

Bifurcation and chaos of Tessiet type food chain chemostat with periodically varying substrate

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Abstract In this paper, we introduce and study a model of Tessiet 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 dilution rate, 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.

Keywords Bifurcation · Tessiet type functional response · Chemostat · Periodic input · Chaos

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

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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 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 washout. 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]. In this paper, we introduce and study a model of Tessier type food chain chemostat with periodically varying substrate, we may write

$$\begin{cases} \frac{dS}{dT} = D[S_0(1 + \varepsilon A(T)) - S] - \frac{\mu_1 \exp(-B_1 S)SH}{\delta_1(A_1 + S)}, \\ \frac{dH}{dT} = \frac{\mu_1 \exp(-B_1 S)SH}{A_1 + S} - DH - \frac{\mu_2 \exp(-B_2 H)HP}{\delta_2(A_2 + H)}, \\ \frac{dP}{dT} = \frac{\mu_2 \exp(-B_2 H)HP}{A_2 + H} - DP, \end{cases} \tag{1.1}$$

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

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

For periodic operation of the chemostat, the dilution rate will be used as the varying parameter, $D(1 + \varepsilon A(T))$. Note that it should be in order to ensure that the dilution rate is nonnegative for all time ($|A(t)| \leq 1, 0 \leq \varepsilon < 1$). The state variables S, H and P represent the concentration of limiting substrate, prey, and predator. 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

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

After some algebra, this yields

$$\begin{cases} \frac{dx}{dt} = 1 + \varepsilon a(t) - x - \frac{m_1 \exp(-b_1 x)xy}{a_1 + x}, \\ \frac{dy}{dt} = \frac{m_1 \exp(-b_1 x)xy}{a_1 + x} - y - \frac{m_2 \exp(-b_2 y)yz}{a_2 + y}, \\ \frac{dz}{dt} = \frac{m_2 \exp(-b_2 y)yz}{a_2 + y} - z, \end{cases} \tag{1.2}$$

with

$$m_1 = \frac{\mu_1}{D}, \quad a_1 = \frac{A_1}{S_0}, \quad b_1 = B_1 S_0; \quad m_2 = \frac{\mu_2}{D}, \quad a_2 = \frac{A_2}{\delta_1 S_0}, \quad b_2 = B_2 S_0 \delta_1;$$

$$a(t) = A(t/D), \quad \int_0^\tau a(t) dt = 0, \quad |a(t)| \leq 1, \quad 0 \leq \varepsilon < 1, \quad \tau = \omega D.$$

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

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

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 $(d(x + y))/(dt) = (1 + \varepsilon a(t)) - (x + y)$. If we take variable changes $s = x + y$ then the system (2.1) can be rewritten as

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

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

$$\tilde{s}(t) := [\tilde{s}(0) + \int_0^t e^l (1 + \varepsilon a(l)) dl] e^{-t},$$

$$\tilde{s}(0) := \frac{1}{e^\tau - 1} \int_0^\tau e^l (1 + \varepsilon a(l)) dl, \quad \int_0^\tau \tilde{s}(t) dt = \tau.$$

The multiplier of τ -period solution $\tilde{s}(t)$ is $e^{-\tau} < 1$, hence it is globally asymptotically stable.

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 $|s(t) - \tilde{s}(t)| \rightarrow 0$ as $t \rightarrow \infty$.*

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 $\lim_{t \rightarrow \infty} |x(t) + y(t) - \tilde{s}(t)| = 0$.*

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 denote*

$$m_1^* := \tau \left(\int_0^\tau \frac{m_1 \tilde{s}(l) \exp(-b_1 \tilde{s}(l))}{a_1 + \tilde{s}(l)} dl \right)^{-1}.$$

(1) If $m_1 < m_1^*$, then the system (2.1) has a unique globally asymptotically stable positive τ -period solution $(x_e(t), y_e(t))$, where

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

(2) If $m_1 > m_1^*$, then the system (2.1) has a unique globally asymptotically stable positive τ -period solution $(x_s(t), y_s(t))$ and the τ -periodic solution $(x_e(t), y_e(t))$ is unstable. The τ -period positive solution $y_s(t)$ satisfies

$$\int_0^\tau \frac{m_1(\tilde{s}(l) - y_s(l)) \exp(-b_1(\tilde{s}(l) - y_s(l)))}{a_1 + (\tilde{s}(l) - y_s(l))} dl = \tau. \tag{2.4}$$

