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Modelling and analysis of a phytoplankton–zooplankton system with continuous and discrete time

S. Kartal^a, M. Kar^b, N. Kartal^c and F. Gurcan^{d,e}

^aDepartment of Mathematics, Faculty of Education, Nevsehir Haci Bektas Veli University, Nevsehir, Turkey;

^bDepartment of Molecular Biology and Genetics, Faculty of Science and Art, Nevsehir Haci Bektas Veli University, Nevsehir, Turkey; ^cAvanos Vocational School, Nevsehir Haci Bektas Veli University, Nevsehir, Turkey; ^dFaculty of Engineering and Natural Sciences, International University of Sarajevo, Sarajevo, Bosnia and Herzegovina;

^eDepartment of Mathematics, Faculty of Science, Erciyes University, Kayseri, Turkey

ABSTRACT

In this study, a phytoplankton–zooplankton system has been modelled using a system of differential equations with piecewise constant arguments, which represents a new approach to modelling phytoplankton–zooplankton interaction. To analyse the dynamic behaviour of the model, we consider the solution of the system in a certain subinterval, which yields a system of difference equations. Some theoretical results on the boundedness character and local stability properties for the discrete dynamical system are obtained. In addition, we explain the biological dynamics of the bloom in the plankton model through Neimark–Sacker bifurcation and obtain the threshold values for different parameters that govern the periodic nature of the bloom. We conclude that, while other studies explained that the bloom depended on only one parameter, this study explains that the bloom depended on three different parameters, namely θ (rate of toxin production per phytoplankton), β (zooplankton growth efficiency) and K (environmental carrying capacity of phytoplankton).

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1. Introduction

Plankton are a diverse group of organisms that live in the water column and cannot swim against the current [1]. Mainly, plankton are broadly divided into two large groups; phytoplankton are usually unicellular and microscopic organisms, and they are consumed by zooplankton. Phytoplankton are very important component of aquatic ecology. They are the base of the aquatic food web, and they also produce 50–80% of the oxygen needs of the world and absorb half of the carbon dioxide, potentially mitigating one cause of global warming. These functions of plankton, which are called beneficial algal blooms, occur in ocean patches where they have favourable nutritional, physical and biological conditions [2].

The dynamics of the rapid increase of the plankton population is known as a ‘bloom’. Algal blooms are broadly divided into two groups; first, spring blooms occur seasonally depending on the temperature and nutrient conditions; second, red tides are the result of localized outbreaks associated with water temperature [3]. If the biomass of an algal bloom has adverse effects on the environment, it is called a harmful algal bloom (HAB). HABs have adverse and disruptive effects on the environment and ecology. HABs fall into two general types: (a) those that secrete secondary metabolites (e.g. toxin and mucus) and cause contamination in the water and damage

aquatic life and (b) those occurring after an extreme biomass increase, thus causing an anoxic situation and harming various organisms.

In recent years, there has been considerable scientific attention focused on HABs [4,5]. Not only does algal nutrient status affect the likelihood of top-down control of these organisms, but any negative impact on grazing pressure will decrease nutrient regeneration, further enhancing algal nutrient stress and unpalatability [6]. For bloom development in immature ecosystems (e.g. during the spring bloom), grazer mismatch is important, but an alternative mechanism is required for growth to exceed grazing losses within mature ecosystems [7].

Modelling of plankton populations is an essential tool to improve our understanding of the physical and biological processes that affect population dynamics. In particular, it is very important to explain the dynamic mechanism of the HAB and its control in the plankton model. In recent years, many authors have used mathematical models to focus on the adverse effect of HAB in order to determine factors that cause bloom [8–13]. Because the dynamics of bloom are not well explained by the ordinary differential equations, many authors prefer to use delay differential equations [14–19]. Chattopadhyay and Sarkar [19] explained the cyclic nature of bloom dynamics of phytoplankton–zooplankton interaction by using the following model:

$$\begin{cases} \frac{dP}{dt} = rP(t) \left(1 - \frac{P(t)}{K}\right) - \alpha P(t)Z(t), \\ \frac{dZ}{dt} = \beta P(t)Z(t) - \mu Z(t) - \frac{\theta P(t-\tau)}{\gamma + P(t-\tau)} Z(t). \end{cases} \quad (1.1)$$

The model includes two predational forms. The first form is $P(t)Z(t)$, which is constructed according to the law of mass action. The second form is the Holling type II functional response, which is given by the last term in the second equation. In addition, they assumed that liberation of toxic substances by the phytoplankton species is not an instantaneous process but instead followed by some time lag. In this way, the mechanism of the periodic nature of blooms was explained by using delay differential equations.

Theoretical studies show that differential equations with piecewise constant arguments are equivalent to integral equations and are very close to delay differential equations [20,21]. This idea was suggested and studied by Cooke and Györi [20]. They provided that differential equations with piecewise constant arguments can be used to obtain the approximate solution of delay differential equations that contain discrete delays. In their method of approximation, the delay equation is first replaced by a differential equation with piecewise constant arguments, and then by a difference equation. With this in mind, they studied the qualitative dynamics of these three equations.

Following this work, using the method of reduction to discrete equations, many authors have analysed various types of biological models consisting of differential equations with piecewise constant arguments [22–29]. In such biological events, differential equations may reflect the dynamics of growth and death of populations; otherwise, difference equations may represent the interaction of two populations, such as competition or predation phenomena [27,28].

By taking into account the work of Chattopadhyay and Sarkar [19], this paper proposes a mathematical model for the phytoplankton–zooplankton interaction including both discrete and continuous time:

$$\begin{cases} \frac{dx_1}{dt} = rx_1(t) \left(1 - \frac{x_1(t)}{K}\right) - \alpha x_1(t)x_2(\llbracket t \rrbracket), \\ \frac{dx_2}{dt} = \beta x_1(\llbracket t \rrbracket)x_2(t) - \mu x_2(t) - \frac{\theta x_1(\llbracket t \rrbracket)}{\gamma + x_1(\llbracket t \rrbracket)} x_2(t). \end{cases} \quad (1.2)$$

In this model, $x_1(t)$ and $x_2(t)$ represent the density of the phytoplankton and zooplankton populations, respectively; $\llbracket t \rrbracket$ denotes the integer part of $t \in [0, \infty)$; and all these parameters are positive. The parameters r , K and α are the intrinsic growth rate, environmental carrying capacity

Table 1. Parameters values used for numerical analysis.

