Complex dynamics of a chemostat with variable yield and periodically impulsive perturbation on the substrate

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In this paper, we consider the dynamic behaviors of a mathematical chemostat model with variable yield and periodically impulsive perturbation on the substrate. The microbial growth rate is the Monod function $\frac{\mu S}{a+S}$ and the variable yield coefficient $\delta(S)$ is quadratic $(1 + cS^2)$. Using Floquet theory and small amplitude perturbation method, we establish the condition under which the boundary periodic solution is globally asymptotically stable. Moreover, the permanence of the system is discussed in detail. Finally, by means of numerical simulation, we demonstrate that with the increasing of the pulsed substrate in the feed the system exhibits the complex dynamics.

KEY WORDS: variable yield, periodically pulsed substrate, permanence, chaotic attractor

AMS subject classification: 34K45, 34K60, 92D25, 92D40

1.   Introduction

The chemostat is a simple and well adopted laboratory apparatus used to culture microorganisms. It can be used to investigate microbial growth and has the advantage that the parameters are easily measurable. Sterile growth medium enters the chemostat at a constant rate; the volume within the chemostat is preserved by allowing excess medium to flow out through a siphon. Modeling microbial growth is an important problem in mathematical biology and theoretical ecology. Smith and Waltman describe a chemostat and formulate various

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mathematical chemostat models [1]. A basic deterministic model of microbial growth in the chemostat takes the following differential equations [2, 3].

$$S'(t) = D(S^0 - S(t)) - \frac{x(t)}{\delta} p(S(t)),$$
$$x'(t) = x(t)(p(S(t)) - D), \tag{1.1}$$

where $S(t)$ and $x(t)$ are concentrations of the substrate and the microorganism in the chemostat, respectively; S^0 is the concentration of the substrate in the feed and D the dilution rate. The function $p(S(t))$ is the microbial growth rate. The stoichiometric yield coefficient δ denotes the ratio of microorganism produced to the mass of the substrate consumed.

When δ is constant and $p(S(t)) = \frac{\mu S(t)}{a + S(t)}$ in system (1.1), the dynamics of the basic model (1.1) are simple: the microorganism $x(t)$ can either become extinct or persist at an equilibrium level [1]. In recent years, the microbial continuous culture has been investigated by many scholars [4–7] and some interesting results have been obtained. The fact that the yield coefficient depends on the substrate concentration has been well analyzed in a series of theoretical studies in chemical engineering literature [8–10]. Pilyugin and Waltman [11] studied multiple limit cycles in the chemostat with variable yield. Zhu and Huang [12] analyzed relative positions of limit cycles in the continuous culture vessel with variable yield. Now many scholars pointed out that it was necessary and important to consider models with periodic perturbations, since these phenomena might be quite naturally exposed in many real world (for instance, mating habits, harvesting). However, there are some other perturbations such as fires, floods, and drainage of sewage which are subject to instantaneous changes. These perturbations bring sudden changes to the system. Systems with sudden changes are involving in impulsive differential equations, which have been studied intensively and systematically in [13, 14]. Impulsive differential equations are found in almost every domain of applied sciences. Authors, in [15, 16], studied population dynamics using the theory of impulsive differential equations and obtained some interest results. The research on the chemostat model with periodically pulsed substrate is not too much yet (See [17, 18] and references therein). However, this is an interest and important problem in mathematical biology and laboratory experiment.

Using the method of [11], we have the dimensionless equations of (1.1) as follows:

$$S' = 1 - S - x\frac{p(S)}{\delta(S)},$$
$$x' = x(p(S) - 1), \tag{1.2}$$
$$S(0) \geqslant 0, x(0) \geqslant 0,$$

where S and x are concentrations of the substrate and the microorganism in the chemostat, respectively. The microbial growth rate $p(S) = \frac{\mu S}{a + S}$, the variable yield coefficient $\delta(S) = 1 + cS^2$.