Proof By Lemma 2.1, we can consider the system (2.1) in its stable invariant manifold $\tilde{s}(t)$, that is

$$\begin{aligned} \frac{dy}{dt} &= \frac{m_1(\tilde{s}(t) - y) \exp(-b_1(\tilde{s}(t) - y))y}{a_1 + (\tilde{s}(t) - y)} - y, \\ 0 &\leq y_0 \leq \tilde{s}(0). \end{aligned} \tag{2.5}$$

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

$$y(t, y_0) = y(0) \exp \left(\int_0^t \left(\frac{m_1(\tilde{s}(l) - y(l, y_0)) \exp(-b_1(\tilde{s}(l) - y(l, y_0)))}{a_1 + (\tilde{s}(l) - y(l, y_0))} - 1 \right) dl \right). \tag{2.6}$$

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

The periodic solutions of (2.5) satisfy the following equation

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

By (i), (ii) and (iii), we know that if $(1/\tau) \int_0^\tau (m_1 \tilde{s}(l) \exp(-b_1 \tilde{s}(l)))/(a_1 + \tilde{s}(l)) dl > 1$, the Eq. 2.6 has a unique solution in $(0, \tilde{s}(0)]$; otherwise, it has no solution in $(0, \tilde{s}(0)]$.

If $m_1 < m_1^*$, it is obvious that

$$y(t) \leq y(0) \exp \left(\int_0^t \frac{m_1 \tilde{s}(l) \exp(-b_1 \tilde{s}(l))}{a_1 + \tilde{s}(l)} dl - t \right). \quad (2.8)$$

By $\int_0^\tau (m_1 \tilde{s}(l) \exp(-b_1 \tilde{s}(l)))/(a_1 + \tilde{s}(l)) dl - \tau < 0$, we obtain that $y(t)$ tends exponentially to zero as $t \rightarrow +\infty$. Considering the system (2.2), we have $x(t) = s(t) - y(t)$. By Lemma 2.2, we have $\lim_{t \rightarrow \infty} |x(t) - \tilde{s}(t)| = 0$. If $m_1 < m_1^*$, then the Eq. 2.5 has a stable periodic solution $y_e(t) = 0$. By Lemma 2.2, we have $\lim_{t \rightarrow \infty} |x(t) - \tilde{s}(t)| = 0$. We have proved in (1).

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

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

which satisfies the following equation

$$\int_0^\tau \frac{m_1(\tilde{s}(t) - y_s(l)) \exp[-b_1(\tilde{s}(t) - y_s(l))]}{a_1 + (\tilde{s}(t) - y_s(l))} dl = \tau. \quad (2.9)$$

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

For proving the stability of the periodic solution $y_s(t)$, we define a function $G(y_0) : y_0 \in (0, \tilde{s}(0))$ as follows:

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

Noticing Eq. 2.5, we have

$$G(y_0) = \frac{y(\tau, y_0)}{y_0}, \quad y_0 \in (0, 1). \tag{2.10}$$

It is obvious that $G(y_0^*) = 1$.

Furthermore, $(\partial y(t, y_0))/(\partial y_0) \geq 0, t \in (0, \tau)$ is hold (otherwise, there exist $t_0 > 0, 0 < y_1 < y_2 < 1$ such that $y(t_0, y_1) = y(t_0, y_2)$, that is a contradiction with the different flows of system (3.5) not to intersect). So we obtain that the function $G(y_0)$ have the following properties:

$$\begin{aligned} G(y_0) &< 1, & \text{if } y_0^* < y_0 < 1, \\ G(y_0) &= 1, & \text{if } y_0 = y_0^*, \\ G(y_0) &> 1, & \text{if } 0 < y_0 < y_0^*. \end{aligned} \tag{2.11}$$

Furthermore, we obtain the following equations

$$\begin{aligned} y_0 > y(\tau, y_0) > \dots > y(n\tau, y_0) > y_0^*, & \text{if } y_0^* < y_0 \leq 1, \\ y_0 < y(\tau, y_0) < \dots < y(n\tau, y_0) < y_0^*, & \text{if } \varepsilon \leq y_0 < y_0^*. \end{aligned} \tag{2.12}$$

