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Study of a Monod–Haldene type food chain chemostat with pulsed substrate

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In this paper, we introduce and study a model of a Monod–Haldene type food chain chemostat with pulsed substrate. We investigate the subsystem with substrate and prey and study the stability of the periodic solutions, which are the boundary periodic solutions of the system. The stability analysis of the boundary periodic solution yields an invasion threshold. By use of standard techniques of bifurcation theory, we prove that above this threshold there are periodic oscillations in substrate, prey, and predator. Simple cycles may give way to chaos in a cascade of period-doubling bifurcations. Furthermore, by comparing bifurcation diagrams with different bifurcation parameters, we can see that the impulsive system shows two kinds of bifurcations, whose are period-doubling and period-halfing.

KEY WORDS: bifurcation, Monod-Haldene growth rates, chemostat, invasion, complexity

1. Introduction

The chemostat represents a basic model of a open system in microbial ecology. Recently many papers studied chemostat model with variations in the supply of nutrients or the washout. Chemostat with periodic inputs are studied in [1–5], those with periodic washout rate in [6, 7], and those with periodic input

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and washout in [8]. Funasaki and Kor [5] studied the dynamics of a bi-trophic food chain model in a chemostat with pulsed inflowing substrate. They have investigated the existence and stability of the periodic solutions of the impulsive subsystem with substrate and prey. Further, they showed that impulsive input substrate cause complex dynamics of system. The goal of this paper is to study a system for a chemostat with bacteria, bacteria, and periodically pulsed substrate, which incorporate the specific growth rates (Monod–Haldene, see Chen [9]) of bacteria and of protozoa saturate at sufficiently high substrate and prey concentrations. The model reads as:

$$\begin{cases} \left.\begin{aligned} \frac{\mathrm{d}S}{\mathrm{d}T} &= -DS - \frac{\mu_1}{\delta_1}\frac{SH}{(A_1+S+B_1S^2)}, \\ \frac{\mathrm{d}H}{\mathrm{d}T} &= \frac{\mu_1 SH}{A_1+S+B_1S^2} - DH - \frac{\mu_2}{\delta_2}\frac{HP}{(A_2+H+B_2H^2)}, \\ \frac{\mathrm{d}P}{\mathrm{d}T} &= \frac{\mu_2 HP}{A_2+H+B_2H^2} - DP, \end{aligned}\right\} & T \neq \frac{n\tau}{D}, \\ S(\frac{n\tau^+}{D}) = S(\frac{n\tau}{D}) + \tau S_0, & T = \frac{n\tau}{D}, \end{cases} \tag{1.1}$$

where τ is the period of the impulsive effect. The state variables S, H, and P represent the concentration of limiting substrate, bacteria, and protozoa. D is the dilution rate; μ_1 and μ_2 are the uptake and predation constances of the bacteria and protozoa; δ_1 is the yield of prey per unit mass of substrate; δ_2 is the biomass yield of protozoa per unit mass of bacteria; A_1, B_1, A_2, B_2, are positive constants; $\frac{\tau}{D}$ is the period of the pulsing; τS_0 is the amount of limiting substrate pulsed each $\frac{\tau}{D}$. DS_0 units of substrate are added, on average, per unit of time. $n \in N$, N is the set of all non-negative integers.

The theory of impulsive differential equation appears as a natural description of several real processes subject to certain perturbations whose duration is negligible in comparison with the duration of the process. Recently, equations of this kind are found in a almost every domain of applied sciences. Numerous examples are given in Bainov's and his collaborator's books [10, 11]. Some impulsive differential equations have been recently introduced in population dynamics in relation to: impulsive birth [12, 13], impulsive vaccination [14, 15], chemotherapeutic treatment of disease [16] and population ecology [17].

There are advantages in analyzing dimensionless equations. In model (1.1), we treat the reciprocal of the dilution rate as natural measure of time:

$$x \equiv \frac{S}{S_0}, \quad y \equiv \frac{H}{\delta_1 S_0}, \quad z \equiv \frac{P}{\delta_1\delta_2 S_0}, \quad t \equiv DT.$$

After some algebra, this yields

$$\left\{\begin{array}{ll}\left.\begin{array}{l}\frac{\mathrm{d}x}{\mathrm{d}t}=-x-\frac{m_1xy}{a_1+x+b_1x^2},\\ \frac{\mathrm{d}y}{\mathrm{d}t}=\frac{m_1xy}{a_1+x+b_1x^2}-y-\frac{m_2yz}{a_2+y+b_2y^2},\\ \frac{\mathrm{d}z}{\mathrm{d}t}=\frac{m_2yz}{a_2+y+b_2y^2}-z,\end{array}\right\} & t\neq n\tau,\\ x(n\tau^+)=x(n\tau)+\tau, & t=n\tau,\end{array}\right. \tag{1.2}$$

with

$$m_1=\frac{\mu_1}{D},\quad a_1=\frac{A_1}{S_0},\quad b_1=B_1S_0;$$
$$m_2=\frac{\mu_2}{D},\quad a_2=\frac{A_2}{\delta_1S_0},\quad b_2=B_2\delta_1S_0.$$

The organizations of the paper are as following. In next section, we investigate the existence and stability of the periodic solutions of the impulsive subsystem with substrate and prey. In section 3, we study the local stability of the boundary periodic solution of the system and obtain the threshold of the invasion of the predator. By use of standard techniques of bifurcation theory, we prove that above this threshold there are periodic oscillations in substrate, prey, and predator. In section 4, the bifurcation diagrams of different coefficients show that with increasing the bifurcation parameters, the system experiences following two kinds of processes: (1) periodic solution → periodic doubling cascade → chaos → periodic halfing cascade → periodic solution, (2) periodic solution → periodic doubling cascade → chaos.

2. Behavior of the substrate bacterium subsystem

In the absence of the protozan predator, system (1.2) reduces to

$$\left\{\begin{array}{ll}\frac{\mathrm{d}x}{\mathrm{d}t}=-x-\frac{m_1xy}{a_1+x+b_1x^2}, & \\ \frac{\mathrm{d}y}{\mathrm{d}t}=\frac{m_1xy}{a_1+x+b_1x^2}-y, & t\neq n\tau,\\ x(n\tau^+)=x(n\tau)+\tau, & t=n\tau,\end{array}\right. \tag{2.1}$$

This nonlinear system has simple periodic solutions. For our purpose, we present these solutions in this sections.

If we add the first and second equations of system (2.1), we have $\frac{d(x+y)}{dt}=-(x+y)$. If we take variable changes $s=x+y$ then system (2.1) can be rewritten as

$$\left\{\begin{array}{ll}\frac{\mathrm{d}s}{\mathrm{d}t}=-s, & t\neq n\tau,\\ s(n\tau^+)=s(n\tau)+\tau, s(0)>0, & t=n\tau.\end{array}\right. \tag{2.2}$$

For system (2.2), we have the following lemma 2.1.

