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Analysis of a Beddington–DeAngelis food chain chemostat with periodically varying substrate

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Abstract In this paper, we introduce and study a model of a Beddington–DeAngelis type food chain chemostat with periodically varying 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. Furthermore, we numerically simulate a model with sinusoidal input, by comparing bifurcation diagrams with different bifurcation parameters, we can see that the periodic system shows two kinds of bifurcations, whose are period-doubling and period-halfing.

Keywords Beddington–DeAngelis functional response · Chemostat · Periodically varying substrate · Periodic solution

1 Introduction

As well known, countless organisms live in seasonally or diurnally forced environment, in which the populations obtain food, so the effects of this forcing may be quite profound. There is evidence, for example, the seasonal variation in contact rates derives the dynamics of childhood disease epidemics [1], and that seasonal or diurnal periodicity in competition coefficients can play a pivotal role in the coexistence of

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some competitors [2]. A chemostat is a common laboratory apparatus used to culture microorganisms. Sterile growth medium enters the chemostat at a constant rate; the volume within the chemostat is held constant. In its simplest form, the system approximates conditions for plankton growth in lakes, where the limiting nutrients such as silica and phosphate are supplied from streams draining the watershed. Recently many papers studied chemostat model with variations in the supply of nutrients or the wash-out. Chemostat with periodic inputs are studied in [3–7], those with periodic washout rate in [8,9], and those with periodic input and washout in [10]. The goal of this paper is to study a system for a chemostat with bacteria, bacteria, and periodically substrate, which incorporate the specific growth rates [11]. The model reads as:

$$\begin{cases} \frac{dS}{dT} = D[S_0(1+\varepsilon A(T)) - S] - \frac{\mu_1}{\delta_1}\frac{SH}{(A_1+S+B_1H)}, \\ \frac{dH}{dT} = \frac{\mu_1 SH}{A_1+S+B_1H} - DH - \frac{\mu_2}{\delta_2}\frac{HP}{(A_2+H+B_2P)}, \\ \frac{dP}{dT} = \frac{\mu_2 HP}{A_2+H+B_2P} - DP, \end{cases} \tag{1.1}$$

where is the ω-period continuous function $A(T)$, with

$$\int_0^\omega A(T)dT = 0,\ |A(T)| \le 1,\ 0 \le \varepsilon < 1.$$

For periodic operation of the chemostat, the periodic input rate will be used as the varying parameter, $S_0(1+\varepsilon A(T))$. Note that it should be in order to ensure that the dilution rate is nonnegative for all time ($|A(T)| \le 1, 0 \le \varepsilon < 1$). The state variables S, H and P represent the concentration of limiting substrate, prey, and predator. D is the dilution rate; S_0 is the concentration of the rate-limiting substrate in the feed; μ_1 and μ_2 are the uptake and predation constants of the prey and predator; δ_1 is the yield of prey per unit mass of substrate; δ_2 is the biomass yield of predator per unit mass of prey.

There are advantages in analyzing dimensionless equations. We choose the non-dimensional variables to be

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

After some algebra, this yields

$$\begin{cases} \frac{dx}{dt} = 1 + \varepsilon a(t) - x - \frac{m_1 xy}{a_1+x+b_1y}, \\ \frac{dy}{dt} = \frac{m_1 xy}{a_1+x+b_1y} - y - \frac{m_2 yz}{a_2+y+b_2z}, \\ \frac{dz}{dt} = \frac{m_2 yz}{a_2+y+b_2z} - z, \end{cases} \tag{1.2}$$

with

$$m_1 = \frac{\mu_1}{D},\quad a_1 = \frac{A_1}{S_0},\quad b_1 = B_1\delta_1;\qquad m_2 = \frac{\mu_2}{D},\ \ a_2 = \frac{A_2}{\delta_1 S_0},\ b_2 = B_2\delta_2;$$
$$a(t) = A(t/D),\qquad \int_0^\tau a(t)dt = 0,\ |a(t)| \le 1,\ 0 \le \varepsilon < 1,\quad \tau = \omega D.$$

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 Sect. 3, we study the locally 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 Sect. 4, we numerically analyze the complexity of a mass-action model with sinusoidally forced inflowing substrate. By comparing bifurcation diagrams with different bifurcation parameters, we can see that the periodic system shows two kinds of bifurcations, whose are period-doubling and period-halving.