Parameters	Default values	Reported ranges
r (Maximum x_1 growth rate)	0.2 ($\text{m}^{-1}\text{day}^{-1}$) ^a	0.07–0.28 ($\text{m}^{-1}\text{day}^{-1}$)
a (Maximum x_2 grazing rate)	0.6 (day^{-1}) ^a	0.6–1.4 (day^{-1})
β (x_2 growth efficiency)	0.25 ^a	0.2–0.5
μ (Natural death rate of x_2)	0.02 ($\text{m}^{-1}\text{day}^{-1}$) ^a	0.015–0.15 ($\text{m}^{-1}\text{day}^{-1}$)
γ (x_2 grazing half-saturation coefficient)	0.06 (gCm^{-3}) ^a	0.02–0.1 (gCm^{-3})
θ (Rate of toxin production per phytoplankton)	0.9 ($\text{m}^{-1}\text{day}^{-1}$) ^a	
K (Environmental carrying capacity of x_1)	5 (m^{-1}) ^b	

^aEdwards and Briendly [30].

^bParameter values within a biologically meaningful range.

and specific predation rate of phytoplankton species, respectively. β represents the ratio of biomass consumption per zooplankton for the production of new zooplankton, μ is the mortality rate of zooplankton, θ denotes the rate of toxin production per phytoplankton, and γ is the half saturation constant. Most of the parameter values are taken from the study of Edwards and Briendly [30] in terms of consistency with the biological facts, and these parameter values are shown in Table 1.

Model (1.2) includes both discrete and continuous time for each population because plankton dynamics have different dynamics properties that can be described using both differential and difference equations. The logistic term $rx_1(t)\left(1 - \frac{x_1(t)}{K}\right)$ and the term $\mu x_2(t)$ include only a time-continuity for the growth of phytoplankton and the death of zooplankton, respectively. In model (1.1), the authors assumed that liberation of toxic substances by the phytoplankton species is not an instantaneous process but instead followed by some time lag. In our model, these time delays are reflected by discrete time in the Holling type II functional response as $\frac{\theta x_1(\lfloor t \rfloor)}{\gamma + x_1(\lfloor t \rfloor)} x_2(t)$. On the other hand, in model (1.1), the authors did not consider another time delay in the interaction phytoplankton and zooplankton system. In a real ecological context, the interaction between phytoplankton and zooplankton, which is described as $x_1(t)x_2(t)$, will not be essentially instantaneous. Instead, the response of zooplankton to contacts with phytoplankton is likely to be delayed due to a gestation period [31–33]. Therefore, we choose a discrete time instead of time delay in the predation term and obtained $x_1(t)x_2(\lfloor t \rfloor)$, $x_1(\lfloor t \rfloor)x_2(t)$, which include both discrete and continuous time for each population. Thus, the phytoplankton–zooplankton interaction is considered in a certain subinterval and is modelled using a system of differential equations with piecewise constant arguments. This approach is a new idea for modelling the phytoplankton–zooplankton system.

2. Local stability analysis

For $t \in [n, n + 1)$, system (1.2) can be written as follows:

$$\begin{cases} \frac{dx_1}{dt} - (r - \alpha x_2(n))x_1(t) = -rkx_1^2(t), \\ \frac{dx_2}{x_2(t)} = \left(\beta x_1(n) - \mu - \frac{\theta x_1(n)}{\gamma + x_1(n)} \right) dt, \end{cases} \quad (2.1)$$

where $\frac{1}{K} = k$.

Solving Equation (2.1) in interval $t \in [n, n + 1)$ and letting t go to $n + 1$, one can obtain a system of difference equation as follows:

$$\begin{cases} x_1(n + 1) = \frac{x_1(n)(r - \alpha x_2(n))}{(r - \alpha x_2(n) - rkx_1(n))e^{-(r - \alpha x_2(n))} + rkx_1(n)}, \\ x_2(n + 1) = x_2(n)e^{\beta x_1(n) - \mu - \frac{\theta x_1(n)}{\gamma + x_1(n)}}. \end{cases} \quad (2.2)$$

Now we obtain the solution of system (1.2) as a system of difference equation that reveals the rich dynamical characteristics and the asymptotic behaviour of the system of differential equations with piecewise constant arguments.

The recurrence relation (2.2) corresponds to the discrete dynamical systems:

$$\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} \rightarrow \begin{pmatrix} \frac{x_1(r-\alpha x_2)}{(r-\alpha x_2-rkx_1)e^{-(r-\alpha x_2)}+rkx_1} \\ x_2 e^{\beta x_1 - \mu - \frac{\theta x_1}{\gamma+1}} \end{pmatrix} \equiv \begin{pmatrix} F_1(x, r, \alpha, k, \beta, \mu, \theta, \gamma) \\ F_2(x, r, \alpha, k, \beta, \mu, \theta, \gamma) \end{pmatrix}, \quad (2.3)$$

where $x = (x_1, x_2)^T$. Map (2.3) has fixed points $E_0 = (0, 0)$ and $E_1 = (\frac{1}{k}, 0)$ for all parameter values. For

$$\theta < \frac{\beta}{k} + \beta\gamma - \mu - k\gamma\mu, \quad (2.4)$$

a nontrivial fixed point $E_* = (\bar{x}_1, \bar{x}_2)$ appears, with the coordinates

$$\bar{x}_1 = \frac{-\beta\gamma + \theta + \mu + \sqrt{(\beta\gamma - \theta - \mu)^2 + 4\beta\gamma\mu}}{2\beta}, \quad \bar{x}_2 = \frac{r}{\alpha}(1 - k\bar{x}_1). \quad (2.5)$$

Now, we first focus on boundedness solution of system (2.2), and later discuss the stability of fixed points of map (2.3).

