \sin 2\theta_1 + \vartheta_2 \sin \theta_1 = 0 \end{cases}, \quad \forall \texttt{R} \texttt{\#} \texttt{ } \cos \theta_1 = \frac{-\vartheta_1 + \sqrt{\vartheta_1^2 - 4(\vartheta_2 - 1)}}{4};$ 由定理2中对(H₁)分析和 $\frac{M_2}{M_1} < \frac{M_3-1}{M_2}$ 知,(6)不存在 $\lambda = \pm 1$ 的根,证毕。

下面讨论模型(1)的分支方向及其稳定性.将(4)式写作如下变换形式:

$$\begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix} \rightarrow \begin{pmatrix} \frac{x_1}{\left[e^{-h_1} + ra_1(1 - e^{-h_1})x_1/h_1\right]} \\ \frac{x_2}{\left[e^{-q_1} + b_2(1 - e^{-q_1})x_2/q_1\right]} \\ x_2 \end{pmatrix} = \begin{pmatrix} F_1(x_1, x_2, x_3) \\ F_2(x_1, x_2, x_3) \\ F_3(x_1, x_2, x_3) \end{pmatrix}$$
(7)

其中, $h_1 = r[1-a_2x_3]$, $q_1 = -s+b_1x_1$, (7)式在平衡态 $E(\bar{x}, \bar{y}, \bar{y})$ 的临界 Jacobi 矩阵:

$$Z_0 = Z(r_0) = \begin{pmatrix} \overline{P} & 0 & \frac{a_2}{a_1}(\overline{P} - 1) \\ -\frac{b_1}{b_2}(e^{-b_2 \overline{y}} - 1) & e^{-b_2 \overline{y}} & 0 \\ 0 & 1 & 0 \end{pmatrix}$$

由定理3可知Z₀存在一对共轭纯虚根 $\lambda_{1,2} = e^{\pm i\theta_0}, \cos\theta_0 = = \frac{-\overline{\vartheta}_1 + \sqrt{\vartheta}_1^2 - 4(\overline{\vartheta}_2 - 1)}{4}, \overline{P} = e^{-r_0 a_1 \bar{x}},$ $\overline{\vartheta} = -(\overline{P} + e^{-b_{\overline{y}}})$ $\overline{\vartheta}_{z} = e^{-b_{\overline{y}}}\overline{P}_{z}$ 矩阵 Z_a和 Z^T 满足·Z_a $a = e^{i\theta_{0}}a_{z}$ Z_a $T_{p} = e^{-i\theta_{0}}p_{z}$ 目其特征向量分别为

$$q \sim \left(\frac{b_2(e^{-b_2\bar{y}+i\theta_0}-e^{2i\theta_0})}{b_1(e^{-b_2\bar{y}}-1)}, e^{i\theta_0}, 1\right)^T, p \sim \left(\frac{a_1}{a_2(\bar{P}-1)}, \frac{a_1b_2(\bar{P}-e^{-i\theta_0})}{a_2b_1(\bar{P}-1)(e^{-b_2\bar{y}}-1)}, e^{i\theta_0}\right)^T$$

$$\bar{R} \qquad q = \left(\frac{b_2(e^{-b_2\bar{y}+i\theta_0}-e^{2i\theta_0})}{b_1(e^{-b_2\bar{y}}-1)}, e^{i\theta_0}, 1\right)^T, p = \frac{1}{n} \left(\frac{a_1}{(\bar{P}-1)}, \frac{a_1b_2(\bar{P}-e^{-i\theta_0})}{a_2b_1(\bar{P}-1)(e^{-b_2\bar{y}}-1)}, e^{i\theta_0}\right)^T$$

