The effects of delayed growth response on the dynamic behaviors of the Monod type chemostat model with impulsive input nutrient concentration[☆]

Xinzhu Meng [a,b], Qian Gao [a,c], Zhenqing Li [a,*]

[a] *State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, PR China*
[b] *College of Information Science and Engineering, Shandong University of Science and Technology, Qingdao 266510, PR China*
[c] *Graduate University Chinese Academy of Sciences, Beijing 100049, PR China*

ARTICLE INFO

ABSTRACT

This paper investigates the effects of delayed growth response on the dynamic behaviors of the Monod type chemostat model with impulsive input nutrient concentration. By the use of the discrete dynamical system determined by the stroboscopic map, we obtain a 'microorganism-extinction' periodic solution, further, prove that the 'microorganism-extinction' periodic solution is globally attractive if the impulsive period satisfies some conditions. Using the theory on delay functional and impulsive differential equation, we obtain sufficient condition with time delay for the permanence of the system, and prove that time delays, impulsive input nutrient can bring obvious effects on the dynamic behaviors of the model.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

The chemostat is a very important laboratory apparatus for the study of microbial population dynamics under nutrient limitation. Sterile medium enters the chemostat at a constant rate; the volume of the chemostat is held constant by allowing excess medium (and microbes) to flow out through a siphon. We introduce this chemostat with a heterotrophic bacterium that has – in the medium – an abundance of all necessary nutrients but one. This last nutrient is the limiting substrate. It has many applications and can be reasonably modelled by differential equations. Moreover, systematic analysis of such models are often mathematically challenging, yet possible. An excellent reference for this subject is the recent book by Smith and Waltman [1]. Recently, many mathematical chemostat models were formulated, and many good results were obtained [1–22]. Transient growth dynamics are of considerable importance in the study of how microorganisms respond to environmental changes, and are pertinent to understanding the control mechanisms for microbial growth [3]. Much research, both theoretical and experimental, has been undertaken regarding the transient behavior of microbial population growth in the chemostat. While the Monod model [4] has some success in describing steady state growth rates [1,5], it has been found to be inadequate to predict transients observed in chemostat experiments where the initial data does not correspond to the globally attracting steady state. Lag phases occur in the growth response of microorganisms to changes in the environment [6]. Ramkrishna et al. [7], in order to introduce a lag phase, assumed that the biomass is composed of two groups of substances which interact with each other and with substances in the environment to produce growth. The

---

[*] Corresponding author.
E-mail addresses: mxz721106@sdust.edu.cn (X. Meng), lizq@ibcas.ac.cn, lizhenqing_12@yahoo.cn (Z. Li).

structure assigned to the organisms in the model accounts for the dependence of growth on the past history of the cells, and hence it is capable of predicting the lag phases and transient oscillations observed in experiments. Many authors have directly incorporated time delays in the modelling equations and, as a result, the models take the form of delay differential equations [8–18]. In [9], Caperon used delay differential equations to describe the time lag in the growth response, and the resulting model successfully predicted the population growth in experiment data under dynamic conditions. In [13], Thingstad and Langeland introduced a discrete delay in the Monod model and showed that persistent oscillations are possible. it was found in [16] that the time delay can affect both the qualitative and quantitative behavior of the solutions, and numerical simulations illustrate that the models with delay may exhibit slightly more oscillations in the transients, when compared with the models without delay. We refer to [19,15], and the references therein, for more detailed discussions on chemostat modelling approaches using delay differential equations. The more details can be seen in [1,14–19].

In recent years, the microbial continuous culture has been investigated in [20–22] and some interesting results were obtained. Many scholars pointed out that it was necessary and important to consider models with periodic perturbations, since these models might be quite naturally exposed in many real world phenomena (for instance, food supply, mating habits, harvesting). In fact, almost perturbations occur in a more-or-less periodic fashion. However, there are some other perturbations such as fires, floods, and drainage of sewage which are not suitable to be considered continually. These perturbations bring sudden changes to the system. Systems with sudden perturbations are involving in impulsive differential equations, which have been studied intensively and systematically in [23,24]. Authors, in [25–29], introduced some impulsive differential equations in population dynamics and obtained some interest results. The research on the chemostat model with impulsive perturbations is not too much yet (see Refs. [30–32] and references therein). However, this is an interest problem in mathematical biology and laboratory experiment.

In view of our arguments above, it is very interesting to introduce delayed growth response and impulsive input nutrient concentration to chemostat model. While delay differential equations have been widely used in modelling population dynamics, some practical problems have to be overcome when applied to models of the chemostat. We remark that the dynamics of impulsive and delayed differential equation are usually more difficult to study than ordinary differential equation. As a result, fewer analytic tools are available for studying the dynamics of impulsive and delayed differential equation. In recently a few age-structured predator–prey models with impulse and delay and epidemic models with impulse and delay were investigated [33,34]. Thus, chemostat model with impulse and delay is not extensive. In this paper, we consider the Monod type chemostat model with impulsive input nutrient concentration and delayed growth response, and investigate how the impulsive perturbation of the substrate and time delay for growth response affect the dynamic behaviors of the chemostat continuous system.

2. Model and preliminaries

The following single-species Monod type chemostat model was introduced by Chen [35]:

$$S'(t) = (S_0 - S(t))D - \frac{\mu_m S(t)x(t)}{\delta(K_m + S(t))},$$

$$x'(t) = x(t)\left(\frac{\mu_m S(t)}{\delta(K_m + S(t))} - D\right). \tag{1}$$

In fact, on the one hand, the nutrient concentration is input periodically not continuously. On the other hand, the taken nutrient cannot translate instantaneously into viable microorganisms, that is, there is a time delay in the growth response that describes the lag involved in the nutrient conversion process. Therefore, impulse and time delay should be considered in system (1). To investigate the effect of delayed growth response and impulsive perturbation on the nutrient concentration on dynamic behaviors of the following chemostat model, we consider a single-species chemostat model with impulsive perturbation and time delay:

$$S'(t) = -DS(t) - \frac{\mu_m S(t)x(t)}{\delta(K_m + S(t))}, \quad t \neq nT, \ n \in N,$$

$$x'(t) = e^{-D\tau}\frac{\mu_m S(t-\tau)x(t-\tau)}{K_m + S(t-\tau)} - Dx(t), \quad t \neq nT, \ n \in N,$$