Set $y_0 \in (0, 1)$. According to (2.12), we suppose that

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

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

Let $\varepsilon > 0$ 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 $0 \leq t \leq \tau$. 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

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

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

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

$$\mu = \exp \left(\int_0^\tau \frac{m_1 x_s(l) y_s(l) (-1 + b_1 x_s(l) + a_1 b_1 x_s^2(l)) \exp(-b_1 x_s)}{(1 + a_1 x_s(l))^2} dl \right) < 1, \quad (2.13)$$

where we have used (2.9). This conclusion will be used in the section . We have proved (2). \square

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*

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

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

For convenience, in the following discussing if $m_1 > m_1^*$, we denote that

$$m_2^* := \tau \left(\int_0^\tau \frac{y_s(l) \exp(-b_2 y_s(l))}{a_1 + y_s(l)} dl \right)^{-1}.$$

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

- (1) *If $m_1 > m_1^*$ and $m_2 < m_2^*$, then the system (1.2) has a unique globally asymptotically stable boundary τ -periodic solution $(x_s(t), y_s(t), 0)$ is globally asymptotically stable.*
- (2) *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 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

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

there may be written

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

where $\Phi(t)$ satisfies $(d\Phi)/(dt) = D^*(t)\Phi(t)$, where

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

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

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

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 $\mu_3 = \exp(\int_0^\tau ((m_2 y_s(l) e^{-b_2 y_s(l)}) / (a_2 + y_s(l)) - 1) dl)$ 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 $m_1 > m_1^*$ 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 $m_1 > m_1^*$ and $m_2 < m_2^*$, the $\mu_3 = \exp(\int_0^\tau ((m_2 y_s(l) e^{-b_2 y_s(l)}) / (a_2 + y_s(l)) - 1) dl) < 1$, the boundary periodic solution $(x_s(t), y_s(t), 0)$ of the system (1.2) is locally asymptotically stable. We have that $z(t) \leq z(0) \exp(\int_0^t ((m_2 y_s(l) e^{-b_2 y_s(l)}) / (a_2 + y_s(l)) - 1) dl)$, hence we obtain that for any solution $(x(t), y(t), z(t))$ with $X(0) > 0$ $z(t) \rightarrow 0$ as $t \rightarrow \infty$. By $\lim_{t \rightarrow \infty} |x(t) + y(t) + z(t) - \tilde{s}(t)| = 0$, we have $\lim_{t \rightarrow \infty} |x(t) + y(t) - \tilde{s}(t)| = 0$. Now using Theorem 2.1, we have $\lim_{t \rightarrow \infty} |y(t) - y_s(t)| = 0$ and $\lim_{t \rightarrow \infty} |x(t) - x_s(t)| = 0$.

If $m_1 > m_1^*$ and $m_2 > m_2^*$, the $\mu_3 = \exp(\int_0^\tau ((m_2 y_s(l) e^{-b_2 y_s(l)}) / (a_2 + y_s(l)) - 1) dl) > 1$, the boundary periodic solution $(x_s(t), y_s(t), 0)$ of the system (1.2) is unstable. We complete the proof. \square

Let B denote the Banach space of continuous, τ -periodic functions $N : [0, \tau] \rightarrow R^2$. 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 [11] we introduce the following Lemmas 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

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

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 $L : B \times B \rightarrow B \times B$ 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 $L_2 : B \rightarrow B$ 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 $L_1 : B \rightarrow B$. Then we have

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

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

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

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

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

Theorem 3.2 For the system (3.7), $m_1 > m_1^*$ is 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 $x = \tilde{s} - y - z > 0$ for all $t > 0$. Hence, the system (3.3) has a positive τ -periodic solution $(\tilde{s} - y - z, y, z)$.