Theorem 2.1. Let $\{(x_1(n), x_2(n))\}_{n=0}^{\infty}$ be a positive solution of system (2.2). If $x_2(n) \in (0, \frac{r}{\alpha})$, then $x_1(n) \in (0, \frac{e^r}{k(e^r-1)})$. If $x_1(n) < \bar{x}_1$, then $x_2(n) \in (0, x_2(0))$.

Proof. It can be easily seen that the function

$$f(u) = \frac{ue^u}{e^u - 1}, \quad u \in \mathbb{R}$$

is increasing on $(-\infty, \infty)$ since

$$f'(u) = \frac{e^u(e^u - 1 - u)}{(e^u - 1)^2} > 0.$$

From the first equation in the system, we get

$$\begin{aligned} x_1(n+1) &= \frac{x_1(n)(r - \alpha x_2(n))e^{r-\alpha x_2(n)}}{r - \alpha x_2(n) + rkx_1(n)(e^{r-\alpha x_2(n)} - 1)} \\ &< \frac{x_1(n)(r - \alpha x_2(n))e^{r-\alpha x_2(n)}}{rkx_1(n)(e^{r-\alpha x_2(n)} - 1)} \\ &= \frac{(r - \alpha x_2(n))e^{r-\alpha x_2(n)}}{rk(e^{r-\alpha x_2(n)} - 1)} \\ &< \frac{re^r}{kr(e^r - 1)} = \frac{e^r}{k(e^r - 1)}. \end{aligned}$$

Similarly, it can be shown that $x_2(n) \in (0, x_2(0))$ under the condition $x_1(n) < \bar{x}_1$.

Theorem 2.2. The fixed points E_0 and E_1 are saddle points.

Proof. The Jacobian matrix at the fixed point E_0 , is the form

$$A_0 = \begin{pmatrix} e^r & 0 \\ 0 & e^{-\mu} \end{pmatrix}$$

and has eigenvalues $\mu_1 = e^r, \mu_2 = e^{-s}$. Consequently, E_0 is a saddle point. On the other hand the Jacobian matrix A_1 at the point E_1 is

$$A_1 = \begin{pmatrix} e^{-r} & -\frac{\alpha - e^{-r}\alpha}{kr} \\ 0 & e^{\frac{\beta}{k} - \frac{\theta}{1+ky} - \mu} \end{pmatrix},$$

which gives eigenvalues $\mu_1 = e^{-r}$ and $\mu_2 = e^{\frac{\beta}{k} - \frac{\theta}{1+ky} - \mu}$. Considering the condition (2.4), we can say that E_1 is a saddle point.

Now, we can investigate the stability of the nontrivial fixed point of the map. The Jacobian matrix A evaluated at the nontrivial fixed point is given by

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \quad (2.6)$$

where

$$\begin{aligned} a_{11} &= \frac{\partial F_1}{\partial x_1}(\bar{x}_1, \bar{x}_2) = e^{-kr\bar{x}_1}, \\ a_{12} &= \frac{\partial F_1}{\partial x_2}(\bar{x}_1, \bar{x}_2) = -\frac{(1 - e^{-kr\bar{x}_1})\alpha}{kr}, \\ a_{21} &= \frac{\partial F_2}{\partial x_1}(\bar{x}_1, \bar{x}_2) = 2\bar{x}_2\beta \frac{\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta)}{(\beta\gamma + \theta + \mu + \Delta)^2}, \\ a_{22} &= \frac{\partial F_2}{\partial x_2}(\bar{x}_1, \bar{x}_2) = 1 \end{aligned}$$

and

$$\Delta = \sqrt{(\beta\gamma - \theta - \mu)^2 + 4\beta\gamma\mu}.$$

The characteristic equation of the matrix A can be obtained as

$$\begin{aligned} p(\mu) &= \mu^2 + \mu(-1 - e^{-kr\bar{x}_1}) \\ &+ \frac{(1 - e^{-kr\bar{x}_1})}{kr} 2\bar{x}_2\beta\alpha \frac{\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta)}{(\beta\gamma + \theta + \mu + \Delta)^2} + e^{-kr\bar{x}_1} = 0. \end{aligned} \quad (2.7)$$

In order to analyse local behaviour of the map through characteristic equation (2.7), we can use the following theorem (Schur–Cohn criterion).

Theorem 2.3 ([34]). The characteristic polynomial

$$p(\mu) = \mu^2 + p_1\mu + p_0 \quad (2.8)$$

has all its roots inside the unit open disk ($|\mu| < 1$) if and only if

$$(a) \quad p(1) = 1 + p_1 + p_0 > 0,$$

$$(b) p(-1) = 1 - p_1 + p_0 > 0,$$

$$(c) D_1^+ = 1 + p_0 > 0, D_1^- = 1 - p_0 > 0.$$

By using Theorem 2.3, we can analyse the dynamic behaviour of the map in the following theorem:

Theorem 2.4. The nontrivial fixed point of map (2.3) is locally asymptotically stable if and only if

$$k > \frac{2\beta(\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta))}{(\beta\gamma + \theta + \mu + \Delta)^2 + (-\gamma\beta + \theta + \mu + \Delta)(\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta))}.$$

Proof. From the characteristic equation, we obtain

$$p_1 = -1 - e^{-kr\bar{x}_1},$$

$$p_0 = \frac{(1 - e^{-kr\bar{x}_1})}{kr} 2\bar{x}_2\beta\alpha \frac{\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta)}{(\beta\gamma + \theta + \mu + \Delta)^2} + e^{-kr\bar{x}_1}.$$