$$S(t^+) = S(t) + \gamma S_0, \quad t = nT, \ n \in N, \tag{2}$$

$$x(t^+) = x(t), \quad t = nT, \ n \in N,$$

$$S(0^+) \geq 0, \qquad x(0^+) \geq 0,$$

where $S(t)$ denotes the concentration of the unconsumed nutrient in the growth vessel at time t and $x(t)$ denotes the biomass of the population of microorganisms at time t. The function $p(S) = \frac{\mu_m S(t)}{\delta(K_m + S(t))}$ represents the species specific per-capita nutrient uptake rate. It also models the rate of conversion of nutrient to viable biomass. The growth yield constant has been scaled out for mathematical convenience. S_0 and D are positive constants and denote, respectively, the concentration of the growth-limiting nutrient and the flow rate of the chemostat (see more details in [14–16]). The first and second equations

hold between pulses, the third and fourth equation describes the actual pulsing. $T = \gamma/D$ is the period of the pulsing, γS_0 is the amount of limiting substrate pulsed each T. DS_0 units of substrate are added, on average, per unit of time. The constant $\tau \geq 0$ denotes the time delay involved in the conversion of nutrient to viable biomass. The constant positive constant, $e^{-D\tau}$, is required, because it is assumed that the current change in biomass depends on the amount of nutrient consumed τ units of time in the past by the microorganisms that were in the growth vessel at that time and managed to remain in the growth vessel the τ units of time required to process the nutrient. $S(nT^+) = \lim_{n \to nT+} S(t)$, and $S(t)$ is left continuous at $t = nT$, i.e., $S(nT) = \lim_{n \to nT-} S(t)$, $x(t)$ is continuous for all $t \geq 0$, the details can be seen in the books of Bainov and Simeonov [23] and Lakshmikantham et al. [24].

Motivated by the application of systems (2) to population dynamics (refer to [36]), we assume that solutions of systems (2) satisfy the initial conditions

$$(\phi_1(s), \phi_2(s)) \in C_+ = C([-\tau, 0], R_+^2), \phi_i(0) > 0 \quad (i = 1, 2). \tag{3}$$

Let $R^+ = [0, \infty)$, $R_+^2 = \{x \in R^2 \mid x \geq 0\}$. Denote $f = (f_1, f_2)$ the map defined by the right hand side of the first two equations of system (2), and N the set of all nonnegative integers. Let $V : R_+ \times R_+^2 \to R_+$, then V is said to belong to class V_0 if
(i) V is continuous in $((k-1)T, kT] \times R_+^2 k \in N$, and for each $x \in R_+^2$, $\lim_{(t,z) \to ((k-1)T^+,x)} V(t, z) = V((k-1)T, x)$ and $\lim_{(t,z) \to (kT^+,x)} V(t, z) = V(kT^+, x)$ exists.
(ii) V is locally Lipschitzian in x.

Definition 2.1. Let $V \in V_0$, then for $(t, x) \in ((k-1)T, kT] \times R_+^2 k \in N$, the upper right derivative of $V(t, x)$ with respect to the impulsive differential system (1) 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 (2), denoted by $X = (S(t), x(t)) : R_+ \to R_+^2$, is continuously differentiable on $((k-1)T, kT] (k \in N)$. Obviously, the global existence and uniqueness of solutions of system (2) is guaranteed by the smoothness properties of f which is the right side (2) (for details see [23,24]).

Lemma 2.1 (*see [23,24]*). *Consider the following impulse differential inequalities:*

$$w'(t) \leq (\geq)p(t)w(t) + q(t), \quad t \neq t_k,$$
$$w(t_k^+) \leq (\geq)d_k w(t_k) + b_k, \quad t = t_k, \ k \in N,$$

where $p(t), q(t) \in C(R_+, R)$, $d_k \geq 0$, and b_k are constants.
Assume
 (A_0) the sequence $\{t_k\}$ satisfies $0 \leq t_0 < t_1 < t_2 < \cdots$, with $\lim_{t \to \infty} t_k = \infty$;
 (A_1) $w \in PC'(R_+, R)$ and $w(t)$ is left continuous at $t_k, k \in N$. Then

$$w(t) \leq (\geq)w(t_0) \prod_{t_0 < t_k < t} d_k \exp\left(\int_{t_0}^t p(s)ds\right) + \sum_{t_0 < t_k < t} \left(\prod_{t_k < t_j < t} d_j \exp\left(\int_{t_k}^t p(s)ds\right)\right) b_k$$
$$+ \int_{t_0}^t \prod_{s < t_k < t} d_k \exp\left(\int_s^t p(\theta)d\theta\right) q(s)ds, \quad t \geq t_0.$$

Lemma 2.2 (*[36]*). *Consider the following delay differential equation*

$$\frac{dx(t)}{dt} = r_1 x(t - \tau) - r_2 x(t),$$

where a, b, τ are all positive constants and $x(t) > 0$ for $t \in [-\tau, 0]$.

 (i) If $r_1 < r_2$, then $\lim_{t \to \infty} x(t) = 0$.
 (ii) If $r_1 > r_2$, then $\lim_{t \to \infty} x(t) = +\infty$.

Lemma 2.3. *There exists a constant $L > 0$ such that $S(t) \leq L$ and $x(t) \leq L$ for each solution of (2) with $t \geq 0$.*

Proof. Let $(s(t), x(t))$ be any solution of system (2) with initial condition (3). We claim that the solution $(s(t), x(t))$ of system (2) is bounded for all $t \geq t_0$. Otherwise, there is a positive integer N and a positive constant $M = \max\{S_0, \delta e^{-D\tau} S_0, e^{-D\tau} S(NT) + \frac{1}{\delta}x(NT) + e^{-D\tau} \int_{NT-\tau}^{NT} \frac{\mu_m S(\theta)x(\theta)}{\delta(K_m + S(\theta))} d\theta\}$, such that $S(t) > M$ or $x(t) > M$ for $t \geq NT$.
Let

$$V(t) = e^{-D\tau} S(t) + \frac{1}{\delta}x(t) + e^{-D\tau} \int_{t-\tau}^t \frac{\mu_m S(\theta)x(\theta)}{\delta(K_m + S(\theta))} d\theta.$$