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

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

where

$$\begin{aligned}
 F_{11}(x_s, y_s) &= \frac{m_1 x_s \exp(-b_1 x_s)}{a_1 + x_s} - 1 - \frac{m_1 y_s \exp(-b_1 x_s)(a_1 - a_1 b_1 x_s - b_1 x_s^2)}{(a_1 + x_s)^2}, \\
 F_{12}(m_2, x_s, y_s) &= \frac{m_1 y_s \exp(-b_1 x_s)(a_1 - a_1 b_1 x_s - b_1 x_s^2)}{(a_1 + x_s)^2} + \frac{m_2 y_s \exp(-b_2 y_s)}{a_2 + y_s}, \\
 F_{22}(m_2, y_s) &= \frac{m_2 y_s \exp(-b_2 y_s)}{a_2 + y_s} - 1.
 \end{aligned}$$

We know that $1/\tau \int_0^\tau (m_2 y_s(l))/(a_2 + y_s(l)) dl - 1 \neq 0$, 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

$$G(x_1, x_2) = (L_1(-F_{12}(x_s, y_s)g_2(x_1, x_2) + g_1(x_1, x_2)), L_2g_2(x_1, x_2)).$$

Here $L^* : B \times B \rightarrow B \times B$ is linear and compact and $G : B \times B \rightarrow B \times B$ 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 $1/\tau \int_0^\tau (m_2^* y_s(l) \exp(-b_2 y_s(l))/(a_2 + y_s(l)) dl = 1$. 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:

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

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

$$\begin{cases} x'_{12} = F_{11}(x_s, y_s)x_{12} - F_{12}(m_2^*, x_s, y_s)x_{22} + G_{12}(x_{11}, x_{11}, \lambda), \\ x'_{22} = F_{22}(m_2^*, x_s, y_s)x_{22} + \frac{x_{21} \exp(-b_2 y_s)}{a_2 + y_s} \left(\lambda y_s + \frac{m_2^* x_{11} (a_2 - a_2 b_2 y_s - b_2 y_s^2)}{a_2 + y_s} \right). \end{cases}$$

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

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

Moreover $x_{11} < 0$ for all t (since $\int_0^\tau ((m_1 x_s e^{-b_1 x_s}) / (a_1 + x_s) - 1 - (m_1 y_s e^{-b_1 x_s} (a_1 - a_1 b_1 x_s - b_1 x_s^2)) / ((a_1 + x_s)^2)) dl = - \int_0^\tau ((m_1 y_s \exp(-b_1 x_s) (a_1 - a_1 b_1 x_s - b_1 x_s^2)) / ((a_1 + x_s)^2)) dl < 0$ implies that the Green’s function for first equation in (4.11) is positive, here we have used (2.14). Using Lemma 3.2 we find that

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

provided with $a_2 - a_2 b_2 y_s - b_2 y_s^2 \geq 0$. 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 τ -periodic. So $x = \tilde{s} - y - z$ is piecewise continuous and τ -periodic. We complete the proof. \square

4 Chemostat chaos

In this section, we will analyze the complexity of the periodic system (1.2). By Theorems 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

$$\begin{cases} \frac{dx}{dt} = 1 + \varepsilon \sin(t) - x - \frac{m_1xy \exp(-b_1x)}{a_1+x}, \\ \frac{dy}{dt} = \frac{m_1xy \exp(-b_1x)}{a_1+x} - y - \frac{m_2yz \exp(-b_2y)}{a_2+y}, \\ \frac{dz}{dt} = \frac{m_2yz \exp(-b_2y)}{a_2+y} - z, \end{cases} \tag{4.1}$$

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. One-dimensional 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 $m_1 \in [1.6, 8]$ as the bifurcation parameter. Figure 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 1.6 to 8, the system experiences process of cycles \rightarrow periodic

