Analysis of a Tessiet type food chain chemostat with k-times' periodically pulsed input

Fengyan Wang* and Shuwen Zhang

College of Science, Jimei University, Xiamen Fujian 361021, People's Republic of China E-mail: wangfy68@163.com

Guoping Pang

Department of Mathematics and Computer Science, Yulin Normal University, Yulin Guangxi 537000, People's Republic of China

Received 28 January 2007; Revised 23 February 2007

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

KEY WORDS: Tessiet growth rate, *k*-times' pulsed input, chaos, quasiperiodic oscillation

1. Introduction and the model

As well known, countless organisms live in seasonally or diurnally forced environment, in which the populations obtain food, so the effects of this forcing may be quite profound. Recently many papers studied chemostat model with variations in the supply of nutrients or the washout. Chemostat with periodic inputs are studied in [1-5], those with periodic washout rate in [6, 7], and those with periodic input and washout in [8]. A chemostat is a common laboratory apparatus used to culture micro-organisms. Sterile growth medium enters the chemostat at a constant rate; the volume within the chemostat is held constant by allowing excess medium (and microbes) to flow out through a siphon. In

*Corresponding author.

this paper we want to study a chemostat with periodically variable pulsed input. We inoculate this chemostat with a heterotrophic bacterium that finds, in the medium, an abundance of all necessary nutrients but one. This last nutrient is the limiting substrate ; it is pulsed in periodically. We also allow for a holozoic predator, e.g, a protist, that feeds on the heterotroph. The specific growth rates of bacteria (Tessiet (1936))(see Chen [9]) and of protozoa saturate at sufficiently high substrate and prey concentrations. The functional responses to be of the Tessiet type. Without loss of generality, we assume that the input occur variable at k-times' ($k \in N$) in period τ . The model takes the form:

$$\left\{ \begin{array}{l} \frac{ds}{dT} = -DS - \frac{\mu_1}{\delta_1} \frac{\exp(-B_1 S)SH}{(A_1 + S)}, \\ \frac{dH}{dT} = \frac{\mu_1 \exp(-B_1 S)SH}{A_1 + S} - DH - \frac{\mu_2}{\delta_2} \frac{\exp(-B_2 H)HP}{(A_2 + H)}, \\ \frac{dP}{dT} = \frac{\mu_2 \exp(-B_2 H)HP}{A_2 + H} - DP, \\ \Delta S\left(\frac{n\tau}{D}\right) = p_i S_0, \quad p_i = \tau_i - \tau_{i-1}, \end{array} \right\} T \neq \frac{n\tau + \tau_i}{D}, (i = 1, 2, \dots, k)$$
(1.1)

where τ is the period of the impulsive effect and $\tau_0 = 0 < \tau_1 < \tau_2 < \cdots < \tau_k = \tau$ are the k-times of the impulsive effects in per period τ . The state variables *S*, *H*, and *P* represent the concentration of limiting substrate, prey, and predator. *D* is the dilution rate; μ_1 and μ_2 are the uptake and predation constance 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; A_i , B_i (i = 1, 2) relate with the functional response of prey and predator; $\frac{\tau}{D}$ is the period of the pulsing; τS_0 is the amount of limiting substrate pulsed each $\frac{\tau}{D}$. DS_0 units of substrate are added, on average, per unit of time. $n \in N$, *N* is the set of all non-negative integers.

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

There are advantages in analyzing dimensionless equations. We treat the reciprocal of the dilution rate as natural measure of time:

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

After some algebra, this yields

$$\frac{dx}{dt} = -x - \frac{m_1 \exp(-b_1 x) xy}{a_1 + x},
\frac{dy}{dt} = \frac{m_1 \exp(-b_1 x) xy}{a_1 + x} - y - \frac{m_2 \exp(-b_2 y) yz}{a_2 + y},
\frac{dz}{dt} = \frac{m_2 \exp(-b_2 y) yz}{a_2 + y} - z,
x((n\tau + \tau_i)^+) = x(n\tau + \tau_i) + p_i, \qquad t = n\tau + \tau_i, (i = 1, 2, ..., k),$$
(1.2)

with

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

The organizations of the paper are as following. In next section, we investigate the existence and stability of the periodic solutions of the impulsive subsystem with substrate and prey. In section 3, we study the 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 section 4, the bifurcation diagrams of different coefficients show that with increasing the bifurcation parameters, the system experiences following two kinds of processes: (1) periodic solution \rightarrow periodic doubling cascade \rightarrow periodic doubling cascade \rightarrow chaos.