The condition (a), (b) and (c) of Theorem 2.3 gives the inequalities

$$p(1) = \frac{(1 - e^{-kr\bar{x}_1})}{kr} 2\bar{x}_2\beta\alpha \frac{(\beta\gamma - \theta)^2 + 2\theta\mu + \theta\Delta + \mu^2 + \mu\Delta + 2\mu\beta\gamma + \beta\gamma\Delta}{(\beta\gamma + \theta + \mu + \Delta)^2} > 0, \quad (2.9)$$

$$p(-1) = 2 + \frac{(1 - e^{-kr\bar{x}_1})}{kr} 2\bar{x}_2\beta\alpha \frac{(\beta\gamma - \theta)^2 + 2\theta\mu + \theta\Delta + \mu^2 + \mu\Delta + 2\mu\beta\gamma + \beta\gamma\Delta}{(\beta\gamma + \theta + \mu + \Delta)^2} + 2e^{-kr\bar{x}_1} > 0 \quad (2.10)$$

and

$$D_1^+ = 1 + \frac{(1 - e^{-kr\bar{x}_1})}{kr} 2\bar{x}_2\beta\alpha \frac{\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta)}{(\beta\gamma + \theta + \mu + \Delta)^2} + e^{-kr\bar{x}_1} > 0, \quad (2.11)$$

which are always held under condition (2.4). From condition (d), we get

$$D_1^- = \frac{(1 - e^{-kr\bar{x}_1})}{kr} 2\bar{x}_2\beta\alpha \frac{\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta)}{(\beta\gamma + \theta + \mu + \Delta)^2} + e^{-kr\bar{x}_1} < 1, \quad (2.12)$$

which reveals

$$k > \frac{2\beta(\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta))}{(\beta\gamma + \theta + \mu + \Delta)^2 + (-\gamma\beta + \theta + \mu + \Delta)(\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta))}.$$

This completes the proof.

To test the conditions of Theorem 2.4, we can use parameter values given in Table 1 and initial conditions $x_1(1) = 3.5, x_2(1) = 1$. Figure 1 shows that, under the conditions given in Theorem 2.4, the nontrivial fixed point $E_* = (\bar{x}_1, \bar{x}_2) = (3.62133, 0.0919116)$ is locally asymptotically stable, where blue and red graphs represent population densities of phytoplankton and zooplankton, respectively.

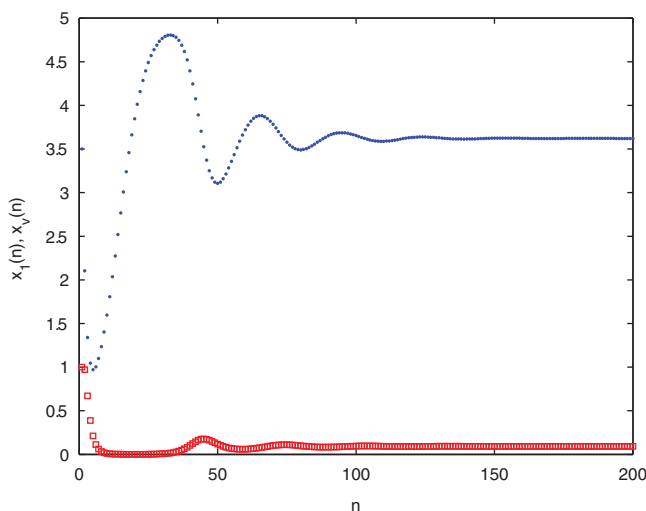


Figure 1. Asymptotically stable fixed point of the map.

3. Bifurcation analysis

In this section, we investigate the existence of stationary bifurcation (fold, transcritical and pitchfork bifurcation), period-doubling bifurcation and Neimark–Sacker bifurcation in map (2.3).

3.1 Stationary bifurcation and period-doubling bifurcation analysis

Stationary bifurcation occurs in a discrete dynamical system when the Jacobian matrix A has one real eigenvalue equal to 1. For a period-doubling bifurcation, the Jacobian matrix A has one real eigenvalue that equals -1 , while the other eigenvalue of A is inside the unit circle. It is well known that replacing condition (a) in Theorem 2.3 by $p(1) = 0$, the algebraic conditions under which the system may undergo stationary bifurcation are obtained. Replacing condition (b) in Theorem 2.3 by $p(-1) = 0$, the conditions of period-doubling bifurcation are obtained.

Because of inequalities (2.9) and (2.10), these conditions do not hold for the system. Thus, stationary bifurcation and period-doubling bifurcation do not exist for the system.

3.2 Neimark–Sacker bifurcation analysis

Theorem 3.1 ([34]). A pair of complex conjugate roots of characteristic polynomial (2.8) lie on the unit circle and the other roots of $p(\mu)$ all lie inside the unit circle if and only if

- (a) $p(1) = 1 + p_1 + p_0 > 0$,
- (b) $p(-1) = 1 - p_1 + p_0 > 0$,
- (c) $D_1^+ = 1 + p_0 > 0$,
- (d) $D_1^- = 1 - p_0 = 0$.

Theorem 3.2. The eigenvalue assignment condition of Neimark–Sacker bifurcation for map (2.3) holds if

$$\bar{k} = \frac{2\beta(\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta))}{(\beta\gamma + \theta + \mu + \Delta)^2 + (-\gamma\beta + \theta + \mu + \Delta)(\beta^2\gamma^2 + (\theta + \mu)(\theta + \mu + \Delta) + \beta\gamma(-2\theta + 2\mu + \Delta))}.$$

Proof. The proof is clear.

Using the condition of Theorem 3.2 with the parameters given in Table 1, we obtain the critical value of the Neimark–Sacker bifurcation parameter as $\bar{K} = 7.6861$.

Theorem 3.3 ([35]). For any generic two dimensional one-parameter system

$$x \mapsto f(x, \alpha)$$

having at $\alpha = 0$ the fixed point $x_0 = 0$ with complex multipliers $\mu_{1,2} = e^{\pm i\theta_0}$, there is a neighbourhood of x_0 in which a unique closed invariant curve bifurcates from x_0 as α passes through zero.

The system has to satisfy the following genericity conditions:

- (1) $r'(0) \neq 0$, where $\mu_{1,2}(\alpha) = r(\alpha)e^{\pm i\varphi(\alpha)}$, $r(0) = 1$, $\varphi(0) = \theta_0$;
- (2) $e^{\pm ik\theta_0} \neq 1, k = 1, 2, 3, 4$;
- (3) $a(0) \neq 0$; where

$$a(0) = \operatorname{Re} \left[\frac{e^{-i\theta_0} g_{21}}{2} \right] - \operatorname{Re} \left[\frac{(1 - 2e^{i\theta_0})e^{-2i\theta_0}}{2(1 - e^{i\theta_0})} g_{20}g_{11} \right] - \frac{1}{2} |g_{11}|^2 - \frac{1}{4} |g_{02}|^2.$$

Theorem 3.4. For map (2.3), a supercritical Neimark–Sacker bifurcation occurs at $\bar{K} = 7.6861$, and the fixed point $E_* = (\bar{x}_1, \bar{x}_2) = (3.62133, 0.176282)$ is surrounded by a closed invariant curve that is stable.