In this paper, we investigate how the periodically pulsed substrate affects the dynamic behaviors of the chemostat with variable yield. The chemostat model takes the form as follows:

$$
\begin{aligned}
S'(t) &= 1 - S(t) - x(t)\frac{p(S(t))}{\delta(S(t))}, & t \neq nT, \\
x'(t) &= x(t)(p(S(t)) - 1), & t \neq nT, \\
\Delta S &= S(nT^+) - S(nT) = T S_1, & n = 1, 2, \ldots, \\
\Delta x &= x(nT^+) - x(nT) = 0, & n = 1, 2, \ldots, \\
S(0^+) &\geqslant 0, x(0^+) \geqslant 0,
\end{aligned}
\tag{1.3}
$$

where the first and second equations hold between pulses, the third and fourth equations describe the actual pulsing. $S(t), x(t)$ are the same as (1.2). T is the period of the pulsing, $T S_1$ the amount of the substrate concentration pulsed each T. S_1 units of substrate are added, on average, per unit of time. the variable yield coefficient $\delta(S)$ is quadratic $(1 + cS^2)$, The function $p(S) = \frac{\mu S}{a+S}$ is the microbial growth rate.

2.   Preliminary results

Let $R_+ = [0, +\infty)$, $R_+^2 = \{X \in R^2 : X \geqslant 0, X = (S, x)\}$, $\Omega = \mathrm{int}\, R_+^2$, N be the set of nonnegative integers. Denote $f = (f_1, f_2)^T$ the map defined by the right-hand of the anterior two equations of system (1.3).

Let $V: R_+ \times R_+^2 \to R_+$. Then V is said to belong to class V_0 if

(i) V is continuous in $(nT, (n + 1)T] \times R_+^2$ and for each $X \in R_+^2, n \in N$,
$$\lim_{(t,y)\to(nT^+,X)} V(t, y) = V(nT^+, X) \text{ exists};$$

(ii) V is locally Lipschitzian in X.

Definition 2.1. Let $V \in V_0$, $(t, X) \in (nT, (n+1)T] \times R_+^2$. The upper right derivative of $V(t, X)$ with respect to the impulsive differential system (1.3) is defined as

$$
D^+ V(t, X) = \limsup_{h\to 0^+} \frac{1}{h}[V(t + h, X + hf(t, X)) - V(t, X)].
$$

The solution of system (1.3) is a piecewise continuous function $X(t) = (S(t), x(t)) : R_+ \to R_+^2$, $X(t)$ is continuous on $(nT, (n + 1)T], n \in N$ and $X(nT^+) = \lim_{t\to nT^+} X(t)$ exists. Obviously, the global existence and uniqueness of solutions of the system (1.3) is guaranteed by the smoothness properties of f (see [13] for details). Hence, we have the following lemma.

Lemma 2.1. Suppose $X(t)$ is a solution of (1.3) with $X(0^+) \geqslant 0$. Then $X(t) \geqslant 0$ for all $t \geqslant 0$. Moreover, if $X(0^+) > 0$, then $X(t) > 0$ for all $t \geqslant 0$.

Definition 2.2. System (1.3) is said to be permanent if there exist constants $M \geqslant m > 0$ such that $m \leqslant S(t) \leqslant M, m \leqslant x(t) \leqslant M$ for t large enough, where $(S(t), x(t))$ is any solution of (1.3) with $S(0^+) > 0, x(0^+) > 0$.

Lemma 2.2 (Comparison Theory, [13, Theorem 3.1.1]). Let $V : R_+ \times R_+^2 \to R_+$ and $V \in V_0$. Assume that

$$
\begin{aligned}
D^+V(t, X(t)) &\leqslant g(t, V(t, X(t))), &t \neq nT, \\
V(t, X(t^+)) &\leqslant \psi_n(V(t, X(t))), &t = nT,
\end{aligned}
\tag{2.1}
$$

where $g : R_+ \times R_+ \to R$ is continuous in $(nT, (n+1)T] \times R_+$ and for each $z \in R_+, n \in N, \lim\limits_{(t,y)\to(nT^+,z)} g(t, y) = g(nT^+, z)$ exist; $\psi_n : R_+ \to R_+$ is nondecreasing. Let $r(t) = r(t, 0, u_0)$ be the maximal solution of the scalar impulsive differential equation

$$
\begin{aligned}
u' &= g(t, u), &t \neq nT, \\
u(t^+) &= \psi_n(u(t)), &t = nT, \\
u(0^+) &= u_0,
\end{aligned}
\tag{2.2}
$$

existing on $[0, \infty)$. Then $V(0^+, X_0) \leqslant u_0$ implies that $V(t, X(t)) \leqslant r(t), t \geqslant 0$, where $X(t) = X(t, 0, X_0)$ is any solution of (1.3) existing on $[0, \infty)$.