2. Behavior of the substrate bacterium subsystem

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

$$\begin{cases} \frac{dx}{dt} = -x - \frac{m_1 \exp(-b_1 x) xy}{a_1 + x}, \\ \frac{dy}{dt} = \frac{m_1 \exp(-b_1 x) xy}{a_1 + x} - y, \\ x((n\tau + \tau_i)^+) = x(n\tau + \tau_i) + p_i, \ t = n\tau + \tau_i, (i = 1, 2, ..., k). \end{cases}$$
(2.1)

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

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

$$\begin{cases} \frac{ds}{dt} = -s, & t \neq n\tau + \tau_i, (i = 1, 2, \dots, k) \\ s(t^+) = s(t) + p_i, s(0) > 0, & t = n\tau + \tau_i, (i = 1, 2, \dots, k). \end{cases}$$
(2.2)

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

Lemma 2.1. The subsystem (2.2) has a positive periodic solution $\tilde{s}(t)$ and for every solution s(t) of (2.2) we have $|s(t) - \tilde{s}(t)| \to 0$ as $t \to \infty$, where

$$\begin{cases} \tilde{s}(t) = s_i^+ \exp(-(t - n\tau - \tau_{i-1})), & t \in (n\tau + \tau_{i-1}, n\tau + \tau_i], \\ \tilde{s}(0) = s_0^+ = \frac{\sum_{j=1}^k p_j \exp(-\tau + \tau_j)}{1 - \exp(-\tau)}, s_i = s_{i-1}^+ \exp(-p_i). & i = 1, 2, \dots, k. \end{cases}$$
(2.3)

Proof. Suppose $s(t, s_0)$ is a solution of equation (2.2), with initial condition $s_0 \in [0, +\infty)$. We have

$$s(t, s_0) = s((n\tau + \tau_{i-1})^+) \exp(-(t - n\tau - \tau_i), t \in (n\tau + \tau_{i-1}, n\tau + \tau_i], (2.4)$$

$$s(t^+) = s(t) + p_i, t = n\tau + \tau_i,$$

for i = 1, 2, ..., k. We introduce a function $U(s_0) = s(t, y_0)$. For (2.4), we have the following properties:

- (i) $0 < s(t, s_0) < \infty, t \in (0, \infty)$ is piecewise continuous function;
- (*ii*) The function $U(s_0) = s(t, s_0), s_0 \in (0, \infty)$ is a increasing function.

By direct calculating, we know that the solution $\tilde{s}(t)$ in (2.3) is a τ -period solution of the equation (2.2); according to (ii), we can see that the solution $\tilde{s}(t)$ is a unique period solution of (2.2). The multiplier μ_s of $\tilde{s}(t)$ is

$$\mu_s := \exp(-\tau) < 1,$$

we can see that $\tilde{s}(t)$ $(t \in (0, \infty))$ is globally asymptotically stable. We complete the proof.

By the lemma 2.1, the following lemma is obvious.

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

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

Theorem 2.1. For the system (2.1), we denote

$$m_1^* := \frac{\tau}{\int_0^\tau \frac{\tilde{s}(l) \exp(-b_1 \tilde{s}(l))}{a_1 + \tilde{s}(l)} \mathrm{d}l}$$

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

$$x_e(t) = 1, y_e(t) = 0;$$

(2) If $m_1 > m_1^*$, then the system (2.1) has a unique globally asymptotically stable positive τ -periodic 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

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

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

$$\frac{d_y}{d_t} = \frac{m_1(\tilde{s}(t) - y) \exp(-b_1(\tilde{s}(t) - y))y}{a_1 + (\tilde{s}(t) - y)} - y, \quad 0 \le y_0 \le \tilde{s}(0).$$
(2.5)