2 Behavior of the substrate bacterium subsystem

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

$$\begin{cases} \frac{dx}{dt} = (1+\varepsilon a(t)) - x - \frac{m_1 xy}{a_1+x+b_1 y}, \\ \frac{dy}{dt} = \frac{m_1 xy}{a_1+x+b_1 y} - y, \end{cases} \tag{2.1}$$

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

If we add the first and second equations of the system (2.1), we have $\frac{d(x+y)}{dt} = (1+\varepsilon a(t)) - (x+y)$. If we take variable changes $s = x + y$ then the system (2.1) can be rewritten as

$$\frac{ds}{dt} = (1+\varepsilon a(t)) - s. \tag{2.2}$$

Equation (2.2) has a period solution $\tilde{s}(t)$, where

$$\begin{aligned} &\tilde{s}(t) := \left[\tilde{s}(0) + \int_0^t e^s(1+\varepsilon a(s))ds\right]e^{-t}, \\ &\tilde{s}(0) := \frac{1}{e^\tau - 1}\int_0^\tau e^s(1+\varepsilon a(s))ds, \\ &\int_0^\tau \tilde{s}(t)dt = \tau. \end{aligned}$$

The multiplier of τ-period solution $\tilde{s}(t)$ is $e^{-\tau} < 1$, hence it is globally asymptotically stable. Then 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 (2.2) we have $|s(t) - \tilde{s}(t)| \to 0$ as $t \to \infty$.

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 $x(0) \geq 0$, $y(0) > 0$, 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 the system (2.1).

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

(1) If $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl < 1$, then the system (3.1) 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 $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl > 1$, then the 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

$$\frac{1}{\tau}\int_0^\tau \frac{m_1(\tilde{s}(l)-y_s(l))}{a_1+\tilde{s}(l)-y_s(l)+b_1y_s(l)}dl = 1.$$

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

$$y(t) \le y(0)\exp\left(\left(\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl - 1\right)t\right)\exp\left(\int_0^t p_1(l)dl\right). \tag{2.4}$$

where $p_1(t) = \frac{m_1\tilde{s}(t)}{a_1+\tilde{s}(t)} - \int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl$; note that $\frac{1}{\tau}\int_0^\tau p(l)dl = 0$ and hence that $p_1(t)$ is τ-periodic piecewise continuous function. Thus, for $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl - 1 < 0$ 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 $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)} > 1$. By lemma 2.1, we can consider the system (2.1) in its stable invariant manifold $\tilde{s}(t)$, that is

$$\begin{aligned} &\frac{dy}{dt} = \frac{m_1(\tilde{s}(t)-y)y}{a_1+(\tilde{s}(t)-y)+b_1y} - y,\\ &0 \le y_0 \le \tilde{s}(0) = 1 + \frac{\varepsilon}{e^\tau-1}\int_0^\tau e^s a(s)ds. \end{aligned} \tag{2.5}$$

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.

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

$$\begin{aligned} &y(t, y_0) = y(n\tau)\exp\left(\int_{n\tau}^t \left(\frac{m_1(\tilde{s}(l)-y(l,y_0))}{a_1+(\tilde{s}(l)-y(l,y_0))+b_1y(l,y_0)} - 1\right)dl\right),\\ &y(n\tau) = y_0. \end{aligned} \tag{2.6}$$

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

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

By (i),(ii) and (iii), we know that if $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl > 1$, the Eq. 2.6 has a unique solution in $(0, \tilde{s}(0)]$; otherwise, it has no solution in $(0, \tilde{s}(0)]$. We denote

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

If $m_1 < m_1^*$, then the Eq. 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 the Eq. 2.5 has uniquely positive periodic solution. We denote this positive periodic solution

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

which satisfies the following equation

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

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:

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

Noticing Eq. 2.5, we have

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

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

For any $y_0 \in (0, \tilde{s}(0))$, by the theorem on the differentiability of the solutions on the initial values, $\frac{\partial y(t,y_0)}{\partial y_0}$ exists. Furthermore, $\frac{\partial y(t,y_0)}{\partial y_0} \geq 0$, $t \in (0, \infty)$ 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

$$\frac{d(F(y(\tau,y_0)))}{dy_0} < 0. \tag{2.11}$$

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

Now we set $0 < \varepsilon_1 < y_0^* < \tilde{s}(0)$. According to (2.11), we have that

$$\begin{array}{ll} \ln y(\tau, y_0) - \ln y_0 < 0, & \text{if} \quad y_0^* < y_0 < \tilde{s}(0), \\ \ln y(\tau, y_0) - \ln y_0 = 0, & \text{if} \quad y_0 = y_0^*, \\ \ln y(\tau, y_0) - \ln y_0 > 0, & \text{if} \quad \varepsilon_1 < y_0 < y_0^*. \end{array} \tag{2.12}$$