Remark. In lemma 2.2, if the directions of the inequalities in (2.1) are reversed, that is,

$$
\begin{aligned}
D^+V(t, X(t)) &\geqslant g(t, V(t, X(t))), &t \neq nT, \\
V(t, X(t^+)) &\geqslant \psi_n(V(t, X(t))), &t = nT,
\end{aligned}
$$

then $V(t, X(t)) \geqslant \rho(t), t \geqslant t_0$, where $\rho(t)$ is the minimal solution of (2.2) on $[0, \infty)$.

The function we will use is in the form $1 - \omega(t)$. For convenience, we give some basic properties of the following system

$$
\begin{aligned}
\omega'(t) &= 1 - \omega(t), &t \neq nT, \\
\omega(t^+) &= \omega(t) + TS_1, &t = nT, \\
\omega(0^+) &= S(0^+) \geqslant 0.
\end{aligned}
\tag{2.3}
$$

Clearly, $\omega^*(t) = 1 + \frac{TS_1 e^{-(t-nT)}}{1-e^{-T}}, t \in (nT, (n+1)T], n \in N, (\omega^*(0^+) = 1 + \frac{TS_1}{1-e^{-T}})$ is a positive periodic solution of (2.3). The solution of (2.3) is $\omega(t) = [\omega(0^+) - \omega^*(0^+)]e^{-t} + \omega^*(t), t \in (nT, (n+1)T], n \in N$. Therefore, the following result holds.

Lemma 2.3. System (2.3) has a positive periodic solution $\omega^*(t)$ and $|\omega(t) - \omega^*(t)| \to 0$ as $t \to \infty$ for any solution $\omega(t)$ of (2.3). Moreover, $\omega(t) \geqslant \omega^*(t)$ if $\omega(0^+) \geqslant \omega^*(0^+)$ and $\omega(t) < \omega^*(t)$ if $\omega(0^+) < \omega^*(0^+)$.

3.   Extinction and permanence

Obviously, system (1.3) has a boundary $T-$periodic solution $(S^*(t), 0)$ representing the absence of microorganism, where $(S^*(t), 0) = (1 + \frac{TS_1 e^{-(t-nT)}}{1-e^{-T}}, 0)$, $t \in (nT, (n+1)T]$.

Theorem 3.1. Periodic solution $(S^*(t), 0)$ of system (1.3) is globally asymptotically stable if $\int_0^T p(S^*(t))dt < T$, i.e. $\mu a \ln \frac{(a+1)(1-e^{-T})+TS_1}{(a+1)(1-e^{-T})+TS_1 e^{-T}} < (a+1-\mu)T$.

Proof.   The local asymptotic stability of boundary periodic solution $(S^*(t), 0)$ may be determined by considering the behavior of small amplitude perturbation of the solution. Let $(S(t), x(t))$ be any solution of (1.3). We define $S(t) = u(t) + S^*(t), x(t) = v(t)$.

The corresponding linear system of (1.3) at $(S^*(t), 0)$ is

$$
\begin{aligned}
u'(t) &= -u - \frac{p(S^*(t))}{\delta(S^*(t))}v, & t \neq nT, \\
v'(t) &= \big[p(S^*(t)) - 1\big]v, & t \neq nT, \\
u(t^+) &= u(t), & t = nT, \\
v(t^+) &= v(t), & t = nT.
\end{aligned}
\tag{3.1}
$$

Let $\Phi(t)$ be a fundamental matrix of (3.1). Then $\Phi(t)$ satisfies

$$
\frac{d\Phi(t)}{dt} = \begin{pmatrix} -1 & -\frac{p(S^*(t))}{\delta(S^*(t))} \\ 0 & p(S^*(t)) - 1 \end{pmatrix} \Phi(t) \triangleq A(t)\Phi(t)
\tag{3.2}
$$

and $\Phi(0) = I$, the identity matrix.