Proof. For $\bar{K} = 7.6861$, the Jacobian matrix of map (2.3) at the nontrivial fixed point is

$$A(\bar{K}) = \begin{pmatrix} 0.910073 & -2.07356 \\ 0.0433682 & 1 \end{pmatrix} \tag{3.1}$$

and has the eigenvalues

$$\mu_{1,2} = 0.955037 \pm 0.296488i = e^{\pm i\theta_0}, \theta_0 = 0.301013.$$

It is clear that (C1) and (C2) are satisfied. To verify the non-degeneracy condition (C3), we have to compute $a(0) \neq 0$. The critical Jacobian matrix $A(\bar{K})$ has the eigenvectors

$$\begin{aligned} A(\bar{K})q &= e^{i\theta_0}q, \\ A(\bar{K})^T p &= e^{-i\theta_0}p, \end{aligned}$$

where

$$q \sim (-0.989704, 0.0214609 + 0.141513i)^T, \tag{3.2}$$

$$p \sim (0.0214609 + 0.141513i, 0.989704)^T. \tag{3.3}$$

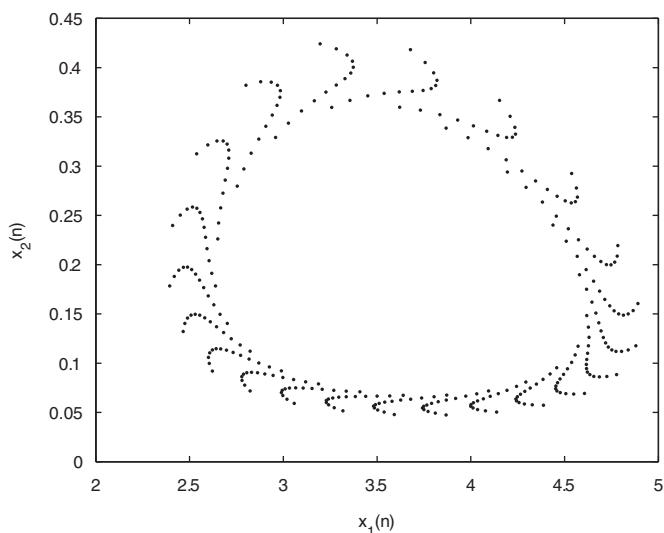


Figure 2. Stable invariant curve in map (2.3) for $\bar{K} = 7.6861$.

To obtain the normalization $\langle p, q \rangle = 1$, we can take

$$q = (-0.989704, 0.0214609 + 0.141513i)^T, \quad (3.4)$$

$$p = (-0.505202 + 0.0766158i, 2.18814 \times 10^{-16} + 3.53325i)^T. \quad (3.5)$$

Now we form

$$x = x^0 + zq + \bar{z}\bar{q}$$

and evaluate the function

$$H(z, \bar{z}) = \langle p, F(x^0 + zq + \bar{z}\bar{q}, \bar{K}) - x^0 \rangle.$$

Computing its Taylor expansion at $(z, \bar{z}) = (0, 0)$,

$$H(z, \bar{z}) = e^{i\theta_0} z + \sum_{2 \leq j+k \leq 3} \frac{1}{j!k!} g_{jk} z^j \bar{z}^k + O(|z|^4),$$

gives

$$g_{20} = -0.209213 - 0.0715625i, g_{11} = -0.000184023 - 0.00134844i,$$

$$g_{21} = 0.0341405 - 0.0055375i, g_{02} = 0.255385 + 0.0759236i,$$

which allows us to find the critical real part

$$a(0) = \operatorname{Re} \left[\frac{e^{-i\theta_0} g_{21}}{2} \right] - \operatorname{Re} \left[\frac{(1 - 2e^{i\theta_0}) e^{-2i\theta_0}}{2(1 - e^{i\theta_0})} g_{20} g_{11} \right] - \frac{1}{2} |g_{11}|^2 - \frac{1}{4} |g_{02}|^2 = -0.00281049.$$

Therefore, a supercritical Neimark–Sacker bifurcation occurs at $\bar{K} = 7.6861$ (Figure 2).

4. Results and discussion

In this paper, we propose and analyse a plankton model with continuous and discrete time. Some theoretical results are obtained for the local behaviour of the model. To test these theoretical results, parameters values (Table 1) are taken from the study of Edwards and Briently [30] in terms of consistency with the biological facts. In addition, we try to explain the dynamics of the bloom, which is the most significant problem in the plankton model. The Neimark–Sacker analysis shows that the parameters θ (rate of toxin production per phytoplankton), β (x_2 growth efficiency) and K (environmental carrying capacity of phytoplankton) play a key role in the dynamics of the bloom.

Theorems 3.2 and 3.4 show that, when the carrying capacity K of phytoplankton crosses a threshold value \bar{K} , the system undergoes a Neimark–Sacker bifurcation. The numerical value of \bar{K} is obtained by using the parameter values given in Table 1, yielding $\bar{K} = 7.6861$ at which the plankton bloom occurs (Figures 2 and 5). This is biologically reasonable because the population density of phytoplankton grows with the increasing carrying capacity [17,36,37]. When the carrying capacity is small, the toxic effect on zooplankton is also small, and both populations can coexist at a stable steady state. Contrary to that, the planktonic bloom has high probability when the carrying capacity increases, and, in that case, the toxin produced by the phytoplankton population plays an important role in the termination of the bloom [38]. Figure 3 shows that the nontrivial fixed point of the map is locally asymptotically stable with damping oscillation for the small value of K . Alternately, the system experiences unstable oscillation for large values of K (Figure 4).