Lemma 2.1. The subsystem (2.2) has a positive periodic solution $\tilde{s}(t)$ and for every solution $s(t)$ of (3.2) we have $|s(t) - \tilde{s}(t)| \to 0$ as $t \to \infty$, where $\tilde{s}(t) = \tau \exp(-(t - n\tau))/1 - \exp(-\tau)$, $t \in (n\tau, (n+1)\tau]$, $n \in N$, $\tilde{s}(0^+) = \tau/1 - \exp(-\tau)$.

By the lemma 2.1, the following lemma is obvious.

Lemma 2.2. Let $(x(t), y(t))$ be any solution of system (2.1) with initial condition $x(0) \geqslant 0$, $y(0) > 0$, then $\lim_{t\to\infty} |x(t) + y(t) - \tilde{s}(t)| = 0$.

The lemma 2.2 says that the periodic solution $\tilde{s}(t)$ is uniquely invariant manifold of system (2.1).

Theorem 2.1. For the system (2.1), we have that:

(1) If $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)}\mathrm{d}l < 1$, then system (2.1) has a unique globally asymptotically stable boundary $\tau-$periodic solution $(x_e(t), y_e(t))$, where

$$x_e(t) = \tilde{s}(t),\ y_e(t) = 0. \tag{2.3}$$

(2) If $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)}\mathrm{d}l > 1$, then system (2.1) has a unique globally asymptotically stable positive $\tau-$periodic solution $(x_s(t), y_s(t))$ and the $\tau-$periodic solution $(x_e(t), y_e(t))$ is unstable. And we have

$$\frac{1}{\tau}\int_0^\tau \frac{m_1(\tilde{s}(l)-y_s(l))}{a_1+\tilde{s}(l)-y_s(l)+b_1(\tilde{s}(l)-y_s(l))^2}\mathrm{d}l = 1.$$

Proof. (1) If $\frac{1}{\tau}\int_0^\tau \tau\frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)} < 1$, it is obvious that

$$y(t) \leqslant y(0)\exp\Big(\Big(\frac{1}{\tau}\int_0^\tau \tau\frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)}\mathrm{d}l - 1\Big)t\Big)\exp\Big(\int_0^t p_1(l)\mathrm{d}l\Big), \tag{2.4}$$

where $p_1(t) = \tau\frac{m_1\tilde{s}(t)}{a_1+\tilde{s}(t)+b_1\tilde{s}^2(t)} - \frac{1}{\tau}\int_0^\tau \tau\frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)}\mathrm{d}l$; note that $\frac{1}{\tau}\int_0^\tau p(l)\mathrm{d}l = 0$ and hence that $p_1(t)$ is τ-periodic piecewise continuous function. Thus, for $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}\mathrm{d}l - 1 < 0$ we find that $y(t)$ tends exponentially to zero as $t \to +\infty$. Consider the system (2.2), we have $x(t) = s(t) - y(t)$. By lemma 2.2, we have $\lim_{t\to\infty} |x(t) - \tilde{s}(t)| = 0$.

(2) Set $\frac{1}{\tau}\int_0^\tau \tau\frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)} > 1$. By lemma 2.1, we can consider the system (2.1) in its stable invariant manifold $\tilde{s}(t)$, that is

$$\begin{aligned} &\frac{\mathrm{d}y}{\mathrm{d}t} = \frac{m_1(\tilde{s}(t)-y)y}{a_1+(\tilde{s}(t)-y)+b_1(\tilde{s}(t)-y)^2} - y,\\ &0 \leqslant y_0 \leqslant s(0) = \frac{\tau}{1-e^{-\tau}}. \end{aligned} \tag{2.5}$$

Now we prove the periodic impulsive equation (2.5) has globally stable periodic solution $y_s(t)$. We have the following properties:

(1) $y(t) = y(t, y_0), t \in [0, \infty)$ is continuous function;
(2) $y(t) = y(t, 0) = 0, t \in [0, \infty)$ is a solution;
(3) $y(t) = y(t, \tilde{s}(0)) = \tilde{s}(t), t \in [0, \tau]$.

Suppose $y(t, y_0)$ is a solution of equation (2.5), with initial condition $y_0 \in [0, 1]$. We have

$$y(t, y_0) = y(n\tau) \exp\left(\int_{n\tau}^{t} \left(\frac{m_1(\tilde{s}(l) - y(l, y_0))}{a_1 + (\tilde{s}(l) - y(l, y_0)) + b_1(\tilde{s}(l) - y(l, y_0))^2} - 1\right) \mathrm{d}l\right),$$

$$y(n\tau) = y_0, \quad t \in (n\tau, (n+1)\tau]. \tag{2.6}$$

For (2.6), we have the following properties:

(i) The function $G(y_0) = y(t, y_0), y_0 \in (0, \tilde{s}(0)]$ is a increasing function;
(ii) $0 < y(t, y_0) < \tilde{s}(t), t \in (0, \infty)$ is continuous function;
(iii) $y(t, 0) = 0, t \in (0, \infty)$ is a solution.

The periodic solutions of (2.5) satisfy the following equation

$$y_0 = y_0 \exp\left(\int_0^{\tau} \left(\frac{m_1(\tilde{s}(l) - y(l, y_0))}{a_1 + (\tilde{s}(l) - y(l, y_0)) + b_1(\tilde{s}(l) - y(l, y_0))^2} - 1\right) \mathrm{d}l\right). \tag{2.7}$$

By (i)–(iii), we know that if $\frac{1}{\tau}\int_0^{\tau} \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)}\mathrm{d}l > 1$, equation (2.6) has a unique solution in $(0, \tilde{s}(0)]$; otherwise, it has no solution in $(0, \tilde{s}(0)]$. We denote

$$m_1^* := \frac{\tau}{\int_0^{\tau} \frac{\tilde{s}(l)\mathrm{d}l}{a_1+\tilde{s}(l)+b_1\tilde{s}(l)^2}}. \tag{2.8}$$

If $m_1 < m_1^*$, then equation (2.5) has stable periodic solution $y_e(t) = 0$. By lemma 2.2, we have $\lim_{t\to\infty} |x(t) - \tilde{s}(t)| = 0$. We have proved in (1).

If $m_1 > m_1^*$, then equation (2.5) has uniquely positive periodic solution. We denote this positive periodic solution

$$y_s(t) = y(t, y_0^*), \qquad x_s(t) = \tilde{s}(t) - y(t, y_0^*),$$

which satisfies the following equation

$$\int_0^{\tau} \frac{m_1(\tilde{s}(l)-y_s(l))\mathrm{d}l}{a_1+(\tilde{s}(l)-y_s(l))+b_1(\tilde{s}(l)-y_s(l))^2} = \tau. \tag{2.9}$$

We denote $y_0^* := y_s(0)$.

