ROCKY MOUNTAIN
JOURNAL OF MATHEMATICS
Volume 42, Number 4, 2012

BIFURCATION AND CHAOS IN A PULSED PLANKTON MODEL WITH INSTANTANEOUS NUTRIENT RECYCLING

SANLING YUAN, YU ZHAO, ANFENG XIAO AND TONGHUA ZHANG

ABSTRACT. This paper deals with a pulsed plankton-nutrient interaction model consisting of phytoplankton, herbivorous zooplankton and dissolved limiting nutrient with general nutrient uptake functions and instantaneous nutrient recycling. We investigate the subsystem with nutrient and phytoplankton and study the stability of the periodic solutions, which are the boundary periodic solutions of the system. Stability analysis of the boundary periodic solution yields the invasion threshold of zooplankton. By use of standard techniques of bifurcation theory, we prove that, above this threshold, there are periodic oscillations in substrate: phytoplankton and zooplankton. 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, which are period-doubling and period-halving.

1. Introduction. Plankton blooms are a widespread phenomenon present in rivers, lakes and oceans all over the world. When large numbers of plankton are concentrated in one area, the color of the water surface changes. For example, in May 2007, a blue-green algae bloomed in Taihu Lake. Analysis of tremendous variations in an abundance of many planktonic communities is very important in aquatic ecosystems. Numerous plankton models have been constructed and studied by researchers in this area [**9, 11, 15**].

The chemostat is an interesting model frequently used for simulating a simple lake, with the input of limiting nutrients such as silica and phosphate from streams draining the surrounding watershed. See [**3,**

2010 AMS *Mathematics subject classification.* Primary 34K45, 37G15, 92C45.
Keywords and phrases. Chemostat, plankton, pulsed, periodic solution, chaos.
Research supported by the National Natural Science Foundation of China (11271260, 10871129) and the Educational Committee Foundation of Shanghai (13ZZ116, 09YZ208).

The first author is the corresponding author.

Received by the editors on July 16, 2009, and in revised form on November 18, 2009.

DOI:10.1216/RMJ-2012-42-4-1387

8, 12, 19, 20, 23] for a detailed description of a chemostat and for various mathematical methods for analyzing chemostat models. As the seasons change, stream drainage patterns change causing variations in the supply of nutrient and washout of lake.

In aquatic ecosystems, the term *plankton* refers to the freely floating and weakly swimming organisms. There are two types of plankton. The plant species, commonly known as phytoplankton, are unicellular and microscopic in size. The animal species, namely zooplankton, live on these phytoplankton [**3**]. The changes of population of plankton have been attributed to several factors, such as seasonal factors, variation of dissolved limiting nutrients or a combination of these. One important observation attracting our attention is that of nutrient recycling by the production of bacterial decomposition of the dead biomass, and thus influence of seasonal succession. The effect of nutrient recycling on aquatic ecosystem has been extensively studied by [**4, 13, 16–18, 20, 27**]. The mathematical analysis of plankton models goes back to Ruan [**17, 18**] who considered persistence and coexistence in plankton models with instantaneous nutrient recycling. Beretta et al. [**3**] considered an open system with a single species feeding on a limiting nutrient which is partially recycled after the death of the organisms. Numerous plankton models with nutrient recycling have been proposed [**4, 16, 22**].

To simulate day/night, seasonal cycles, or other variations in open systems, models described by impulsive differential equations have been studied by many authors, see, for example, Funasaki and Kor [**7**], Xiang and Song [**26**], Wang et al. [**24**], Smith and Wolkowicz [**21**], Fan and Wolkowicz [**6**], Wang et al. [**25**] and the references therein for recent studies on this subject. Recently, impulsive differential equations have been introduced in almost every domain of applied sciences. Numerous examples are given in Bainov's and his collaborators' books [**1, 2**]. In this paper, we focus on a pulsed chemostat type plankton model with instantaneous nutrient recycling. We suppose that zooplankton does not ingest nutrient directly, and all dead zooplankton and phytoplankton are recycled back into nutrient (see Figure 1). This model might be more suitable in chemostat or lakes than in oceanic regions. Assuming that the specific growth rates of the organisms take the general monotone form, we want to explore whether some new dynamical behaviors could occur in impulsive perturbations and under what conditions phytoplankton and zooplankton can survive in the chemostat.

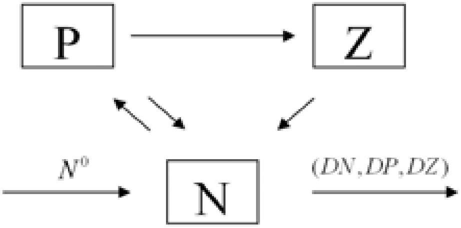


FIGURE 1. The Z-P-N model with pulsed input and washout. Arrows indicate nutrient flow pathways between phytoplankton (P), zooplankton (Z) and nutrient (N).

The organization of this paper is as follows. In the next section, we present the model under periodic pulsed chemostat conditions. In Section 3, we investigate existence and stability of periodic solutions of the impulsive subsystem with nutrient and phytoplankton. In Section 4, we study local stability of the boundary periodic solution of the system and obtain the threshold of the invasion of the zooplankton. Using standard techniques of bifurcation theory, we prove that above this threshold there are periodic oscillations in nutrient and plankton. In Section 5, numerical simulations are carried out to illustrate our results and prognosticate the complexity of the system. Finally, a brief discussion is presented in Section 6.

2. The model. Let $N(t)$ be the dissolved limiting nutrient at time t, $P(t)$ the phytoplankton at time t and $Z(t)$ the herbivorous zooplankton at time t. The plankton model with instantaneous nutrient recycling and pulsed input and washout can be described by the following impulsive differential equations:

(2.1)
$$\begin{cases} \left.\begin{aligned} dN/dt &= -aPU(N) + (1-\delta)cZ\omega(P) + \gamma_1 P + \eta_1 Z, \\ dP/dt &= aPU(N) - cZ\omega(P) - \gamma P, \\ dZ/dt &= \delta c\omega(P)Z - \eta Z, \end{aligned}\right\} \quad t \neq n\tau, \\ \left.\begin{aligned} \Delta N(t) &= D(N^0 - N(t)) \\ \Delta P(t) &= -DP(t), \\ \Delta Z(t) &= -DZ(t), \end{aligned}\right\} \quad t = n\tau, \\ N(0^+) = N_0 > 0, \quad P(0^+) = P_0 > 0, \quad Z(0^+) = Z_0 > 0, \end{cases}$$

where all parameters are positive and are interpreted as follows: a is the maximal nutrient uptake rate of the phytoplankton, c is the maximal zooplankton ingestion rate, N^0 is the input concentration of the nutrient, D is the rate of input and washout flow, γ is the phytoplankton mortality rate, η is the zooplankton death rate, γ_1 is the nutrient recycle rate after the death of the phytoplankton, $\gamma_1 \le \gamma$, η_1 is the nutrient recycle rate after the death of the zooplankton, $\eta_1 \le \eta$; a mathematical simplification arises if we assume that $\gamma = \gamma_1$, $\eta = \eta_1$. δ is the fraction of zooplankton nutrient conversion, $0 < \delta \le 1$. The function $U(N)$ describes the nutrient uptake rate of phytoplankton. $U(N)$ is a continuous function defined on $[0, \infty)$ and satisfies

$$U(N) = 0, \quad \frac{dU}{dN} > 0, \qquad \lim_{N \to \infty} U(N) = 1. \tag{2.2}$$

This kind of function includes Holling's II type, that is,

$$U(N) = \frac{N}{k + N}, \tag{2.3}$$

where k is the half saturation constant.