It is easy to see that $V \geq 0$ and $V \to +\infty$ when $|(S, x)| \to +\infty$. The upper right derivative of $V(t)$ along the trajectories of (2) is

$$
\begin{aligned}
\dot{V}(t) &= -De^{-D\tau}S(t) - e^{-D\tau}\frac{\mu_m S(t)x(t)}{\delta(K_m + S(t))} + \frac{1}{\delta}e^{-D\tau}\frac{\mu_m S(t-\tau)x(t-\tau)}{K_m + S(t-\tau)} - \frac{D}{\delta}x(t) \\
&\quad + e^{-D\tau}\frac{\mu_m S(t)x(t)}{\delta(K_m + S(t))} - e^{-D\tau}\frac{\mu_m S(t-\tau)x(t-\tau)}{\delta(K_m + S(t-\tau))} \\
&= -De^{-D\tau}S(t) - \frac{D}{\delta}x(t).
\end{aligned}
\tag{4}
$$

Integrating and solving the Eq. (4) between pulses, yields

$$
V(t) = V(nT) - \int_{nT}^{t} De^{-D\tau}S(\theta) + \frac{D}{\delta}x(\theta)d\theta, \quad t \in (nT, (n+1)T], \ n \geq N.
$$

Then

$$
V((n+1)T) = V(nT) - \int_{nT}^{(n+1)T} De^{-D\tau}S(\theta) + \frac{D}{\delta}x(\theta)d\theta,
$$

and

$$
\begin{aligned}
V((n+1)T^+) &= V((n+1)T) + \Delta V \\
&= V(nT) - \int_{nT}^{(n+1)T} De^{-D\tau}S(\theta) + \frac{D}{\delta}x(\theta)d\theta + \gamma e^{-D\tau}S_0.
\end{aligned}
$$

So we have

$$
\begin{aligned}
V((n+1)T^+) &\leq V(nT) - \int_{nT}^{(n+1)T} De^{-D\tau}S(\theta)d\theta + \gamma e^{-D\tau}S_0 \\
&< V(nT) - \int_{nT}^{(n+1)T} De^{-D\tau}Md\theta + \gamma e^{-D\tau}S_0 \\
&= V(nT) - TDe^{-D\tau}M + \gamma e^{-D\tau}S_0 \\
&\leq V(nT)
\end{aligned}
$$

or

$$
\begin{aligned}
V((n+1)T^+) &\leq V(nT) - \int_{nT}^{(n+1)T} \frac{D}{\delta}x(\theta)d\theta + \gamma e^{-D\tau}S_0 \\
&< V(nT) - \int_{nT}^{(n+1)T} \frac{D}{\delta}Md\theta + \gamma e^{-D\tau}S_0 \\
&= V(nT) - T\frac{D}{\delta}M + \gamma e^{-D\tau}S_0 \\
&\leq V(nT).
\end{aligned}
$$

This contradict that $V \to +\infty$ when $|(S, x)| \to +\infty$. Therefore, there exists a constant $L > 0$ such that $S(t) \leq L$ and $x(t) \leq L$ for each solution of (2) with $t \geq 0$. The proof is complete.

3. Extinction

In this section, we investigate the extinction of the microorganism species, that is, microorganism are entirely absent from the chemostat permanently, i.e.,

$$
x(t) = 0, \quad t \geq 0.
\tag{5}
$$

This is motivated by the fact that $x^* = 0$ is an equilibrium solution for the variable $x(t)$, as it leaves $x'(t) = 0$. Under these conditions, we show below that the nutrient concentration oscillates with period T in synchronization with the periodic impulsive input nutrient concentration.

From the second equation of system (2), we have

$$
x'(t) \leq \mu_m e^{-D\tau}x(t-\tau) - Dx(t).
\tag{6}
$$

By Lemma 2.2, if $\mu_m e^{-D\tau} < D$, then $\lim_{t \to \infty} x(t) = 0$, that is, the microorganism species becomes ultimately extinct. This show that the specific growth of the microorganism species cannot supply the losing of the microorganism species to flow out no matter how much input the nutrient. Therefore, we assume $\mu_m e^{-D\tau} > D$ in the rest of this paper.

Assuming (5), we know that the nutrient concentration oscillates in the time-interval $nT < t \le (n+1)T$ and give some basic properties of the following subsystem of (2)

$$
\begin{aligned}
&S'(t) = -DS(t), \quad t \ne nT, n \in N, \\
&S(t^+) = S(t) + \gamma S_0, \quad t = nT, \ n \in N, \\
&S(0^+) > 0.
\end{aligned}
\tag{7}
$$

Clearly,

$$
S^*(t) = \frac{\gamma S_0 e^{-D(t-nT)}}{1 - e^{-DT}}, \quad t \in (nT, (n+1)T], \ n \in N, \qquad S^*(0^+) = \frac{\gamma S_0}{1 - e^{-DT}}
$$

is a positive periodic solution of (7). The solution of (7) is $S(t) = (S(0^+) - S^*(0^+))e^{-Dt} + S^*(t), t \in (nT, (n+1)T], n \in N$. Therefore, we have the following Lemma 3.1.

Lemma 3.1. *System* (7) *has a unique positive periodic solution* $S^*(t)$, *that is, the system* (2) *has a 'microorganism-extinction' periodic solution* $(S^*(t), 0)$ *for* $t \in (nT, (n+1)T], n \in N$, *for any solution* $(S(t), x(t))$ *of* (2) *we have* $S(t) \to S^*(t)$ *as* $t \to \infty$.

The positive periodic solution $(S^*(t), 0)$ corresponds to washout of the single population of microorganism from the chemostat.

By the following theorem we give conditions for extinction of the microorganisms species:

Theorem 3.1. *Periodic solution* $(S^*(t), 0)$ *of system* (2) *is globally attractive if*

$$
\gamma S_0 < \frac{DK_m(1 - e^{-DT})}{\mu_m e^{-D\tau} - D},
\tag{8}
$$

where $\gamma = TD$.