In the plankton system, chaotic behaviour can arise due to interactions between seasons and internal biological rhythms [39]. The role of chaos was identified and recognized by Huisman and Weissing [40]. From the mathematical point of view, if a dynamical system has a positive largest Lyapunov exponent, then the system exhibits chaotic dynamics. For map (2.3), the maximum

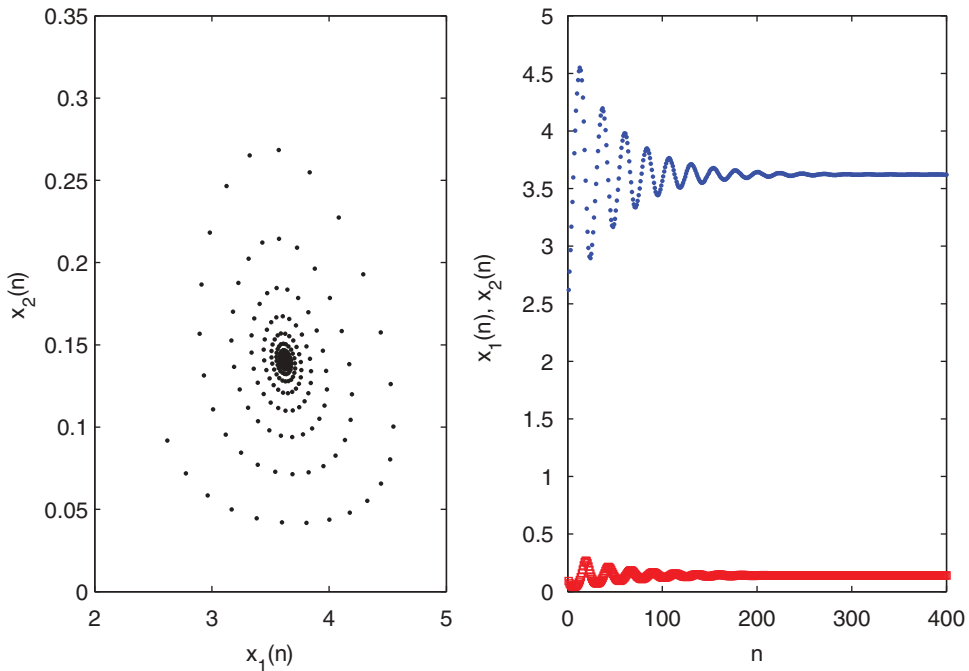


Figure 3. Stable focus in the map for $K = 6.25$. Initial conditions and other parameters are the same as in Figure 1.

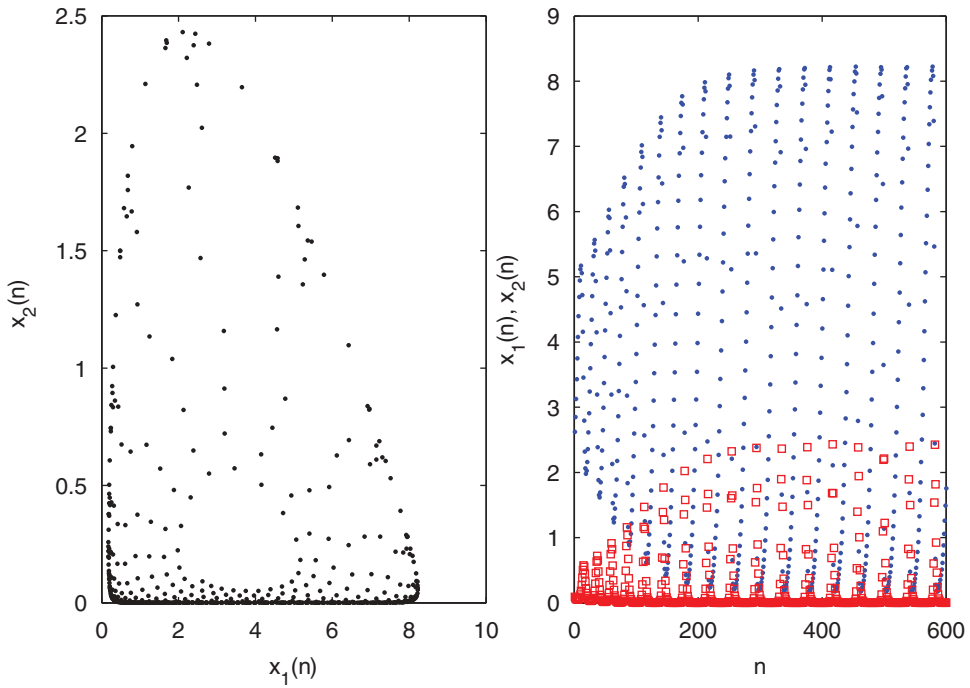


Figure 4. Unstable fixed point of the map for $K = 9.09091$. Initial conditions and other parameters are the same as in Figure 1.

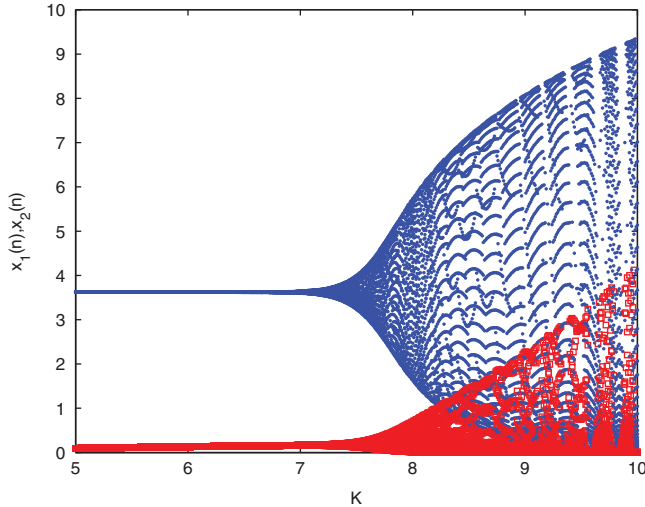


Figure 5. Bifurcation diagram of the map with respect to parameter K .