Furthermore, we obtain the following equations

$$\begin{array}{ll} y_0 > y(\tau, y_0) > \cdots > y(n\tau, y_0) > y_0^*, & \text{if} \quad y_0^* < y_0 \le \tilde{s}(0), \\ y_0 < y(\tau, y_0) < \cdots < y(n\tau, y_0) < y_0^*, & \text{if} \quad \varepsilon_1 \le y_0 < y_0^*. \end{array} \tag{2.13}$$

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 Eq. 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 $\varepsilon_1 > 0$ be given. By the theorem 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 $0 \le t \le \tau$. 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

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

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

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 $s = x + y + z$, 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

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

The lemma 3.1 says that the periodic solution $\tilde{s}(t)$ is an invariant manifold of system (1.2).

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

(1) If $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl > 1$ and $\frac{1}{\tau}\int_0^\tau \frac{m_2 y_s(l)}{a_2+y_s(l)}dl < 1$, then the system (1.2) has a unique globally asymptotically stable boundary $\tau-$periodic solution $(x_s(t), y_s(t), 0)$ is globally asymptotical stable.

(2) If $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl > 1$ and $\frac{1}{\tau}\int_0^\tau \frac{m_2\tilde{y}(l)}{a_2+\tilde{y}(l)}dl > 1$, then the periodic boundary solution $(\tilde{s}(t) - y_s(t), y_s(t), 0)$ of the system (1.2) is unstable.

Proof 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

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

there may be written

$$\begin{pmatrix} u(t) \\ v(t) \\ w(t) \end{pmatrix} = \Phi(t) \begin{pmatrix} u(0) \\ v(0) \\ w(0) \end{pmatrix} \qquad 0 \le t < \tau$$

where $\Phi(t)$ satisfies

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

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

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

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

The eigenvalues of the matrix $\Phi(\tau)$ are $\mu_3 = \exp\left(\int_0^\tau \left(\frac{m_2 y_s(l)}{a_2+y_s} - 1\right) dl\right)$ 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 the system (2.1) provided with $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl > 1$ at the asymptotically stable periodic solution $(x_s(t), y_s(t))$, according to Theorem 2.1, we have that $\mu_1 < 1, \mu_2 < 1$.

If $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl > 1$ and $\frac{1}{\tau}\int_0^\tau \frac{m_2 y_s(l)}{a_2+y_s(l)}dl < 1$, the $\mu_3 = \exp\left(\int_0^\tau \left(\frac{m_2 y_s(l)}{a_2+y_s(l)} - 1\right) dl\right) < 1$, the boundary periodic solution $(x_s(t), y_s(t), 0)$ of the system (1.2) is locally asymptotically stable. We have that $z(t) \leq z(0)\exp\left(\int_0^t\left(\frac{m_2 y_s(l)}{a_2+y_s(l)}-1\right)dl\right)$, 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 2.1, we have $\lim_{t\to\infty}|y(t)-y_s(t)| = 0$ and $\lim_{t\to\infty}|x(t)-x_s(t)| = 0$.

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

Let B denote the Banach space of continuous, $\tau-$periodic functions $N : [0, \tau] \to R^2$. In the set B introduce the norm $|N|_0 = \sup_{0\leq t\leq\tau}|N(t)|$ with which B becomes a Banach space with the uniform convergence topology.

For convenience, just like [12] we introduce the following lemma 3.2 and 3.3.