For proving the period solution $y_s(t)$, we define a function $F(y(t, y_0))$: $(t, y_0) \to R, \in [0, \infty) \times [0, \tilde{s}(0)]$ as following:

$$F(y(t, y_0)) = \int_0^{t} \frac{m_1(\tilde{s}(l)-y(l,y_0))}{a_1+(\tilde{s}(l)-y(l,y_0))+b_1(\tilde{s}(l)-y(l,y_0))^2}\mathrm{d}l - t.$$

Noticing equation (2.5), we have

$$F(y(\tau, y_0)) = \ln\left(\frac{y(\tau, y_0)}{y_0}\right), \quad y_0 \in (0, \tilde{s}(0)]. \tag{2.10}$$

It is obvious that $F(y(n\tau, y_0^*)) = 0$.

For any $y_0 \in (0, \tilde{s}(0))$, by theorem 2.10 [10] on the differentiability of the solutions on the initial values, $\frac{\partial y(t,y_0)}{\partial y_0}$ exists. Furthermore, $\frac{\partial y(t,y_0)}{\partial y_0} \geqslant 0, t \in (0, \infty)$ is hold (otherwise, there exist $t_0 > 0, 0 < y_1 < y_2 < \tilde{s}(0)$ such that $y(t_0, y_1) = y(t_0, y_2)$, that is a contradiction with the different flows of system (2.5) not to intersect). And we can have $\tilde{s}(l) > y(l, y_0))$, for $l \in [0, \tau]$. So we obtain that

$$\frac{\mathrm{d}(F(y(\tau,y_0)))}{\mathrm{d}y_0} < 0. \tag{2.11}$$

So $F(y(\tau, y_0)), y_0 \in [0, \tilde{s}(0)]$ is monotonously decreasing continuous function.

Now we set $0 < \varepsilon < y_0^* < \frac{\tau e^\tau}{e^\tau - 1}$. According to (2.11), we have that

$$\begin{array}{ll} \ln y(\tau, y_0) - \ln y_0 < 0, & \text{if } \ y_0^* < y_0 < \frac{\tau}{1-e^{-\tau}}, \\ \ln y(\tau, y_0) - \ln y_0 = 0, & \text{if } \ y_0 = y_0^*, \\ \ln y(\tau, y_0) - \ln y_0 > 0, & \text{if } \ \varepsilon < y_0 < y_0^*. \end{array} \tag{2.12}$$

Furthermore, we obtain the following equations

$$\begin{array}{ll} y_0 > y(\tau, y_0) > \cdots > y(n\tau, y_0) > y_0^*, & \text{if } \ y_0^* < y_0 \leqslant \frac{\tau}{1-e^{-\tau}}, \\ y_0 < y(\tau, y_0) < \cdots < y(n\tau, y_0) < y_0^*, & \text{if } \ \varepsilon \leqslant y_0 < y_0^*. \end{array} \tag{2.13}$$

Set $y_0 \in (0, \tilde{s}(0)]$. According to (2.12), we suppose that

$$\lim_{n\to\infty} y(n\tau, y_0) = a.$$

We shall prove that the solution $y(t, a)$ is $\tau-$periodic. We note that the functions $y_n(t) = y(t+n\tau, y_0)$, due to the $\tau-$periodicity of equation (2.5), are also its solutions and $y_n(0) \to a$ as $n \to \infty$. By the continuous dependence of the solutions on the initial values we have that $y(\tau, a) = \lim_{n\to\infty} y_n(\tau) = a$. Hence the solution $y(t, a)$ is $\tau-$periodic. The periodic solution $y(t, y_0^*)$ is unique, so $a = y_0^*$.

Let $\varepsilon > 0$ be given. By theorem 2.9 [10] on the continuous dependence of the solutions on the initial values, there exists a $\delta > 0$ such that

$$|y(t, y_0) - y(t, y_0^*)| < \varepsilon,$$

if $|y_0 - y_0^*| < \delta$ and $0 \leqslant t \leqslant \tau$. Choose $n_1 > 0$ so that $|y(n\tau, y_0) - y_0^*| < \delta$ for $n > n_1$. Then $|y(t, y_0) - y(t, y_0^*)| < \varepsilon$ for $t > n\tau$ which proves that

$$\lim_{n\to\infty} |y(t, y_0) - y(t, y_0^*)| = 0, \qquad y_0 \in (0, \tilde{s}(0)].$$

For system (2.1), by lemma 2.2, we obtain that for any solution $(x(t), y(t))$ with initial condition $x(0) \geqslant 0, y(0) > 0, |x - x_s| \to 0, |y - y_s| \to 0$ as $t \to \infty$.

From τ-period solution y_s being globally asymptotically stable, we can obtain that the multiplier μ of y_s, which satisfies

$$\mu = \exp\left(\int_0^\tau \frac{m_1 x_s(l)(a_1 - b_1 x_s^2)}{(a_1 + x_s(l) + b_1 x_s^2(l))^2}\mathrm{d}l\right) < 1, \tag{2.14}$$

where we have used (2.7). This conclusion will be used in section 3. We have proved (2).

3. The bifurcation of the system

In order to investigate the invasion of the predator of system (1.2), we add the first, second, and third equations of it and take variable changes $s = x + y + z$, then we obtain the following system

$$\begin{cases} \frac{ds}{dt} = -s, & t \neq n\tau, \\ s(n\tau^+) = s(n\tau) + \tau, s(0) > 0, & t = n\tau. \end{cases}$$

By lemma 2.1, the following lemma is obvious.

Lemma 3.1. Let $(x(t), y(t), z(t))$ be any solution of system (1.2) with $X(0) > 0$, then

$$\lim_{t\to\infty} |x(t) + y(t) + z(t) - \tilde{s}(t)| = 0. \tag{3.1}$$

Lemma 3.1 says that the periodic solution $\tilde{s}(t)$ is an invariant manifold of the system (2.3).
For convenance, in the following discussing if $m_1 > m_1^*$, we denote that

$$m_2^* := \frac{\tau}{\int_0^\tau \frac{y_s(l)}{a_2 + y_s(l) + b_2 y_s^2(l)} dl}.$$

Theorem 3.1. Let $(x(t), y(t), z(t))$ be any solution of system (1.2) with $X(0) > 0$.

(1) If $m_1 < m_1^*$, then system (3.1) has a unique globally asymptotically stable positive τ−periodic solution $(\tilde{s}(t), 0, 0)$.
(2) If $m_1 > m_1^*$ and $m_2 < m_2^*$, then system (1.2) has a unique globally asymptotically stable boundary τ−periodic solution $(x_s(t), y_s(t), 0)$ is globally asymptotical stable.
(3) If $m_1 > m_1^*$ and $m_2 > m_2^*$, then the periodic boundary solution $(\tilde{s}(t) - y_s(t), y_s(t), 0)$ of system (1.2) is unstable.

