

Study of a chemostat model with Beddington–DeAngelis functional response and pulsed input and washout at different times

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Abstract In the paper, we considered a food chain chemostat model with a Beddington–DeAngelis functional response of predator, with periodical input and washout occurring at different fixed times. We obtained exact periodic solutions for the model with substrate and prey only. The stability analysis for this periodic solutions yields an invasion threshold for period of pulses of the predator. When the impulsive period is greater than the threshold, there are periodic oscillations in substrate, prey, and predator. If the impulsive period is increased further, the system undergoes the complex dynamic process. By analyzing bifurcation diagrams, we can see that the impulsive system shows two kinds of bifurcations; period-doubling and period-halving.

Keywords Predator–prey system · Impulsive invasion and washout · Chemostat · Complexity

1 Introduction

The chemostat is an important laboratory apparatus use culture microorganisms. It plays an important role as a model in mathematical biology. In 1977, Hsu et al. [1] and Hsu [2] studied a chemostat model in which the response function was modelled by Michaelis–Menten dynamics. Then, many papers [3,4] studied a chemostat model with the Michaelis–Menten functional response. But, there are few papers which study a chemostat model with Beddington–DeAngelis functional response. The Beddington–DeAngelis functional response is different from the traditional monotone or non-monotone functional response. It was introduced by Beddington and

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DeAngelis et al. [5]. It is similar to the well-known Holling type II functional response but has an extra term $by_1(t)$ in the denominator that models mutual interference in a species. It can be derived mechanistically via considerations of time utilization [6,7] or spatial limits on predation [8]. Harrison [9] showed that the Beddington–DeAngelis functional response (for intraspecific interference competition) was superior to functional response without such competition in a microbial predator–prey interaction.

Many papers have studied a chemostat with periodic input [10] or periodic washout rate [11] or periodic input and washout [12,13] and different removal rate [14]. It is well-known that countless organisms live in seasonally or diurnally forced environments, in which the populations obtain food, so the effects of forcing may be quite profound (for example, seasonal effects of weather, food supply, mating habits, etc.). We all know that nutrients are input into lakes and lakes washed out during floods. There are still some other perturbations, such as fires, earthquakes, etc., that are not suitable to be considered as continuous. These perturbations bring sudden change to the system. So, it is natural to describe these cases by impulsive differential equation models in which extend impulses can occur. Impulsive differential equations are used in almost every domain of applied science and has been studied investigations [15–20].

Periodic forcing and impulsive effects are two different approaches to simulating seasonal or other variations. Recently, it has been of interest to investigate the possible existence of chaos in biological population. The models of predator–prey system in periodic forcing and impulsive perturbation environments have attracted the attention of many scholars. The papers [21–23] have shown that periodic forcing systems possess complex dynamics. Many authors [24,25] have studied predator–prey system with impulsive perturbations, and the impulsive perturbations bring complexity to the system. Funasaki and Kot [26] studied the model of a chemostat with predator, prey and periodically pulsed substrate. They have investigated the existence and stability of the periodic solutions of the impulsive subsystem with substrate and prey. Further, they have shown that impulsive invasion cause complex dynamics of system, and obtained way to chaos in a cascade of period-doubling bifurcation.

The goal of this paper is to study the system for a chemostat with predator, prey and periodically pulsed substrate and washout at different fixed moments which incorporate the Beddington–DeAngelis functional response of predator. The model takes the form

$$\left. \begin{aligned} \left. \begin{aligned} s'_1(t) &= -\frac{k_1}{\delta_1} s_1(t)x_1(t), \\ x'_1(t) &= k_1 s_1(t)x_1(t) - \frac{k_2}{\delta_2} \frac{x_1(t)y_1(t)}{B+x_1(t)+by_1(t)}, \\ y'_1(t) &= \frac{k_2 x_1(t)y_1(t)}{B+x_1(t)+by_1(t)}, \\ s_1(t^+) &= s_1(t) + Ds_0, \\ x_1(t^+) &= x_1(t), \\ y_1(t^+) &= y_1(t), \end{aligned} \right\} t \neq nT, t \neq (n+l-1)T \\ \left. \begin{aligned} s_1(t^+) &= s_1(t) - Ds_1(t), \\ x_1(t^+) &= x_1(t) - Dx_1(t), \\ y_1(t^+) &= y_1(t) - Dy_1(t), \end{aligned} \right\} t = (n+l-1)T. \end{aligned} \right\} \quad (1.0)$$