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

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

$$y(0) = y_0, \qquad t \in (n\tau, (n+1)\tau].$$
(2.6)

For (2.6), we have the following properties:

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

The periodic solutions of (2.5) satisfy the following equation

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

By (i),(ii), and (iii), we know that if $\frac{1}{\tau} \int_0^{\tau} \frac{m_1 \tilde{s}(l) \exp(-b_1 \tilde{s}(l))}{a_1 + \tilde{s}(l)} dl > 1$, the equation (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

$$y(t) \leq y(0) \exp((\int_0^t \frac{m_1 \tilde{s}(l) \exp(-b_1 \tilde{s}(l))}{a_1 + \tilde{s}(l)} dl - 1)t).$$
(2.8)

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

If $m_1 > m_1^*$, then the equation (2.5) has 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

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

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

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

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

Noticing equation (2.5), we have

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

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

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

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

So $F(y(\tau, y_0)), y_0 \in [0, \tilde{s}(0)]$ is monotonously decreasing continuous function. Now we set $0 < \varepsilon < y_0^* < \tilde{s}(0)$. According to (2.11), we have that

$$\ln y(\tau, y_0) - \ln y_0 < 0, \quad \text{if} \quad y_0^* < y_0 < \tilde{s}(0), \\ \ln y(\tau, y_0) - \ln y_0 = 0, \quad \text{if} \quad y_0 = y_0^*, \\ \ln y(\tau, y_0) - \ln y_0 > 0, \quad \text{if} \quad \varepsilon < y_0 < y_0^*.$$

$$(2.12)$$

Furthermore, we obtain the following equations

$$y_0 > y(\tau, y_0) > \dots > y(n\tau, y_0) > y_0^*, if \quad y_0^* < y_0 \le \tilde{s}(0), y_0 < y(\tau, y_0) < \dots < y(n\tau, y_0) < y_0^*, if \quad \varepsilon \le y_0 < y_0^*.$$
(2.13)

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

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

We shall prove that the solution y(t, a) is τ -periodic. We note that the functions $y_n(t) = y(t + n\tau, y_0)$, due to the τ -periodicity of equation (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 $y(\tau, a) = \lim_{n \to \infty} y_n(\tau) = a$. 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 2.9 [10] on the continuous dependence of the solutions on the initial values, there exists a $\delta > 0$ such that

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

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

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

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

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

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

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

3. Bifurcation of the system

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

$$\begin{cases} \frac{\mathrm{d}s}{\mathrm{d}t} = -s, & t \neq n\tau + \tau_i, (i = 1, 2, \dots, k) \\ s(t^+) = s(t) + p_i, s(0) > 0, & t = n\tau + \tau_i, (i = 1, 2, \dots, k). \end{cases}$$

By the lemma 2.1, the following lemma is obvious.

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

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

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

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

$$m_2^* := \frac{\tau}{\int_0^\tau \frac{y_s(l) \exp(-b_2 y_s(l))}{a_1 + y_s(l)} \mathrm{d}l}$$

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

(1) If $m_1 < m_1^*$, then the system (1.2) has a unique globally asymptotically stable positive τ -periodic solution ($x_e(t)$, $y_e(t)$, 0).

- (2) 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 asymptotical stable.
- (3) If $m_1 > m_1^*$ and $m_2 > m_2^*$, then the periodic boundary solution $(\tilde{s}(t) y_s(t), y_s(t), 0)$ of the system (1.2) is unstable.

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

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

there may be written

$$\begin{pmatrix} u(t) \\ v(t) \\ w(t) \end{pmatrix} = \Phi_i(t) \begin{pmatrix} u(\tau_{i-1}^+) \\ v(\tau_{i-1}^+) \\ w(\tau_{i-1}^+) \end{pmatrix} \qquad \tau_{i-1} < t < \tau_i, (i = 1, 2, \dots, k),$$

where $\Phi_i(t)$ satisfies

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

and $\Phi_i(\tau_{i-1}) = I$, the identity matrix. Hence the fundamental solution matrix is

$$\Phi_{i}(\tau_{i}) = \begin{pmatrix} \phi_{1i}(\tau_{i}) & \phi_{2i}(\tau_{i}) & * \\ \phi_{3i}(\tau_{i}) & \phi_{4i}(\tau_{i}) & ** \\ 0 & 0 & \exp(\int_{\tau_{i-1}}^{\tau_{i}} (\frac{m_{2}y_{s}(l)\exp(-b_{2}y_{s}(l))}{a_{2}+y_{s}(l)} - 1)dl) \end{pmatrix}.$$
 (3.2)