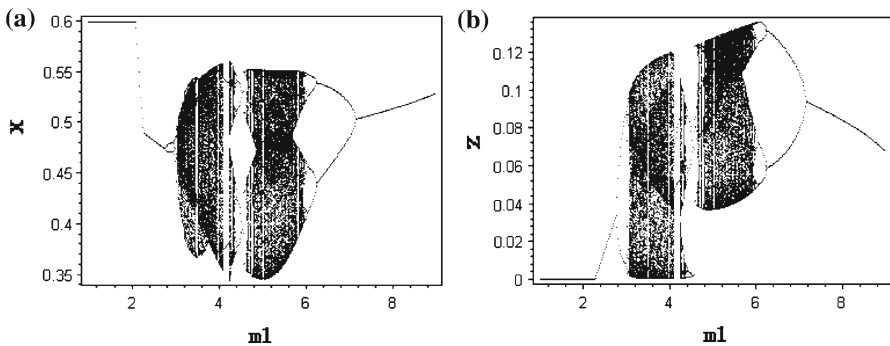


Fig. 1 (a, b) Bifurcation diagrams of *Poincaré* section for the substrate x and predator z in system (4.1) under $m_2 = 8, \varepsilon = 0.8, a_1 = 0.8, a_2 = 1, b_1 = 0.1, b_2 = 0.2, \tau = 2\pi$ and m_1 is varied in $[0.2, 8]$

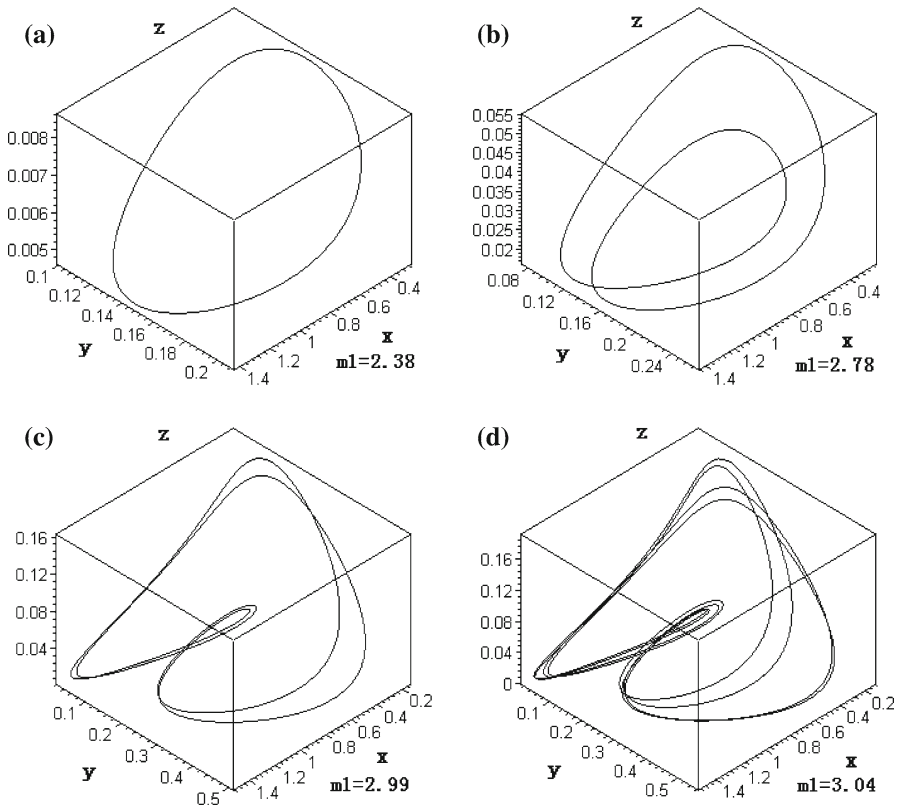


Fig. 2 Periodic-doubling bifurcations. In Eq. 4.1, $m_2 = 8$, $\varepsilon = 0.8$, $a_1 = 0.8$, $a_2 = 1$, $b_1 = 0.1$, $b_2 = 0.2$, $\tau = 2\pi$, (a–d) are the complete trajectories of τ , 2τ , 4τ and 8τ -periodic solutions over the time interval from $t = 300\pi$ to $t = 500\pi$, corresponding with $m_1 = 2.38, 2.78, 2.99$ and 3.04

doubling cascade (Fig. 2) \rightarrow chaos (Fig. 3) \rightarrow periodic windows \rightarrow chaos \rightarrow periodic halving cascade (Fig. 4) \rightarrow cycles, which is characterized by (1) period doubling, (2) period halving.