Proof. The proof of (1) is easy, we want to prove (2) and (3). The local stability of periodic solution $(x_s(t), y_s(t), 0)$ may be determined by considering the behavior of small amplitude perturbations of the solution. Define

$$x(t) = u(t) + x_s(t), \qquad y(t) = v(t) + y_s(t), \qquad z(t) = w(t)$$

there may be written

$$\begin{pmatrix} u(t) \\ v(t) \\ w(t) \end{pmatrix} = \Phi(t) \begin{pmatrix} u(0) \\ v(0) \\ w(0) \end{pmatrix}, \quad 0 \leqslant t < \tau,$$

where $\Phi(t)$ satisfies

$$\frac{\mathrm{d}\Phi}{\mathrm{d}t} = \begin{pmatrix} -1 - \frac{m_1 y_s (a_1 - b_1 x_s^2)}{(a_1 + x_s + b_1 x_s^2)^2} & -\frac{m_1 x_s}{a_1 + x_s + b_1 x_s^2} & 0 \\ \frac{m_1 y_s (a_1 - b_1 x_s^2)}{(a_1 + x_s + b_1 x_s^2)^2} & \frac{m_1 x_s}{a_1 + x_s + b_1 x_s^2} - 1 & -\frac{m_2 y_s}{a_2 + y_s + b_2 y_s^2} \\ 0 & 0 & \frac{m_2 y_s}{a_2 + y_s + b_2 y_s^2} - 1 \end{pmatrix} \Phi(t)$$

and $\Phi(0) = I$, the identity matrix. Hence the fundamental solution matrix is

$$\Phi(T) = \begin{pmatrix} \phi_{11}(\tau) & \phi_{12}(\tau) & * \\ \phi_{21}(\tau) & \phi_{22}(\tau) & ** \\ 0 & 0 & \exp(\int_0^\tau (\frac{m_2 y_s(l)}{a_2 + y_s(l) + b_2 y_s^2(l)} - 1)\mathrm{d}l) \end{pmatrix}. \tag{3.2}$$

It is no need to give the exact form of $(*)$ and $(**)$ as it is not required in the analysis that follows. The linearization of impulsive subsystem (1.2) become

$$\begin{pmatrix} u(nT^+) \\ v(nT^+) \\ w(nT^+) \end{pmatrix} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} u(nT) \\ v(nT) \\ w(nT) \end{pmatrix}.$$

Hence, if both eigenvalues of

$$M = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} \Phi(T).$$

The eigenvalues of the matrix $\Phi(\tau)$ are $\mu_3 = \exp(\int_0^\tau (\frac{m_2 y_s(l)}{a_2 + y_s + b_1 y_s^2} - 1)\mathrm{d}l)$ and the eigenvalues μ_1, μ_2 of the following matrix

$$\begin{pmatrix} \phi_{11}(\tau) & \phi_{12}(\tau) \\ \phi_{21}(\tau) & \phi_{22}(\tau) \end{pmatrix}. \tag{3.3}$$

The μ_1, μ_2 are also the multipliers the locally linearizing system of system (2.1) provided with $m_1 > m_1^*$ at the asymptotically stable periodic solution $(x_s(t), y_s(t))$, according to theorem 3.1, we have that $\mu_1 < 1, \mu_2 < 1$.

If $m_1 > m_1^*$ and $m_2 < m_2^*$, the $\mu_3 = \exp\left(\int_0^\tau \left(\frac{m_2 y_s(l)}{a_2 + y_s(l) + b_1 y_s^2(l)} - 1\right) dl\right) < 1$, the boundary periodic solution $(x_s(t), y_s(t), 0)$ of system (2.5) is locally asymptotically stable. We have that $z(t) \leqslant z(0) \exp\left(\int_0^t \left(\frac{m_2 y_s(l)}{a_2 + y_s(l) + b_1 y_s^2(l)} - 1\right) \mathrm{d}l\right)$, hence we obtain that for any solution $(x(t), y(t), z(t))$ with $X(0) > 0$, $z(t) \to 0$ as $t \to \infty$. By $\lim_{t\to\infty} |x(t)+y(t)+z(t)-\tilde{s}(t)| = 0$, we have $\lim_{t\to\infty} |x(t)+y(t)-\tilde{s}(t)| = 0$. Now using theorem 3.1, we have $\lim_{t\to\infty} |y(t) - y_s(t)| = 0$ and $\lim_{t\to\infty} |x(t) - x_s(t)| = 0$.

If $m_1 > m_1^*$ and $m_2 < m_2^*$,the $\mu_3 = \exp\left(\int_0^\tau \left(\frac{m_2 y_s(l)}{a_2+y_s(l)+b_1 y_s^2(l)} - 1\right) \mathrm{d}l\right) > 1$, the boundary periodic solution $(x_s(t), y_s(t), 0)$ of system (1.2) is unstable. We complete the proof.

Let B denote the Banach space of piecewise continuous, τ−periodic functions $N : [0, \tau] \to R^2$ and have points of discontinuity τ, where they are continuous from the left. In the set B introduce the norm $|N|_0 = \sup_{0\leqslant t\leqslant\tau} |N(t)|$ with which B becomes a Banach space with the uniform convergence topology.

For convenience, just like [18] we introduce the following lemmas 3.3 and 3.4.

Lemma 3.2. Suppose $a_{ij} \in B$. (a) If $\int_0^\tau a_{22}(s)\mathrm{d}s \neq 0$, $\int_0^\tau a_{11}(s)\mathrm{d}s \neq 0$, then the linear homogenous system

$$\begin{aligned} \frac{\mathrm{d}y_1}{\mathrm{d}t} &= a_{11}y_1 + a_{12}y_2, \\ \frac{\mathrm{d}y_2}{\mathrm{d}t} &= a_{22}y_2, \end{aligned} \tag{3.4}$$

has no nontrivial solution in $B \times B$. In this case, the nonhomogeneous system

$$\begin{aligned} \frac{\mathrm{d}x_1}{\mathrm{d}t} &= a_{11}x_1 + a_{12}x_2 + f_1, \\ \frac{\mathrm{d}x_2}{\mathrm{d}t} &= a_{22}x_2 + f_2, \end{aligned} \tag{3.5}$$

has, for every $(f_1, f_2) \in B \times B$, a unique solution $(x_1, x_2) \in B \times B$ and the operator L: $B \times B \to B \times B$ defined by $(x_1, x_2) = L(f_1, f_2)$ is linear and compact. If we define that $x_2' = a_{22}x_2 + f_2$ has a unique solution $x_2 \in B$ and the operator $L_2 : B \to B$ defined by $x_2 = L_2 f_2$ is linear and compact. Furthermore, $x_1' = a_{11}x_1 + f_3$ for $f_3 \in B$ has a unique solution (since $\int_0^\tau a_{11}(s)\mathrm{d}s \neq 0$) in B and $x_1 = L_1 f_3$ defines a linear, compact operator L_1: $B \to B$. Then we have

$$L(f_1, f_2) \equiv (L_1(a_{12}L_2 f_2 + f_1), L_2 f_2). \tag{3.6}$$

(b) If $\int_0^\tau a_{22}(s)\mathrm{d}s = 0$, $\int_0^\tau a_{11}(s)\mathrm{d}s \neq 0$, then (3.4) has exactly one independent solution in $B \times B$.

Lemma 3.3. Suppose $a \in B$ and $\frac{1}{\tau}\int_0^\tau a(l)\mathrm{d}l = 0$. Then $x' = ax + f$, $f \in B$, has a solution $x \in B$ if and only if $\frac{1}{\tau}\int_0^\tau f(l)(\exp(-\int_0^l a(s)\mathrm{d}s))\mathrm{d}l = 0$.