Proof. Let $(S(t), x(t))$ be any solution of system (2) with initial condition (3). From (8), we have

$$
\frac{\mu_m e^{-D\tau} \frac{\gamma S_0}{1 - e^{-DT}}}{K_m + \frac{\gamma S_0}{1 - e^{-DT}}} < D.
$$

Since $p(z) = \frac{\mu_m e^{-D\tau} z}{K_m + z}$ is strictly increasing for all $z \ge 0$, we may choose a sufficiently small positive constant ε such that

$$
\frac{\mu_m e^{-D\tau} \eta}{K_m + \eta} < D,
\tag{9}
$$

where

$$
\eta = \frac{\gamma S_0}{1 - e^{-DT}} + \varepsilon.
$$

It follows from that the first equation of system (2) that $S'(t) \le -DS(t)$. So we consider the following impulse differential inequalities:

$$
\begin{aligned}
&S'(t) \le -DS(t), \quad t \ne nT, \ n \in N, \\
&S(t^+) = S(t) + \gamma S_0, \quad t = nT, \ n \in N.
\end{aligned}
$$

By using Lemma 2.1, we have

$$
\limsup_{t \to \infty} S(t) \le \frac{\gamma S_0}{1 - e^{-DT}}.
$$

Hence, there exist a positive integer n_1 and a arbitrarily small positive constant ε such that for all $t \ge n_1 T$,

$$
S(t) \le \frac{\gamma S_0}{1 - e^{-DT}} + \varepsilon =: \eta.
\tag{10}
$$

From (10) and the second equation of (3), we get that, for $t > n_1 T + \tau$,

$$
x'(t) \le \frac{\mu_m \eta e^{-D\tau}}{K_m + \eta} x(t - \tau) - Dx(t).
\tag{11}
$$

Consider the following comparison equation

$$
\frac{dz(t)}{dt} = \frac{\mu_m \eta e^{-D\tau}}{K_m + \eta} z(t - \tau) - Dz(t).
\tag{12}
$$

By Lemma 2.2 and (9), we obtain that

$$\lim_{t\to\infty} z(t) = 0.$$

Since $x(s) = z(s) = \phi_2(s) > 0$ for all $s \in [-\tau, 0]$, by the comparison theorem in differential equation and the nonnegativity of solution (with $x(t) \geq 0$), we have that $x(t) \to 0$ as $t \to \infty$.

Without loss of generality, we may assume that $0 < x(t) < \varepsilon$ for all $t \geq 0$, by the first equation of system (2), we have

$$S'(t) \geq -\left(D + \frac{\mu_m \varepsilon}{\delta K_m}\right) S(t).$$

Then we have $\widetilde{z_1}(t) \leq S(t)$ and $\widetilde{z_1}(t) \to S^*(t)$, as $\varepsilon \to 0$, where $\widetilde{z_1}(t)$ is a unique globally asymptotically stable positive periodic solution of

$$
\begin{aligned}
&z_1'(t) = -\left(D + \frac{\mu_m \varepsilon}{\delta K_m}\right) z_1(t), \quad t \neq nT, \ n \in N, \\
&z_1(t^+) = z_1(t) + \gamma S_0, \quad t = nT, \ n \in N, \\
&z_1(0^+) = S(0^+).
\end{aligned}
\tag{13}
$$

From (13), we have that, for $nT < t \leq (n+1)T$,

$$\widetilde{z_1}(t) = \frac{\gamma S_0 e^{-\left(D + \frac{\mu_m \varepsilon}{\delta K_m}\right)(t - nT)}}{1 - e^{-\left(D + \frac{\mu_m \varepsilon}{\delta K_m}\right)T}}.$$

By using comparison theorem of impulsive equation (see Theorem 3.1.1 in [24]), for any $\varepsilon_1 > 0$ there exists such a $T_1 > 0$ that, for $t > T_1$,

$$S(t) > \widetilde{z_1}(t) - \varepsilon_1.
\tag{14}$$

On the other hand, from the first equation of (2), it follows that

$$S'(t) \leq -DS(t).$$

Consider the following comparison system

$$
\begin{aligned}
&z_2'(t) = -Dz_2(t), \quad t \neq nT, \ n \in N, \\
&z_2(t^+) = z_2(t) + \gamma S_0, \quad t = nT, \ n \in N, \\
&z_2(0^+) = S(0^+).
\end{aligned}
\tag{15}
$$

Then we have

$$S(t) < \widetilde{z_2}(t) + \varepsilon_1
\tag{16}$$

as $t \to \infty$ and $\widetilde{z_2}(t) = S^*(t)$, where $\widetilde{z_2}(t)$ is a unique positive periodic solution of (15).

Let $\varepsilon \to 0$, then it follows from (14) and (16) that

$$S^*(t) - \varepsilon_1 < S(t) < S^*(t) + \varepsilon_1,
\tag{17}$$

for t large enough, which implies $S(t) \to S^*(t)$ as $t \to \infty$. This completes the proof.

By Theorem 3.1, we can easily get the following Corollary 3.1.

Corollary 3.1. *Periodic solution* $(S^*(t), 0)$ *of system* (3) *is globally attractive if*

$$\frac{TS_0 \left(\mu_m e^{-D\tau} - D\right)}{K_m(1 - e^{-DT})} < 1.
\tag{18}$$

Clearly, the inequality (8) is equivalent to

$$S_0 T + \frac{K_m}{\mu_m e^{-D\tau} - D} e^{-DT} - \frac{K_m}{\mu_m e^{-D\tau} - D} < 0.$$

Denote

$$f(T) = S_0 T + \frac{K_m}{\mu_m e^{-D\tau} - D} e^{-DT} - \frac{K_m}{\mu_m e^{-D\tau} - D}.$$

Since function $f(T)$ is continuous for all $T \geq 0$, then we have

$$f'(T) \leq 0, \quad 0 \leq T \leq \frac{1}{D} \ln \frac{DK_m}{S_0(\mu_m e^{-D\tau} - D)}$$

and

$$f'(T) > 0, \quad \frac{1}{D} \ln \frac{DK_m}{S_0(\mu_m e^{-D\tau} - D)} < T < \infty.$$

Also

$$f\left(\frac{1}{D} \ln \frac{DK_m}{S_0(\mu_m e^{-D\tau} - D)}\right) = \frac{S_0}{D}\left(1 + \ln \frac{DK_m}{S_0(\mu_m e^{-D\tau} - D)}\right) - \frac{K_m}{\mu_m e^{-D\tau} - D} < 0, f(+\infty) > 0.$$

Hence there exists a $T_0 \in (\frac{1}{D} \ln \frac{DK_m}{S_0(\mu_m e^{-D\tau} - D)}, +\infty)$ such that $f(T_0) = 0$. We can clearly see that $f(T) < 0$ for $T \in (0, T_0)$. Further, we have the following corollary.

Corollary 3.2. *There exists a $T_0 \in \left(\frac{1}{D} \ln \frac{DK_m}{S_0(\mu_m e^{-D\tau} - D)}, +\infty\right)$ such that when $T \in (0, T_0)$, then the periodic solution $(S^*(t), 0)$ is globally attractive.*

In Section 3, we give the conditions for the population of microorganisms will eventually be washed out of the chemostat. In the following, we investigate the permanence of the microorganisms species.