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

$$\begin{cases} \frac{dy_1}{dt} = a_{11}y_1 + a_{12}y_2, \\ \frac{dy_2}{dt} = a_{22}y_2, \end{cases} \tag{3.4}$$

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

$$\begin{cases} \frac{dx_1}{dt} = a_{11}x_1 + a_{12}x_2 + f_1, \\ \frac{dx_2}{dt} = a_{22}x_2 + f_2, \end{cases} \tag{3.5}$$

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

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

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

$$\begin{cases} \frac{dy}{dt} = \frac{m_1(\tilde{s}(t)-y-z)y}{a_1+\tilde{s}(t)+(b_1-1)y-z} - y - \frac{m_2 yz}{a_2+y+b_2 z}, \\ \frac{dz}{dt} = \frac{m_2 yz}{a_2+y+b_2 z} - z, \\ y(0) > 0,\ z(0) \geq 0,\ y(0) + z(0) \leq \tilde{s}(0). \end{cases} \tag{3.7}$$

If $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl > 1$, for the system (3.7), by the theorem 3.1 the boundary periodic solution $(y_s(t), 0)$ is locally asymptotically stable provided with $\frac{1}{\tau}\int_0^\tau \frac{m_2 y_s(l)}{a_2+y_s(l)}dl < 1$, and it is unstable provided with $\frac{1}{\tau}\int_0^\tau \frac{m_2 y_s(l)}{a_2+y_s(l)}dl > 1$, hence the value $m_2^* = \tau/\int_0^\tau \frac{y_s(l)}{a_2+y_s(l)}dl$ practises as a bifurcation threshold. For the system (3.7), we have the following results.

Theorem 3.2 For the system (3.7), $\frac{1}{\tau}\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl > 1$ is hold, then there exists a constant $\lambda_0 > 0$, 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, the system (3.3) 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

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

where

$$F_{11}(x_s, y_s) = \frac{m_1 x_s}{a_1 + x_s + b_1 y_s} - 1 - \frac{m_1(a_1 + b_1 x_s + b_1 y_s)y_s}{(a_1 + x_s + b_1 y_s)^2},$$
$$F_{12}(m_2, x_s, y_s) = \frac{m_1(a_1+b_1x_s+b_1y_s)y_s}{(a_1+x_s+b_1y_s)^2} + \frac{m_2 y_s}{a_2 + y_s}, \quad F_{22}(m_2, y_s) = \frac{m_2 y_s}{a_2 + y_s} - 1.$$

We know that $\frac{1}{\tau}\int_0^\tau \frac{m_2 y_s(l)}{a_2+y_s(l)}dl - 1 \neq 0$, by the lemma 3.3, using L we can equivalently write the system (3.8) 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 $G = o(|(x_1, x_2)|_0)$ 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 the 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

$$\begin{cases} \frac{dy_1}{dt} = F_{11}(x_s, y_s)y_1 - F_{12}(x_s, y_s)y_2, \\ \frac{dy_2}{dt} = F_{22}(x_s, y_s)y_2. \end{cases} \tag{3.11}$$

and conversely. Using Lemma 3.2 (b), we see that (3.11) and hence (3.10) has one nontrivial solution in $B \times B$ if and only if $\frac{1}{\tau}\int_0^\tau \frac{m_2^* y_s(l)}{a_2 + y_s(l)} dl = 1$. 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

$$\begin{cases} x_{11}' = F_{11}(x_s, y_s)x_{11} - F_{12}(m_2^*, x_s, y_s)x_{21}, \\ x_{21}' = F_{22}(m_2^*, y_s)x_{21}. \end{cases}$$

and

$$\begin{cases} x_{12}' = F_{11}(x_s, y_s)x_{12} - F_{12}(m_2^*, x_s, y_s)x_{22} + G_{12}(x_{11}, x_{11}, \lambda), \\ x_{22}' = F_{22}(m_2^*, x_s, y_s)x_{22} + \frac{x_{21}}{a_2 + y_s}\left(\lambda y_s + \frac{m_2^*(a_2 x_{11} - b_2 y_s x_{21})}{a_2 + y_s}\right). \end{cases}$$

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

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

Moreover $x_{11} < 0$ for all t $\left(\text{since } \int_0^\tau \left(\frac{m_1 x_s(l)}{a_1 + x_s(l) + b_1 y_s(l)} - 1 - \frac{m_1(a_1 + b_1(y_s(l) + x_s(l)))y_s(l)}{(a_1 + x_s(l) + b_1 y_s(l))^2}\right)\right.$ $dl = -\int_0^\tau \left(\frac{m_1(a_1 + b_1 y_s(l) + b_1 x_s(l))y_s(l)}{(a_1 + x_s(l) + b_1 y_s(l))^2}\right) dl < 0)$ implies that the Green's function for first equation in (3.11) is positive). Using Lemma 3.3 we find that