The function $\omega(P)$ represents the response function describing herbivore grazing. It is also assumed that $\omega(P)$ is continuous on $[0, \infty)$ and satisfies

$$\omega(0) = 0, \quad \frac{d\omega}{dP} > 0, \qquad \lim_{P \to \infty} \omega(P) = 1. \tag{2.4}$$

Usually, Ivlev's [**10**] functional response formulation

$$\omega(P) = 1 - e^{-\lambda P} \tag{2.5}$$

is used to describe the zooplankton grazing, where λ is the rate at which saturation is achieved with increasing phytoplankton levels (per unit concentration). Alternatively, Mayzaud and Poulet formulation [**14**],

$$\omega(P) = \lambda P(1 - e^{-\lambda P}) \tag{2.6}$$

is also used to describe the food-acclimatized herbivore grazing.

In the following, we assume that $\gamma = \gamma_1$, $\eta = \eta_1$. Then system (2.1) becomes

(2.7)
$$\begin{cases} \left.\begin{aligned} dN/dt &= -aPU(N) + (1-\delta)cZ\omega(P) + \gamma P + \eta Z, \\ dP/dt &= aPU(N) - cZ\omega(P) - \gamma P, \\ dZ/dt &= \delta c\omega(P)Z - \eta Z, \end{aligned}\right\} & t \neq n\tau, \\ \left.\begin{aligned} \Delta N(t) &= D(N^0 - N(t)) \\ \Delta P(t) &= -DP(t), \\ \Delta Z(t) &= -DZ(t), \end{aligned}\right\} & t = n\tau, \\ N(0^+) = N_0 > 0, \quad P(0^+) = P_0 > 0, \quad Z(0^+) = Z_0 > 0. \end{cases}$$

From the point of biology, we need only consider system (2.7) in the biological meaning region $R_+^3 = \{(N, P, Z) \mid N, P, Z \geq 0\}$. The form of the equations in system (2.7) implies the global existence and uniqueness of its solutions.

3. Dynamical behaviors of the nutrient and phytoplankton subsystem.

In the absence of the herbivorous zooplankton, system (2.7) reduces to

$$\begin{cases} \left.\begin{aligned} dN/dt &= -aPU(N) + \gamma P, \\ dP(t)/dt &= aPU(N) - \gamma P, \end{aligned}\right\} & t \neq n\tau, \\ \left.\begin{aligned} \Delta N(t) &= D(N^0 - N(t)) \\ \Delta P(t) &= -DP(t), \end{aligned}\right\} & t = n\tau, \\ N(0^+) = S_0 > 0, \quad P(0^+) = P_0 > 0. \end{cases} \tag{3.1}$$

This nonlinear system has simple periodic solutions. If we add the first and second equations in system (3.1), we have $d(N(t) + P(t))/dt = 0$. Let $\Sigma(t) = N(t) + P(t)$; then system (3.1) can be written as:

$$\begin{cases} d\Sigma(t)/dt = 0, & t \neq n\tau, \\ \Sigma(n\tau^+) = D + (1-D)\Sigma(n\tau), & t = n\tau, \\ \Sigma(0^+) = \Sigma_0 > 0. \end{cases} \tag{3.2}$$

For system (3.2), we have the following lemma.

Lemma 3.1. *System* (3.2) *has a positive solution* $\widetilde{\Sigma}(t)$ *and, for every solution* $\Sigma(t)$ *of* (3.2), *we have* $|\Sigma(t) - \widetilde{\Sigma}(t)| \to 0$ *as* $t \to \infty$, *where* $\widetilde{\Sigma}(t) = N^0$, $t \in (n\tau, (n+1)\tau]$, $n \in N$.

By Lemma 3.1, the following lemma is obvious.

Lemma 3.2. *Let* $(N(t), P(t))$ *be any solution of system* (3.1) *with initial conditions* $N(0) > 0$, $P(0) > 0$. *Then* $\lim_{t\to\infty} |N(t) + P(t) - N^0| = 0$.

Lemma 3.2 says that the periodic solution $\widetilde{\Sigma}(t) = N^0$ is a unique invariant manifold of the system (3.1). Denote

$$a^* = \frac{-\ln(1-D) + \gamma\tau}{U(N^0)\tau}. \tag{3.3}$$

Theorem 3.1. *For system* (3.1), *we have*

(1) *If* $a < a^*$, *then system* (3.1) *has a unique globally asymptotically stable boundary* τ*-periodic solution* $(N_e(t), P_e(t))$, *where* $N_e(t) = N^0$, $P_e(t) = 0$.

(2) *If* $a > a^*$, *then system* (3.1) *has a unique globally asymptotically stable positive* τ*-periodic solution* $(N_s(t), P_s(t))$, *and the* τ*-periodic solution* $(N_e(t), P_e(t))$ *is unstable. The* τ*-periodic solution* $P_s(t)$ *satisfies*

$$\frac{1}{1-D} = \exp\left(\int_0^\tau (aU(N^0 - P(l, P_0)) - \gamma)\, dl\right). \tag{3.4}$$

Proof. By Lemma 3.2, we can consider system (3.1) in its stable invariant manifold $\widetilde{\Sigma}(t) = N^0$. That is,

$$\begin{cases} dP/dt = aPU(N^0 - P) - \gamma P, & t \neq n\tau, \\ \Delta P = -DP, & t = n\tau, \\ 0 \le P_0 \le N^0. \end{cases} \tag{3.5}$$

Suppose $P(t, P_0)$ is a solution of equation (3.5); with initial condition $P_0 \in [0, N^0]$, we have

$$\begin{aligned} &P(t, P_0) = P(n\tau^+) \exp\left(\int_{n\tau}^t (aU(N^0 - P(l, P_0)) - \gamma)\, dl\right), \\ &\qquad\qquad\qquad\qquad t \in (n\tau, (n+1)\tau], \\ &P(n\tau^+) = (1-D)P(n\tau),\ P(0^+) = P_0, \quad t = n\tau. \end{aligned} \tag{3.6}$$

For (3.6), we have the following properties:

(i) For $P_0 \in (0, N^0]$, $0 < P(t, P_0) \leq N^0$, $t \in (0, \infty)$ is a piecewise continuous function;

(ii) the function $F(P_0) = P(t, P_0)$, $P_0 \in (0, N^0]$ is an increasing function;

(iii) $P(t, 0) = 0$, $t \in (0, \infty)$ is a solution.

Periodic solutions of (3.5) satisfy the following equation:

$$P_0 = (1 - D) P_0 \exp\bigg(\int_0^\tau (aU(N^0 - P(l, P_0)) - \gamma)\, dl \bigg). \tag{3.7}$$

By (i) and (ii), we know that if $1 < [1/(1 - D)] < \exp(aU(N^0) - \gamma)\tau$, that is, $a > a^*$, then equation (3.7) has a unique solution P_0^* in $(0, N^0)$; otherwise, it has no solution in $(0, N^0]$.