By lemma 3.1, in its invariant manifold $\tilde{s} = x(t) + y(t) + z(t)$, system (1.2) reduce to a equivalently nonautonomous system as following

$$\begin{aligned} \frac{dy}{dt} &= \frac{m_1(\tilde{s}-y-z)y}{a_1+(\tilde{s}-y-z)+b_1(\tilde{s}-y-z)^2} - y - \frac{m_2 yz}{a_2+y+b_2y^2}, \\ \frac{dz}{dt} &= \frac{m_2 yz}{a_2+y+b_2y^2} - z, \\ & y(0) > 0, z(0) \geqslant 0, y(0) + z(0) \leqslant \tilde{s}(0). \end{aligned} \tag{3.7}$$

If $m_1 > m_1^*$, for system (3.7), by theorem 3.1, the boundary periodic solution $(y_s(t), 0)$ is locally asymptotically stable provided with $m_2 < m_2^*$, and it is unstable provided with $m_2 > m_2^*$, hence the value m_2^* practises as a bifurcation threshold. For the system (3.7), we have following results.

Theorem 3.2. For system (3.7), $m_1 > m_1^*$ and $a_2 - b_2 y_s^2 \geqslant 0$ for $t \in (0, \tau]$ hold, then there exists a constance $\lambda_0 > 0$, such that for each $m_2 \in (m_2^*, m_2^* + \lambda_0)$, there exists a solution $(y, z) \in B \times B$ of (3.7) satisfying $0 < y < y_s, z > 0$ and $x = \tilde{s}(t) - y - z > 0$ for all $t > 0$. Hence, system (1.2) has a positive τ−periodic solution $(\tilde{s}(t) - y - z, y, z)$.

Proof. Let $x_1 = y - y_s(t), x_2 = z$ in (3.7), then

$$\begin{aligned} \frac{dx_1}{dt} &= F_{11}(x_s, y_s)x_1 - F_{12}(m_2, x_s, y_s)x_2 + g_1(x_1, x_2), \\ \frac{dx_2}{dt} &= F_{22}(m_2, y_s)x_2 + g_2(x_1, x_2), \end{aligned} \tag{3.8}$$

where

$$\begin{aligned} F_{11}(x_s, y_s) &= \frac{m_1 x_s}{a_1+x_s+b_1x_s^2} - 1 - \frac{m_1(a_1-b_1x_s^2)y_s}{(a_1+x_s+b_1x_s^2)^2}, \\ F_{12}(m_2, x_s, y_s) &= \frac{m_1(a_1-b_1x_s^2)y_s}{(a_1+x_s+b_1x_s^2)^2} + \frac{m_2 y_s}{a_2+y_s+b_2y_s^2}, \\ F_{22}(m_2, y_s) &= \frac{m_2 y_s}{a_2+y_s+b_2y_s^2} - 1. \end{aligned}$$

We know that $\int_0^\tau \left(\frac{m_2 y_s(l)}{a_2+y_s(l)+b_2y_s^2(l)} - 1\right) dl \neq 0$, by lemma 3.3, using L we can equivalently write system (4.8) as the operator equation

$$(x_1, x_2) = L^*(x_1, x_2) + G(x_1, x_2), \tag{3.9}$$

where

$$G(x_1, x_2) = (L_1(-F_{12}(x_s, y_s)g_2(x_1, x_2) + g_1(x_1, x_2)), L_2 g_2(x_1, x_2)).$$

Here $L^* : B\times B \to B\times B$ is linear and compact and $G : B\times B \to B\times B$ is continuous and compact (since L_1 and L_2 are compact) and satisfies $G = 0(|(x_1, x_2)|_0)$ near (0,0). A nontrivial solution $(x_1, x_2) \neq (0, 0)$ for some $m_2 > 1$ yields a solution $(y, z) = (y_s + x_1, x_2)$ of system (3.7). Solutions $(y, z) \neq (y_s, 0)$ will be called nontrivial solutions of system (3.7).

We apply well-known local bifurcation techniques to (3.9). As is well known, bifurcation can occur only at the nontrivial solution of the linearized problem

$$(y_1, y_2) = L^*(y_1, y_2), m_2 > 0. \tag{3.10}$$

If $(y_1, y_2) \in B \times B$ is a solution of (3.10) for some $m_2 > 0$, then by the very manner in which L^* was defined, (y_1, y_2) solves the system

$$\begin{aligned} \frac{\mathrm{d}y_1}{\mathrm{d}t} &= F_{11}(x_s, y_s)y_1 - F_{12}(x_s, y_s)y_2, \\ \frac{\mathrm{d}y_2}{\mathrm{d}t} &= F_{22}(x_s, y_s)y_2. \end{aligned} \tag{3.11}$$

and conversely. Using lemma 3.3 (b), we see that (3.11) and hence (3.10) has one nontrivial solution in $B \times B$ if and only if $\frac{1}{\tau}\int_0^\tau \frac{m_2^* y_s(l)}{a_2+y_s(l)+b_2y_s^2(l)}\mathrm{d}l = 1$. Hence there exists a continuum $C = \{(m_2; x_1, x_2)\} \subseteq (0, \infty) \times B \times B$ nontrivial solutions of (3.10) such that the closure $\bar{C}$ contains $(m_2^*; 0, 0)$. This continuum gives rise to a continuum $C_1 = \{(m_2; y, z)\} \subseteq (0, \infty) \times B \times B$ of the solutions of (3.7) whose closure $\bar{C}_1$ contains the bifurcation point $(m_2^*; y_s, 0)$.

To see that solutions in C_1 correspond to solutions (y, z) of (3.7), we investigate the nature of the continuum C near the bifurcation point $(m_2^*; 0, 0)$ by expending m_2 and (x_1, x_2) in Lyapunov-Schmidt series:

$$\begin{aligned} m_2 &= m_2^* + \lambda\varepsilon + \cdots, \\ x_1 &= x_{11}\varepsilon + x_{12}\varepsilon^2 + \cdots, \\ x_2 &= x_{21}\varepsilon + x_{22}\varepsilon^2 + \cdots \end{aligned}$$

for $x_{ij} \in B$ where ε is a small parameter. If we substitute these series into the differential system (3.7) and equate coefficients of ε and ε^2 we find that

$$\begin{aligned} x'_{11} &= F_{11}(x_s, y_s)x_{11} - F_{12}(m_2^*, x_s, y_s)x_{21}, \\ x'_{21} &= F_{22}(m_2^*, y_s)x_{21} \end{aligned}$$

and

$$\begin{aligned} x'_{12} &= F_{11}(x_s, y_s)x_{12} - F_{12}(m_2^*, x_s, y_s)x_{22} + G_{12}(x_{11}, x_{11}, \lambda), \\ x'_{22} &= F_{22}(m_2^*, x_s, y_s)x_{22} + \frac{x_{21}y_s}{a_2+y_s+b_2y_s}\left(\lambda + \frac{m_2^* x_{11}(a_2-b_2y_s^2)}{a_2+y_s+b_2y_s}\right), \end{aligned}$$

respectively. Thus, $(x_{11}, x_{21}) \in B \times B$ must be a solution of (3.10). We choose the specific solution satisfying the initial conditions $x_{21}(0) = 1$. Then

$$x_{21} = \exp\left(\int_0^t \left(\frac{m_2^* y_s(l)}{a_2+y_s(l)} - 1\right)\mathrm{d}l\right) > 0.$$