$$\lambda = -\frac{\int_0^\tau \frac{m_2^* x_{21}(l)(a_2 x_{11}(l) - b_2 y_s(l) x_{21}(l))}{(a_2 + y_s(l))^2} \exp\left(\int_0^l \left(\frac{m_2^* y_s(t)}{a_2 + y_s(t)} - 1\right) dt\right) dl}{\int_0^\tau \frac{y_s(l) x_{21}(l)}{a_2 + y_s(l)} \exp\left(\int_0^l \left(\frac{m_2^* y_s(t)}{a_2 + y_s(t)} - 1\right) dt\right) dl} > 0.$$

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 (subcontinua) branches corresponding to $\varepsilon < 0, \varepsilon > 0$ respectively:

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

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 the 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 periodic system (1.2). By theorem 2.1, 3.1 and 3.2, we know that if $m_1 < m_1^*$, the periodic solution $(\tilde{s}(t), 0, 0)$ is globally asymptotically stable; if $m_1 > m_1^*$ and $m_2 < m_2^*$, then the $(x_s(t), y_s(t), 0)$ is globally asymptotically stable. According to Theorem 3.2, if $m_1 > m_1^*$ and $m_2 > m_2^*$, the predator begins to invade the system. In the following we apply the forced model equations are

$$\begin{cases} \frac{dx}{dt} = (1 + \varepsilon \sin(t)) - x - \frac{m_1 xy}{a_1 + x + b_1 y}, \\ \frac{dy}{dt} = \frac{m_1 xy}{a_1 + x + b_1 y} - y - \frac{m_2 yz}{a_2 + y + b_2 z}, \\ \frac{dz}{dt} = \frac{m_2 yz}{a_2 + y + b_2 z} - z, \end{cases} \tag{4.1}$$

We shall numerically integrate Eq. (4.1) and seek the long-term behavior of the solutions (after the transients have disappeared).

A traditional approach to gain preliminary insight into the properties of dynamic system is to carry out a one-dimensional bifurcation analysis. Onedimensional bifurcation diagrams of *Poincaré* maps provide information about the dependence of the dynamics on a certain parameter. The analysis is expected to reveal the type of attractor to which the dynamics will ultimately settle down after passing the initial transient phase and within which the trajectory will then remain forever.

Firstly, we want to investigate the influence of m_1. In system (4.1), set $m_2 = 8$, $\varepsilon = 0.8$, $a_1 = 0.8$, $a_2 = 1$, $b_1 = 0.1$, $b_2 = 0.2$, $\tau = 2\pi$, and we choose $m_1 \in [0.2, 7]$ as the bifurcation parameter. Fig. 1 illustrates the bifurcation diagram of *Poincaré* map for Eq. (4.1). The resulting bifurcation diagrams (Fig. 1) clear show that: with increasing m_1 from 0.2 to 8, the system experiences process of cycles → periodic doubling cascade (Fig. 2)→chaos (Fig. 3)→periodic windows →chaos → periodic halfing cascade (Fig. 4)→ cycles, which is characterized by (1)period doubling, (2) periodic windows, (3) period halfing.

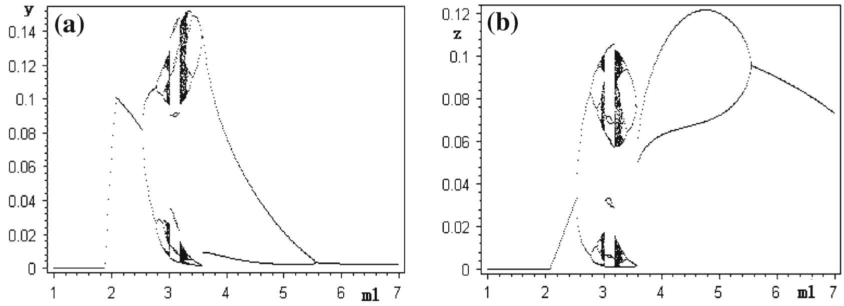

Fig. 1 (**a**, **b**) Bifurcation diagrams of *Poincaré* section for the prey y and predator z in system (4.1) under $m_2 = 8$, $\varepsilon = 0.8$, $a_1 = 0.8$, $a_2 = 1$, $b_1 = 0.1$, $b_2 = 0.2$, $\tau = 2\pi$ and m_1 is varied in [0.2,7]