where $s_1(t)$, $x_1(t)$ and $y_1(t)$ represent the concentrations of limiting substrate, prey and predator, $0 \leq l < 1$, $0 \leq D < 1$ is the washout proportion of the chemostat each time; k_1 and k_2 are the uptake and predation constants of the prey and predator; δ_1 is the yield of prey per unit mass of substrate; δ_2 is the biomass yield of predator per unit mass of prey; Ds_0 is the amount of limiting substrate pulsed each T ; T is the period of

the impulsive effect; B, b are positive constants. $n \in N, N$ is the set of non-negative integers.

For the sake of simplicity, we put the model equations (1.0) in dimensionless, i.e.

$$s = \frac{s_1}{s_0}, \quad x = \frac{x_1}{\delta_1 s_0}, \quad y = \frac{y_1}{\delta_1 \delta_2 s_0}$$

We obtain the following impulsive differential equations

$$\left\{ \begin{array}{l} s'(t) = -ks(t)x(t), \\ x'(t) = ks(t)x(t) - \frac{hx(t)y(t)}{a+x(t)+cy(t)}, \\ y'(t) = \frac{hx(t)y(t)}{a+x(t)+cy(t)}, \\ s(t^+) = s(t) + D, \\ x(t^+) = x(t), \\ y(t^+) = y(t), \end{array} \right\} \quad \left. \begin{array}{l} t \neq nT, t \neq (n+l-1)T \\ \\ \\ \\ \\ \end{array} \right\} \quad (1.1)$$

$$\left. \begin{array}{l} s(t^+) = s(t) - Ds(t), \\ x(t^+) = x(t) - Dx(t), \\ y(t^+) = y(t) - Dy(t), \end{array} \right\} \quad t = (n+l-1)T$$

where $k = k_1 s_0, h = k_2, a = \frac{B}{\delta_1 s_0}, c = b\delta_2$.

The organization of the paper is as follows: In Sect. 2, we investigate the dynamic behaviors of impulsive subsystem with substrate and prey. In Sect. 3, we study the stability of the predator-free periodic solution. By using Floquet theorem [27] of impulsive differential equations and the small amplitude perturbation method, we obtain that the threshold of periodic oscillations in predator, prey, and substrate. In Sect. 4, we show bifurcation diagrams of different bifurcation parameters, and discuss the the complexity of system (1.1). A brief conclusion is given in the last section.

2 Dynamic behaviors of the substrate–prey subsystem

In the absence of the predator, system (1.1) reduces to

$$\left\{ \begin{array}{l} s'(t) = -ks(t)x(t), \\ x'(t) = ks(t)x(t), \end{array} \right\} \quad t \neq nT, t \neq (n+l-1)T \quad (2.1)$$

$$\left\{ \begin{array}{l} s(t^+) = s(t) + D, \\ x(t^+) = x(t), \end{array} \right\} \quad t = nT, \quad \left. \begin{array}{l} s(t^+) = s(t) - Ds(t), \\ x(t^+) = x(t) - Dx(t), \end{array} \right\} \quad t = (n+l-1)T.$$

This nonlinear system possesses a simple periodic solution. We investigate the stability of this periodic solution.

Theorem 2.1 (1) If $T < \frac{1}{k(D+(1-D))} \ln \frac{1}{1-D}$, then the T -periodic solution $(s_1(t), x_1(t))$ is asymptotically stable, where

$$\left\{ \begin{array}{l} s_1(t) = \begin{cases} 1 & t \in (nT, (n+l)T] \\ 1 - D & t \in ((n+l)T, (n+1)T] \end{cases} \\ x_1(t) = \begin{cases} 0 & t \in (nT, (n+l)T] \\ 0 & t \in ((n+l)T, (n+1)T] \end{cases} \end{array} \right. \quad (2.2)$$