If $a < a^*$, then equation (3.5) has a periodic solution $P_e(t) = 0$. By Lemma 3.2, we have $\lim_{t \to \infty} |N(t) - \widetilde{\Sigma}(t)| = 0$. We have proved (1).

If $a > a^*$, then equation (3.5) has a unique positive periodic solution $P_s(t) = P(t, P_0^*)$. The multiplier μ_1 of $P_s(t)$ is

$$\begin{aligned} \mu_1 &= (1 - D) \exp\bigg(\int_0^\tau \Big(aU(N_s) - aP \frac{\partial N(N_s)}{\partial P} - \gamma\Big)\, dl \bigg) \\ &= \exp\bigg(\int_0^\tau -aP \frac{\partial N(N_s)}{\partial P}\, dl \bigg) < 1, \end{aligned} \tag{3.8}$$

where $N_s(t) = 1 - P_s(t)$, (2.2) and (3.7) have been used. Thus, the periodic solution $P_s(t)$ of (3.5) is locally stable.

To prove the global attractivity of periodic solution $P_s(t)$, we define a function $G(P_0) : P_0 \in (0, N^0)$ as follows:

$$G(P_0) = (1 - D) \exp\bigg(\int_0^\tau (aU(N^0 - P(l, P_0)) - \gamma)\, dl \bigg). \tag{3.9}$$

Noticing equation (3.6), we have

$$G(P_0) = \frac{P(\tau, P_0)}{P_0}, \quad P_0 \in (0, N^0).$$

It is obvious that $G(P_0^*) = 1$.

Furthermore, $[\partial P(t, P_0)]/\partial P_0 \geq 0$, $t \in (0, \tau)$ (otherwise, there exist $t_0 > 0$ and $0 < P_0^{(1)} < P_0^{(2)} < 1$ such that $P(t_0, P_0^{(1)}) = P(t_0, P_0^{(2)})$, a contradiction, since different flows of system (3.5) do not intersect). Thus, the function $G(P_0)$ has the following properties:

$$\begin{aligned} &G(P_0) < 1, \quad \text{if } P_0^* < P_0 < 1,\\ &G(P_0) = 1, \quad \text{if } P_0 = P_0^*,\\ &G(P_0) > 1, \quad \text{if } 0 < P_0 < P_0^*. \end{aligned} \tag{3.10}$$

Furthermore, we obtain the following inequalities:

$$\begin{aligned} P_0 > P(\tau, P_0) > \cdots > P(n\tau, P_0) > \cdots > P_0^*, \quad &\text{if } P_0^* < P_0 \leq 1,\\ P_{10} < P(\tau, P_0) < \cdots < P(n\tau, P_0) < \cdots < P_0^*, \quad &\text{if } 0 < P_0 < P_0^*. \end{aligned} \tag{3.11}$$

Let $P_0 \in (0, N^0)$. According to (3.11), we suppose that $\lim_{n\to\infty} P(n\tau, P_0) = \alpha$. We shall prove that solution $P(t, \alpha)$ is τ-periodic. We note that the functions $P_n(t) = P(t + n\tau, P_0)$, due to the τ-periodicity of equation (3.5), are also its solutions and $P_n(\tau) \to \alpha$, as $n \to \infty$. By the continuous dependence of solutions on the initial values, we have that $P(\tau, \alpha) = \lim_{n\to\infty} P_n(\tau) = \alpha$. Hence, the solution $P(t, \alpha)$ is τ-periodic. Since the periodic solution $P(t, P_0^*)$ is unique, thus we have $\alpha = P_0^*$.

Let $\varepsilon > 0$ be given. By Theorem 2.9 [**2**] on the continuous dependence of solutions on the initial values, there exists a $\delta > 0$ such that if $|P_0 - P_0^*| < \delta$ and $0 \leq t \leq \tau$, then

$$|P(t, P_0) - P(t, P_0^*)| < \varepsilon.$$

Choose $n_1 > 0$ such that $|P(n\tau, P_0) - P_0^*| < \delta$ for $n > n_1$. Then $|P(t, P_0) - P(t, P_0^*)| < \varepsilon$ for $t > n\tau$, which implies that

$$\lim_{t\to\infty} |P(t, P_0) - P(t, P_0^*)| = 0.$$

By Lemma 3.2, for any solution $(N(t), P(t))$ of system (3.1) with initial conditions $N(0) > 0$, $P(0) > 0$, we have that

$$\lim_{t\to\infty} |P(t) - P_s(t)| = 0, \qquad \lim_{t\to\infty} |N(t) - N_s(t)| = 0.$$

The proof of Theorem 3.1 (2) is thus completed. $\square$

4. Existence of the positive τ-periodic solution. In this section we investigate the invasion of the herbivorous zooplankton of system (2.7). Denote $\Sigma(t) = N(t) + P(t) + Z(t)$. It follows from system (2.7) that

$$\begin{cases} d\Sigma(t)/dt = 0, & t \neq n\tau, \\ \Sigma(n\tau^+) = DN^0 + (1-D)\Sigma(n\tau), & t = n\tau, \\ \Sigma(0^+) > 0. \end{cases} \tag{4.1}$$

By Lemma 3.1, the following lemma is obvious.

Lemma 4.1. *Let* $(N(t), P(t), Z(t))$ *be any solution of system* (2.3) *with initial values* $N(0) > 0$, $P(0) > 0$ *and* $Z(0) > 0$. *Then*

$$\lim_{t\to\infty} |N(t) + P(t) + Z(t) - N^0| = 0. \tag{4.2}$$

Lemma 4.1 says that the periodic solution $\widetilde{\Sigma}(t) = N^0$ of (4.1) is an invariant manifold of system (2.3).

By Theorem 3.1, we know that system (2.7) has two nonnegative boundary τ-periodic solutions

$$(N_e(t), P_e(t), Z_e(t)) = (N^0, 0, 0), \qquad (N_s(t), P_s(t), 0)(\text{if } a > a^*).$$

4.1. Stability of the boundary periodic solutions. For convenience, in the following discussion, if $a > a^*$, we denote

$$c^* = \frac{-\ln(1-D) + \eta\tau}{\int_0^\tau \delta\omega(P)dl}. \tag{4.3}$$

Theorem 4.1. *For system* (2.7), *we have*

(1) *If* $a < a^*$, *then system* (2.7) *has a unique globally asymptotically stable boundary* τ*-periodic solution* $(N^0, 0, 0)$.

(2) *If* $a > a^*$ *and* $c < c^*$, *then system* (2.7) *has a unique globally asymptotically stable boundary* τ*-periodic solution* $(N_s(t), P_s(t), 0)$.