The resetting impulsive conditions of (3.1) becomes

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

The stability of the boundary $T-$periodic solution $(S^*(t), 0)$ is determined by the eigenvalues of the monodromy matrix

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

From (3.2), we can obtain $\Phi(T) = \Phi(0) \exp\left(\int_0^T A(t)dt\right)$. Therefore, the Floquet multipliers of system (3.1) are

$$
\mu_1 = \exp(-T) < 1, \qquad \mu_2 = \exp\left(\int_0^T [p(S^*(t)) - 1]dt\right).
$$

According to Floquet theory ([14, theorem 3.5]), the boundary T−periodic solution $(S^*(t), 0)$ is asymptotically stable if $|\mu_2| < 1$, i.e. $\mu a \ln \frac{(a+1)(1-e^{-T})+TS_1}{(a+1)(1-e^{-T})+TS_1 e^{-T}} < (a + 1 - \mu)T$.

In the sequel, we prove the global attractability of the boundary periodic solution $(S^*(t), 0)$. Note that $S'(t) \leqslant 1 - S(t)$ and the comparison system (2.3). We have $S(t) \leqslant \omega(t)$ and $S(t) \to \omega^*(t) = S^*(t)$ as $t \to \infty$ by lemmas 2.2 and 2.3.

From the condition of theorem 3.1, we can choose $\epsilon > 0$ small enough such that $\bar{\sigma} = \int_0^T p(S^*(t)+\epsilon)dt - T < 0$ and $S(t) \leqslant S^*(t)+\epsilon$ for t large enough. Without loss of generality, we can assume $S(t) \leqslant S^*(t)+\epsilon$ for all $t \geqslant 0$. From system (1.3), we have

$$x'(t) \leqslant x(t)[p(S^*(t) + \epsilon) - 1]. \tag{3.3}$$

Integrating (3.3) on $(nT, (n + 1)T]$, we have

$$x((n + 1)T) \leqslant x(nT^+) \exp\left(\int_{nT}^{(n+1)T} [p(S^*(t) + \epsilon) - 1]dt\right) = x(nT)e^{\bar{\sigma}}.$$

Therefore, $x(nT) \leqslant x(0^+) \exp(n\bar{\sigma})$ and $x(nT) \to 0$ as $n \to \infty$. Since $0 \leqslant x(t) \leqslant x(nT) \exp(\int_0^T p(S^*(t) + \epsilon)dt) \leqslant x(nT) \exp(T) \leqslant x(0^+) \exp(n\bar{\sigma} + T)$ for any $t \in (nT, (n + 1)T]$, we have $x(t) \to 0$ as $t \to \infty$. The proof is completed. □

Theorem 3.2. There exists a constant $M > 0$ such that $S(t) \leqslant M, x(t) \leqslant M$ for each solution $(S(t), x(t))$ of (1.3) with all t large enough.

Proof. Suppose $(S(t), x(t))$ is any solution of (1.3) in Ω. Then $S(t)$ satisfies the inequality $\limsup S(t) \leqslant 1 + TS_1$. In particular, there exists $\mathcal{T} \geqslant 0$ such that $S(t) \leqslant 2 + TS_1 \triangleq \bar{S}$ for all $t > \mathcal{T}$. Let $q = \max_{[0,\bar{S}]} \delta(S)$ and $V(t) = S(t) + \frac{x(t)}{q}$. Then $V \in V_0$ and

$$D^+V(t) = 1 - S(t) + (\tfrac{1}{q} - \tfrac{1}{\delta(S)})p(S(t))x(t) - \tfrac{Dx(t)}{q} \leqslant 1 - V(t), \quad t \neq nT.$$
$$V(nT^+) = V(nT) + TS_1, \quad n = 1, 2, \dots.$$

Obviously, we can choose $K > 0$ such that

$$D^+V(t) \leqslant -V(t) + (K + 1), \quad t \neq nT,$$
$$V(nT^+) = V(nT) + TS_1, \quad n = 1, 2, \dots.$$

By Comparison Theory, we have

$$V(t) \leqslant (V(0^+) - (K + 1))e^{-t} + \frac{TS_1(1 - e^{-nT})}{1 - e^{-T}}e^{-(t-nT)} + (K + 1),$$
$$t \in (nT, (n + 1)T].$$

Therefore, $V(t)$ is ultimately bounded by a constant and there exists a constant $M > 0$ such that $S(t) \leqslant M, x(t) \leqslant M$ for any solution $(S(t), x(t))$ of system (1.3) with all t large enough. The proof is completed. □

Now we investigate the permanence of the system (1.3).