When m_1 is small ($m_1 < m_1^* = 2.08$), the solution $(\bar{s}(t), 0, 0)$ is stable. When $m_1 > m_1^*$, the prey begins invade the system and the solution $(x_s, y_s, 0)$ is stable if $m_1 < q_1 \approx 2.27 (> q_0)$. 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 $m_1 < q_2 \approx 2.75$. However, when $m_1 > q_2$, the stability of τ -periodic solution is destroyed and 2τ -periodic solution occurs (Fig. 2b) and is stable if $m_1 < q_3 \approx 2.95$. When $m_1 > q_3$, it is unstable and there is a cascade of period doubling bifurcations leading to chaos (Fig. 3a, b). A typical chaotic oscillation is captured when $m_1 = 3.29$ (Fig. 3). When $m_1 > 5.8$ is followed by a cascade of periodic halving bifurcations from chaos to cycles (Fig. 5). This periodic-doubling route to chaos is the hallmark of the logistic and Ricker maps [12, 13] and has been studied extensively by Mathematicians [14]. Periodic halving is the flip bifurcation in the opposite direction, which is also observed in [13].

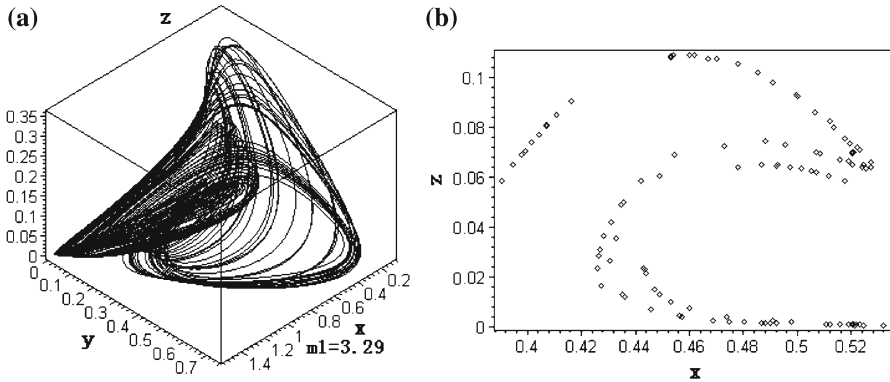


Fig. 3 Strange attractors (chaos) of the flow by Eq. 4.1. Compare a *Poincaré* section (b) with the complete chaotic trajectory (a) ($m_1 = 3.29$). *Poincaré* points 150–250 are plotted in (b), and the corresponding complete trajectory over the time interval from $t = 300\pi$ to $t = 500\pi$ are plotted in (a)