It is no need to give the exact form of (*) and (**) as it is not required in the analysis that follows. The linearization of impulsive subsystem (2.3) become

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

We denote that

$$M_i = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} \Phi_i(\tau), (i = 1, 2, \dots, k).$$

Hence, we obtain the fundamental solution matrix M is

$$M = M_k \cdots M_2 M_1 = \begin{pmatrix} \phi_{11}(\tau) & \phi_{12}(\tau) & * \\ \phi_{21}(\tau) & \phi_{22}(\tau) & ** \\ 0 & 0 & \exp(\int_0^\tau (\frac{m_2 y_s(l) \exp(-b_2 y_s(l))}{a_2 + y_s(l)} - 1) dl) \end{pmatrix}.$$

The eigenvalues of the matrix M are $\mu_3 = \exp(\int_0^{\tau} (m_2 y_s(l) - 1) dl)$ and the eigenvalues μ_1, μ_2 of the following matrix

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

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

If $\frac{1}{\tau} \int_0^{\tau} \frac{m_1 \tilde{s}(l) \exp(-b_1 \tilde{s}(l))}{a_1 + \tilde{s}(l)} dl > 1$ and $\frac{1}{\tau} \int_0^{\tau} \frac{m_2 \exp(-b_1 y_s(l))}{a_2 + y_s(l)} dl < 1$, then we get that $\mu_3 = \exp(\int_0^{\tau} (\frac{m_2 y_s(l) \exp(-b_2 y_s(l))}{a_2 + y_s(l)} - 1) dl) < 1$, the boundary periodic solution $(x_s(t), y_s(t), 0)$ of the system (1.2) is locally asymptotically stable. We have that

$$z(t) \leq z(0) \exp(\int_0^t (\frac{m_2 y_s(l) \exp(-b_2 y_s(l))}{a_2 + y_s(l)} - 1) dl),$$

hence we obtain that for any solution (x(t), y(t), z(t)) with $X(0) > 0, z(t) \to 0$ as $t \to \infty$. By $\lim_{t\to\infty} |x(t) + y(t) + z(t) - \tilde{s}(t)| = 0$, we have $\lim_{t\to\infty} |x(t) + y(t) - \tilde{s}(t)| = 0$. Now using theorem 2.1, we have $\lim_{t\to\infty} |y(t) - y_s(t)| = 0$ and $\lim_{t\to\infty} |x(t) - x_s(t)| = 0$.

If $\frac{1}{\tau} \int_0^{\tau} \frac{m_1 \tilde{s}(l) \exp(-b_1 \tilde{s}(l))}{a_1 + \tilde{s}(l)} dl > 1$ and $\frac{1}{\tau} \int_0^{\tau} \frac{m_2 \exp(-b_1 y_s(l))}{a_2 + y_s(l)} dl > 1$, then we obtain that $\mu_3 = \exp(\int_0^{\tau} (\frac{m_2 y_s(l) \exp(-b_2 y_s(l))}{a_2 + y_s(l)} - 1) dl) > 1$, the boundary periodic solution $(x_s(t), y_s(t), 0)$ of the system (1.2) is unstable. We complete the proof.

Let *B* denote the Banach space of piecewise continuous, τ -periodic functions $N: [0, \tau] \to R^2$ and have points of discontinuity $\tau_i, (i=1, 2, ..., k)$, where they are continuous from the left. In the set *B* introduce the norm $|N|_0 = \sup_{0 \le t \le \tau} |N(t)|$ with which *B* becomes a Banach space with the uniform convergence topology.

For convenience, just like [18] we introduce the following lemma 3.2 and 3.3.