Theorem 3.3. System (1.3) is permanent if $\int_0^T p(S^*(t))dt > T$, i.e.
$$\mu a \ln \frac{(a+1)(1-e^{-T})+TS_1}{(a+1)(1-e^{-T})+TS_1e^{-T}} > (a+1-\mu)T.$$

Proof. Suppose $(S(t), x(t))$ is any solution of (1.3) with $(S(0^+), x(0^+)) > 0$. From theorem 3.2, we can assume $S(t) \leqslant M, x(t) \leqslant M$ for $t \geqslant 0$. Choose $\epsilon_1 > 0$ small enough such that $m_1 = 1 + \frac{TS_1}{e^T-1} - \epsilon_1 > 0$ and $\sigma_0 = p(m_1) - 1 < 0$. It follows from lemmas 2.2 and 2.3 that $S(t) > m_1$ for all t large enough.

Next, we prove that there exists an $m_2 > 0$ such that $x(t) > m_2$ for all t large enoughin two steps.

Step 1. Since $\int_0^T p(S^*(t))dt > T$, we can choose $m_3 > 0, \epsilon_2 > 0$ small enough such that $\sigma = \int_0^T p(\bar{y}(t) - \epsilon_2)dt - T > 0$, where $\bar{y}(t) = \frac{a}{a+\mu m_3} + \frac{TS_1 \exp\{-(1+\frac{\mu m_3}{a})(t-nT)\}}{1-\exp\{-(1+\frac{\mu m_3}{a})T\}}$, $t \in (nT, (n+1)T]$. We claim that $x(t) < m_3$ cannot hold for all $t \geqslant 0$, otherwise,

$$S'(t) \geqslant 1 - \left(1 + \frac{\mu m_3}{a}\right)S(t).$$

By lemmas 2.2 and 2.3, we have $S(t) \geqslant y(t)$ and $y(t) \to \bar{y}(t), t \to \infty$, where $y(t)$ is the solution of

$$\begin{aligned} y'(t) &= 1 - (1 + \frac{\mu m_3}{a})y(t), & t \neq nT, \\ \Delta y &= y(t^+) - y(t) = TS_1, & t = nT, \\ y(0^+) &= S(0^+) > 0 \end{aligned} \tag{3.4}$$

and $\bar{y}(t)$ is the positive periodic solution of (3.4).

Therefore, there exists a $T_1 > 0$ such that $S(t) \geqslant y(t) \geqslant \bar{y}(t) - \epsilon_2$ and

$$x' \geqslant x[p(\bar{y}(t) - \epsilon_2) - 1] \tag{3.5}$$

for $t \geqslant T_1$.

Let $N_1 \in N$ and $N_1 T \geqslant T_1$. Integrating (3.5) on $(nT, (n+1)T], n \geqslant N_1$, we have

$$x((n+1)T) \geqslant x(nT^+)\exp\left\{\int_{nT}^{(n+1)T} p(\bar{y}(t) - \epsilon_2)dt - T\right\} = x(nT)e^{\sigma}.$$

Then $x((N_1+k)T) \geqslant x(N_1T)e^{k\sigma} \to \infty$ as $k \to \infty$, which is a contradiction. Hence, there exists a $t_1 > 0$ such that $x(t_1) \geqslant m_3$.

Step 2. If $x(t) \geqslant m_3$ for all $t \geqslant t_1$, then our goal is obtained. Hence, we need only to consider those solutions which leave the region $\Omega_1 = \{X \in R_+^2 : x(t) < m_3\}$ and enter it again. Let $t^* = \inf\{t \geqslant t_1 : x(t) < m_3\}$. Then $x(t) \geqslant m_3$ for $t \in [t_1, t^*)$ and $x(t^*) = m_3$ since $x(t)$ is continuous. Suppose
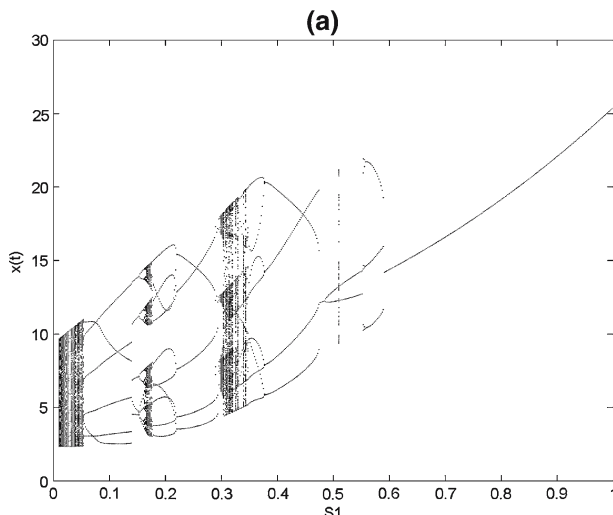
(a)