Lyapunov exponents corresponding to Figure 5 are calculated and plotted in Figure 10(a) [41], which demonstrates the existence of the chaotic regions in the parametric space.

There is also a variety of evidence that the toxic substance plays a key role in the growth of the zooplankton population in controlling the dynamics of bloom [14,18,19,42–44]. This result is also valid for our system. The parameter θ is determined as a bifurcation parameter to show the existence of Neimark–Sacker bifurcation around the nontrivial fixed point. When the value of the

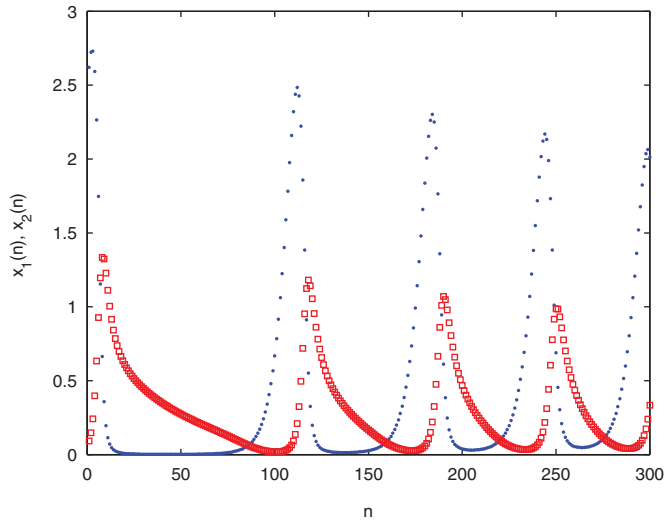


Figure 6. Periodic solutions of the map for $\bar{\theta} = 0.167996$ due to the Neimark–Sacker bifurcation, where $x_1(1) = 3.6213, x_2(1) = 0.0919$ and other parameters are taken from Table 1.

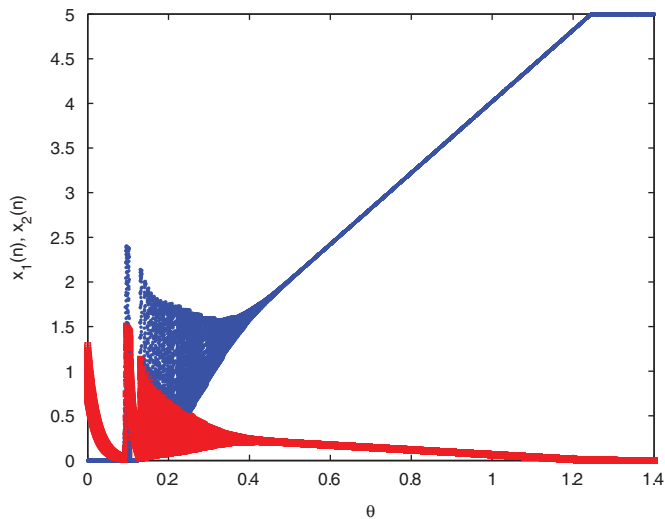


Figure 7. Bifurcation diagram of the map with respect to parameter θ .

rate of toxin production is $\bar{\theta} = 0.167996$, a periodic solution occurs as a result of Neimark–Sacker bifurcation (Figures 6 and 7). The phytoplankton bloom occurs between the 47th and 112th days. When the phytoplankton population reaches the first peak at the 112th day, it releases too much of the toxic substance such that it controls the bloom of the zooplankton and also its own bloom. After the bloom, the phytoplankton population decreases and finally attains very low densities at the 139th day. In this period, the zooplankton population decreases between the 8th and 102nd day. Alternately, zooplankton bloom occurs between the 102nd and 118th day. After the zooplankton bloom, the zooplankton population starts to decrease, and it reaches low density at the 173rd day. When there is a low concentration of toxin, both populations lead to another bloom and the process continues (Figure 6). Results from Chattopadhyay et al. [14] support our

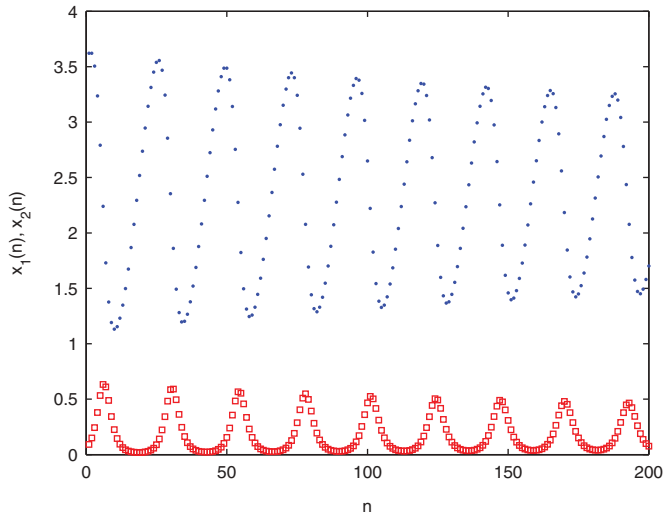


Figure 8. Periodic solutions of the map for $\bar{\beta} = 0.384513$ due to the Neimark–Sacker bifurcation. Initial conditions and other parameters are taken from Figure 1.

findings. In addition, the system exhibits chaotic dynamics for some values of the parameter θ (Figures 7 and 10(b)).

In contrast, if θ is increased beyond $\bar{\theta}$, the zooplankton population becomes extinct and the phytoplankton population reaches its environmental carrying capacity (Figure 7). In this situation, the system tends to fixed point $E_1 = (K, 0)$.