(2) If $T > \frac{1}{k(lD+(1-D))} \ln \frac{1}{1-D}$, then T -periodic solution $(s_2(t), x_2(t))$ is asymptotically stable, where

$$\begin{cases} s_2(t) = \begin{cases} \frac{D \exp(-k(t-nT))}{1 - \exp(-K) - D + D \exp(-k(t-nT))} & t \in (nT, (n+l)T] \\ \frac{(1-D)D \exp(-klDT) \exp(-k(1-D)(t-nT))}{1 - \exp(-K) - D + D \exp(-klDT) \exp(-k(1-D)(t-nT))} & t \in ((n+l)T, (n+1)T] \end{cases} \\ x_2(t) = \begin{cases} \frac{1 - \exp(-K) - D}{1 - \exp(-K) - D + D \exp(-k(t-nT))} & t \in (nT, (n+l)T] \\ \frac{(1-D)(1 - \exp(-K) - D)}{1 - \exp(-K) - D + D \exp(-klDT) \exp(-k(1-D)(t-nT))} & t \in ((n+l)T, (n+1)T] \end{cases} \end{cases} \tag{2.3}$$

where $K = kT(lD + (1 - D))$.

Proof Adding the first and second equations of system (2.1)

$$s'(t) + x'(t) = 0 \tag{2.4}$$

We integrate and solve for the concentration in the chemostat over the pulse period, and we obtain

$$s(t) + x(t) = \begin{cases} s_n + x_n & t \in (nT, (n+l)T] \\ (1-D)(s_n + x_n) & t \in ((n+l)T, (n+1)T] \end{cases} \tag{2.5}$$

where s_n and x_n are the initial concentrations of substrate and prey at time nT . Thus, Eq. 2.5 allows us to decouple the equations

$$\begin{cases} s'(t) = \begin{cases} -k(s_n + x_n)s(t) + k(s_n + x_n)s^2(t) & t \in (nT, (n+l)T] \\ -k(s_{n+l} + x_{n+l})s(t) + k(s_{n+l} + x_{n+l})s^2(t) & t \in ((n+l)T, (n+1)T] \end{cases} \\ x'(t) = \begin{cases} k(s_n + x_n)x(t) + k(s_n + x_n)x^2(t) & t \in (nT, (n+l)T] \\ k(s_{n+l} + x_{n+l})x(t) + k(s_{n+l} + x_{n+l})x^2(t) & t \in ((n+l)T, (n+1)T] \end{cases} \end{cases} \tag{2.6}$$

where

$$\begin{cases} s_{n+l} = \frac{(1-D)(s_n+x_n)s_n \exp(-k(s_n+x_n)lT)}{x_n+s_n \exp(-k(s_n+x_n)lT)} \\ x_{n+l} = \frac{(1-D)(s_n+x_n)x_n}{x_n+s_n \exp(-k(s_n+x_n)lT)} \end{cases}$$

Solving Eq. 2.6, we get

$$\begin{cases} s(t) = \begin{cases} \frac{(s_n+x_n)s_n \exp(-k(s_n+x_n)(t-nT))}{x_n+s_n \exp(-k(s_n+x_n)(t-nT))} & t \in (nT, (n+l)T] \\ \frac{(1-D)(s_n+x_n)s_n \exp(-k(s_n+x_n)lDT) \exp(-k(1-D)(s_n+x_n)(t-nT))}{x_n+s_n \exp(-k(s_n+x_n)lDT) \exp(-k(1-D)(s_n+x_n)(t-nT))} & t \in ((n+l)T, (n+1)T] \end{cases} \\ x(t) = \begin{cases} \frac{(s_n+x_n)x_n}{x_n+s_n \exp(-k(s_n+x_n)(t-nT))} & t \in (nT, (n+l)T] \\ \frac{(1-D)(s_n+x_n)x_n}{x_n+s_n \exp(-k(s_n+x_n)lDT) \exp(-k(1-D)(s_n+x_n)(t-nT))} & t \in ((n+l)T, (n+1)T] \end{cases} \end{cases} \tag{2.7}$$

Equation 2.7 hold during period of the pulse. We can obtain the following difference equations:

$$\begin{aligned}
 s_{n+1} &= D + \frac{(1-D)(s_n+x_n)s_n \exp(-k(s_n+x_n)lDT) \exp(-k(1-D)(s_n+x_n)T)}{x_n+s_n \exp(-k(s_n+x_n)lDT) \exp(-k(1-D)(s_n+x_n)T)} \\
 x_{n+1} &= \frac{(1-D)(s_n+x_n)x_n}{x_n+s_n \exp(-k(s_n+x_n)lDT) \exp(-k(1-D)(s_n+x_n)T)}
 \end{aligned}
 \tag{2.8}$$

Difference equations (2.8) describe the substrate and prey concentrations at a impulsive time $t = nT$ in terms of values at the previous pulse $t = (n + 1)T$. We are, in other words, stroboscopically sampling the chemostat at its forcing period. The limiting behavior of system (2.8) coupled with (2.7), determines the asymptotic behavior within the chemostat.