(3) *If* $a > a^*$ *and* $c > c^*$*, then the periodic boundary solution* $(N_s(t), P_s(t), 0)$ *of system* (2.7) *is unstable.*

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

$$N(t) = u(t) + N_s(t), \qquad P(t) = v(t) + P_s(t), \qquad Z(t) = w(t).$$

Then we have

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

where $\Phi(t)$ satisfies

$$\frac{d\Phi(t)}{dt} = \begin{pmatrix} -aP[\partial U(N)/\partial N] & -aU(N) + \gamma & (1-\delta)c\omega(P) + \eta \\ aP[\partial U(N)/\partial N] & aU(N) - \gamma & -c\omega(P) \\ 0 & 0 & \delta c\omega(P) - \eta \end{pmatrix} \Phi(t)$$

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

$$\Phi(\tau) = \begin{pmatrix} \phi_{11}(\tau) & \phi_{12}(\tau) & * \\ \phi_{21}(\tau) & \phi_{22}(\tau) & ** \\ 0 & 0 & \exp(\int_0^\tau (\delta c\omega(P) - \eta)\, dl) \end{pmatrix}. \tag{4.4}$$

The linearization of impulsive subsystem (2.3) can be written as

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

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

$$M = \begin{pmatrix} 1-D & 0 & 0 \\ 0 & 1-D & 0 \\ 0 & 0 & 1-D \end{pmatrix} \Phi(\tau),$$

which are $\mu_3 = (1-D)\exp(\int_0^\tau (\delta c\omega(P) - \eta)\, dl)$ and the eigenvalues μ_1, μ_2 of the following matrix:

$$(1-D)\begin{pmatrix} \phi_{11}(\tau) & \phi_{12}(\tau) \\ \phi_{21}(\tau) & \phi_{22}(\tau) \end{pmatrix}.$$

μ_1, μ_2 are also the multipliers of the locally linearization system of system (3.1) provided with $D \in (0, D_0)$ at the asymptotically stable periodic solution $(N_s(t), P_s(t))$, where $D_0 = 1 - [1/(\exp((a^* U(N^0) - \gamma)\tau))]$. According to Theorem 3.1, we have that $\mu_1 < 1$, $\mu_2 < 1$.

If $c < c^*$, then $\mu_3 = (1-D)\exp(\int_0^\tau (\delta c\omega(P) - \eta)\, dl) < 1$, the boundary periodic solution $(N_s(t), P_s(t), 0)$ of system (2.7) is locally stable. We obtain that

(4.5)
$$Z(t) = Z(0)(1-D)^n \exp\left(\int_0^t (\delta c\omega(P) - \eta)\, dl\right), \quad t \in (n\tau, (n+1)\tau].$$

Hence, we obtain that, for any solution $(N(t), P(t), Z(t))$ of system (2.7) with initial value $N(0) > 0$, $P(0) > 0$, $Z(0) > 0$, $Z(t) \to 0$ as $t \to \infty$. By Lemma 4.1, we have $\lim_{t\to\infty} |N(t) + P(t) - N^0| = 0$. Now, using Theorem 3.1, we have $\lim_{t\to\infty} |N(t) - N_s(t)| = 0$ and $\lim_{t\to\infty} |P(t) - P_s(t)| = 0$.

If $c > c^*$, then $\mu_3 > 1$, the boundary periodic solution $(N_s(t), P_s(t), 0)$ of system (2.7) is unstable. The proof of Theorem 4.1 is completed. □

4.2. Bifurcation analysis of the boundary periodic solution $(N_s(t), P_s(t), 0)$. Let $\mathscr{B}$ denote the Banach space of piecewise continuous, τ-periodic function $\mathbf{N} : [0, \tau] \to R^2$ and have points of discontinuity τ, where they are continuous from the left. In the set $\mathscr{B}$, we introduce the norm $\|\mathbf{N}\|_0 = \sup_{0 \le t \le \tau} \|\mathbf{N}(t)\|$, with which $\mathscr{B}$ becomes a Banach space with uniform convergence topology.

For convenience, we introduce the following Lemmas 4.2 and 4.3 from Cushing [**5**] with small modifications.

Lemma 4.2. *Suppose* $a_{ij} \in \mathscr{B}$ *and* $0 \le d_i < 1$ $(i = 1, 2)$.

(a) *If* $(1-d_2)\exp(\int_0^\tau a_{22}(s)\, ds) \neq 1$, $(1-d_1)\exp(\int_0^\tau a_{11}(s)\, ds) \neq 1$, *then the linear impulsive homogenous system*

$$\left\{\begin{array}{c} \left.\begin{array}{c} dy_1/dt = a_{11}y_1 + a_{12}y_2, \\ dy_2/dt = a_{22}y_2, \end{array}\right\} \quad t \neq n\tau, \\ \left.\begin{array}{c} \triangle y_1 = -d_1y_1, \\ \triangle y_2 = -d_2y_2, \end{array}\right\} \quad t = n\tau \end{array}\right. \tag{4.6}$$

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

$$\left\{\begin{array}{c} \left.\begin{array}{c} dx_1/dt = a_{11}x_1 + a_{12}x_2 + f_1, \\ dx_2/dt = a_{22}x_2 + f_2, \end{array}\right\} \quad t \neq n\tau, \\ \left.\begin{array}{c} \triangle x_1 = -d_1x_1, \\ \triangle x_2 = -d_2x_2, \end{array}\right\} \quad t = n\tau \end{array}\right. \tag{4.7}$$

has, for every $(f_1, f_2) \in \mathscr{B}\times\mathscr{B}$, *a unique solution* $(x_1, x_2) \in \mathscr{B}\times\mathscr{B}$ *and the operator* $L : \mathscr{B}\times\mathscr{B} \to \mathscr{B}\times\mathscr{B}$ *defined by* $(x_1, x_2) = L(f_1, f_2)$ *is linear and compact.*

(b) *If* $(1-d_2)\exp(\int_0^\tau a_{22}(s)\,ds) = 1$, $(1-d_1)\exp(\int_0^\tau a_{11}(s)\,ds) \neq 1$, *then* (4.6) *has exactly one independent solution in* $\mathscr{B}\times\mathscr{B}$.

Remark 4.1. In fact, under the conditions of Lemma 4.1 (a),

$$\begin{cases} dx_2/dt = a_{22}x_2 + f_2, & t \neq n\tau, \\ \triangle x_2 = -d_2x_2, & t = n\tau \end{cases} \tag{4.8}$$

has a unique solution $x_2 \in \mathscr{B}$, and the operator $L_2 : \mathscr{B} \to \mathscr{B}$ defined by $x_2 = L_2f_2$ is linear and compact. Furthermore, the equation

$$\begin{cases} dx_1/dt = a_{11}x_1 + f_3, & t \neq n\tau, \\ \triangle x_1 = -d_1x_1, & t = n\tau \end{cases} \tag{4.9}$$

for $f_3 \in \mathscr{B}$ has a unique solution (since $(1-d_1)\exp(\int_0^\tau a_{11}(s)\,ds) \neq 1$) in $\mathscr{B}$, and $x_1 = L_1f_3$ defines a linear, compact operator $L_1 : \mathscr{B} \to \mathscr{B}$. Then we have

$$L(f_1, f_2) = (L_1(a_{12}L_2f_2 + f_1), L_2f_2).$$

Lemma 4.3. *Suppose that* $a \in \mathscr{B}$, $0 \le d < 1$, $(1-d)\exp(\int_0^\tau a(s)\,ds) = 1$ *and* $f \in \mathscr{B}$. *Then the impulsive equation*

$$\begin{cases} dx/dt = ax + f, & t \neq n\tau, \\ \triangle x = -dx, & t = n\tau \end{cases} \tag{4.10}$$

has a solution $x \in \mathscr{B}$ *if and only if* $\int_0^\tau f(l)\exp(-\int_0^l a(s)\,ds)\,dl = 0$.