Figure 1. Bifurcation diagrams system (1.3) with $X_0 = (0.58, 10)$: (a) the microorganism $x(t)$ is plotted for 500 values of S_1 over $[0.01, 1]$.

$t^* \in [n_1 T, (n_1 + 1)T), n_1 \in N$. Choose $n_2, n_3 \in N$ such that $n_2 T > T_2 = \frac{a}{a + \mu m_3} \ln \frac{(M + TS_1)(a + \mu m_3) + a}{\epsilon_2(a + \mu m_3)}$ and $e^{(n_2 + 1)\sigma_0 T} e^{n_3 \sigma} > 1$.

Let $T_3 = n_2 T + n_3 T$. We claim that there exists a $t_2 \in [(n_1 + 1)T, (n_1 + 1)T + T_3]$ such that $x(t_2) \geqslant m_3$. Otherwise, $x(t) < m_3, t \in [(n_1 + 1)T, (n_1 + 1)T + T_3]$. Consider (3.4) with $y((n_1 + 1)T^+) = S((n_1 + 1)T^+)$, we have

$$
y(t) = \left[y((n_1 + 1)T^+) - \left(\frac{a}{a + \mu m_3} + \frac{TS_1}{1 - \exp\{-(1 + \frac{\mu m_3}{a})T\}} \right) \right]
$$
$$
e^{-(1 + \frac{\mu m_3}{a})(t - (n_1 + 1)T)} + \bar{y}(t)
$$

for $t \in (nT, (n + 1)T], n_1 + 1 \leqslant n \leqslant n_1 + 1 + n_2 + n_3$.

Thus

$$
|y(t) - \bar{y}(t)| < \left[M + \left(\frac{a}{a + \mu m_3} + TS_1 \right) \right] \exp\left\{ -\left(D + \frac{\mu m_3}{a} \right) n_2 T \right\} < \epsilon_2
$$

and $S(t) \geqslant y(t) \geqslant \bar{y}(t) - \epsilon_2$, for $t \in [(n_1 + 1 + n_2)T, (n_1 + 1)T + T_3]$, which implies (3.5) holds for $t \in [(n_1 + 1 + n_2)T, (n_1 + 1)T + T_3]$.

Integrating (3.5) on $[(n_1 + 1 + n_2)T, (n_1 + 1)T + T_3]$, we have

$$
x((n_1 + 1 + n_2 + n_3)T) \geqslant x((n_1 + 1 + n_2)T)e^{n_3 \sigma}.
$$

It follows from the second equation of (1.3) that

$$
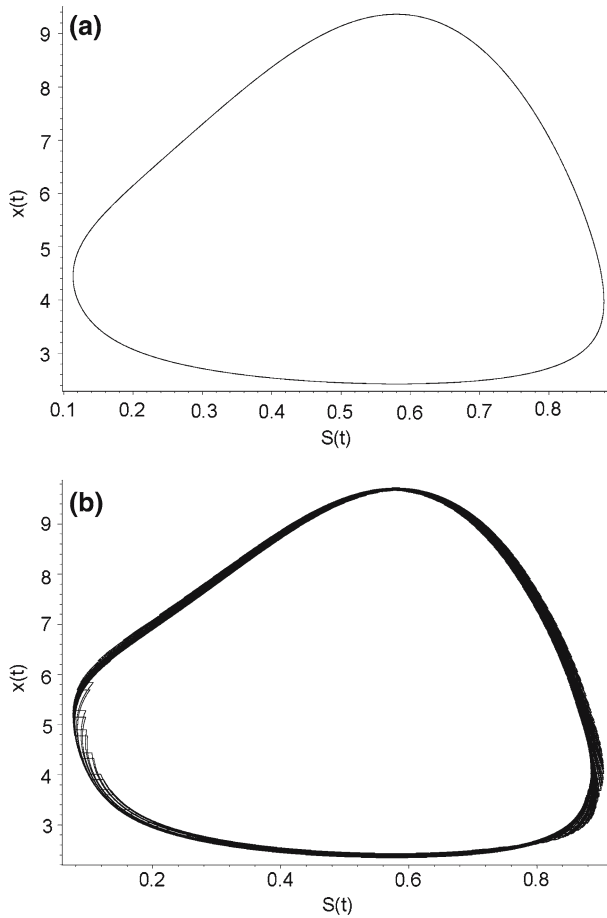x'(t) \geqslant x(t)[p(m_1) - 1] = \sigma_0 x(t).
$$