4. Permanence

Before starting our theorem, we give the following definition.

Definition 4.1. System (2) is said to be permanent if there exists a compact region $D \subset$ int Ω such that every solution of system (2) with initial conditions (3) will eventually enter and remain in region D.

Theorem 4.1. *The system (2) is permanent if*

$$\gamma S_0 > \frac{DK_m(e^{DT} - 1)}{\mu_m e^{-D\tau} - D}. \tag{19}$$

Proof. Suppose that $(S(t), x(t))$ is any positive solution of system (2) with initial conditions (3). The second equation of system (2) may be rewritten as follow:

$$x'(t) = \left[\mu_m e^{-D\tau} \frac{S(t)}{K_m + S(t)} - D\right] x(t) - \mu_m e^{-D\tau} \frac{d}{dt} \int_{t-\tau}^t \frac{S(\theta)x(\theta)}{K_m + S(\theta)} d\theta. \tag{20}$$

Define

$$V(t) = x(t) + \mu_m e^{-D\tau} \int_{t-\tau}^t \frac{S(\theta)x(\theta)}{K_m + S(\theta)} d\theta.$$

Calculating the derivative of $V(t)$ along the solution of (2), it follows from (20) that

$$\frac{dV(t)}{dt} = D\left[\mu_m e^{-D\tau} \frac{S(t)}{D(K_m + S(t))} - 1\right] x(t). \tag{21}$$

Let

$$m_2^* = \frac{1}{2} \frac{\delta K_m}{\mu_m}\left(\frac{1}{T} \ln\left(1 + \frac{TS_0(\mu_m e^{-D\tau} - D)}{K_m}\right) - D\right).$$

From inequality (19), it is clear that $m_2^* > 0$. For this m_2^*, we can choose a positive constant ε_1 small enough such that

$$\frac{\mu_m e^{-D\tau} \varrho}{D(K_m + \varrho)} > 1, \tag{22}$$

where

$$\varrho = \frac{\gamma S_0 e^{-\left(D + \frac{\mu_m m_2^*}{\delta K_m}\right)T}}{1 - e^{-\left(D + \frac{\mu_m m_2^*}{\delta K_m}\right)T}} - \varepsilon_1 > 0.$$

For any positive constant t_0, we claim that the inequality $x(t) < m_2^*$ cannot hold for all $t \geq t_0$. Otherwise, there is a positive constant t_0, such that $x(t) < m_2^*$ for all $t \geq t_0$. From the first and third equations of system (2), we have

$$S'(t) \geq -\left(D + \frac{\mu_m m_2^*}{\delta K_m}\right) S(t), \quad t \neq nT,$$

$$S(t^+) = S(t) + \gamma S_0, \quad t = nT.$$

By Lemma 2.1, there exists such $T_1 \geq t_0 + \tau$, for $t \geq T_1$ that

$$S(t) > \frac{\gamma S_0 e^{-\left(D + \frac{\mu_m m_2^*}{\delta K_m}\right)T}}{1 - e^{-\left(D + \frac{\mu_m m_2^*}{\delta K_m}\right)T}} - \varepsilon_1 =: \varrho. \tag{23}$$

From (21) and (23), we have

$$\frac{dV(t)}{dt} > D\left[\mu_m e^{-D\tau} \frac{\varrho}{D(K_m + \varrho)} - 1\right] x(t), \quad t \geq T_1. \tag{24}$$

Let

$$x^l = \min_{t \in [T_1, T_1 + \tau]} x(t).$$

We show that $x(t) \geq x^l$ for all $t \geq T_1$. Otherwise, there exists a nonnegative constant T_2 such that $x(t) \geq x^l$ for $t \in [T_1, T_1 + \tau + T_2]$, $x(T_1 + \tau + T_2) = x^l$ and $x'(T_1 + \tau + T_2) \leq 0$. Thus from the second equation of (2) and (22), we easily see that

$$\begin{aligned} x'(T_1 + \tau + T_2) &> \left[\mu_m e^{-D\tau} \frac{\varrho}{K_m + \varrho} - D\right] x^l \\ &= D\left[\mu_m e^{-D\tau} \frac{\varrho}{D(K_m + \varrho)} - 1\right] x^l \\ &> 0, \end{aligned}$$

which is a contradiction. Hence we get that $x(t) \geq x^l > 0$ for all $t \geq T_1$. From (24), we have

$$\frac{dV(t)}{dt} > D\left[\mu_m e^{-D\tau} \frac{\varrho}{D(K_m + \varrho)} - 1\right] x^l > 0,$$

which implies $V(t) \to +\infty$ as $t \to +\infty$. This is a contradiction to $V(t) \leq (1 + \mu_m \tau e^{-D\tau})L$. Therefore, for any positive constant t_0, the inequality $x(t) < m_2^*$ cannot hold for all $t \geq t_0$.

On the one hand, if $x(t) \geq m_2^*$ holds true for all t large enough, then our aim is obtained. On the other hand, $x(t)$ is oscillatory about m_2^*.

Let

$$m_2 = \min\left\{\frac{m_2^*}{2}, m_2^* e^{-D\tau}\right\}.$$

In the following, we shall show that $x(t) \geq m_2$. There exist two positive constants $\bar{t}$, ω such that

$$x(\bar{t}) = x(\bar{t} + \omega) = m_2^*$$

and

$$x(t) < m_2^*, \quad \text{for } \bar{t} < t < \bar{t} + \omega.$$

When $\bar{t}$ is large enough, the inequality $S(t) > \varrho$ holds true for $\bar{t} < t < \bar{t} + \omega$. Since $x(t)$ is continuous and bounded and is not effected by impulses, we conclude that $x(t)$ is uniformly continuous. Hence there exists a constant T_3 (with $0 < T_3 < \tau$ and T_3 is independent of the choice of $\bar{t}$) such that $x(t) > \frac{m_2^*}{2}$ for all $\bar{t} \leq t \leq \bar{t} + T_3$. If $\omega \leq T_3$, our aim is obtained. If $T_3 < \omega \leq \tau$, from the second equation of (2) we have that $x'(t) \geq -Dx(t)$ for $\bar{t} < t \leq \bar{t} + \omega$. Then we have $x(t) \geq m_2^* e^{-D\tau}$ for $\bar{t} < t \leq \bar{t} + \omega \leq \bar{t} + \tau$ since $x(\bar{t}) = m_2^*$. It is clear that $x(t) \geq m_2$ for $\bar{t} < t \leq \bar{t} + \omega$. If $\omega \geq \tau$, then we have that $x(t) \geq m_2$ for $\bar{t} < t \leq \bar{t} + \tau$. Thus, proceeding exactly as the proof for above claim, we can obtain $x(t) \geq m_2$ for $\bar{t} + \tau \leq t \leq \bar{t} + \omega$. Since the interval $[\bar{t}, \bar{t} + \omega]$ is arbitrarily chosen (we only need $\bar{t}$ to be large), we get that $x(t) \geq m_2$ for t large enough. In view of our arguments above, the choice of m_2 is independent of the positive solution of (2) which satisfies that $x(t) \geq m_2$ for sufficiently large t.