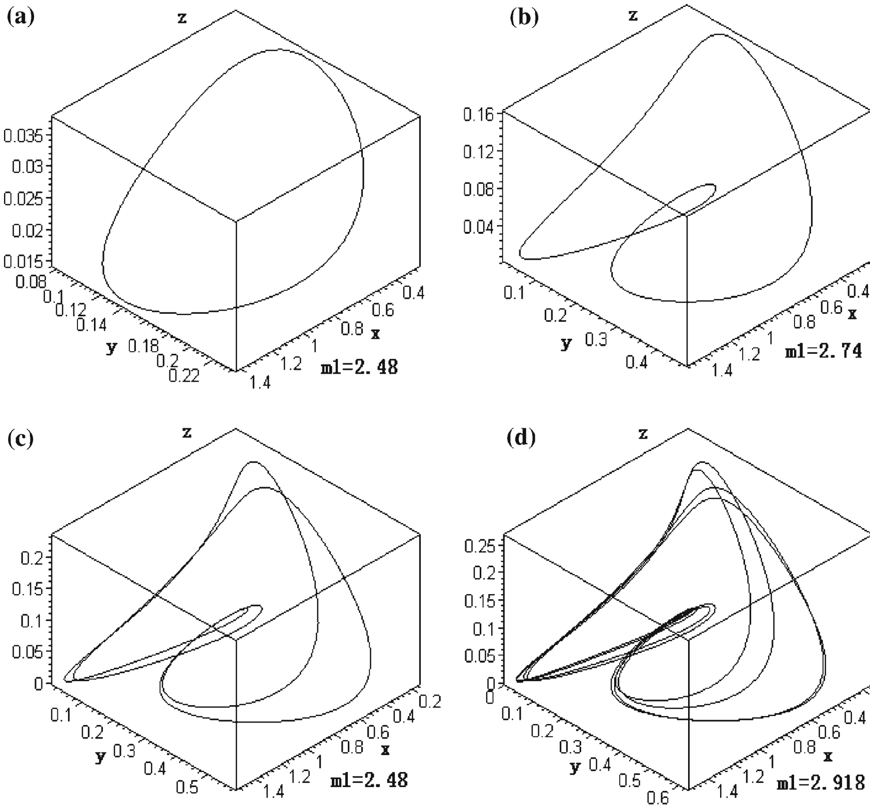

Fig. 2 Periodic-doubling bifurcations. In Eq. (4.1), $m_2 = 8$, $\varepsilon = 0.8$, $a_1 = 0.8$, $a_2 = 1$, $b_1 = 0.1$, $b_2 = 0.2$, $\tau = 2\pi$, (**a**–**d**) are the complete trajectories of τ, 2τ, 4τ and 8τ-periodic solutions over the time interval from $t = 300\pi$ to $t = 500\pi$, corresponding with $m_2 = 2.48$, 2.74, 2.86 and 2.918

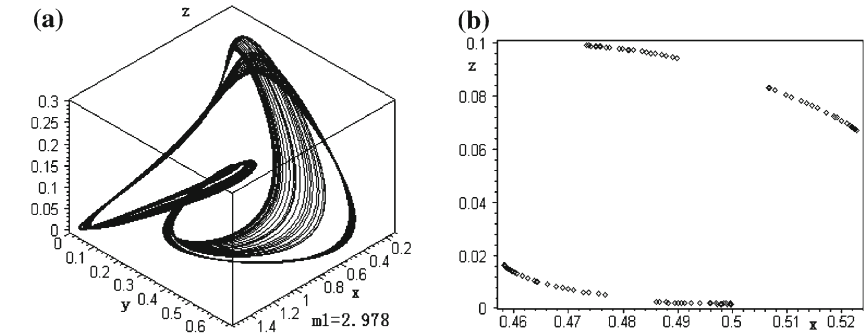

Fig. 3 Strange attractors (chaos) of the flow by Eq. (4.1). Compare a *Poincaré* section (**b**) with the complete chaotic trajectory (**a**)($m_1 = 2.978$). *Poincaré* points 150–250 are plotted in (**b**), and the corresponding complete trajectory over the time interval from $t = 300\pi$ to $t = 500\pi$ are plotted in (**a**)