Figure 2. Phase portraits of system (1.3) with $X_0 = (0.58, 10)$. The system is integrated 500 pulsing cycles and the last 200 pulsing cycles are plotted: (a)$S_1 = 0$, and (b) $S_1 = 0.01$.

Integrating it on $[t^*, (n_1 + 1 + n_2)T]$, we have

$$x((n_1 + 1 + n_2)T) \geqslant x(t^*)e^{(n_2+1)\sigma_0 T} = m_3 e^{(n_2+1)\sigma_0 T}.$$

Thus $x((n_1 + 1 + n_2 + n_3)T) \geqslant m_3 e^{n_3\sigma} e^{\sigma_0(n_2+1)T} > m_3$, which is a contradiction.

Let $\bar{t} = \inf\{t \geqslant t^* : x(t) \geqslant m_3\}$. Then $x(\bar{t}) \geqslant m_3$. For $t \in [t^*, \bar{t})$, we have $x(t) \geqslant x(t^*)e^{\sigma_0(t-t^*)} \geqslant m_3 e^{\sigma_0(1+n_2+n_3)T} \triangleq m_2$. For $t > \bar{t}$, the same arguments can be continued since $x(\bar{t}) \geqslant m_3$. Hence, we have $x(t) \geqslant m_2$ for all $t \geqslant t_1$. Therefore, let $m = \min\{m_1, m_2\}$, then for any solution $(S(t), x(t))$ of system (1.3) with $S(0^+) > 0, x(0^+) > 0$ there exists an enough large $\tilde{T} > 0$ such that $m \leqslant S(t) \leqslant M, m \leqslant x(t) \leqslant M$ for all $t > \tilde{T}$. The proof is complete.   □
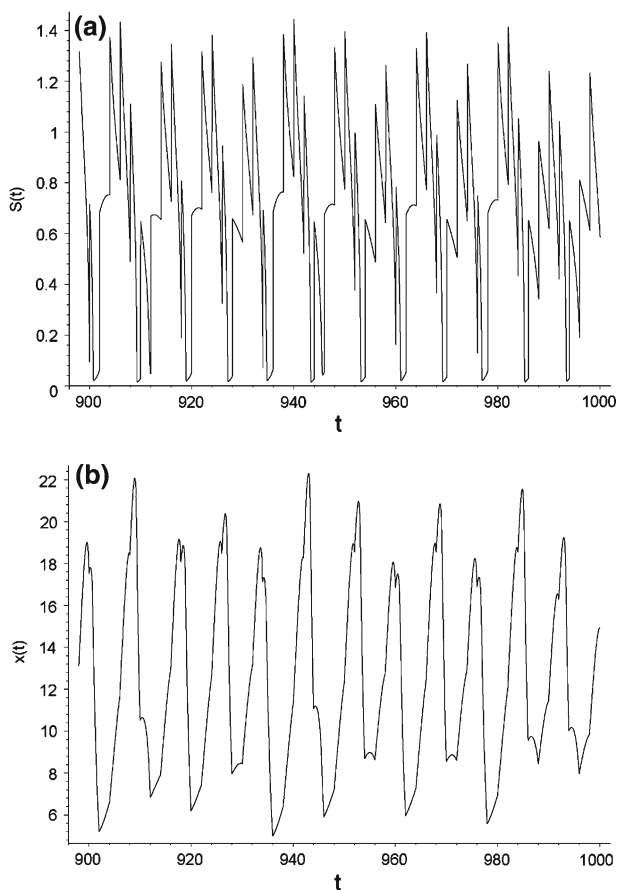
Figure 3. The time series for the last 50 pulsing cycles with $S_1 = 0.31$: (a) time series of the substrate $S(t)$ with $X_0 = (0.58, 10)$, and (b) time series of the microorganism $x(t)$ with $X_0 = (0.58, 10)$.