$$|| \langle q, p \rangle = \sum_{i=1}^{3} \bar{q}_{i} p_{i} = 1, \\ || \psi ||_{\kappa} = \frac{a_{1} b_{2} \left[(e^{-b_{2}\bar{y}-i\theta_{0}} - e^{-2i\theta_{0}}) + (\bar{P}e^{-i\theta_{0}} - e^{-2i\theta_{0}}) \right]}{a_{2} b_{1} (e^{-b_{2}\bar{y}} - 1) (\bar{P} - 1)} + e^{i\theta_{0}}, \\ \bar{q}_{i} \\ || \psi ||_{\kappa} = \frac{a_{1} b_{2} \left[(e^{-b_{2}\bar{y}} - i\theta_{0} - e^{-2i\theta_{0}}) + (e^{-i\theta_{0}} - e^{-2i\theta_{0}}) \right]}{a_{2} b_{1} (e^{-b_{2}\bar{y}} - 1) (\bar{P} - 1)} + e^{i\theta_{0}}, \\ \bar{q}_{i} \\ || \psi ||_{\kappa} = \frac{a_{1} b_{2} \left[(e^{-b_{2}\bar{y}} - i\theta_{0} - e^{-2i\theta_{0}}) + (e^{-i\theta_{0}} - e^{-2i\theta_{0}}) \right]}{a_{2} b_{1} (e^{-b_{2}\bar{y}} - 1) (\bar{P} - 1)} + e^{i\theta_{0}}, \\ \bar{q}_{i} \\ || \psi ||_{\kappa} = \frac{a_{1} b_{2} \left[(e^{-i\theta_{0} - e^{-2i\theta_{0}}}) + (e^{-i\theta_{0}} - e^{-2i\theta_{0}}) \right]}{a_{2} b_{1} (e^{-i\theta_{0}} - e^{-2i\theta_{0}}) + (e^{-i\theta_{0}} - e^{-2i\theta_{0}}) \right]} + e^{i\theta_{0}}, \\ \bar{q}_{i} \\ || \psi ||_{\kappa} = \frac{a_{1} b_{2} \left[(e^{-i\theta_{0} - e^{-2i\theta_{0}}}) + (e^{-i\theta_{0} - e^{-2i\theta_{0}}}) \right]}{a_{2} b_{1} (e^{-i\theta_{0} - e^{-2i\theta_{0}}}) + (e^{-i\theta_{0} - e^{-2i\theta_{0}}}) \right]} + e^{i\theta_{0}}, \\ \bar{q}_{i} \\ || \psi ||_{\kappa} = \frac{a_{1} b_{2} \left[(e^{-i\theta_{0} - e^{-2i\theta_{0}}}) + (e^{-i\theta_{0} - e^{-2i\theta_{0}}}) \right]}{a_{2} b_{1} (e^{-i\theta_{0} - e^{-2i\theta_{0}}}) + (e^{-i\theta_{0} - e^{-2i\theta_{0}}}) \right]} + e^{i\theta_{0}}, \\ \bar{q}_{i} \\ || \psi ||_{\kappa} = \frac{a_{1} b_{2} \left[(e^{-i\theta_{0} - e^{-2i\theta_{0}}) + (e^{-i\theta_{0} - e^{-2i\theta_{0}}) \right]}{a_{2} b_{1} (e^{-i\theta_{0} - e^{-2i\theta_{0}}}) - (e^{-i\theta_{0} - e^{-2i\theta_{0}}}) \right]} + e^{i\theta_{0}}, \\ \bar{q}_{i} \\ || \psi ||_{\kappa} = \frac{a_{1} b_{2} \left[(e^{-i\theta_{0} - e^{-2i\theta_{0}}) + (e^{-i\theta_{0} - e^{-2i\theta_{0}}) \right]}{a_{2} b_{1} (e^{-i\theta_{0} - e^{-2i\theta_{0}}}) - (e^$$

将(7)式写为如下形式:

$$x \rightarrow Z_0 x + F(x) = \begin{pmatrix} \overline{P} & 0 & \frac{a_2}{a_1}(\overline{P} - 1) \\ -\frac{b_1}{b_2}(e^{-b_2 \overline{y}} - 1) & e^{-b_2 \overline{y}} & 0 \\ 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix} + \begin{pmatrix} G_1(x) \\ G_2(x) \\ 0 \end{pmatrix}$$