Moreover, $x_{11} < 0$ for all t (since $m_1 > m_1^*$ and (2.14), $\int_0^\tau \left(\frac{m_1 x_s}{a_1+x_s+b_1x_s^2} - 1 - \frac{m_1(a_1-b_1x_s^2)y_s}{(a_1+x_s+b_1x_s^2)^2}\right)\mathrm{d}l = -\int_0^\tau \left(\frac{m_1(a_1-b_1x_s^2)y_s}{(a_1+x_s+b_1x_s^2)^2}\right)\mathrm{d}l < 0$ implies that the Green's function for first equation in (3.11) is positive). Using lemma 3.3, we find that

$$\lambda = -\frac{\int_0^\tau \frac{m_2^* x_{21}(t)x_{11}(t)(a_2-b_2y_s^2(t))}{(a_2+y_s(t)+b_2y_s^2(t))^2} \exp\left(\int_0^t (\frac{m_2 y_s(l)}{a_2+y_s(l)+b_2y_s^2(l)} - 1)\mathrm{d}l\right)\mathrm{d}t}{\int_0^\tau \frac{y_s(t)x_{21}(t)}{a_2+y_s(t)+b_2y_s^2(t)} \exp\left(\int_0^t \left(\frac{m_2 y_s(t)}{a_2+y_s(l)+b_2y_s^2(l)} - 1\right)\mathrm{d}l\right)\mathrm{d}t} > 0$$

provided with $a_2 - b_2y_s^2 \geqslant 0$. Thus, we see that near the bifurcation point $(m_2^*; 0, 0)$ (say, for $0 < |m_2 - m_2^*| = \lambda|\varepsilon| < \lambda_0$) the continuum C has two (sub-continua) branches corresponding to $\varepsilon < 0, \varepsilon > 0$, respectively:

$$C^+ = \{(m_2; x_1, x_2) : m_2^* < m_2 < m_2^* + \lambda_0, x_1 < 0, x_2 > 0\},$$
$$C^- = \{(m_2; x_1, x_2) : m_2^* - \lambda_0 < m_2 < m_2^*, x_1 > 0, x_2 < 0\}.$$

The solution is on C^+ which prove the theorem, since $\lambda > 0$ is equivalent to $m_2 > m_2^*$. We have left only to show that $y = x_1 + y_s > 0$ for all t. This is easy, for if λ_0 is small, then y is near y_s in the sup norm of B; thus since y_s is bounded away from zero, so is y. At same time, by theorem 3.1, for system (1.2), y is near y_s means that x is near x_s; thus $x = \tilde{s} - y - z > 0$. We notice that the periodic solution (y, z) is continuous $\tau-$periodic. So $x = \tilde{s} - y - z$ is piecewise continuous and $\tau-$periodic. We complete the proof.

4. Chemostat chaos

In this section, we will analyze the complexity of the impulsive system (1.2). By theorems 2.1, 3.1, and 3.2, we know that if $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)}\mathrm{d}l < 1$, the periodic solution $(\tilde{s}(t), 0, 0)$ is globally asymptotically stable; if $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)}\mathrm{d}l > 1$ and $\frac{1}{\tau}\int_0^\tau \frac{m_2 y_s(l)}{a_2+y_s(l)+b_1y_s^2(l)}\mathrm{d}l < 1$, then the $(x_s(t), y_s(t), 0)$ is globally asymptotically stable; if $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)}\mathrm{d}l > 1$ and $\frac{1}{\tau}\int_0^\tau \frac{m_2 y_s(l)}{a_2+y_s(l)+b_1y_s^2(l)}\mathrm{d}l > 1$, hence the value $m_2^* = \tau/\int_0^\tau \frac{y_s(l)}{a_2+y_s(l)+b_1y_s^2(l)}\mathrm{d}l$ practises as a bifurcation threshold.

We want to investigate the influence of m_1. Set $m_2 = 10$ and $\tau = 6$, $a1 = 1.2, a2 = 0.8, b1 = 0.2, b2 = 0.3$. The influences of m_1 may be documented by stroboscopically sampling some of the variables over a range of m_1 values. We numerically integrated system (1.2) for 500 pulsing cycles at each value of m_1. For each m_1, we plotted the last 200 measures of the prey y and the predator z. Since, we sampled at the forcing period, periodic solutions of period τ appear as fixed points, periodic solutions of period 2τ appear as two cycles, and so forth. The resulting bifurcation diagrams (figure 1) clear show that: with increasing m_1

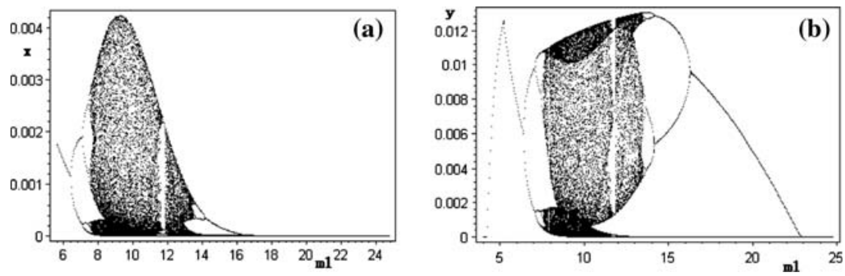

Figure 1. Bifurcation diagrams of system (1.1) with $m2 = 10, a1 = 1.2, a2 = 0.8, b1 = 0.2, b2 = 0.3$, and $T = 6$, $5.6 < m1 \leqslant 24.6$ and initial values $x_0 = 1$, $y_0 = 1$, $z_0 = 0.5$.