Adding the two equations of Eq. 2.8, we can get a simple difference equation

$$s_{n+1} + x_{n+1} = D + (1 - D)(x_n + s_n)
 \tag{2.9}$$

Equation 2.9 is linear, and may be solved exactly

$$s_{n+1} + x_{n+1} = 1 - (1 - D)^{n+1} + (1 - D)^{n+1}(s_0 + x_0)$$

Moreover, we get $\lim_{n \rightarrow \infty} (s_n + x_n) = 1$. Decoupling stroboscopic map (2.8), we obtain the following difference equations:

$$\begin{aligned}
 s_{n+1} &= D + \frac{(1-D)s_n \exp(-kT(lD+(1-D)))}{s_n+x_n \exp(-kT(lD+(1-D)))} \\
 x_{n+1} &= \frac{(1-D)x_n}{x_n+s_n \exp(-kT(lD+(1-D)))}
 \end{aligned}
 \tag{2.10}$$

Equation 2.10 possess two equilibria, corresponding to extinction $(s_1^*, x_1^*) = (1, 0)$, or survival of the predaton $(s_2^*, x_2^*) = (\frac{D}{1-\exp(-kT(lD+(1-D)))}, 1 - \frac{D}{1-\exp(-kT(lD+(1-D)))})$. The stability of equilibrium is determined by the slope λ of difference equation (2.10) at that equilibrium. If $|\lambda| < 1$, that this equilibrium is stable. Evaluating the derivatives of Eq. 2.10 at equilibria (s_1^*, x_1^*) and (s_2^*, x_2^*) , respectively, we get $\lambda_1 = (1 - D) \exp(-kT(lD + (1 - D)))$ and $\lambda_2 = \frac{1}{(1-D) \exp(-kT(lD+(1-D)))}$

For $T < \frac{1}{k(lD+(1-D))} \ln \frac{1}{1-D}$, equilibrium (s_1^*, x_1^*) is stable. The prey wash out of the chemostat. The equilibrium of stroboscopic map corresponds to the periodic solution of system (2.1). For this range of T , the trajectories of system of system (2.1) approach the periodic solution (2.2).

For $T > \frac{1}{k(lD+(1-D))} \ln \frac{1}{1-D}$, the equilibrium (s_2^*, x_2^*) is stable. For this range of T , the trajectories of system of system (2.1) approach the periodic solution (2.3). This completes the proof. □

Remark At $T = T_0 = \frac{1}{k(lD+(1-D))} \ln \frac{1}{1-D}$, there is a transcritical bifurcation of periodic solutions, as $(s_1(t), x_1(t))$ and $(s_2(t), x_2(t))$ pass through each other and exchange stability.

3 Invasion of the predator

In order to investigate the invasion of the predator of system (1.1), we discuss the stability of the predator-free periodic solution $(s_2(t), x_2(t), 0)$.

Theorem 3.1 *Let $(s(t), x(t), y(t))$ be any solution of (1.1), then $(s_2(t), x_2(t), 0)$ is asymptotically stable provided that $T > \frac{1}{k(D+(1-D))} \ln \frac{1}{1-D}$ and $\int_0^T \frac{hx_2(t)}{a+x_2(t)} dt < \ln \frac{1}{1-D}$.*