其中 $F(x) = O(||x||^2)$ 是光滑函数且在平衡态 $E(\bar{x}, \bar{y}, \bar{y})$ 的 Taylor 展开式为:

$$F(x) = \frac{1}{2}B(x,x) + \frac{1}{6}C(x,x,x) + O(||x||^4)$$

B(x,y)和 C(x,y,z)分量分别为:

$$B_i(x,y) = \sum_{j,k=1}^3 \frac{\partial^2 F_i(\xi)}{\partial \xi_j \partial \xi_k} \bigg|_{\xi=0} x_j y_k, C_i(x,y,z) = \sum_{j,k,l=1}^3 \frac{\partial^3 F_i(\xi)}{\partial \xi_j \partial \xi_k \partial \xi_l} \bigg|_{\xi=0} x_j y_k z_l, i=1,2,\ldots,n$$

当 $e^{ik\theta_0} \neq 1(k=1,2,3,4)$ 时,映射(7)经坐标变换可化成: $\eta \rightarrow e^{i\theta_0}\eta(1+\zeta |\eta|^2) + O(|\eta|^4)$,其中 ζ 决定闭不 变曲线的分支方向,可由下面公式计算:

$$z_{13}|_{(\bar{x},\bar{y},\bar{y})}(x_2y_2z_1+x_1y_2z_2+x_2y_1z_2)+z_{14}|_{(\bar{x},\bar{y},\bar{y})}x_2y_2z_2,0)^T$$
(9)

将 q, q 代入(8) 和(9) 式可得:

В

$$(q,q) = (\Omega_1, \Omega_2, 0)^T, B(q,\bar{q}) = (\Omega_3, \Omega_4, 0)^T, C(q,q,\bar{q}) = (\Omega_5, \Omega_6, 0)^T$$

其中:

$$\begin{split} & \Omega_{1} = \Big[\frac{b_{2} \Big(e^{-b_{2}\bar{y} + i\theta_{0}} - e^{2i\theta_{0}} \Big)}{b_{1} (e^{-b_{2}\bar{y}} - 1)} \Big]^{2} z_{1} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + \frac{2b_{2} \Big(e^{-b_{2}\bar{y} + i\theta_{0}} - e^{2i\theta_{0}} \Big)}{b_{1} (e^{-b_{2}\bar{y}} - 1)} z_{2} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + z_{3} \Big|_{(\bar{x}, \bar{y}, \bar{y})} \\ & \Omega_{2} = \Big[\frac{b_{2} \Big(e^{-b_{2}\bar{y} + i\theta_{0}} - e^{2i\theta_{0}} \Big)}{b_{1} \Big(e^{-b_{2}\bar{y}} - 1 \Big)} \Big]^{2} z_{4} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + \frac{2b_{2} \Big(e^{-b_{2}\bar{y} + 2i\theta_{0}} - e^{3i\theta_{0}} \Big)}{b_{1} \Big(e^{-b_{2}\bar{y}} - 1 \Big)} z_{5} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + e^{2i\theta_{0}} z_{6} \Big|_{(\bar{x}, \bar{y}, \bar{y})} \\ & \Omega_{3} = \frac{b_{2}^{-2} \Big(e^{-2b_{2}\bar{y}} - e^{-b_{2}\bar{y} + i\theta_{0}} - e^{-b_{2}\bar{y} - i\theta_{0}} + 1 \Big)}{b_{1}^{-2} \Big(e^{-b_{2}\bar{y}} - 1 \Big)^{2}} z_{1} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + \frac{b_{2} \Big[e^{-b_{2}\bar{y}} \Big(e^{i\theta_{0}} + e^{-i\theta_{0}} \Big) - \Big(e^{2i\theta_{0}} + e^{-2i\theta_{0}} \Big) \Big]}{b_{1} \Big(e^{-b_{2}\bar{y}} - 1 \Big)} \times z_{2} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + z_{3} \Big|_{(\bar{x}, \bar{y}, \bar{y})} \\ & \Omega_{4} = \frac{b_{2}^{-2} \Big(e^{-2b_{2}\bar{y}} - e^{-b_{2}\bar{y} + i\theta_{0}} - e^{-b_{2}\bar{y} - i\theta_{0}} + 1 \Big)}{b_{1}^{-2} \Big(e^{-b_{2}\bar{y} - 1} \Big)^{2}} z_{4} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + \frac{b_{2} \Big(e^{-b_{2}\bar{y} - e^{-b_{2}\bar{y} + i\theta_{0}} - e^{i\theta_{0}} - e^{3i\theta_{0}} \Big)}{b_{1} \Big(e^{-b_{2}\bar{y}} - 1 \Big)} \times z_{5} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + z_{6} \Big|_{(\bar{x}, \bar{y}, \bar{y})} \\ & \Omega_{5} = \Big[\frac{b_{2}^{-3} \Big(e^{-b_{2}\bar{y} + i\theta_{0} - e^{2i\theta_{0}} \Big)^{2} \Big(e^{-b_{2}\bar{y} - i\theta_{0}} - e^{-2i\theta_{0}} \Big)}{b_{1}^{-3} \Big(e^{-b_{2}\bar{y} - 1} \Big)^{3}} z_{7} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + \Big\{ \frac{b_{2} \Big(e^{-b_{2}\bar{y} + i\theta_{0} - e^{2i\theta_{0}} \Big)}{b_{1} \Big(e^{-b_{2}\bar{y}} - 1 \Big)} \Big]^{2} + \frac{2b_{2}^{-2} \Big(e^{-2b_{2}\bar{y} - 1} \Big)^{2}}{b_{1}^{-2} \Big(e^{-b_{2}\bar{y} - i\theta_{0}} - e^{-2i\theta_{0}} \Big)}{b_{1}^{-2} \Big(e^{-b_{2}\bar{y} - i\theta_{0}} + 1 \Big)^{2}} z_{8} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + \Big[\frac{2b_{2} \Big(e^{-b_{2}\bar{y} + i\theta_{0} - e^{2i\theta_{0}} \Big)}{b_{1} \Big(e^{-b_{2}\bar{y}} - 1 \Big)} \Big] z_{9} \Big|_{(\bar{x}, \bar{y}, \bar{y})} + z_{10} \Big|_{(\bar{x}, \bar{y}, \bar{y})} \Big|_{(\bar{x}, \bar{y}, \bar{y})} \Big] z_{9} \Big|_{(\bar{x}, \bar{y}, \bar{y$$