By Lemma 4.1, in its invariant manifold $\widetilde{\Sigma}(t) = N(t) + P(t) + Z(t) = N^0$, system (2.7) reduces to an equivalently nonautonomous system as follows:

$$(4.11)\quad \begin{cases} \left.\begin{aligned} dP/dt &= aPU(N^0 - P - Z) - cZ\omega(P) - \gamma P, \\ dZ/dt &= \delta c\omega(P)Z - \eta Z, \end{aligned}\right\} & t \neq n\tau, \\ \left.\begin{aligned} \triangle P &= -DP, \\ \triangle Z &= -DZ, \end{aligned}\right\} & t = n\tau, \\ P_0 > 0, \quad Z_0 > 0, \quad P_0 + Z_0 \leq N^0. \end{cases}$$

If $a > a^*$, for system (4.11), by Theorem 4.1, the boundary periodic solution $(N_s(t), 0)$ is locally asymptotically stable provided that $c < c^*$; hence, the value c^* plays an important role as a bifurcation threshold.

For system (4.11), we have the following results.

Theorem 4.2. *For system* (4.11)*, assume that $a > a^*$ holds. Then a constant $\lambda_0 > 0$ exists such that, for each $c \in (c^*, c^* + \lambda_0)$, there exists a solution $(P, Z) \in \mathscr{B} \times \mathscr{B}$ of* (4.11) *satisfying $0 < P < P_s$, $Z > 0$ and $N = N^0 - P - Z > 0$ for all $t > 0$. Hence, system* (2.7) *has a positive τ-periodic solution (N, P, Z).*

Proof. Let $y_1 = P - P_s$, $y_2 = Z$ in (4.11). Then

$$(4.12)\quad \begin{cases} \left.\begin{aligned} dy_1/dt &= F_{11}(N_s, P_s)y_1 + F_{12}(c, N_s, P_s)y_2 + g_1(y_1, y_2), \\ dy_2/dt &= F_{22}(c, P_s)y_2 + g_2(y_1, y_2), \end{aligned}\right\} & t \neq n\tau, \\ \left.\begin{aligned} \triangle y_1 &= -Dy_1, \\ \triangle y_2 &= -Dy_2 \end{aligned}\right\} & t = n\tau, \\ P_0 > 0, \quad Z_0 > 0, \quad P_0 + Z_0 \leq N^0, \end{cases}$$

where

$$\begin{aligned} F_{11}(N_s, P_s) &= aU(N^0 - P_s) - aP\frac{\partial U(N_s)}{\partial N} - r, \\ F_{12}(c, N_s, P_s) &= -aP\frac{U(N_s)}{\partial N} - c\omega(P_s), \\ F_{22}(c, P_s) &= \delta c\omega(P_s) - \eta. \end{aligned}$$

Since $(1 - D)\exp(\int_0^\tau (\delta c\omega(P) - \eta)\, dl) \neq 1$, by Lemma 4.2, using L we can equivalently write the system (4.12) as the operator equation

$$(4.13)\qquad (y_1, y_2) = L^*(y_1, y_2) + G(y_1, y_2),$$

where

$$G(y_1,y_2)=(L_1(F_{12}(c,N_s,P_s)L_2g_2(y_1,y_2)+g_1(y_1,y_2)),L_2g_2(y_1,y_2)).$$

Here $L^*:\mathscr{B}\times\mathscr{B}\to\mathscr{B}\times\mathscr{B}$ is linear and compact (since L_1 and L_2 are compact) and satisfies $G=o(|(y_1,y_2)|_0)$ near $(0,0)$. A nontrivial solution $(y_1,y_2)\neq(0,0)$ for some $c>c^*$ yields a solution $(P,Z)=(P_s+y_1,y_2)$ of system (4.11). Solution $(P,Z)\neq(P_s,0)$ is called a nontrivial solution of system (4.11).

We apply the well-known local bifurcation techniques to (4.13). As is well known, bifurcation can occur only at the nontrivial solution of the linearized problem

$$(y_1,y_2)=L^*(y_1,y_2). \tag{4.14}$$

If $(y_1,y_2)\in\mathscr{B}\times\mathscr{B}$ is a solution of (4.14) for some $c>0$, then by the very manner in which L^* was defined, (y_1,y_2) solves the system

$$\begin{cases} \left.\begin{aligned} dy_1/dt &= F_{11}(N_s,P_s)y_1+F_{12}(c,N_s,P_s)y_2,\\ dy_2/dt &= F_{22}(c,P_s)y_2,\end{aligned}\right\} & t\neq n\tau,\\ \left.\begin{aligned} \triangle y_1 &= -Dy_1,\\ \triangle y_2 &= -Dy_2,\end{aligned}\right\} & t=n\tau,\end{cases} \tag{4.15}$$

and conversely. Using Lemma 4.2 (b), we see that (4.15), and hence (4.14), has one nontrivial solution in $\mathscr{B}\times\mathscr{B}$ if and only if $c=c^*$. Hence, a continuum $C=(c;y_1,y_2)\subseteq(0,\infty)\times\mathscr{B}\times\mathscr{B}$ of nontrivial solutions of (4.14) exists such that the closure $\overline{C}$ contains $(c^*;0,0)$. This continuum gives rise to a continuum $C_1=(c;P,Z)\subseteq(0,\infty)\times\mathscr{B}\times\mathscr{B}$ of solutions of (4.11) whose closure $\overline{C}_1$ contains the bifurcation point $(c^*;P_s,0)$.

To see that solutions in C_1 correspond to solutions (P,Z) of (4.11), we investigate the nature of continuum C near the bifurcation point $(c^*;0,0)$ by expending c and (y_1,y_2) in a Lyapunov-Schmidt series:

$$\begin{aligned} c &= c^*+\lambda\varepsilon+\cdots,\\ y_1 &= y_{11}\varepsilon+y_{12}\varepsilon^2+\cdots,\\ y_2 &= y_{21}\varepsilon+y_{22}\varepsilon^2+\cdots,\end{aligned}$$

for $y_{ij}\in\mathscr{B}$ where ε is a small parameter. If we substitute these series into differential system (4.11) and equate coefficients of ε and ε^2, we find that

$$(4.16)\quad \begin{cases} \left.\begin{array}{c} dy_{11}/dt = F_{11}(N_s, P_s)y_{11} + F_{12}(c^*, N_s, P_s)y_{21}, \\ dy_{21}/dt = F_{22}(c^*, P_s)y_{21}, \end{array}\right\} \quad t \neq n\tau, \\ \left.\begin{array}{c} \triangle y_{11} = -Dy_{11}, \\ \triangle y_{21} = -Dy_{21}, \end{array}\right\} \quad t = n\tau \end{cases}$$

and

$$(4.17)\quad \begin{cases} \left.\begin{array}{c} \frac{dy_{12}}{dt} = F_{11}(N_s, P_s)y_{12} + F_{12}(c^*, N_s, P_s)y_{22} + G_{12}(y_{11}, y_{12}, \lambda), \\ \frac{dy_{22}}{dt} = F_{22}(c^*, P_s)y_{22} + \delta\lambda\omega(P)y_{21} + \delta c^* \frac{\partial\omega(P)}{\partial P} y_{11}y_{21}, \end{array}\right\} t \neq n\tau, \\ \left.\begin{array}{c} \triangle y_{21} = -Dy_{21}, \\ \triangle y_{22} = -Dy_{22}, \end{array}\right\} \quad t = n\tau, \end{cases}$$

respectively. Thus, $(y_{11}, y_{21}) \in \mathscr{B} \times \mathscr{B}$ must be a solution of (4.13). We choose the specific solution satisfying initial conditions $y_{21}(0) = 1$. Then

$$y_{21} = \exp\left(\int_{n\tau}^{t} (\delta c^*\omega(P) - \eta)\, dl\right) > 0, \quad n\tau < t \leq (n+1)\tau,$$
$$y_{21}(0) = 1.$$