By Lemma 2.3, we have $x(t) \leq L$ for $t \geq 0$. Hence, from the first equation of (2), we have that,

$$S'(t) \geq -\left(D + \frac{\mu_m L}{\delta K_m}\right) S(t).$$

Then we have $S(t) \geq \widetilde{z_3}(t)$, where $\widetilde{z_3}(t)$ is unique a globally asymptotically stable positive periodic solution of

$$\begin{aligned} z_3'(t) &= -\left(D + \frac{\mu_m L}{\delta K_m}\right) z_3(t), \quad t \neq nT, \ n \in N, \\ z_3(t^+) &= z_3(t) + \gamma s_0, \quad t = nT, \ n \in N, \\ z_3(0^+) &= S(0^+) > 0. \end{aligned}$$
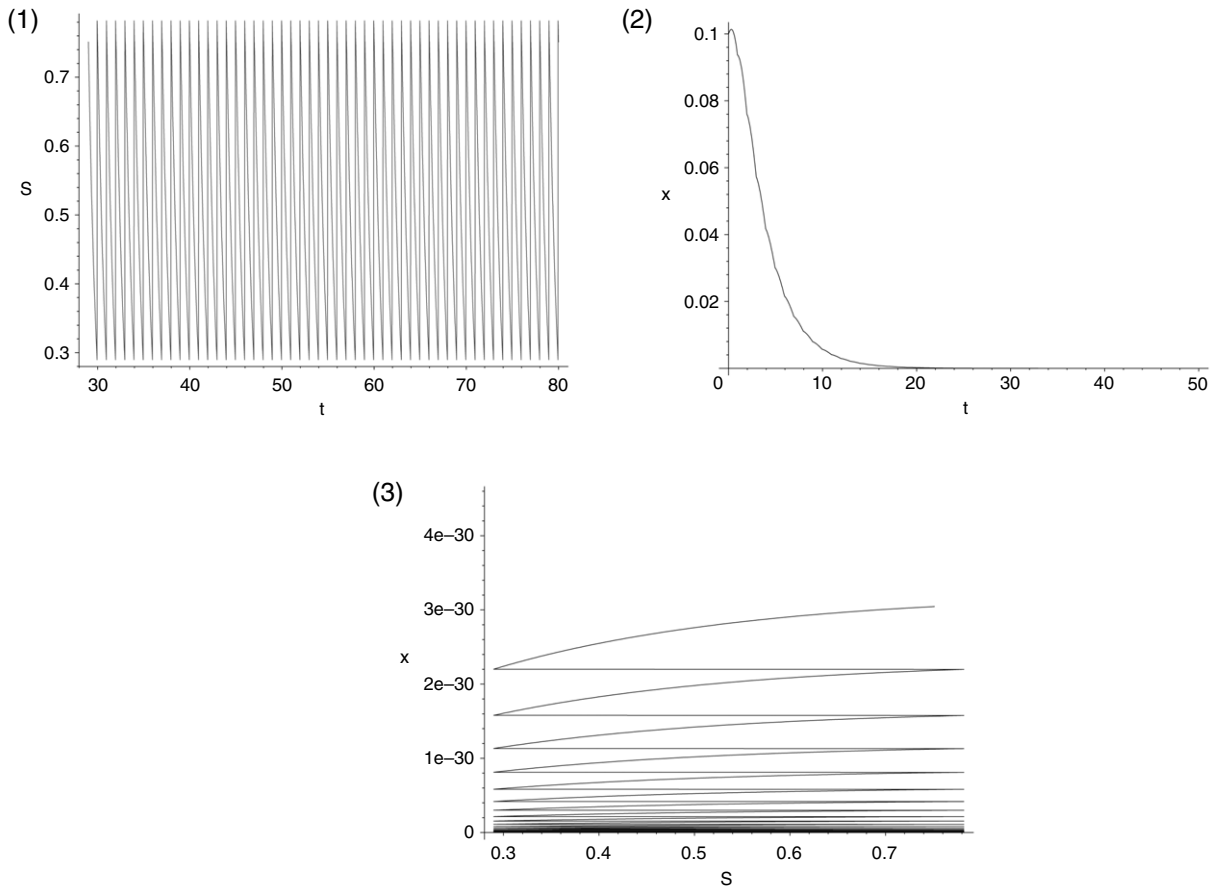
Fig. 1. Dynamical behavior of system (2) with $\mu_m = 1.5$, $K_m = 0.6$, $D = 1$, $\delta = 10$, $T = 1$, $\tau = 0$, $S_0 = 0.7$. (1) Time series of the concentration of the unconsumed nutrient (S) for periodic oscillation; (2) Time series of the microorganism population (x) for extinction; (3) Phase portrait of the nutrient and the microorganism population for global attractivity of the 'microorganism-eradication' periodic solution ($S^*(t), 0$).

There exists a $\varepsilon > 0$ small enough such that for sufficiently large t,

$$S(t) \geq \widetilde{z_3}(t) - \varepsilon \geq \frac{\gamma S_0 e^{-\left(D + \frac{\mu_m L}{\delta K_m}\right)T}}{1 - e^{-\left(D + \frac{\mu_m L}{\delta K_m}\right)T}} - \varepsilon =: m_1.$$

Set

$$D = \{(S, x) \in R_+^2 \,|\, m_1 \leq S(t) \leq L, m_2 \leq x(t) \leq L\}.$$

Then D is a bounded compact region which has positive distance from coordinate axes. In view of our arguments above, one obtains that every solution of system (2) with the initial condition (3) eventually enters and remains in the region D. The proof is complete.