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

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

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

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

has, for every $(f_1, f_2) \in B \times B$, a unique solution $(x_1, x_2) \in B \times B$ and the operator $L: B \times B \to B \times B$ defined by $(x_1, x_2) = L(f_1, f_2)$ is linear and compact. If we define that $x'_2 = a_{22}x_2 + f_2$ has a unique solution $x_2 \in B$ and the operator $L_2: B \to B$ defined by $x_2 = L_2 f_2$ is linear and compact. Furthermore, $x'_1 = a_{11}x_1 + f_3$ for $f_3 \in B$ has a unique solution (since $\int_0^\tau a_{11}(s)ds \neq 0$) in B and $x_1 = L_1 f_3$ defines a linear, compact operator $L_1: B \to B$. Then we have

$$L(f_1, f_2) \equiv (L_1(a_{12}L_2f_2 + f_1), L_2f_2).$$
(3.6)

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

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

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

$$\begin{cases} \frac{dy}{dt} = \frac{m_1 \exp(-b_1(\tilde{s}(t) - y - z))(\tilde{s}(t) - y - z)y}{a_1 + (\tilde{s}(t) - y - z)} - y - \frac{m_2 \exp(-b_2 y)yz}{a_2 + y}, \\ \frac{dz}{dt} = \frac{m_2 \exp(-b_2 y)yz}{a_2 + y} - z, \\ y(0) > 0, z(0) \ge 0, y(0) + z(0) \le \tilde{s}(0). \end{cases}$$
(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^* practises as a bifurcation threshold. For the system (3.7), we have the following results.

Theorem 3.2. For the system (3.7), $m_1 > m_1^*$ and $a_2 - a_2b_2y_s - b_2y_s^2 \ge 0$ for $t \in (0, \tau]$ hold, then there exists a constance $\lambda_0 > 0$, such that for each $m_2 \in (m_2^*, m_2^* + \lambda_0)$, there exists a solution $(y, z) \in B \times B$ of (3.7) satisfying $0 < y < y_s, z > 0$ and $x = \tilde{s}(t) - y - z > 0$ for all t > 0. Hence, the system (1.2) has a positive τ -periodic solution $(\tilde{s}(t) - y - z, y, z)$.

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

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

where

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

We know that $\frac{1}{\tau} \int_0^{\tau} \frac{m_2 y_s(l)}{a_2 + y_s(l)} dl - 1 \neq 0$, by the lemma 4.3, using *L* we can equivalently write the system (3.8) as the operator equation

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

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

$$(y_1, y_2) = L^*(y_1, y_2), m_2 > 0.$$
 (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

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

and conversely. Using Lemma 3.2 (b), we see that (3.11) and hence (3.10) has one nontrivial solution in $B \times B$ if and only if $\frac{1}{\tau} \int_0^{\tau} \frac{m_2^* y_s(l) \exp(-b_2 y_s(l))}{a_2 + y_s(l)} dl = 1$. 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 \overline{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 \overline{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:

$$m_2 = m_2^* + \lambda \varepsilon + \cdots,$$

$$x_1 = x_{11}\varepsilon + x_{12}\varepsilon^2 + \cdots,$$

$$x_2 = x_{21}\varepsilon + x_{22}\varepsilon^2 + \cdots.$$

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

$$\begin{cases} x_{12}' = F_{11}(x_s, y_s)x_{12} - F_{12}(m_2^*, x_s, y_s)x_{22} + G_{12}(x_{11}, x_{11}, \lambda), \\ x_{22}' = F_{22}(m_2^*, x_s, y_s)x_{22} + \frac{x_{21}\exp(-b_2y_s)}{a_2+y_s}(\lambda y_s + \frac{m_2^*x_{11}(a_2-a_2b_2y_s-b_2y_s^2)}{a_2+y_s}), \end{cases}$$