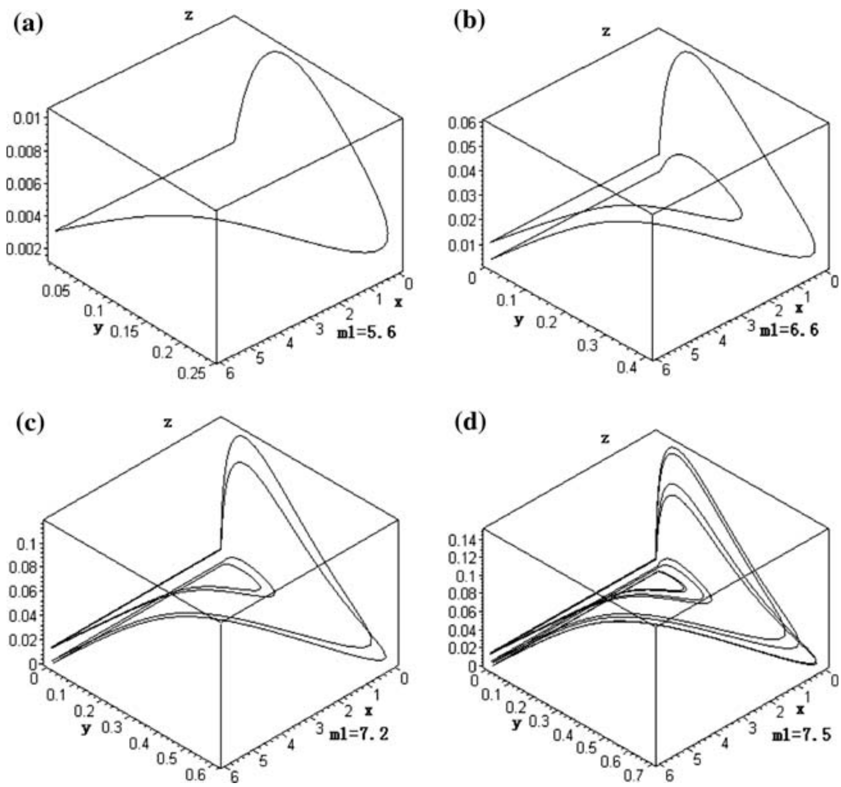

Figure 2. Doubling bifurcation. (a)–(d) Phase portraits of τ, 2τ, 4τ and 8τ-period solutions for $m1$=5.6, 6.6, 7.2, and 7.5, respectively.

from 4 to 24.6, the system experiences process of cycles → periodic doubling cascade (figure 2)→chaos(figure 3) → periodic halfing cascade (figure 4)→ cycles, which is characterized by (1) period doubling, (2) period halfing.

When m_1 is small ($m_1 < q_0 \approx 4.16$), the solution $(\tilde{s}(t), 0, 0)$ is stable. When $m_1 > q_0$, the prey begins invade the system and the solution $(x_s, y_s, 0)$ is sta-

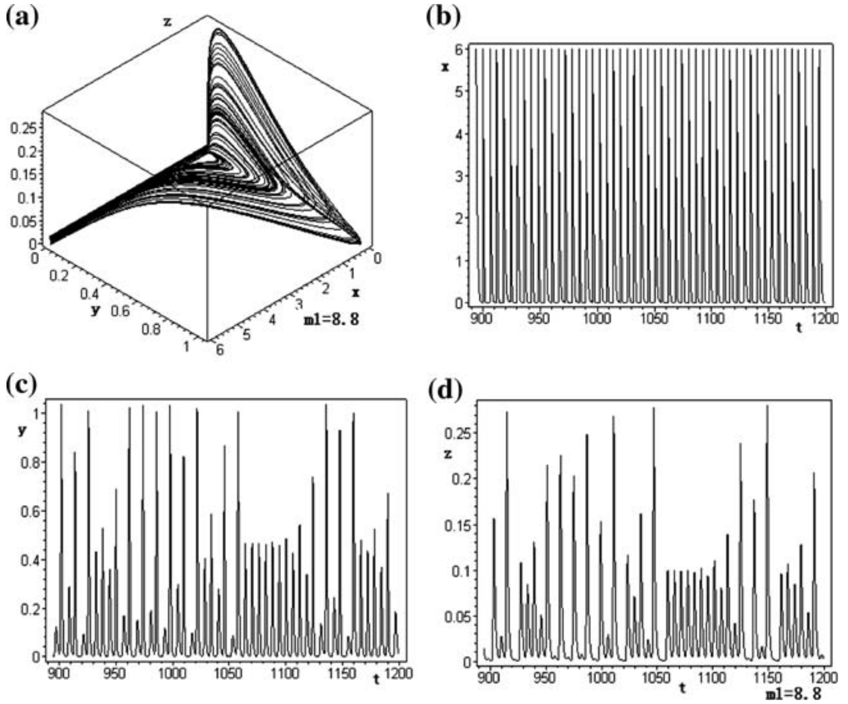

Figure 3. A strange attractor: (a) phase portrait of system (1.1) of m1=8.8, (b)–(d) time series of x, y, z solution initial values $x_0 = 1$, $y_0 = 1$, $z_0 = 0.5$.

ble if $m_1 < q_1$. When $m_1 > q_1$, the predator begins invade and a stable positive period solution is bifurcated from $(x_s, y_s, 0)$ if $m_1 < q_2 \approx 5.19$. However, when $m_1 > q_3 \approx 6.4$, the stability of $\tau-$periodic solution is destroyed and $2\tau-$periodic solution occurs (figure 2(b)) and is stable if $m_1 < q_4 \approx 7.08$. When $m_1 > q_4$, it is unstable and there is a cascade of period doubling bifurcations leading to chaos (figure 2 (c) and (d) and figure 3). Continuously increasing m_1, it is followed by a cascade of periodic halfing bifurcations from chaos to cycles (figure 4). A typical chaotic oscillation is captured when $m_1 = 8.8$. This periodic-doubling route to chaos is the hallmark of the logistic and Ricker maps [19, 20] and has been studied extensively by Mathematicians [21]. Periodic halving is the flip bifurcation in Klebanott and Hastings the opposite direction, which is also observed in [22].

We want to investigate the influence of m_2. Set $m_1 = 8, a1 = 1.2, a2 = 0.8, b1 := 0.2, b2 = 0.3$, and $\tau = 6$. We numerically integrated system (2.3) for 500 pulsing cycles at each value of m_2. For each m_2, we plotted the last 200 stroboscopic measures of the prey y and the predator z. The resulting bifurcation diagrams (figure 5) show: (1) the invasion of predator at $m_2^* \approx 5.26$, (2) the first