5. Numerical analysis and discussion

In this paper, we introduce a growth response time delay and pulse input nutrient into the Monod type chemostat model, and theoretically analyze the influence of them on the extinction of the population of the microorganism and the permanence of the system. To facilitate the interpretation of our mathematical findings and possible lab or field implementation of the model and to investigate the effect of the impulsive input nutrient by numerical analysis, we consider the hypothetical set of parameter values as $\mu_m = 1.5$, $K_m = 0.6$, $D = 1$, $\delta = 10$, $T = 1$, $\tau = 0$.

Whether the microorganism is extinct or not is determined completely by the input amount of the substrate S_0 for the fixed period T. If $S_0 = 0.5$, by Theorem 3.1, we know that when $\gamma S_0 = TDS_0 = 0.5 < \frac{DK_m(1 - e^{-DT})}{\mu_m e^{-D\tau} - D} \approx 0.7588$, the 'microorganism-extinction' periodic solution ($S^*(t), 0$) is globally attractive, the substrate $S(t)$ presents periodic oscillation and the microorganism $x(t)$ is extinct as $t \to \infty$, (see Fig. 1). If $S_0 = 2.1$, by Theorem 4.1, we know that when $\gamma S_0 = TDS_0 = 2.1 > \frac{DK_m(e^{DT} - 1)}{\mu_m e^{-D\tau} - D} \approx 1.9598$, the system (2) is permanent, the substrate $S(t)$ and the microorganism
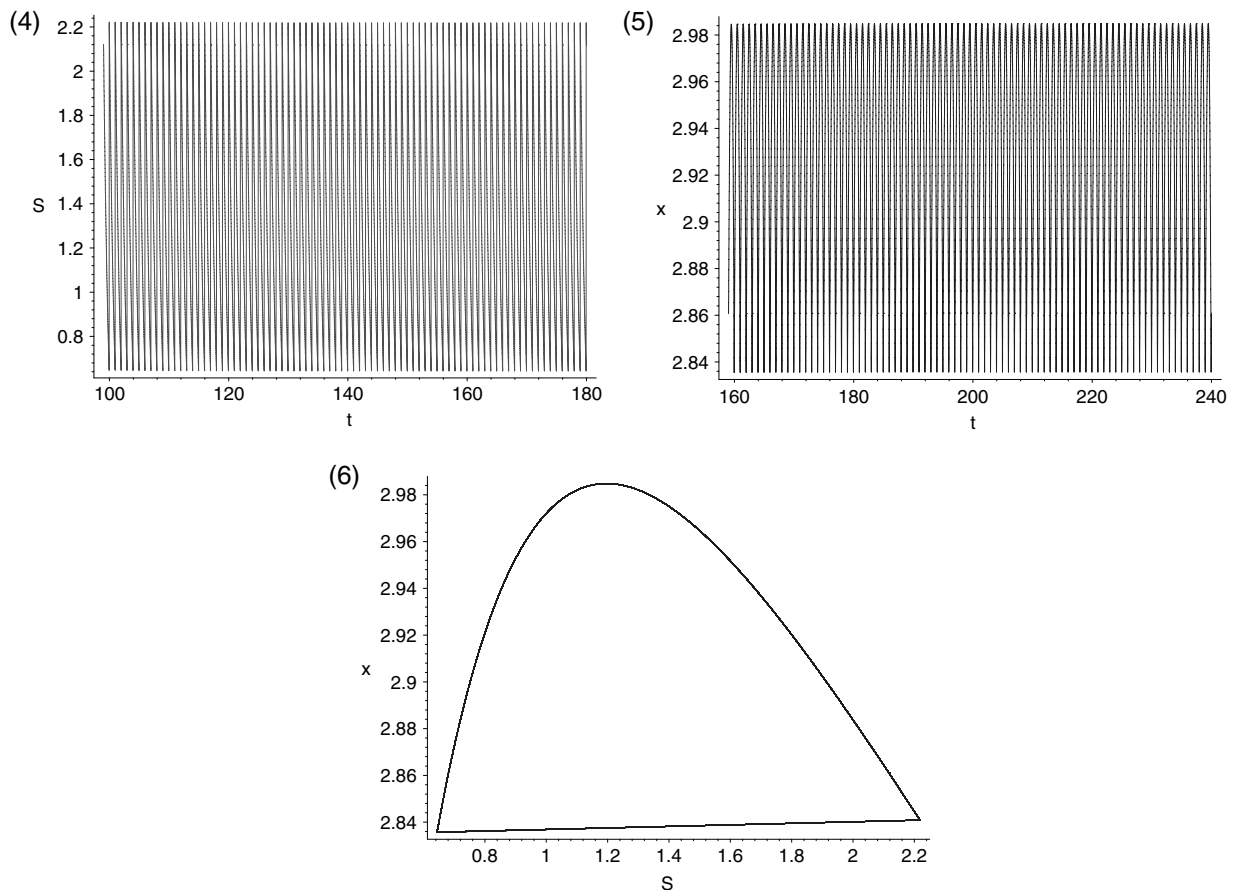
Fig. 2. Dynamical behavior of system (2) with $\mu_m = 1.5, K_m = 0.6, D = 1, \delta = 10, T = 1, \tau = 0, S_0 = 2.1$. (4) Time series of the nutrient (S) for permanence and periodic oscillation; (5) Time series of the microorganism population (x) for permanence and periodic oscillation; (6) Phase portrait (T-periodic solution) of the nutrient and the microorganism population of system (2).

$x(t)$ present periodic oscillation as $t \rightarrow \infty$, (see Fig. 2). In this case, the microorganism is obtained. Obviously, if both the continuous culture and the impulsive culture can obtain the microorganism, the latter is better than the former since the impulsive culture can save the substrate.

From Theorems 3.1 and 4.1, we can see the extinction and permanence of the microorganism are dependent of the time delay for growth response of the microorganism. Ultimately, when the time delay for growth response is too long, the permanence of system disappears and the consumer population of the microorganism dies out. This shows the sensitivity of the model dynamics on time delay (growth response). The ultimate scenario makes intuitive biological sense: if it takes too long to grow then the highest possible recruitment rate to the microorganism species ($\mu_m e^{-D\tau}$) will drop below the losing rate to flow out D, leading to the extinction of x. This implies that time delay brings great effect on the dynamics behaviors of the model. Therefore, it is very important to consider time delay for the growth response of the microorganism in chemostat model.