Proof The local stability of periodic solution $(s_2(t), x_2(t), 0)$ may be determined by considering the behavior of small amplitude perturbations of the solution. Define

$$s(t) = u(t) + s_2(t), x(t) = v(t) + x_2(t), y(t) = w(t) + 0,$$

one can write

$$\begin{pmatrix} u(t) \\ v(t) \\ w(t) \end{pmatrix} = \Phi(t) \begin{pmatrix} u(0) \\ v(0) \\ w(0) \end{pmatrix},$$

where $\Phi(t)$ satisfies

$$\frac{d\Phi}{dt} = \begin{pmatrix} -kx_2(t) & -ks_2(t) & 0 \\ kx_2(t) & ks_2(t) & -\frac{hx_2(t)}{a+x_2(t)} \\ 0 & 0 & \frac{hx_2(t)}{a+x_2(t)} \end{pmatrix} \Phi(t),$$

and $\Phi(0) = I$, the identity matrix. The resetting impulsive condition of (1.1) becomes

$$\begin{pmatrix} u((n+l-1)T^+) \\ v((n+l-1)T^+) \\ w((n+l-1)T^+) \end{pmatrix} = \begin{pmatrix} 1-D & 0 & 0 \\ 0 & 1-D & 0 \\ 0 & 0 & 1-D \end{pmatrix} \begin{pmatrix} u((n+l-1)T) \\ v((n+l-1)T) \\ w((n+l-1)T) \end{pmatrix},$$

and

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

The stability of the periodic solution $(s_2(t), x_2(t), 0)$ is determined by the eigenvalues of

$$M = \begin{pmatrix} 1-D & 0 & 0 \\ 0 & 1-D & 0 \\ 0 & 0 & 1-D \end{pmatrix} \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} \varphi_{11}(T) & \varphi_{12}(T) & \star \\ \varphi_{21}(T) & \varphi_{22}(T) & \star\star \\ 0 & 0 & \exp\left(\int_0^T \frac{hx_2(t)}{a+x_2(t)} dt\right) \end{pmatrix}.$$

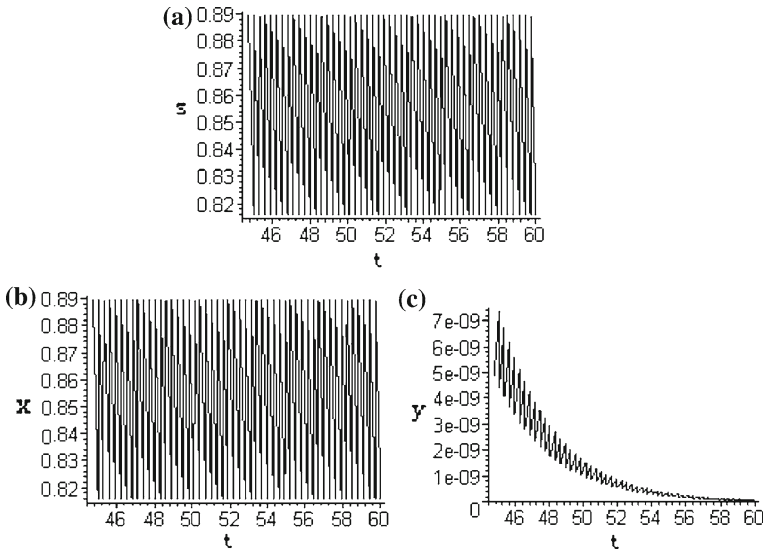


Fig. 1 Time series of system (1.1) at $T = 0.4$ with $l = 0.2$, $D = 0.4$, $k = 2$, $h = 0.2$, $a = 0.1$, $c = 0.2$

There are no need to calculate the exact values of (\star) and $(\star\star)$, as it is not required in the analysis that follows.

The eigenvalues of the matrix M are $\lambda_3 = (1 - D) \exp\left(\int_0^T \frac{hx_2(t)}{a+x_2(t)} dt\right)$ and the eigenvalues λ_1 and λ_2 of the following matrix

$$\begin{pmatrix} \varphi_{11}(T) & \varphi_{12}(T) \\ \varphi_{21}(T) & \varphi_{22}(T) \end{pmatrix}.$$

The eigenvalues λ_1, λ_2 are also the multipliers of the locally linearizing system of system (2.1) provided with $T > \frac{1}{k(D+(1-D))} \ln \frac{1}{1-D}$ at the asymptotically stable periodic solution $(s_2(t), x_2(t))$. According to Theorem 2.1, we have that $\lambda_1 < 1, \lambda_2 < 1, \lambda_3 < 1$ if and only if $\int_0^T \frac{hx_2(t)}{a+x_2(t)} dt < \ln \frac{1}{1-D}$. According to Floquet theory of impulsive differential equation, the periodic solution $(s_2(t), x_2(t), 0)$ is asymptotically stable. This completes the proof. \square