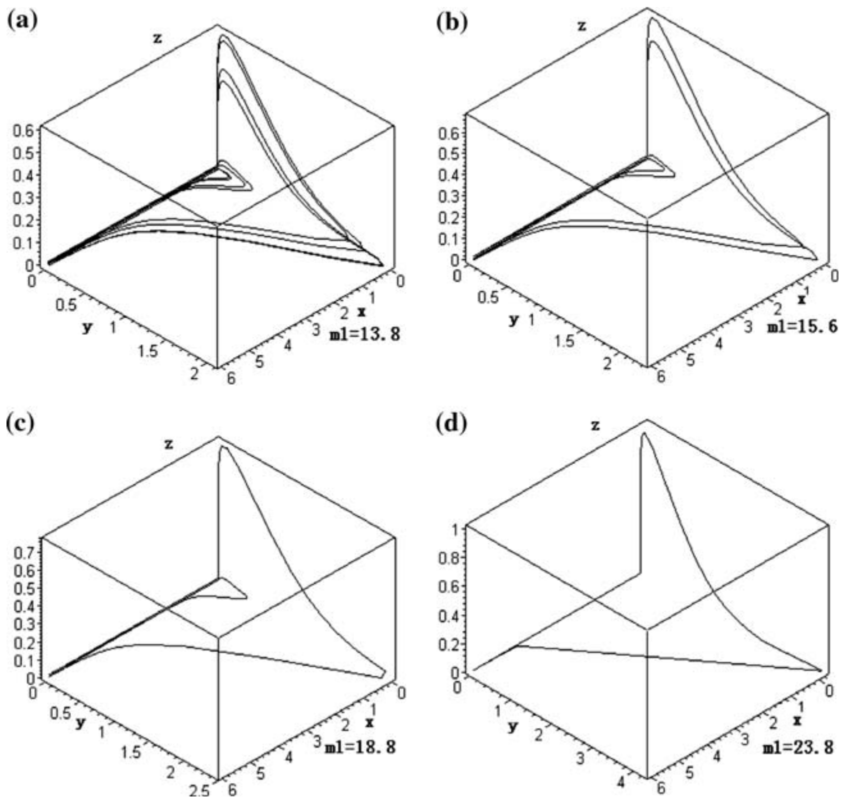

Figure 4. Halving bifurcation. (a)–(d) Phase portraits of 8τ, 4τ, 2τ and τ-period solutions for $m1$=13.8, 15.6, 18.8, and 23.8, respectively.

period-doubling at $m_2 \approx 7.85$, (3) a cascade of period doubling, (4) chaotic solutions, and (5) periodic windows within the chaotic regime.

Comparable changes occur with an increase in the pulse period τ. Set $m1 = 10, m2 = 12, a1 = 1.2, a2 = 0.8, b1 = 0.2$, and $b2 = 0.3$. The resulting bifurcation diagrams (figure 6) clear show that: with increasing τ from 0.2 to 8.2, the system experiences process of quasiperiodic oscillations $\rightarrow$ cycles $\rightarrow$ periodic doubling cascade $\rightarrow$chaos $\rightarrow$ periodic halving cascade $\rightarrow$ cycles, which is characterized by quasi-periodic oscillating, period doubling and period halving. figure 7 shows a phase portrait of quasi-periodic oscillating solution at $\tau = 0.5$.

5. Conclusions

In this paper, we introduce and study a model of a Monod–Haldene type food chain chemostat with pulsed substrate. First, we find the invasion threshold

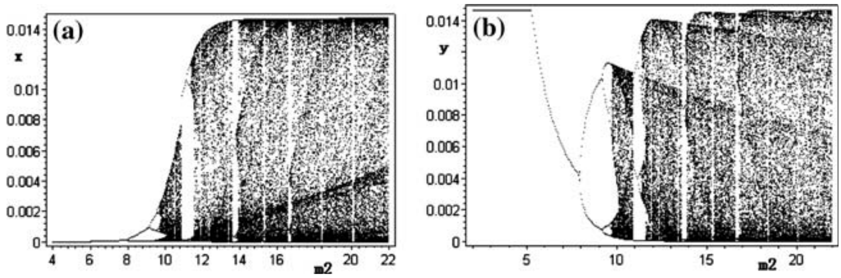

Figure 5. Bifurcation diagrams of system (1.1) with $m_1 = 8, a1 = 1.2, a2, = 0.8, b1 = 0.2, b2 = 0.3$, and $\tau = 6$ and initial values $x_0 = 1,\ y_0 = 1,\ z_0 = 0.5$.

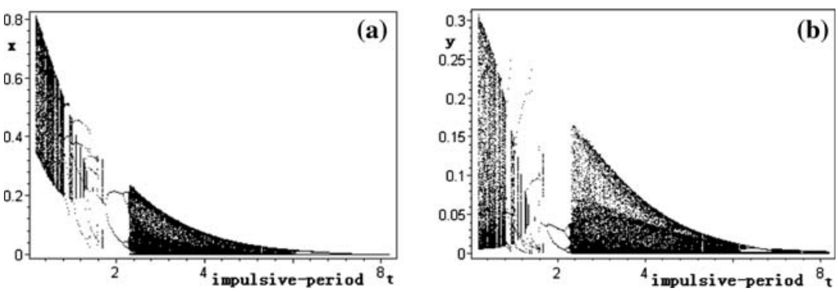

Figure 6. Bifurcation diagrams of system (1.1) with $m_1 = 10, m2 = 12, a1 = 1.2, a2 = 0.8$, $b1 = 0.2, b2 = 0.3$, and $0.03 < \tau \leqslant 8$ and initial values $x_0 = 1,\ y_0 = 1,\ z_0 = 0.5$.

of the prey, which is $m_1^* = \frac{\tau}{\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)+b_1\tilde{s}^2(l)}\mathrm{d}l}$. If $m_1 < m_1^*$, the periodic–periodic solution $(\tilde{s}(t), 0, 0)$ is globally asymptotically stable and if $m_1 > m_1^*$, the prey starts to invade the system. Furthermore, by using Floquet theorem and small amplitude perturbation skills, we have proved that if $m_1 > m_1^*$, there exists

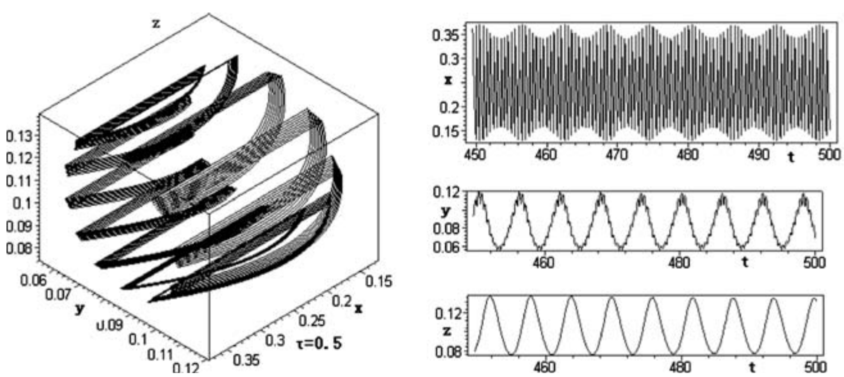

Figure 7. Quasiperiodic oscillation at $\tau = 0.5$ and the time series of x, y, z solution with initial values $x_0 = 1,\ y_0 = 1,\ z_0 = 0.5$.

$m_2^* = \frac{\tau}{\int_0^\tau \frac{m_2 y_s(l)}{a_2+y_s(l)+b_2 y_s^2(l)} dl}$ to play as the invasion threshold of the predator, that is to say, if $m_2 < m_2^*$ the boundary solution $(x_s, y_s, 0)$ is globally asymptotically stable and if $m_2 > m_2^*$ the solution $(x_s, y_s, 0)$ is unstable.

Choosing different coefficients m_1, m_2, and pulsed period τ as bifurcation parameters, we have obtained bifurcation diagrams (figures 1, 5 and 6). Bifurcation diagrams have shown that there exists complexity for system (1.2) including quasi-periodic oscillation, periodic-doubling cascade, periodic windows, and periodic halving cascade. All these results show that dynamical behavior of system (1.2) becomes more complex under periodically impulsive inputting substrate.

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