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

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

Moreover $x_{11} < 0$ for all t (since $\int_0^{\tau} (m_1 x_s \exp(-b_1 x_s)/a_1 + x_s - 1 - \frac{m_1 y_s \exp(-b_1 x_s)(a_1 - a_1 b_1 x_s - b_1 x_s^2)}{(a_1 + x_s)^2}$) $dl = -\int_0^{\tau} (\frac{m_1 y_s \exp(-b_1 x_s)(a_1 - a_1 b_1 x_s - b_1 x_s^2)}{(a_1 + x_s)^2} dl < 0$ implies that the Green's function for first equation in (4.11) is positive). Using Lemma 3.3 we find that

$$\lambda = -\frac{\int_{0}^{\tau} \frac{m_{2}^{*x_{21}(t)x_{11}(t)\exp(-b_{2}y_{s}(t))(a_{2}-a_{2}b_{2}y_{s}(t)-b_{2}y_{s}^{2}(t))}{(a_{2}+y_{s}(t))^{2}}\exp(\int_{0}^{t} (\frac{m_{2}y_{s}(l)\exp(-b_{2}y_{s}(l))}{a_{2}+y_{s}(l)}-1)dl)dt}{\int_{0}^{\tau} \frac{\exp(-b_{2}y_{s}(t))y_{s}(t)x_{21}(t)}{a_{2}+y_{s}(t)}\exp(\int_{0}^{t} (\frac{m_{2}y_{s}(l)\exp(-b_{2}y_{s}(l))}{a_{2}+y_{s}(l)}-1)dl)dt} > 0,$$

provided with $a_2 - a_2b_2y_s - b_2y_s^2 \ge 0$. 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:

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

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

The solution is on C^+ which prove the theorem, since $\lambda > 0$ is equivalent to $m_2 > m_2^*$. We have left only to show that $y = x_1 + y_s > 0$ for all t. This is easy, for if λ_0 is small, then y is near y_s in the sup norm of B; thus since y_s is bounded away from zero, so is y. At same time, by theorem 3.1, for the system (3.3), 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.



Figure 1. Bifurcation diagrams of system (1.2) with $m_2 = 8, a_1 = 1, b_1 = 0.1, a_2 = 0.9, b_2 = 0.2, \tau_1 = 0.6\tau, \tau = 8, 2 < m_1 \leq 18.$

4. Chemostat chaos

In this section, we will analyze the complexity of the impulsive system (2.3). If $\frac{1}{\tau} \int_0^{\tau} \frac{m_1 \tilde{s}(l) \exp(-b_1 \tilde{s}(l))}{a_1 + \tilde{s}(l)} dl > 1$, for the system (4.7), by the theorem 4.1 the boundary periodic solution $(y_s(t), 0)$ is locally asymptotically stable provided with the following equation $\frac{1}{\tau} \int_0^{\tau} \frac{m_2 y_s(l) \exp(-b_2 y_s(l))}{a_2 + y_s(l)} dl < 1$, and it is unstable provided with the condition $\frac{1}{\tau} \int_0^{\tau} \frac{m_2 y_s(l) \exp(-b_2 y_s(l))}{a_2 + y_s(l)} dl > 1$, hence the value $m_2^* = \tau / \int_0^{\tau} \frac{y_s(l) \exp(-b_2 y_s(l))}{a_2 + y_s(l)} dl$ practises as a bifurcation threshold.

We want to investigate the influence of m_1 . Set $m_2=8$, $a_1=1$, $b_1=0.1$, $a_2=0.9$, $b_2=0.2$, $\tau_1=0.6\tau$, $\tau=8$, $2 < m_1 \leq 18$. The influences of m_1 may be documented by stroboscopically sampling some of the variables over a range of m_1 values. We numerically integrated system (1.2) for 500 pulsing cycles at each value of m_1 . For each m_1 , we plotted the last 200 measures of the prey y and the predator z. Since we sampled at the forcing period, periodic solutions of period τ appear as fixed points, periodic solutions of period 2τ appear as two cycles, and so forth. The resulting bifurcation diagrams (figure 1) clear show that: with increasing m_1 from 2 to 18, the system experiences process of cycles \rightarrow periodic doubling cascade \rightarrow cycles, which is characterized by (1) doubling bifurcations, (2) period halfing.