Let $l = 0.2, D = 0.4, k = 2, h = 0.2, a = 0.1, c = 0.2, T = 0.4$. Then $\frac{1}{k(D+(1-D))} \ln \frac{1}{1-D} \approx 0.375$. Thus, the conditions of Theorem 3.1 are satisfied, and the system (1.1) has the periodic solution $(s_2(t), x_2(t), 0)$. A typical periodic solution $(s_2(t), x_2(t), 0)$ is shown in Fig. 1.

When $T > \frac{1}{k(D+(1-D))} \ln \frac{1}{1-D}$ and $\int_0^T \frac{hx_2(t)}{a+x_2(t)} dt > \ln \frac{1}{1-D}$, and is sufficiently small, substrate, prey, predator coexist periodically. The predator has succeeded in invading the chemostat.

4 Chemostat chaos

In this section, we will study the dynamics of system (1.1) with periodically input and washout at different fixed times. Bifurcation diagrams for different bifurcation parameters are obtained, and incarnates the dynamic behavior of the system.

Set $k = 2$, $h = 0.5$, $a = 0.01$, $c = 0.5$, $D = 0.4$, $l = 0.2$. We want to investigate the influence of T . The effect of T may be documented by stroboscopically sampling one of the variables over a range of T values. In Fig. 2, we have displayed bifurcation diagrams for impulsive period T as T increases from 4 to 13 with initial values $(s(0), x(0), y(0)) = (0.2, 0.3, 0.04)$. By Theorem 3.1, when $T > \frac{1}{K} \ln \frac{1}{1-D} \approx 2.235$ and $\int_0^T \frac{0.5x_2(t)}{0.01+x_2(t)} dt > \ln 5$, periodic solution $(s_2(t), x_2(t), 0)$ is unstable and a T -periodic solution for substrate, prey, and predator coexisting is stable (Fig. 3a). when $T \geq 5.8$, T -periodic solution is unstable and system (1.1) comes into chaotic area (Fig. 3b) with periodic windows (Fig. 4).

Let $h = 5$, $a = 1$, $c = 0.2$, $D = 0.9$, $l = 0$, $T = 8$. We have got bifurcation diagrams (Fig. 5) of the system (1.1) showing the effect of k . The bifurcation diagrams (Fig. 5) clearly show that: when $k > 0.31$, there is a cascade of period doubling bifurcations leading to chaos (Fig. 6). Which is followed by a cascade of periodic halving bifurcations from chaos to periodic solution. This periodic doubling route to chaos is the hallmark of the logistic and Ricker maps [28] and has been studied extensively by mathematicians [29]. Periodic halving is the flip bifurcation in the opposite direction, which is also observed in [30]

Bifurcation diagrams Fig. 7 tell us that: with h increasing from 1 to 7, the system experiences the processes of periodic doubling cascade to chaos.