Moreover, $y_{11} < 0$ for all t (since $a > a^*$ and (3.8), hence

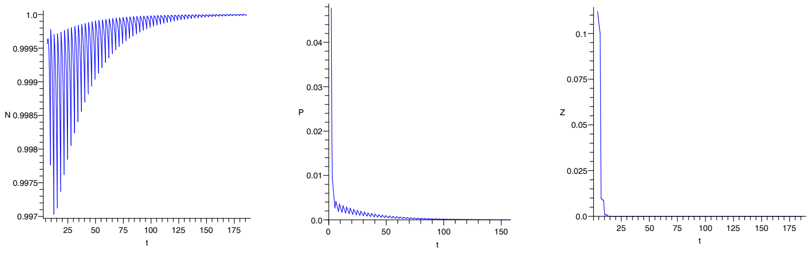
$$\int_0^\tau -aP[\partial N(N_s)/\partial P]\, dl < 0,$$

which implies that Green's function for the first equation in (4.14) is positive). Using Lemma 4.3, we find that

$$\lambda = -\frac{\int_0^\tau \delta c^*[\partial\omega(P)/\partial P]y_{11}y_{21} \exp(-\int_0^l (\delta c^*\omega(P) - \eta)\, dl)\, dt}{\int_0^\tau \delta\omega(P)y_{21} \exp(-\int_0^l (\delta c^*\omega(P) - \eta)\, dl)\, dt} > 0.$$

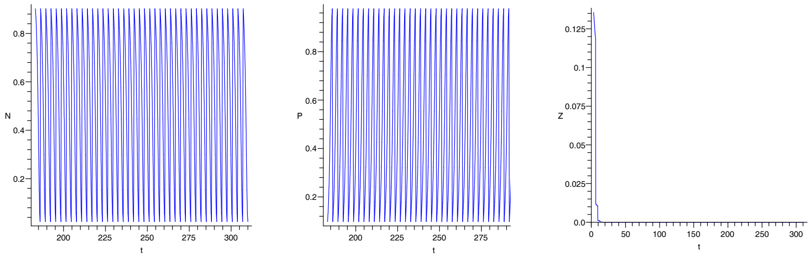
Thus, we see that near the bifurcation point $(c^*, 0, 0)$ the continuum C has two branches corresponding to $\varepsilon < 0$, $\varepsilon > 0$, respectively,

$$C^+ = (c; P, Z) : c^* < c < c^* + \lambda_0, \quad P < 0,\ Z > 0,$$
$$C^- = (c; P, Z) : c^* - \lambda_0 < c < c^*, \quad P > 0,\ Z < 0.$$



(a) (b) (c)

FIGURE 2. Time series of system (2.7) with initial value $(1, 0.5, 0.5)$ and $a = 1$, $c = 3$, $k = 0.2$, $\lambda = 0.7$, $\gamma = 0.08$, $\eta = 0.05$, $D = 0.9$, $\delta = 0.9$, $N^0 = 1$ and $\tau = 3$.



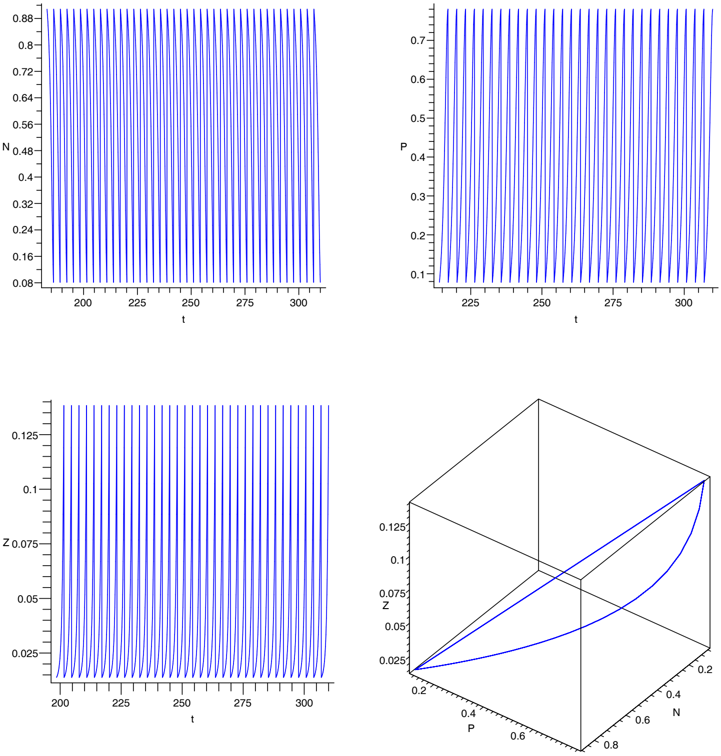
(a) (b) (c)

FIGURE 3. Time series of system (2.7) with initial value $(1, 0.5, 0.5)$ and $a = 1.3$, $c = 3$, $k = 0.2$, $\lambda = 0.7$, $\gamma = 0.08$, $\eta = 0.05$, $D = 0.9$, $\delta = 0.9$, $N^0 = 1$ and $\tau = 3$.

The solution is on C^+ which proves the theorem since $\lambda > 0$ is equivalent to $c > c^*$. We only have left to show that $P = y_1 + P_s$ for all t. This is easy for, if λ_0 is small, then P is near P_s in the sup norm of B; thus, since P_s is bounded away from zero, so is P. At the same time, by Theorem 4.1, for system (2.7), Z is near Z_s means that P is near P_s; thus, $N = N^0 - P - Z > 0$. We notice that the periodic solution (P, Z) is τ-periodic. So $N = N^0 - P - Z > 0$ is piecewise continuous and τ-periodic. The proof is thus completed. □

5. Numerical simulations.

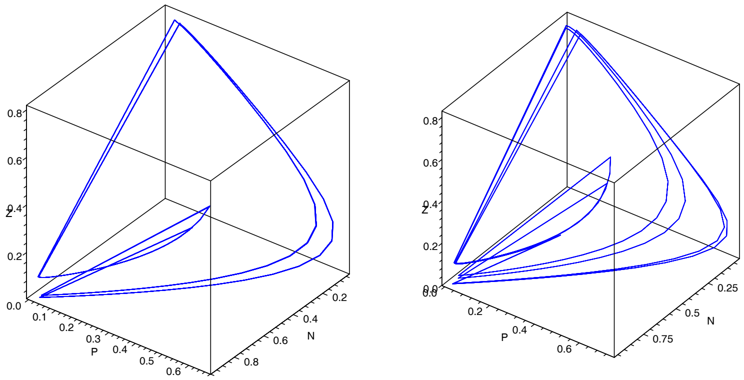
To study the dynamic complexity of plankton models in a pulsed chemostat with instantaneous nutrient



(c) (d)

FIGURE 4. (a–c) Time series of N, P, Z, (d) phase portrait of system (2.7) with initial value $(1, 0.5, 0.5)$ and $a = 1.3$, $c = 4$, $k = 0.2$, $\lambda = 0.7$, $\gamma = 0.08$, $\eta = 0.05$, $D = 0.9$, $\delta = 0.9$, $N^0 = 1$ and $\tau = 3$.

recycling, the solution of system (2.7) with initial conditions in the first quadrant is obtained numerically for a biologically feasible range of parametric values, and the bifurcation diagram provides a summary of essential dynamical behavior of the system. To justify the theoretic results we obtained in Section 4, we give two examples which concern the results in Theorem 4.1 and Theorem 4.2, respectively. Here we assume in system (2.7) that $U(N) = N/(k + N)$ and $\omega(P) = (1 - e^{-\lambda P})$.