References

[1] H.L. Simth, P. Waltman, The Theory of the Chemostat, Cambridge University Press, Cambridge, 1995.
[2] S.B. Hsu, S.P. Hubbell, P. Waltman, A mathematical theory for single nutrient competition in continuous cultures of micro-organisms, SIAM J. Appl. Math. 32 (1977) 366–383.
[3] A.M. Picket, Growth in a changing environment, in: M.J. Bazin (Ed.), Microbial Population Dynamics, CRC Press, Florida, 1982, pp. 91–124.
[4] J. Monod, La technique de culture continue; théorie et applications, Ann. Inst. Pasteur 79 (1950) 390–401.
[5] S.R. Hansen, S.P. Hubbell, Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes, Science 207 (1980) 1491–1493.
[6] J.P. Barford, N.B. Pamment, R.J. Hall, Lag phases and transients, in: M.J. Bazin (Ed.), Microbial Population Dynamics, CRC Press, Florida, 1982, pp. 55–89.
[7] D. Ramkrishna, A.G. Fredrickson, H.M. Tsuchiya, Dynamics of microbial propagation: models considering inhibitors and variable cell composition, Biotechnol. Bioeng. 9 (1967) 129–170.
[8] A.W. Bush, A.E. Cook, The effect of time delay and growth rate inhibition in the bacterial treatment of wastewater, J. Theoret. Biol. 63 (1976) 385–395.
[9] J. Caperon, Time lag in population growth response of isochrysis galbana to a variable nitrate environment, Ecology 50 (1969) 188–192.
[10] W. Ma, M. Song, Y. Takeuchi, Global stability of an SIR epidemicmodel with time delay, Appl. Math. Lett. 17 (2004) 1141–1145.

[11] G. Fu, W. Ma, Hopf bifurcations of a variable yield chemostat model with inhibitory exponential substrate uptake, Chaos Solitons Fractals 30 (2006) 845–850.
[12] S. Ruan, G.S.K. Wolkowicz, Bifurcation analysis of a chemostat model with a distributed delay, J. Math. Anal. Appl. 204 (1996) 786–812.
[13] T.F. Thingstad, T.I. Langeland, Dynamics of chemostat culture: the effect of a delay in cell response, J. Theoret. Biol. 48 (1974) 149–159.
[14] S.F. Ellermeyer, Competition in the chemostat: global asymptotic behavior of a model with delayed response in growth, SIAM J. Appl. Math. 54 (1994) 456–465.
[15] G.S.K. Wolkowicz, H. Xia, Global asymptotic behavior of a chemostat model with discrete delays, SIAM J. Appl. Math. 57 (1997) 1019–1043.
[16] G.S.K. Wolkowicz, H. Xia, S. Ruan, Competition in the chemostat: a distributed delay model and its global asymptotic behavior, SIAM J. Appl. Math. 57 (1997) 1281–1310.
[17] H. Xia, G.S.K. Wolkowicz, L. Wang, Transient oscillations induced by delayed growth response in the chemostat, J. Math. Biol. 50 (2005) 489–530.
[18] T. Zhao, Global periodic solutions for a differential delay system modelling a microbial population in the chemostat, J. Math. Anal. Appl. 193 (1995) 329–352.
[19] N. MacDonald, Time delays in chemostat models, in: M.J. Bazin (Ed.), Microbial Population Dynamics, CRC Press, Florida, 1982.
[20] J.K. Hale, A.S. Somolinas, Competition for fluctuating nutrient, J. Math. Biol. 18 (1983) 255–280.
[21] G.J. Buler, S.B. Hsu, P. Waltman, A mathematical model of the chemostat with periodic washout rate, SIAM J. Appl. Math. 45 (1985) 435–449.
[22] G.S.K. Wolkowicz, X.Q. Zhao, N-spicies competition in a periodic chemostat, Differ. Integral Equ. 11 (1998) 465–491.
[23] D.D. Bainov, P.S. Simeonov, Impulsive Differential Eqations: Periodic Solutions and Applications, Longman Scientific and Technical, Burnt Mill, 1993.
[24] V. Lakshmikantham, D.D. Bainov, P.S. Simeonov, Theory of Impulsive Differential Equations, World Scientific, Singapore, 1989.
[25] X. Liu, L. Chen, Complex dynamics of Holling type II Lotka–Volterra predator–prey system with impulsive perturbations on the predator, Chaos Solitons Fractals 16 (2003) 311–320.
[26] B. Liu, Y. Zhang, L. Chen, The dynamical behaviors of a Lotka–Volterra predator–prey model concerning integrated pest management, Nonlinear Anal. RWA 6 (2005) 227–243.
[27] G. Ballinger, X. Liu, Permanence of population growth models with impulsive effects, Math. Comput. Modelling 26 (1997) 59–72.
[28] Y. Li, J. Cui, X. Song, Dynamics of a predator–prey system with pulses, Appl. Math. Comput. 204 (2008) 269–280.
[29] H. Zhang, P. Georgescu, L. Chen, An impulsive predator–prey system with Beddington–Deangelis functional response and time delay, Int. J. Biomath. 1 (2008) 1–17.
[30] E. Funasaki, M. Kot, Invasion and chaos in a periodically pulsed mass-action chemostat, Theor. Popul. Biol. 44 (1993) 203–224.
[31] R.J. Smith, G.S.K. Wolkowicz, Analysis of a model of the nutrient driven self-cycling fermentation process, Dyn. Contin. Discrete Impul. Syst. Ser. B 11 (2004) 239–265.
[32] S. Sun, L. Chen, Dynamic behaviors of Monod type chemostat model with impulsive perturbation on the nutrient concentration, J. Math. Chemistry 42 (2007) 837–847.
[33] X. Meng, J. Jiao, L. Chen, The dynamics of an age structured predatorCprey model with disturbing pulse and time delays, Nonlinear Anal. RWA 9 (2008) 547–561.
[34] S. Gao, Z. Teng, D. Xie, The effects of pulse vaccination on SEIR model with two time delays, Appl. Math. Comput. 201 (2008) 282–292.
[35] L. Chen, J. Chen, Nonlinear Biological Dynamic Systems, Science Press, Beijing, 1993 (in Chinese).
[36] Y. Kuang, Delay Differential Equations with Applications in Population Dynamics, Academic Press, INC., San Diego, CA, 1993.