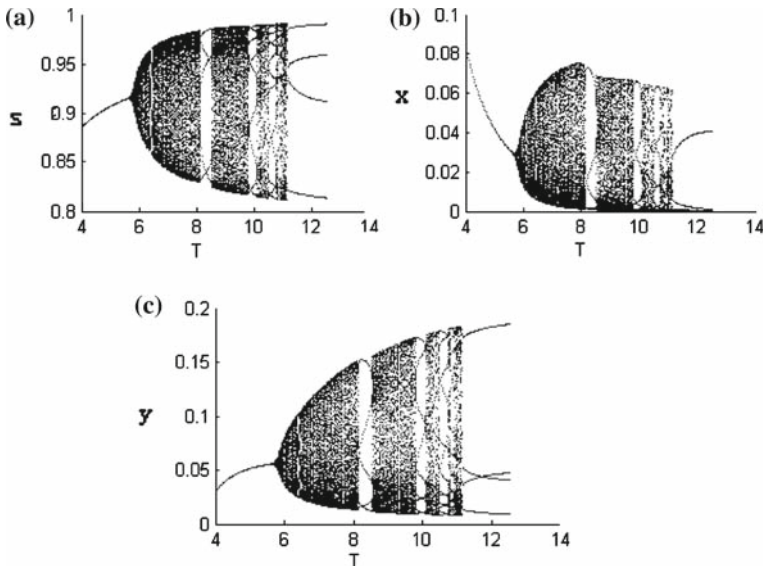


Fig. 2 Bifurcation diagrams of system (1.1) with $l = 0.2$, $D = 0.4$, $k = 2$, $h = 0.5$, $a = 0.01$, $c = 0.5$. (a), (b) and (c) s , x , y are plotted for T over $[4, 13]$, respectively

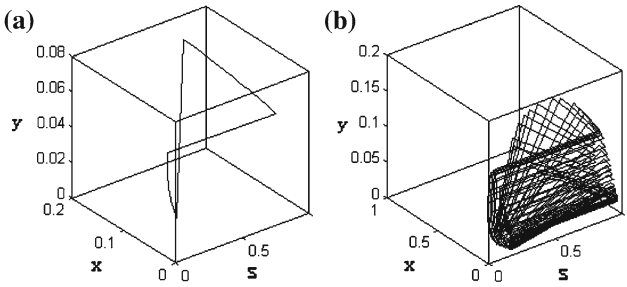


Fig. 3 Period solution and chaos: (a) phase portrait of T -periodic solution for $T = 5$, (b) phase portrait of chaos solution for $T = 7$

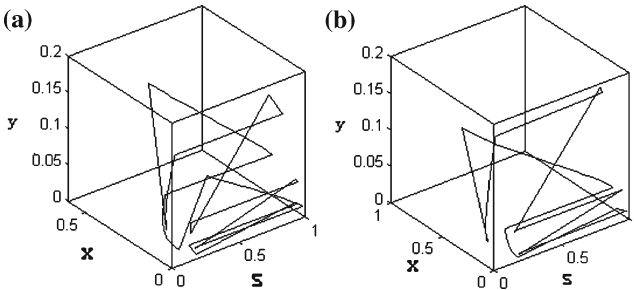


Fig. 4 Period windows. (a) Phase portrait of $5T$ -periodic solution for $T = 8.3$, (b) phase portrait of $4T$ -periodic solution for $T = 12$

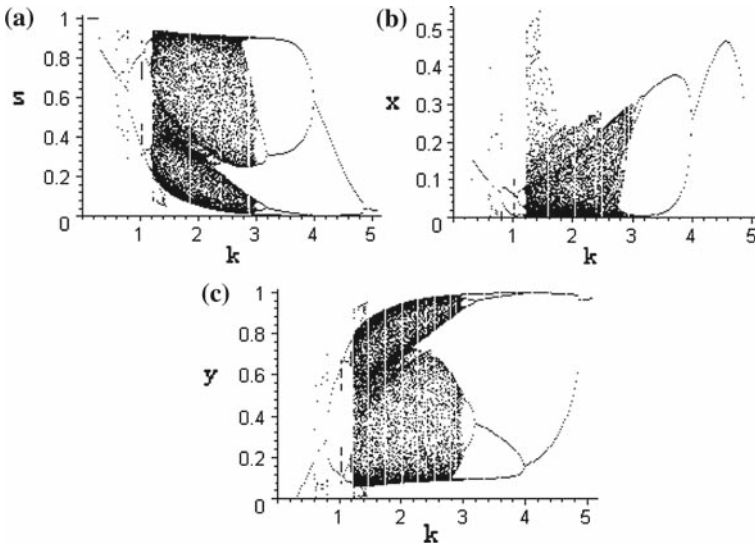


Fig. 5 Bifurcation diagrams of system (1.1) with $l = 0, D = 0.9, h = 1, a = 1, c = 0.2, T = 8$. (a), (b) and (c) s, x, y are plotted for k over $[0.1, 5]$ respectively