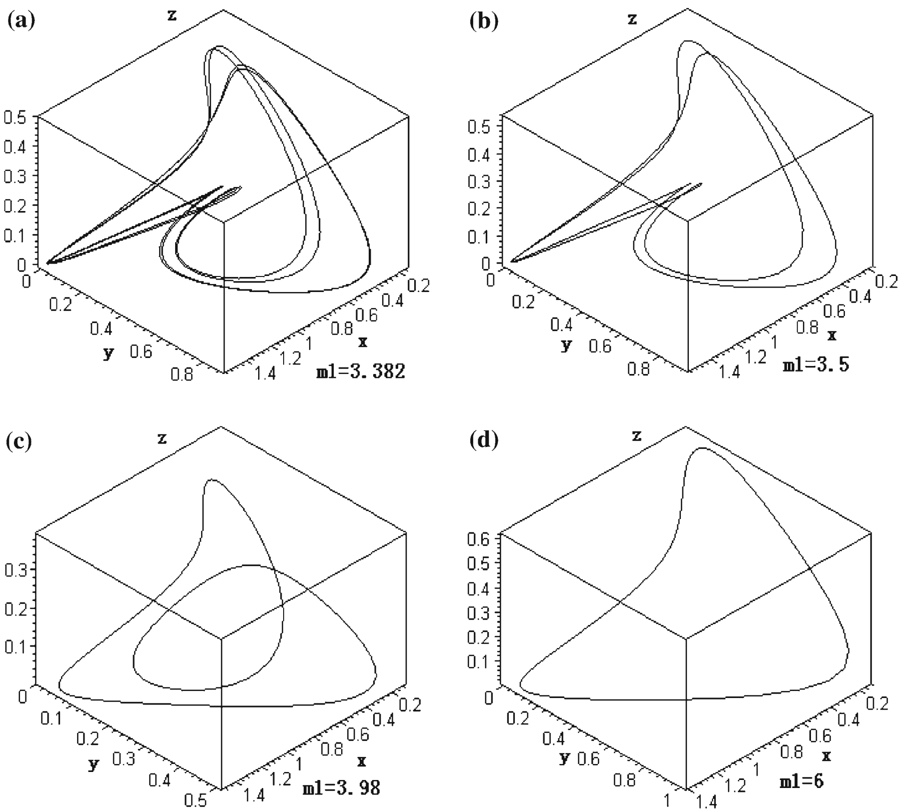

Fig. 4 Periodic-halving bifurcations. In Eq. (4.1), $m_2 = 6$, $\varepsilon = 0.8$, $a_1 = 0.8$, $a_2 = 1$, (**a**–**d**) are the complete trajectories of 8τ, 4τ, 2τ and τ-periodic solutions over the time interval from $t = 300\pi$ to $t = 500\pi$, corresponding with $m_2 = 3.382$, 3.5, 3.98 and 6

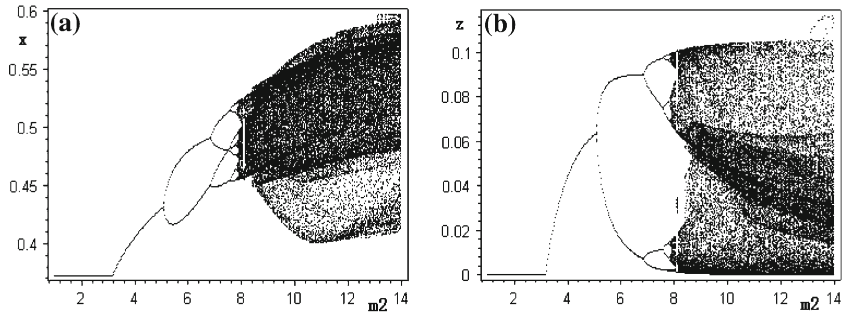

Fig. 5 (**a**, **b**) Bifurcation diagrams of *Poincaré* section for the substrate x and predator z in system (4.1) under $m_1 = 3, \varepsilon = 0.8, a_1 = 0.8, a_2 = 1$ and m_2 is varied in [1,14]