When m_1 is small $(m_1 < q_0 \approx 3)$, the solution $(\tilde{s}(t), 0, 0)$ is stable. When $m_1 > q_0$, the prey begins invade the system and the solution $(x_s, y_s, 0)$ is stable if $m_1 < q_1 \approx 3.76$. When $m_1 > q_1$, the predator begins invade and a stable positive period solution is bifurcated from $(x_s, y_s, 0)$ if $m_1 > q_1$. However, when $m_1 > q_2 \approx 4.36$, the stability of τ -periodic solution is destroyed and 2τ -periodic solution occurs and is stable if $m_1 < q_3 \approx 4.79$. When $m_1 > q_3$, it is uns-



Figure 2. Doubling bifurcation. (a)–(d) Phase portraits of τ , 2τ , 4τ , and 8τ -period solutions for m1 = 4.18, 4.58, 4.8, and 4.98, respectively.

table and there is a cascade of period doubling bifurcations (to see figure 2) leading to chaos (to see figure 3). Continuously increasing m_1 , it is followed by a cascade of periodic halving bifurcations from chaos to cycles (figure 4). A typical chaotic oscillation is captured when $m_1 = 5.83$. This periodic-doubling route to chaos is the hallmark of the logistic and Ricker maps [19, 20] and has been studied extensively by Mathematicians [21]. Periodic halving is the flip bifurcation in the opposite direction, which is also observed in [22].

We want to investigate the influence of m_2 . Set $m_1=6$, $a_1=1$, $b_1=0.2$, $a_2=0.9$, $b_2=0.1$, $\tau_1=0.6\tau$, $\tau = 8$, and $0.8 < m_2 \leq 21$. We numerically integrated system (1.2) for 500 pulsing cycles at each value of m_2 . For each m_2 , we plotted the last 200 stroboscopic measures of the prey y and the predator z. The resulting bifurcation diagrams (figure 5) show: (1) the invasion of predator at $m_2^* \approx 4.93$, (2)



Figure 3. Strange attractors: the phase portraits of system (1.2) of m1 = 5.83; the time series of y, z solution on the right sides are corresponding with the portraits on the left with initial values x0 = 1, y0 = 1, z0 = 0.5.

the first period-doubling at $m_2 \approx 6.7$, (3) a cascade of period doubling, (4) chaotic solutions, and (5) periodic windows within the chaotic regime.

Comparable changes occur with an increase in the pulse period τ . Set $m_1 = 6$, $m_2=8$, $a_1=1$, $b_1=0.1$, $a_2=0.9$, $b_2=0.2$, $\tau_1 = 0.6\tau$ and $0.1 < \tau \leq 11.8$. The resulting bifurcation diagrams (figure 6) clear show that: with increasing τ from 0.1 to 11.8, the system experiences process of quasiperiodic oscillation \rightarrow cycles \rightarrow periodic doubling cascade \rightarrow chaos \rightarrow periodic halfing cascade \rightarrow cycles. When impulsive period τ is small, there exists quasiperiodic oscillation in impulsive system. figure 7 shows a phase portrait of quasiperiodic oscillating solution at $\tau = 0.2$.



Figure 4. Halving bifurcation. (a)–(d) Phase portraits of 8τ , 4τ , 2τ , and τ -period solutions for m1 = 11.68, 11.8, 13.8, and 18.8, respectively.



Figure 5. Bifurcation diagrams of system (1.2) with $m_1=6, a_1=1, b_1=0.2, a_2=0.9, b_2=0.1, \tau_1 = 0.6\tau, \tau = 8$, and $2 < m_2 \leq 22$ and initial values x0 = 0.2, y0 = 0.1, z0 = 0.05.



Figure 6. Bifurcation diagrams of system (1.2) with $m_1 = 6, m_2 = 8, a_1 = 1, b_1 = 0.1, a_2 = 0.9, b_2 = 0.2, \tau_1 = 0.6\tau$, and $0.2 < \tau \leq 18$ and initial values $x_0 = 0.2, y_0 = 0.1, z_0 = 0.05$.



Figure 7. Quasiperiodic oscillation at $\tau = 0.2$ and the time series of x, y, z solution with initial values x0 = 1, y0 = 1, z0 = 0.5.