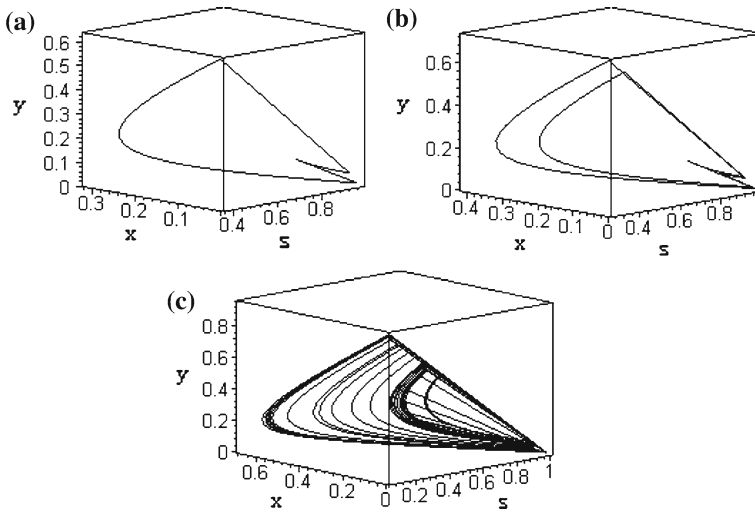


Fig. 6 Period doubling cascade to chaos: (a) phase portrait of $2T$ -periodic solution for $k = 1$, (b) phase portrait of $4T$ -periodic solution for $k = 1.12$, (c) Phase portrait of chaos solution for $k = 2$

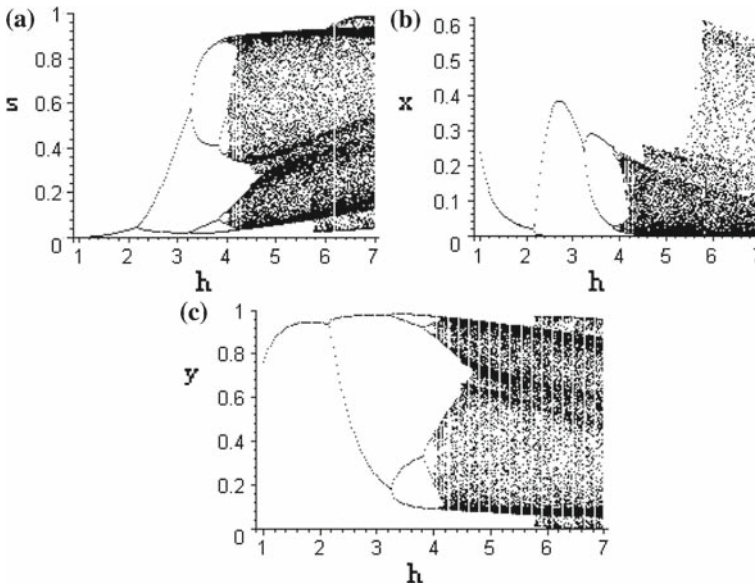


Fig. 7 Bifurcation diagrams of system (1.1) with $l = 0$, $D = 0.9$, $k = 2$, $a = 1$, $c = 0.2$, $T = 8$. (a), (b) and (c) s , x , y are plotted for k over $[1,7]$, respectively

5 Conclusion

In this paper, we have investigated a food chain chemostat model with Beddington–DeAngelis functional response and periodically input and washout at different fixed time. First, we find the invasion threshold of the predation, which is $T_0 = \frac{1}{K} \ln \frac{1}{1-D}$.

Furthermore, by Floquet theorem and the small amplitude perturbation method, we have proven the predator eradication periodic solution $(s_2(t), x_2(t), 0)$ is locally asymptotically stable for $T < \frac{1}{k(lD+(1-D))} \ln \frac{1}{1-D}$. When $T > \frac{1}{k(lD+(1-D))} \ln \frac{1}{1-D}$ and $\int_0^T \frac{hx_2(t)}{a+x_2(t)} dt > \ln \frac{1}{1-D}$, predator can invade and there are periodic oscillations in substrate, prey, predator. If the period of pulses is further increased, the system will exhibit complicated dynamical behaviors.

We have obtained bifurcation diagrams (Figs. 2, 5, 6) for different bifurcation parameters T, k, h . Bifurcation diagrams have shown that the system (1.1) exhibits the rich dynamics, which include: (1) periodic solution, (2) periodic doubling cascade, (3) chaos (chaotic region with periodic windows), (4) periodic halving cascade. All these results show that dynamical behavior of system (1.1) becomes more complex under periodically impulsive perturbations.

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