4.   Numerical simulation

In this section, we will demonstrate our main results by means of numerical simulation. Let $\mu = 2.0$, $a = 0.58$, $T = 2$, $c = 50$, $S(0^+) = 0.58$, $x(0^+) = 10$. Then dynamic behavior of system (1.3) is determined completely by the amount of the pulsed substrate in the feed. If $S_1 = 0$, then the system (1.3) is a continuous system (1.2), we have known system (1.2) has limit cycles [11] (figure 2(a)). We will study the influences of S_1 on this inherent oscillation by means of numerical simulation. System (1.3) is integrated numerically for 500 pulsing cycles at each value of S_1. We plotted the last 300 stroboscopic measurements of the microorganism $x(t)$. The resulting bifurcation diagrams (figure 1) clearly show that with S_1 increasing over $[0.01, 1]$ system (1.3) experiences complex dynamic process of
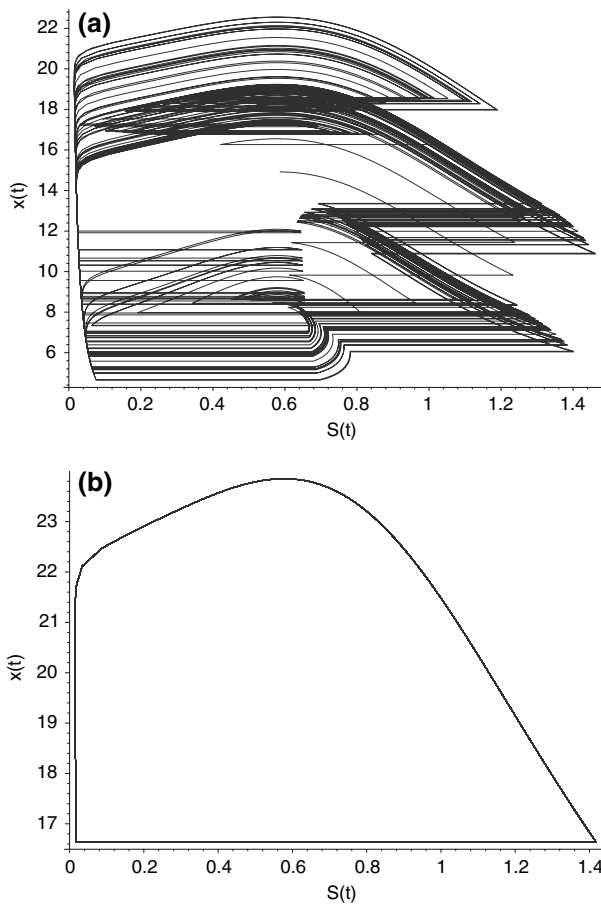
Figure 4. Phase portraits of system (1.3) (a) chaotic attractor of system (1.3) with $S_1 = 0.31$, and (b) T−Periodic solution of system (1.3) with $S_1 = 0.7$.

quasi-periodic oscillating $\rightarrow$ cycles $\rightarrow$ periodic doubling cascade $\rightarrow$ chaos $\rightarrow$ periodic halfing cascade $\rightarrow$ cycles.

When $S_1 = 0.01$ is sufficiently small, the periodic impulsive perturbation cannot destroy the inherent oscillation of the continuous system, the solutions of system (1.3) will ultimately oscillate around the limit cycle (figure 2(b)). But, with the increasing of S_1, the system (1.3) exhibits complex dynamic behavior. When $S_1 = 0.31$, the substrate $S(t)$ and the microorganism $x(t)$ exhibit anomalous sustained oscillation (figure 3) and a typical chaotic attractor is captured (figure 4(a)). When $S_1 = 0.7$, the substrate $S(t)$ and the microorganism $x(t)$ exhibit periodic sustained oscillation and coexist in the chemostat (figure 4(b)).

In conclusion, the fact that the microorganism cultures with variable yields exhibit sustained oscillations has an important implication for coexistence. In a

sense, our results may provide a theoretical policy for the microorganism cultures in experiment.

Acknowledgment

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