5. Conclusions

In this paper, we introduce and study a model of a Tessiet type food chain chemostat with pulsed substrate. First we find the invasion threshold of the prey, which is $m_1^* = \frac{\tau}{\int_0^{\tau} \frac{m_1 \hat{s}(l) \exp(-b_1 \hat{s}(l)}{a_1 + \hat{s}(l)} dl}$. If $m_1 < m_1^*$, the periodic periodic solution ($\hat{s}(t)$, 0, 0) is globally asymptotically stable and if $m_1 > m_1^*$, the prey starts to invade the system. Furthermore, by using Floquet theorem and small amplitude perturbation skills, we have proved that if $m_1 > m_1^*$, there exists $m_2^* = \frac{\tau}{\int_0^{\tau} \frac{m_2 y_s(l) \exp(-b_2 y_s(l))}{a_1 + y_s(l)} dl}$ to play as the invasion threshold of the predator, that is to say, if $m_2 < m_2^*$ the boundary solution ($x_s, y_s, 0$) is globally asymptotically stable and if $m_2 > m_2^*$ the solution ($x_s, y_s, 0$) is unstable.

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

Acknowledgments

The research of Fengyan Wang was supported by the Youth Science Foundation of Fujian Province (2006F3091) and the Science Foundation of Jimei University, China. The research of Guoping Pang was supported by NSF of China (10526015), the NSF of Guangxi Province (0728249), the SRF of Guangxi Education Office (2006243) and Yulin Normal University Foundation (2007YJZD08).

References

- [1] J.K. Hale and A.S. Somolinos, J. Math. Biol. 18 (1983) 255-280.
- [2] S.B. Hsu, J. Math. Biol. 18 (1980) 115–132.
- [3] G. Alessandra, D.F. Oscar and R. Sergio, Bull. Math. Biol. 60 (1998) 703-719.
- [4] K. Mark, G.S. Sayler and T.W. Waltman, Bull. Math. Biol. 54 (1992) 619-648.
- [5] F. Eric and K. Mark, Theoretical Population Biol. 44 (1993) 203-224.
- [6] G.J. Butler, S.B. Hsu and P. Waltman, SIAM J. Appl. Math. 45 (1985) 435-449.
- [7] P. Lenas and S. Pavlou, Math. Biosci. 129 (1995) 111-142.
- [8] D.L. DeAnglis, R.A. Goldstein, and R.V. O'Neill, Ecology 56 (1975) 881-892.
- [9] L. Chen and J. Chen, Nonlinear Biodynamical Systems (in Chinese), (Science, Beijing, 1993).
- [10] D. Bainov and P. Simeonor, Pitman Monogr. surreys pure Appl. Math. 66 (1993) 22–23.
- [11] V. Laksmikantham, D.D. Bainov and P.S. Simeonov, *Theory of Impulsive Differential Equa*tions, (World Scientific, Singapore, 1989).
- [12] S.Y. Tang and L.S. Chen, J. Math. Biol. 44 (2002) 185-199.

- [13] G. Ballinger and X. Liu, Math. Comput. Model. 26 (1997) 59-72.
- [14] B. Shulgin, L. Stone and I. Agur, Bull. Math. Biol. 60 (1998) 1-26.
- [15] A. D'Onofrio, Bull. Math. Biol. 60 (2002) 1-26.
- [16] J.C. Panetta, Bull. Math. Biol. 58 (1996) 425-447.
- [17] F. Wang, S. Zhang, L. Chen and L. Sun, Int. J. Nonlin. Sci. Numer. Simul. 6(2) (2005) 169– 180.
- [18] J.M. Cushing, SIAM J. Appl. Math. 10 (1977) 384-400.
- [19] R.M. May, Science 186 (1974) 645-647.
- [20] S. Gakkhar and M.A. Naji, Chaos solitons Fractal 18 (2003) 229-239.
- [21] A. Klebanoff and A. Hastings, J. Math. Biol. 32 (1994) 427-451.
- [22] M.G. Neubert and H. Caswell, J. Math. Biol. 41 (2000) 103-121.