(a) (b)

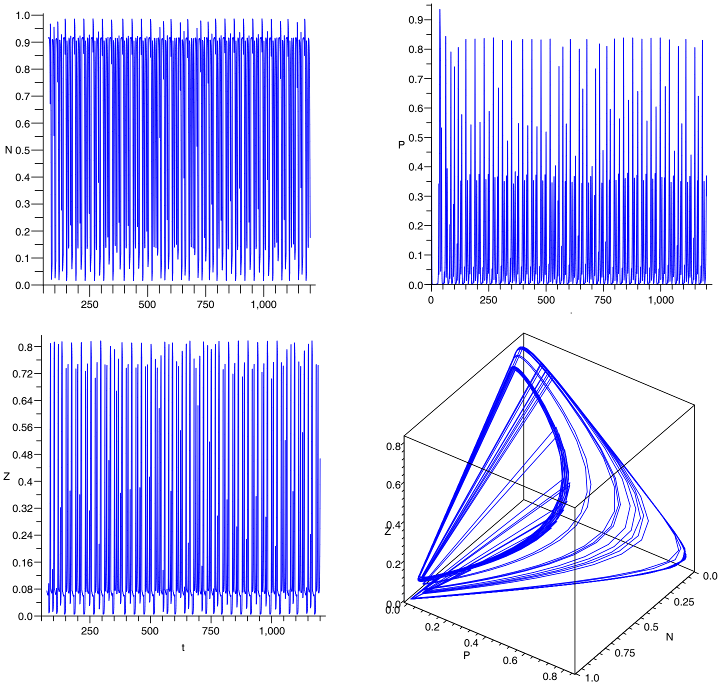
FIGURE 5. Periodic-doubling bifurcation. (a,b) Phase portraits of 2τ and 4τ-period solution for $\tau = 6$ and $\tau = 6.4$, respectively.

Example 1. In system (2.7), set $c = 3$, $k = 0.2$, $\lambda = 0.7$, $\gamma = 0.08$, $\eta = 0.05$, $D = 0.9$, $\delta = 0.9$, $N^0 = 1$, $\tau = 3$, $a^* \approx 1.05$. By Theorem 4.1, we know that, if $a < a^*$, the periodic solution $(1, 0, 0)$ is globally asymptotically stable; if $a > a^*$, the phytoplankton begins to invade the system and the periodic solution $(N_s(t), P_s(t), 0)$ is globally asymptotically stable. Our simulations support these results (see Figures 2 and 3, where $a = 1$ and $a = 1.3$, respectively).

Example 2. In system (2.7), set $a = 1.3$ ($> a^*$) and $k, \lambda, \gamma, \eta, D, \delta, N^0, \tau$ have similar values as in Example 1. We can estimate numerically that $c^* \doteq 3.5$ (since we cannot compute the exact value from the expression of c^* in (4.3)). By Theorem 4.2, we know that, if $c > c^*$, the zooplankton begins to invade the system and, in this case, system (2.7) has a positive periodic solution $(N(t), P(t), Z(t))$. Our simulations support this result (see Figure 4, where $c = 4$).

The following example describes the influence of impulsive period τ in system (2.7).

Example 3. Set $a = 1.3$, $c = 4$, $k = 0.2$, $\lambda = 0.7$, $\gamma = 0.08$, $\eta = 0.05$, $D = 0.9$, $\delta = 0.9$ and $N^0 = 1$. When $\tau < \tau_1 \approx 3.2$, the solution $(N(t), P(t), Z(t))$ is stable (see Figure 4). When $\tau = 4 > \tau_1$, stability of the τ-periodic solution is destroyed, the 2τ-periodic solution occurs (see Figure 5 (a)) and it is stable. If $\tau > \tau_2 \approx 6.4$, then the 2τ-periodic solution is destroyed and the 4τ-periodic solution occurs (see Figure

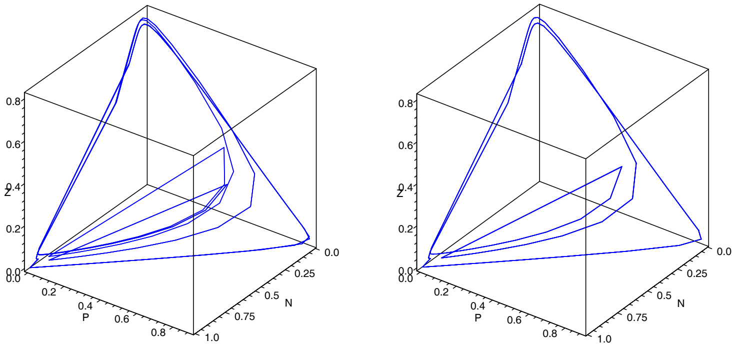


(c) (d)

FIGURE 6. A strange attractor: (a–c) Time series of N, P, Z, (d) phase portrait of system (2.7) with initial values $(1, 0.5, 0.5)$ and $\tau = 8$.

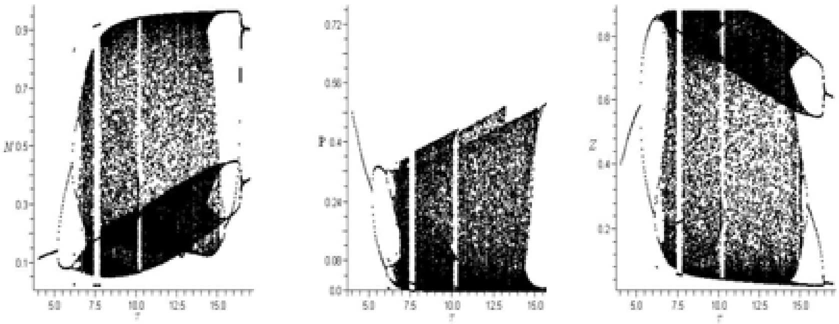
5 (b)). Continuously increasing τ, it follows a cascade of periodic-doubling bifurcations (see Figure 6) leading to chaos (see Figure 8), as τ continuously increases, producing periodic-halving bifurcation (see Figure 7). System (2.7) experiences a process of cycles → of periodic-doubling cascade → chaos → periodic-halving cascade, which is characterized by (1) periodic-doubling, (2) periodic-halving.