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$$\begin{split} \Omega_{6} &= \big[\frac{b_{2}^{-3} \left(e^{-b_{2}\bar{y}+i\theta_{0}} - e^{2i\theta_{0}} \right)^{2} \left(e^{-b_{2}\bar{y}-i\theta_{0}} - e^{-2i\theta_{0}} \right)}{b_{1}^{-3} \left(e^{-b_{2}\bar{y}} - 1 \right)^{3}} z_{11} \left|_{(\bar{x},\bar{y},\bar{y})} + \big\{ \frac{b_{2} \left(e^{-b_{2}\bar{y}+i\theta_{0}} - e^{2i\theta_{0}} \right)}{b_{1} \left(e^{-b_{2}\bar{y}} - 1 \right)} \big]^{2} e^{-i\theta_{0}} + \frac{2b_{2}^{-2} \left(e^{-2b_{2}\bar{y}+i\theta_{0}} - e^{-b_{2}\bar{y}+2i\theta_{0}} - e^{-b_{2}\bar{y}} + e^{i\theta_{0}} \right)}{b_{1}^{-2} \left(e^{-b_{2}\bar{y}} - 1 \right)^{2}} z_{12} \left|_{(\bar{x},\bar{y},\bar{y})} + \big[\frac{b_{2} \left(e^{-b_{2}\bar{y}+i\theta_{0}} - e^{2i\theta_{0}} \right)}{b_{1} \left(e^{-b_{2}\bar{y}} - 1 \right)^{2}} + \frac{2b_{2} \left(e^{-b_{2}\bar{y}+i\theta_{0}} - e^{2i\theta_{0}} \right)}{b_{1} \left(e^{-b_{2}\bar{y}} - 1 \right)^{2}} \big] z_{13} \left|_{(\bar{x},\bar{y},\bar{y})} + e^{i\theta_{0}} z_{14} \right|_{(\bar{x},\bar{y},\bar{y})} \end{split}$$