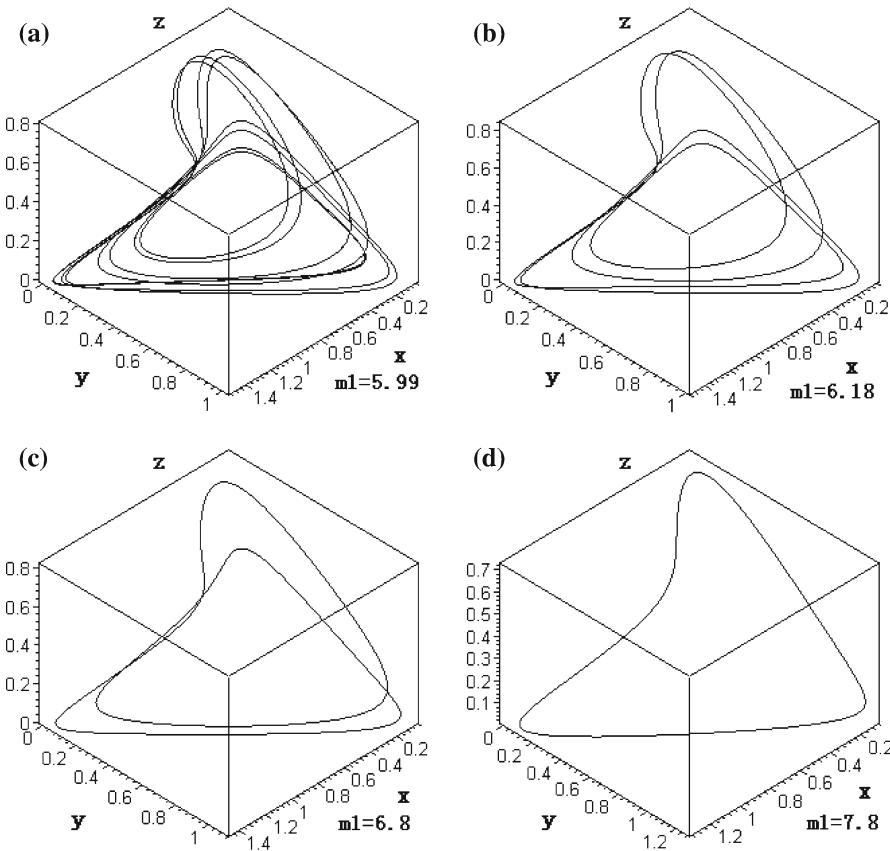


Fig. 4 Periodic-halving bifurcations. In Eq. 4.1, $m_2 = 8, \varepsilon = 0.8, a_1 = 0.8, a_2 = 1$, (a–d) are the complete trajectories of $8\tau, 4\tau, 2\tau$ and τ -periodic solutions over the time interval from $t = 300\pi$ to $t = 500\pi$, corresponding with $m_2 = 5.99, 6.18, 6.8$ and 7.8

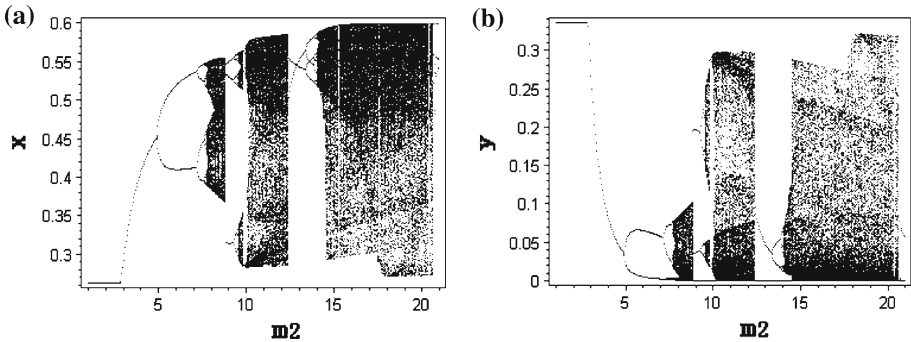


Fig. 5 (a, b) Bifurcation diagrams of *Poincaré* section for the substrate x and predator z in system (4.1) under $m_1 = 3.6, \varepsilon = 0.8, a_1 = 0.8, a_2 = 1$ and m_2 is varied in $[1, 21]$

Secondly, we investigate the influence of m_2 . In system (4.1), set $m_1 = 5.8, \varepsilon = 0.8, a_1 = 0.8, a_2 = 1, b_1 = 0.1, b_2 = 0.2\tau = 2\pi$, and we choose $m_2 \in [1, 14]$ as the bifurcation parameter. The resulting bifurcation diagrams (Fig. 5) show: with increasing m_2 from 1.6 to 8, the system undergoes process of a one-period bifurcation \rightarrow a three-period bifurcation \rightarrow a two-period bifurcation $\rightarrow \dots$. The invasion of predator at $m_2^* \approx 2.79$; by using Theorem 3.1, when $m_2 > m_2^*$ to be not very large, the system shows stable period-one cycles; 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. As the parameter m_2 is slightly increased beyond 8.73 or 12.38, the chaotic attractors abruptly shrink to 3τ -periodic or 2τ -periodic cycles, after which is a Feigenbaum cascade of period-doubling bifurcations leading to a chaotic region.

Comparable changes occur with an increase in the amplitude ε of the forcing term. Set $m_1 = 6, m_2 = 10, a_1 = 0.8, a_2 = 1, b_1 = 0.1, b_2 = 0.2 \tau = 2\pi$. When $\varepsilon = 0$, system (4.1) has a stable limit cycle in positive quadrant. Figure 6 is the resulting bifurcation diagrams of *Poincaré* map for (4.1). Quasiperiodic range $\varepsilon \in (0, 0.22)$ often includes frequency locking in this case, too (see Fig. 7). In the plane of $x - z$ is