6. Discussion. The phenomenon of plankton bloom has received much attention among experimental ecologists as well as mathematical ecologists. Though the process by which these population outbursts occur are not clearly understood, researchers are attempting to explain bloom phenomenon by different approaches. There is a large body of



(a) (b)

FIGURE 7. Periodic-halving bifurcation. (a,b) Phase portraits of 4τ and 2τ-period solution for $\tau = 16.6$ and $\tau = 16.8$, respectively.



(a) (b) (c)

FIGURE 8. Bifurcation diagrams of system (2.7) with initial value $(1, 0.5, 0.5)$ and $a = 1.3$, $c = 4$, $k = 0.2$, $\lambda = 0.7$, $\gamma = 0.08$, $\eta = 0.05$, $D = 0.9$, $\delta = 0.9$, $N^0 = 1$ and $4 < \tau < 17$.

literature where plankton blooms have been modelled using different modifications of classical food chain models by introducing nonlinear functional responses of the plankton populations or using environmental forcing [**4**].

Unlike the existing literature on plankton models with nutrient recycling, in this paper, we investigate a nutrient-phytoplankton-zooplankton model in a chemostat with instantaneous nutrient recycling and impulsive perturbation. Firstly, we obtain the invasion threshold of the phytoplankton, which is a^*. If $a < a^*$, the periodic solution $(N^0, 0, 0)$ is globally asymptotically stable (see Figure 2), and, if $a > a^*$, zooplankton begin to invade the system. c^* plays an important role as the invasion threshold of the zooplankton. If $c < c^*$, the periodic solution $(N_s, P_s, 0)$ is globally stable (see Figure 3). If $c > c^*$, by using standard techniques of local bifurcation theory, we prove that there are periodic oscillations in nutrient, phytoplankton and zooplankton (see Figure 4).

Choosing different values of the pulsed period τ as bifurcation parameters, and using numerical simulation, we obtain bifurcation diagrams (Figure 8). Bifurcation diagrams indicate that the system has complexity, including periodic-doubling cascade, periodic windows and periodic-halving cascade. All these results show that the dynamical behavior of system (2.7) becomes more complex under impulsive perturbation.

For the situation when we assume nutrient recycling is not instantaneous, that is, if we consider the affect of the time delay involved in nutrient recycling on resilience, what new dynamical behaviors will occur? We leave this for future work.

REFERENCES

1. D.D. Bainov and P.S. Simeonov, *Impulsive differential equations: Asymptotic properties of the solutions*, World Scientific, 1995.

2. ———, *Impulsive differential equations: Periodic solution and application*, Pitman Monogr. Surv. Pure Appl. Math., 1993.

3. E. Beretta, G.I. Bischi and F. Solimano, *Stability in chemostat equations with delayed nutrient recycling*, J. Math. Biol. **28** (1990), 99–111.

4. S. Busenberg, S.K. Kumar, P. Austin and G. Wake, *The dynamics of a model of a plankton-nutrient interaction*, Bull. Math. Biol. **52** (1990), 677–696.

5. J.M. Cushing, *Periodic time-dependent predator-prey systems*, SIAM J. Appl. Math. **32** (1977), 82–95.

6. G. Fan and Gail S.K. Wolkowicz, *Analysis of a model of nutrient driven self-cycling fermentation allowing unimodal response functions*, Dynam. Contin., Discr. Impuls. Syst.: Appl. Algorithms **8** (2007), 801–831.

7. E. Funasaki and M. Kor, *Invasion and chaos in periodically periodically pulsed mass-action chemostat*, Theor. Popul. Biol. **44** (1993), 203–224.

8. J.K. Hale and A.S. Somolinos, *Competition for fluctuating nutrient*, J. Math. Biol. **18** (1983), 255–280.

9. T.G. Hallam, *Controlled persistence in rudimentary plankton models*. Math. Model. **4** (1977), 2081–2088.

10. V.S. Ivlev, *Experimental ecology of the feeding of fishes*, Yale University Press, New Haven, 1961.

11. S.R.J. Jang and J. Baglama, *Persistence in variable-yield nutrient-plankton models*, Math. Comp. Model. **38** (2003), 281–298.

12. B. Li and Y. Kuang, *Simple food chain in a chemostat with distinct removal rates*, J. Math. Anal. Appl. **242** (2000), 75–92.

13. Z. Lu and K.P. Hadeler, *Model of plasmid-bearing, plasmid-free competition in the chemostat with nutrient recycling and an inhibitor*, Math. Biosci. **148** (1998), 147–159.

14. P. Mayzaud and S.A. Poulet, *The importance of the time factor in the response of zooplankton to varying concentrations of naturally occurring particulate matter*, Limnol. Oceanogr. **23** (1978), 1144–1154.

15. B. Mukhopadhyay and R. Bhattacharyya, *Modelling phytoplankton allelopathy in a nutrient-plankton model with spatial heterogeneity*, Ecol. Model. **198** (2006), 163–173.

16. R.M. Nisbet, J. Mckinstry and W.S.C. Gurney, *A strategic model of material cycling in a closed ecosystem*, Math. Biosci. **64** (1983), 99–113.

17. S. Ruan, *Persistence and coexistence in zooplankton-phytoplankton-nutrient models with instantaneous nutrient recycling*, J. Math. Biol. **31** (1993), 633–654.

18. ———, *Oscillations in plankton models with nutrient recycling*, J. Theor. Biol. **208** (2001), 15–26.

19. H. Smith and P. Waltman, *The theory of the chemostat*, Cambridge University, Cambridge, UK, 1995.

20. H.L. Smith, *Competitive coexistence in an oscillating chemostat*, SIAM J. Appl. Math. **40** (1981), 498–522.

21. R.J. Smith and Gail S.K. Wolkowicz, *Growth and competition in the nutrient driven self-cycling fermentation process*, Canad. Appl. Math. Quart. **10** (2003), 171–177.

22. J.H. Steele and E.W. Henderson, *The role of predation in plankton models*, J. Plankton Res. **14** (1992), 157–172.

23. P.A. Taylor and J.L. Williams, *Theoretical studies on the coexistence of competing species under continuous-flow conditions*, Canad. J. Microbiol. **21** (1975), 90–98.

24. F. Wang, C. Hao and L. Chen, *Bifurcation and chaos in a monod type food chain chemostat with pulsed input and washout*, Chaos, Soliton Fract. **31** (2007), 826–839.

25. W. Wang, H. Wang and Z. Li, *Chaotic behavior of a three-species Beddington-type system with impulsive perturbations*, Chaos, Soliton Fract. **37** (2008), 438–443.

26. Z. Xiang and X. Song, *A model of competition between plasmid-bearing and plasmid-free organisms in a chemostat with periodic input*, Chaos, Soliton Fract. **32** (2007), 1419–1428.

27. S. Yuan, D. Xiao and M. Han, *Competition between plasmid-bearing and plasmid-free organisms in a chemostat with nutrient recycling and an inhibitor*, Math. Biosci. **202** (2006), 1–28.

College of Science, Shanghai University for Science and Technology, Shanghai 200093, China
Email address: sanling@usst.edu.cn

College of Science, Shanghai University for Science and Technology,
Shanghai 200093, China
Email address: zhaoyuzy123@163.com

College of Bioengineering, Jimei University, Xiamen 361021, China
Email address: xxaaffeng@jmu.edu.cn

Mathematics, H38, FEIS, Swinburne University of Technology, Hawthorn,
VIC. 3122, Australia
Email address: tonghuazhang@swin.edu.au