经计算:

$$(I_3 - Z_0)^{-1} = \frac{1}{\Psi_1} (a_{ij})_{3\times 3}, (e^{2i\theta_0}I_3 - Z_0)^{-1} = \frac{1}{\Psi_2} (b_{ij})_{3\times 3}$$

其中:

$$\begin{split} &a_{11} = 1 - e^{-b_{2}\bar{y}}, a_{12} = b_{12} = \frac{a_{2}}{a_{1}} (\bar{P}-1), a_{13} = \frac{a_{2}}{a_{1}} (1 - e^{-b_{2}\bar{y}}) (\bar{P}-1), a_{22} = (1 - \bar{P}), \\ &a_{21} = a_{31} = b_{31} = \frac{b_{1}}{b_{2}} (1 - e^{-b_{2}\bar{y}}), a_{23} = b_{23} = \frac{a_{2}b_{1}}{a_{1}b_{2}} (1 - \bar{P}) (e^{-b_{2}\bar{y}}-1), a_{32} = (\bar{P}-1), \\ &a_{33} = (1 - e^{-b_{2}\bar{y}}) (1 - \bar{P}), b_{11} = e^{2i\theta_{0}} (e^{2i\theta_{0}} - e^{-b_{2}\bar{y}}), b_{13} = \frac{a_{2}}{a_{1}} (e^{2i\theta_{0}} - e^{-b_{2}\bar{y}}) (\bar{P}-1), \\ &b_{21} = \frac{b_{1}}{b_{2}} e^{2i\theta_{0}} (e^{2i\theta_{0}} - e^{-b_{2}\bar{y}}), b_{22} = e^{2i\theta_{0}} (e^{2i\theta_{0}} - \bar{P}), b_{32} = (\bar{P} - e^{2i\theta_{0}}) b_{33} = (e^{2i\theta_{0}} - e^{-b_{2}\bar{y}}) (e^{2i\theta_{0}} - \bar{P}), \\ &\Psi_{1} = (1 - e^{-b_{2}\bar{y}}) (1 - \bar{P}) (\frac{a_{2}b_{1}}{a_{1}b_{2}} + 1) \\ &\Psi_{2} = e^{2i\theta_{0}} (e^{2i\theta_{0}} - \bar{P}) (e^{2i\theta_{0}} - e^{-b_{2}\bar{y}}) + \frac{a_{2}b_{1}}{a_{1}b_{2}} (1 - e^{-b_{2}\bar{y}}) (1 - \bar{P}) \\ &(I_{3} - Z_{0})^{-1} B(q, \bar{q}) = \frac{1}{\Psi_{1}} (a_{11}\Omega_{3} + a_{12}\Omega_{4}, a_{21}\Omega_{3} + a_{22}\Omega_{4}, a_{31}\Omega_{3} + a_{32}\Omega_{4})^{\mathrm{T}} \\ &(e^{2i\theta_{0}}I_{2} - Z_{0})^{-1} B(q, q) = \frac{1}{\Psi_{2}} (b_{11}\Omega_{1} + b_{12}\Omega_{2}, b_{21}\Omega_{1} + b_{22}\Omega_{2}, b_{31}\Omega_{1} + b_{32}\Omega_{2})^{\mathrm{T}} \\ &B(q, (I_{3} - Z_{0})^{-1} B(q, \bar{q})) = (\Omega_{7}, \Omega_{8}, 0)^{\mathrm{T}}, B(\bar{q}, (e^{2i\theta_{0}}I_{3} - Z_{0})^{-1} B(q, q)) = (\Omega_{9}, \Omega_{10}, 0)^{\mathrm{T}} \end{split}$$