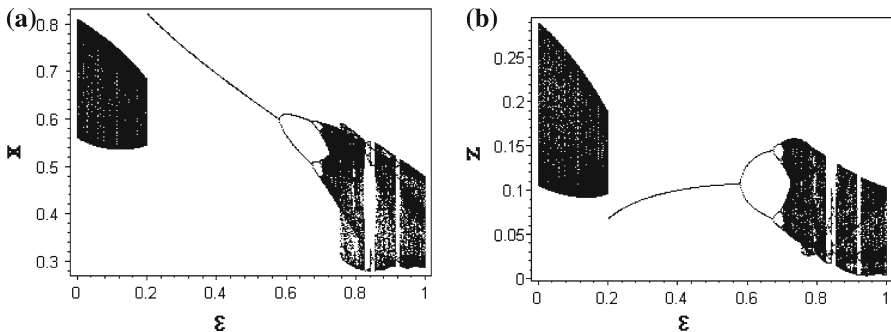


Fig. 6 (a, b) Bifurcation diagrams of *Poincaré* section for the substrate x and predator z in system (4.1) under $m_1 = 6, m_2 = 10, a_1 = 0.8, a_2 = 1, b_1 = 0.1, b_2 = 0.2 \tau = 2\pi$ and ε is varied in $[0, 1]$

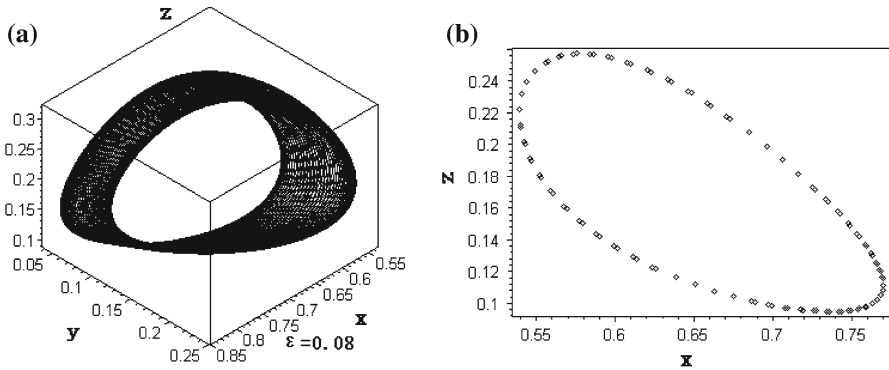


Fig. 7 A typical quasiperiodic solution in the region $\varepsilon \in (0, 0.22)$ with $\varepsilon = 0.08$. Compare a *Poincaré* section **(b)** with the complete quasiperiodic trajectory **(a)**. *Poincaré* points 150–250 are plotted in **(b)**, and the corresponding complete trajectory over the time interval from $t = 300\pi$ to $t = 500\pi$ are plotted in **(a)**

appearance of a closed curve (Fig. 7b), where the point never coincide, is an indication of quasiperiodicity of Eq. 4.1. Further increasing ε , the system experiences process cycles \rightarrow periodic doubling cascade \rightarrow chaos.

Pitchfork bifurcations and tangent (saddle node) bifurcations are abundantly evident in cycles in Figs. 1, 5 and 6, as well as attractor crises (the phenomenon of “crisis” in which chaotic attractors suddenly appear or disappear, or change size discontinuously as or change size discontinuously as a parameter smoothly varies, was first extensively analyzed by Grebogi et al. [15]). For instance, in Fig. 5, when m_1 is slightly increased beyond 8.73 or 12.38, the chaotic attractor abruptly disappears, thus constituting a type of crisis.

5 Conclusions

In this paper, we introduce and study a model of Tessiet type food chain chemostat with periodically varying dilution rate. Firstly we find the invasion threshold of the prey, which is $m_1^* = \tau (\int_0^\tau (\tilde{s}(l) \exp(-b_1 \tilde{s}(l)) / (a_1 + \tilde{s}(l)) dl)^{-1}$. If $m_1 < m_1^*$, the periodic solution $(1, 0, 0)$ 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 $m_2^* = \tau (\int_0^\tau (y_s(l) \exp(-b_2 y_s(l)) / (a_1 + y_s(l)) dl)^{-1}$ 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. By using standard techniques of bifurcation theory, we prove that above this threshold there are periodic oscillations in substrate, prey and predator.

Choosing different coefficients m_1 and m_2 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 halving cascade. All these results show that dynamical behavior of system (4.1) becomes more complex under periodically varying conditions.

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