When m_1 is small ($m_1 < m_1^* = 1.86$), the solution $(\tilde{s}(t), 0, 0)$ is stable. When $m_1 > m_1^*$, the prey begins invade the system and the solution $(x_s, y_s, 0)$ is stable if $m_1 < q_1 \approx 2.08(> q_0)$. When $m_1 > q_1$, the predator begins invade and a stable positive period solution (Fig. 2a) is bifurcated from $(x_s, y_s, 0)$ if $m_1 < q_2 \approx 2.54$. However, when $m_1 > q_2$, the stability of $\tau-$periodic solution is destroyed and $2\tau-$periodic solution occurs (Fig. 2b) and is stable if $m_1 < q_3 \approx 2.78$. When $m_1 > q_4 \approx 2.89$, it is unstable and there is a cascade of period doubling bifurcations leading to chaos (Fig. 3a,b). Continuously increasing $m_1 \approx 3.02$, the chaotic solution suddenly shrinks to a τ-period solution and further the system shows next doubling bifurcations. A typical chaotic oscillation is captured when $m_1 = 2.978$ (Fig. 3). When $m_1 > 5.18$ is followed by a cascade of periodic halfing bifurcations from chaos to cycles (Fig 5). This periodic-doubling route to chaos is the hallmark of the logistic and Ricker maps [13,14] and has been studied extensively by Mathematicians [15]. Periodic halving is the flip bifurcation in the opposite direction, which is also observed in [16].

Secondly, we investigate the influence of m_2. In system (4.1), set $m_1 = 3, \varepsilon = 0.8, a_1 = 0.8, a_2 = 1, b_1 = 0.1, b_2 = 0.2, \tau = 2\pi$, and we choose $m_2 \in [1, 14]$ as the bifurcation parameter. The resulting bifurcation diagrams (Fig. 3) show: the invasion of predator at $m_2^* \approx 3.18$; by using theorem 4.1, when $m_2 > m_2^*$ to be not very large, the system shows stable period-one cycles; as the parameter m_2 increases from

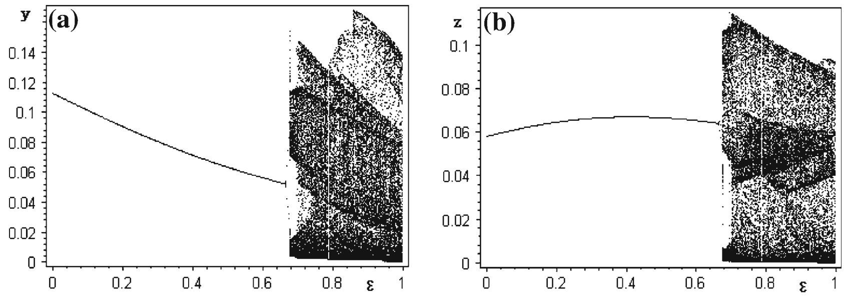

Fig. 6 (**a**, **b**) Bifurcation diagrams of *Poincaré* section for the prey y and predator z in system (4.1) under $m_1 = 3, m_2 = 10, a_1 = 0.8, a_2 = 1, b_1 = 0.1, b_2 = 0.2, \tau = 2\pi$, and ε is varied in [0,1]

5.06, the τ-period behavior bifurcates to a 2τ-periodic cycles, after which period-doubling bifurcations ensure these culminate in a Feigenbaum cascade of period-doubling bifurcations leading to a chaotic region. The main routs to chaos are Feigenbaum cascades.

Comparable changes occur with an increase in the amplitude ε of the seasonal variation. In system (4.1), set $m_1 = 3, m_2 = 10, a_1 = 0.8, a_2 = 1, b_1 = 0.1, b_2 = 0.2, \tau = 2\pi$, and $0 \leq \varepsilon < 1$. Figure 6 shows a cascade of period-doubling route to chaos.

5 Conclusions

In this paper, we introduce and study a model of a Beddington–DeAngelis type food chain chemostat with periodic varying substrate. Firstly we find the invasion threshold of the prey , which is $m_1^* = \frac{\tau}{\int_0^\tau \frac{m_1\tilde{s}(l)}{a_1+\tilde{s}(l)}dl}$. If $m_1 < m_1^*$, the 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 $m_2^* = \frac{\tau}{\int_0^\tau \frac{y_s(l)}{a_2+y_s(l)}dl}$ 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 ε as bifurcation parameters, we have obtained bifurcation diagrams (Figs. 1,5,6). Bifurcation diagrams have shown that there exists complexity for system (4.1) including periodic doubling cascade, periodic windows, periodic halfing cascade. All these results show that dynamical behavior of system (4.1) becomes more complex under periodically inputting substrate.

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