其中:

$$\begin{split} \Omega_{7} &= \frac{1}{\Psi_{1}} \{ \frac{b_{2}(e^{-b_{2}\bar{y}+i\theta_{0}}-e^{2i\theta_{0}})}{b_{1}(e^{-b_{2}\bar{y}}-1)} (a_{11}\Omega_{3}+a_{12}\Omega_{4})z_{1} |_{(\bar{x},\bar{y},\bar{y})} + [\frac{b_{2}(e^{-b_{2}\bar{y}+i\theta_{0}}-e^{2i\theta_{0}})}{b_{1}(e^{-b_{2}\bar{y}}-1)} (a_{31}\Omega_{3}+a_{32}\Omega_{4}) \\ &(a_{11}\Omega_{3}+a_{12}\Omega_{4})]z_{2} |_{(\bar{x},\bar{y},\bar{y})} + (a_{31}\Omega_{3}+a_{32}\Omega_{4})z_{3} |_{(\bar{x},\bar{y},\bar{y})} \} \\ \Omega_{8} &= \frac{1}{\Psi_{1}} \{ \frac{b_{2}(e^{-b_{2}\bar{y}+i\theta_{0}}-e^{2i\theta_{0}})}{b_{1}(e^{-b_{2}\bar{y}}-1)} (a_{11}\Omega_{3}+a_{12}\Omega_{4})z_{4} |_{(\bar{x},\bar{y},\bar{y})} + \frac{b_{2}(e^{-b_{2}\bar{y}+i\theta_{0}}-e^{2i\theta_{0}})}{b_{1}(e^{-b_{2}\bar{y}}-1)} (a_{21}\Omega_{3}+a_{22}\Omega_{4}) \\ &(a_{11}\Omega_{3}+a_{12}\Omega_{4})e^{i\theta_{0}}]z_{5} |_{(\bar{x},\bar{y},\bar{y})} + (a_{21}\Omega_{3}+a_{22}\Omega_{4})e^{i\theta_{0}}z_{6} |_{(\bar{x},\bar{y},\bar{y})} \} \\ \Omega_{9} &= \frac{1}{\Psi_{2}} \{ \frac{b_{2}(e^{-b_{2}\bar{y}-i\theta_{0}}-e^{-2i\theta_{0}})}{b_{1}(e^{-b_{2}\bar{y}}-1)} (b_{11}\Omega_{1}+b_{12}\Omega_{2})z_{1} |_{(\bar{x},\bar{y},\bar{y})} + [\frac{b_{2}(e^{-b_{2}\bar{y}-i\theta_{0}}-e^{-2i\theta_{0}})}{b_{1}(e^{-b_{2}\bar{y}}-1)} (b_{31}\Omega_{1}+b_{32}\Omega_{2}) \\ &(b_{11}\Omega_{1}+b_{12}\Omega_{2})]z_{2} |_{(\bar{x},\bar{y},\bar{y})} + (b_{31}\Omega_{1}+b_{32}\Omega_{2})z_{3} |_{(\bar{x},\bar{y},\bar{y})} \} \\ \Omega_{10} &= \frac{1}{\Psi_{2}} \{ \frac{b_{2}(e^{-b_{2}\bar{y}-i\theta_{0}}-e^{-2i\theta_{0}})}{b_{1}(e^{-b_{2}\bar{y}}-1)} (b_{11}\Omega_{1}+b_{12}\Omega_{2})z_{4} |_{(\bar{x},\bar{y},\bar{y})} + \frac{b_{2}(e^{-b_{2}\bar{y}-i\theta_{0}}-e^{-2i\theta_{0}})}{b_{1}(e^{-b_{2}\bar{y}}-1)} (b_{21}\Omega_{1}+b_{22}\Omega_{2})z_{4} |_{(\bar{x},\bar{y},\bar{y})} \} \\ \Omega_{10} &= \frac{1}{\Psi_{2}} \{ \frac{b_{2}(e^{-b_{2}\bar{y}-i\theta_{0}}-e^{-2i\theta_{0}})}{b_{1}(e^{-b_{2}\bar{y}}-1)} (b_{11}\Omega_{1}+b_{12}\Omega_{2})z_{4} |_{(\bar{x},\bar{y},\bar{y})} + \frac{b_{2}(e^{-b_{2}\bar{y}-i\theta_{0}}-e^{-2i\theta_{0}})}{b_{1}(e^{-b_{2}\bar{y}}-1)} (b_{21}\Omega_{1}+b_{22}\Omega_{2}) \\ &(b_{11}\Omega_{1}+b_{12}\Omega_{2}) e^{-i\theta_{0}}]z_{5} |_{(\bar{x},\bar{y},\bar{y})} + (b_{21}\Omega_{1}+b_{22}\Omega_{2}) e^{-i\theta_{0}}z_{6} |_{(\bar{x},\bar{y},\bar{y})} \} \end{cases}$$