Another important parameter controlling the bloom is β . If the growth efficiency of the population of zooplankton passes a threshold value, $\bar{\beta} = 0.384513$, the system undergoes a Neimark–Sacker bifurcation and the bloom occurs (Figures 8 and 9). Due to the increase of β , the zooplankton population increase triggers the zooplankton bloom. In this period, the zooplankton requires more phytoplankton, and they consume too much phytoplankton; as a result,

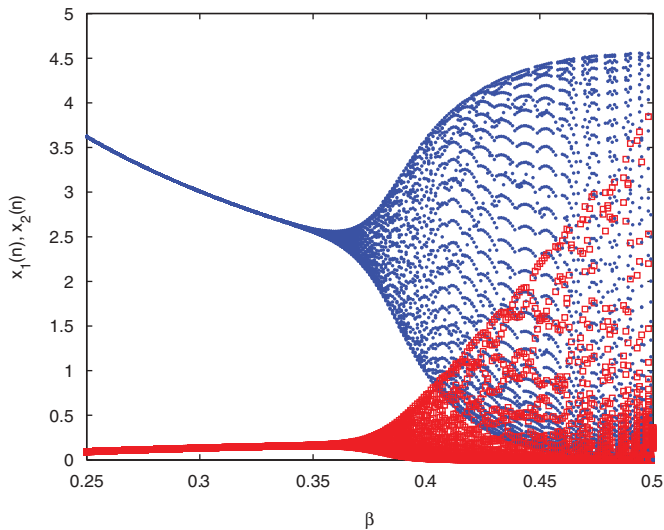


Figure 9. Bifurcation diagram of the map with respect to parameter β .

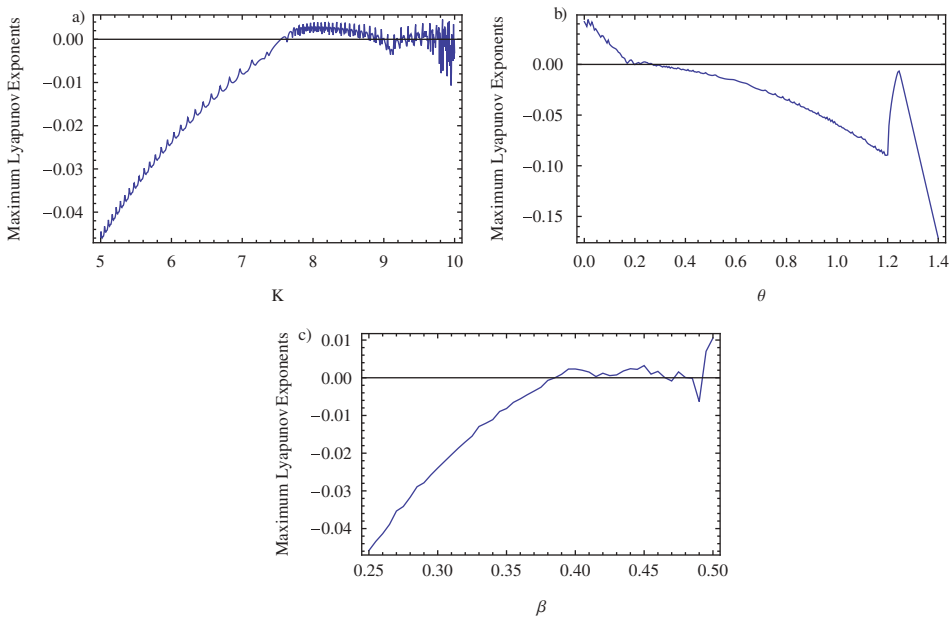


Figure 10. Maximum Lyapunov exponents corresponding to [Figure 5\(a\)](#), [Figure 7\(b\)](#) and [Figure 9\(c\)](#).

the zooplankton leads to a reduction of the phytoplankton population. As the phytoplankton population decreases, the zooplankton cannot consume sufficient nutrients, so the population tends to decrease. If β exceeds $\hat{\beta}$, the system exhibits chaotic dynamics where the populations of phytoplankton and zooplankton cannot be controlled ([Figures 9 and 10\(c\)](#)).

5. Conclusion

In this study, we prefer to use differential equations with piecewise constant arguments instead of delay differential equations for two important reasons. The first reason is that analysing of delay differential equations is usually very difficult because the state space of these equations are infinite dimensional. Therefore, a numerical approach may be needed for delay differential equations. In this paper, this is done by using differential equations with piecewise constant arguments.

The second reason for using differential equations with piecewise constant arguments is related to biology. It is well known that the macroscopic biological state is continuous and the microscopic biological state is discrete. However, using a mathematical model that considers the population interactions from the microscopic level and the macroscopic level at the same time could allow us to better understand the biological phenomenon. Our model that combine properties both differential and difference equations considers the microscopic state and the macroscopic state at the same time.

We note that our model is different from model (1.1), in which the delay only occurs in the Holling type II functional response due to the liberation of toxic substances by the phytoplankton species. This is reflected by discrete time in our model. In addition, Model (1.2) also includes another time lag, which is reflected by discrete time, due to a gestation period.

Model (1.1) and the discrete version of model (1.2), which is given as (2.2), have both same and different dynamic properties. For example, the equilibrium points of system (1.1) and (2.2) are the same. In addition, the periodic solution occurs as a result of Hopf bifurcation in model (1.1) at the delay parameter. For model (2.2), the Neimark–Sacker bifurcation, which is a discrete version of the Hopf bifurcation in the discrete dynamical

system, occurs for three different parameters. While the study [19] explained that the bloom depends on one parameter, we explain that the bloom depends on three different parameters, namely θ (rate of toxin production per phytoplankton), β (x_2 growth efficiency) and K (environmental carrying capacity of phytoplankton). This result is biologically reasonable because the population density of phytoplankton grows with the increasing carrying capacity (K) where the planktonic bloom has high probability [17,36,37]. Another reason behind population succession and bloom is the toxin produced (θ). Plankton ecology studies show that phytoplankton start to release toxic chemicals or become toxic very quickly in the presence of dense zooplankton population; as a result, the grazing pressure decreases, and the toxic effect on zooplankton will help in the termination of blooms [14,18,19,42–44]. In addition, due to the increase of β , the zooplankton population increase triggers the zooplankton bloom. In this period, the zooplankton requires more phytoplankton, and they consume too much phytoplankton. So, the presence of low concentration of toxin leads to zooplankton bloom [14]. Finally, we can say that our model also explains the chaotic dynamics in the plankton system.

Disclosure statement

No potential conflict of interest was reported by the authors.

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