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经计算可知:

$$\langle p, C(q,q,\bar{q}) \rangle = \frac{1}{\bar{\kappa}} \left[\frac{a_1}{a_2(\bar{P}-1)} \Omega_5 + \frac{a_1 b_2(\bar{P}-e^{i\theta_0})}{a_2 b_1(\bar{P}-1) (e^{-b_2 \bar{y}}-1)} \Omega_6 \right] \langle p, B(q,(I_3-Z_0)^{-1} B(q,\bar{q})) \rangle$$

$$= \frac{1}{\bar{\kappa}} \left[\frac{a_1}{a_2(\bar{P}-1)} \Omega_7 + \frac{a_1 b_2(\bar{P}-e^{i\theta_0})}{a_2 b_1(\bar{P}-1) (e^{-b_2 \bar{y}}-1)} \Omega_8 \right]$$

$$\langle p, B(\bar{q}, (e^{2i\theta_0} I_3 - Z_0)^{-1} B(q,q)) \rangle = \frac{1}{\bar{\kappa}} \left[\frac{a_1}{a_2(\bar{P}-1)} \Omega_9 + \frac{a_1 b_2(\bar{P}-e^{i\theta_0})}{a_2 b_1(\bar{P}-1) (e^{-b_2 \bar{y}}-1)} \Omega_{10} \right]$$

其中 κ 为 κ 的共轭复数。

由以上计算知ζ的表达式如下:

$$\begin{split} \zeta &= \frac{1}{2} \operatorname{Re} \left\{ \operatorname{e}^{-i\theta_0} \left[\left\langle p, C(q, q, \bar{q}) \right\rangle + 2 \left\langle p, B(q, (I_3 - Z_0)^{-1} B(q, \bar{q})) \right\rangle + \left\langle p, B(\bar{q}, (\operatorname{e}^{2i\theta_0} I_3 - Z_0)^{-1} B(q, q)) \right\rangle \right] \right\} \\ &= \frac{1}{2} \operatorname{Re} \left\{ \frac{\operatorname{e}^{-i\theta_0} \kappa}{|\kappa|} \left[\frac{a_1}{a_2(\bar{P} - 1)} (\Omega_5 + 2\Omega_7 + \Omega_9) + \frac{a_1 b_2(\bar{P} - \operatorname{e}^{i\theta_0})}{a_2 b_1(\bar{P} - 1) (\operatorname{e}^{-b_2 \bar{y}} - 1)} (\Omega_6 + 2\Omega_8 + \Omega_{10}) \right] \right\} \end{split}$$

由如上分析和推理可得如下定理4。

定理 4^[14]当 $r=r_0 = -\frac{\ln(P)}{a_1\bar{x}}$ 时(P由定理 3 确定),模型(1)在正平衡态 $E(\bar{x},\bar{y})$ 产生 Neimark-sacker 分支; 若 $\zeta < 0(>0)$,则模型(1)从正平衡态 $E(\bar{x},\bar{y})$ 分支出惟一(不)稳定的超(亚)临界 Neimark-sacker 分支。

3 数值计算

本节将通过实例,运用 Matlab 软件绘出相应的分支图,验证以上理论的可行性,并通过图形说明该模型 复杂的动力学行为。

例 在模型(1)中,取 a1=0.5, a2=0.4, b1=4, b2=2.5, s=0.1 计算可得:

 $M_3 = 1.2400, M_4 = -1.8426, \Delta = 2.7092, \zeta = -0.4851 < 0, P_1 = 0.3304 > (M_3 - 1)/M_3 = 0.1935$

则分支参数的临界值 r_0 = 2.4852, 惟一正平衡态 E(0.8912, 1.3860)

对应分支图为图1。由图1可知,当*r<r*₀=2.4852,正平衡态*E*局部渐近稳定(图2,图3);当*r*=*r*₀=2.4852时,产生 N-S分支(图4)及像平面图和解图(图5);当*r>r*₀=2.4852时,模型(1)出现复杂的动力学行为(图1)。



Fig.1 r-x, r-y bifurcation map

4 总结

本文应用 Schur-Cohn 判据、分支理论及中心流形投影等理论给出了具有时滞与分段常数变量捕食-食饵



Fig.4 N-S bifurcation map

模型的稳定性及 Neimark-sacker 分支的存在性以及稳定性条件。通过模型的分析得到如下两个主要结论:

H,)在捕食-食饵系统中考虑捕食者只在一定时间段或整数时刻且具有滞后效应捕食时,由定理2可知, 系统的稳定性(捕食者和食饵共存且数量保持稳定)将会变得非常复杂。

H₂)由实例可知,系统在其它参数不变的情况下,当食饵的内禀增长率 r<2.4852 时,由图 1—图 3 可知捕 食者和食饵的数量处于稳定状态;当r=2.4852,由图4,图5知捕食者和食饵的数量将呈现周期性变化,系统 产生 Neimark-sacker 分支;当 r>2.4852 时,由图 1 知系统的正平衡态由稳定到不稳定。

综上所述,在捕食-食饵系统中,若考虑捕食者只在一定时间段或整数时刻且具有滞后效应捕食时,模型

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0.9

r 0.89

1.37

0.885 0.89 0.895 0.90 x 0.885 0.89 0.895 0.90 x 0.88 0 0.

Fig.5 phase plane and space solution map of x and y $(r=r_0=2.4852)$

动力学行为将变得更为错综复杂;食饵的内禀增长率达到确定的临界值时,种群数量将失去原有的稳定性,模型将产生惟一稳定的超临界 Neimark-Sacker 分支。

参考文献(References):

- [1] 祁君,苏志勇.具有捕食正效应的捕食-食饵系统.生态学报,2011,31(24):7471-7478.
- [2] 杨立,李维德.利用元胞自动机研究一类捕食食饵模型中的斑块扩散现象.生态学报,2012,32(6):1773-1782.
- [3] Kot M. Elements of Mathematical Ecology. London: The Cambridge University Press, 2001: 107-160.
- [4] He Z M, Lai X. Bifurcation and chaotic behavior of a discrete-time predator-prey system. Nonlinear Analysis: Real world Applications, 2011, 12 (1): 403-417.
- [5] Wang W M, Ling L. Stability and Hopf bifurcation analysis of a delayed predator-prey model with constant rate harvesting. Journal of Mathematical Biology, 2009, 24(4): 1-14.
- [6] Wang J F, Shi J P, Wei J J. Predator-prey system with strong Allee effect in prey. Journal of Mathematical Biology, 2011, 62(3): 291-331.
- [7] Beretta E, Kuang Y. Global analyses in some delayed ratio-dependent predator-prey systems. Nonlinear Analysis: Theory, Methods & Applications, 1988, 32(3): 381-408.
- [8] Skalski G T, Gilliam J F. Functional responses with predator interference: viable alternatives to the Holling type II model. Ecology, 2001, 82(11): 3083-3092.
- [9] Mischaikow K, Wolkowicz G. A predator-prey system involving group defense: a connection matrix approach. Nonlinear Analysis: Theory, Methods & Applications, 1990, 14(11): 955-969.
- [10] Jost C, Arditi R. From pattern to process: identifying predator-prey models from time-series data. Population Ecology, 2001, 43(3): 229-243.
- [11] Salt G W. Predator and prey densities as controls of the rate of capture by the predator Didinium nasutum. Ecology, 1974, 55(2): 434-439.
- [12] Martin A, Ruan S G. Predator-prey models with delay and prey harvesting. Journal of Mathematical Biology, 2001, 43(3): 247-267.
- [13] Jury E I. Theory and Application of the Z-transform Method. New York: Wiley, 1964.
- [14] Kuznetsov Y A. Elements of Applied Bifurcation Theory. New York: Springer-Verlag, 2004.

1.405 1.400

1.395

1.390

1.385

1.380

1.375

1.370

0.88

1000

500

n