Nonlinear Dyn (2015) 81:1895–1906
DOI 10.1007/s11071-015-2114-1

ORIGINAL PAPER

Modelling and analysis of spatio-temporal dynamics of a marine ecosystem

Kunal Chakraborty · Vamsi Manthena

Received: 7 November 2014 / Accepted: 21 April 2015 / Published online: 1 May 2015

Abstract This paper examines the spatio-temporal dynamics of a marine ecosystem. The system is described by two reaction–diffusion equations. We consider a phytoplankton–zooplankton system with Ivlev-type grazing function. The dynamics of the reaction–diffusion system of phytoplankton–zooplankton interaction has been studied with both constant and variable diffusion coefficients. Periodic oscillations of the phytoplankton and zooplankton populations are shown with constant and variable diffusion coefficients. In order to obtain spatio-temporal patterns, we perform numerical simulations of the coupled system describing phytoplankton–zooplankton dynamics in the presence of diffusive forces. We explain how the concentration of species changes due to local reactions and diffusion. Our results suggest that patchiness is one of the basic characteristics of the functioning of an ecological system. Two-dimensional spatial patterns of phytoplankton–zooplankton dynamics are self-organized and, therefore, can be considered to provide a theoretical framework to understand patchiness in marine environments.

Keywords Reaction–diffusion equations · Marine ecosystem · Diffusion-driven instability · Spatio-temporal dynamics · Patchiness

1 Introduction

The stability of ecological systems, interactions, and persistence of species in an ecosystem are the fundamental concerns of ecology. In this regard, there has been ongoing research in the field of stability of interactions for the last 40 years. The formulation of a marine ecosystem using mathematical models is quite a difficult task. We generally consider different types of differential equations to describe the dynamics of such systems [1–4]. Prey–predator interaction is one of the major areas of interest. Mathematical models have been used to study these systems [5–8]. These models have been used for prediction and analysis of ecological phenomena.

Most of the ecological phenomena, including but not limited to population dynamics, species abundance, and individual behavior, exhibit spatial variation. Partial differential equations could be used to model various ecological phenomena [9]. Incorporation of diffusion into the prey–predator equations made the systems more realistic [10]. Reaction–diffusion equations were used to describe such systems. Low diffusion values

K. Chakraborty (✉)
Information Services and Ocean Sciences Group, Indian National Centre for Ocean Information Services, Hyderabad, Ocean Valley, Pragathinagar (BO), Nizampet (SO), Hyderabad 500090, India
e-mail: kunal.c@incois.gov.in

V. Manthena
School of Mathematics and Statistics, University of Hyderabad, Hyderabad 500046, India
e-mail: vamsi.manthena@gmail.com

led a periodic Lotka–Volterra system to an aperiodic system over time. It was also observed that the system was sensitive to initial conditions of the system, and diffusion induces chaos [11].

The effects of predator response functions were studied by several researchers [12,13]. The stability of the system was strongly dependent on the predator response function [14]. For ratio-dependent systems, local asymptotic stability does not necessarily imply persistence and hence cannot imply global stability [15]. The system becomes unstable with diffusion, and a Turing bifurcation was observed [16]. This ratio-dependent prey–predator model with diffusion was taken forward by Wang and Qu [17]. They also incorporated disease into the model.

Pattern formation, in prey–predator models, was studied to show the instability driven by diffusion or by dispersion. The system was described with two reaction–diffusion equations. It was shown that, for a wide range of initial conditions, the system led to the formation of irregular patterns corresponding to spatio-temporal chaos. The chaotic pattern was first observed in the subdomain of the system. As time passes, the chaotic pattern grows and eventually the entire space becomes chaotic, completely replacing the regular pattern [18].

Cross diffusion induces stationary patterns in the models. These patterns may give greater insight into the understanding of the dynamics of the ecosystem [19]. Migration has a significant effect on the pattern formation of the population. In the presence of migration, the Turing pattern changes to travelling pattern. Both migration and diffusion lead to dynamical complexity that is encountered in natural ecosystems [20].

Dormancy is considered to be a method of escaping from unfavorable environmental conditions. Dormancy of predators is not a generator but an enhancer of spatio-temporal Turing patterns in prey–predator reaction–diffusion systems [21]. It was considered that the stability of the plankton ecosystem mainly depended on the nutrient uptake rate by the phytoplankton and zooplankton grazing rate, but nutrient recycling is an important factor for the coexistence of the plankton species [22].

Toxin production by phytoplankton plays an important role in planktonic interactions and therefore in regulating planktonic blooms. The qualitative behaviors of the models are likely to alter in the presence of toxin-producing phytoplankton (TPP) and hence, while modelling plankton dynamics, the inhibitory effect of TPP should be considered very carefully [23]. Zooplankton should be more patchy than phytoplankton, a property that is often seen in natural settings [24]. Periodic toxin liberation by phytoplankton can be regarded as a mechanism for plankton patchiness [25]. There are subtle but relevant differences in the roles played by phytoplankton and zooplankton in promoting patchiness. The interaction between toxin-producing phytoplankton and zooplankton in marine environments may be partly driven by the forces of diffusion [26].

Eruption of algal bloom results from increasing the nutrient concentration. Zooplankton only plays a role in alleviating the scale of algal bloom. This could be used to explain the mechanism of algal bloom occurrence in many natural waters [27].

This paper is organized as follows. In Sect. 2, the qualitative properties of the system are described, and subsequently, the model is developed with diffusion coefficients. In Sect. 3, the existence of coexisting equilibrium is discussed, and the criterion for the stability of the system is derived around coexisting equilibrium. In Sect. 4, the dynamics of both the one-dimensional and the two-dimensional reaction–diffusion systems of phytoplankton–zooplankton interaction is studied. Numerical simulation is carried out in Sect. 5. A brief conclusion of the biological significance of our findings is provided in the final section.

2 Qualitative properties of the system and model formulation

We consider a two-component phytoplankton–zooplankton model. The ecological setup of the system is based on some major assumptions such as the growth of phytoplankton is assumed to be modified Leslie–Gower type [28,29]. This means that in the case of severe scarcity of nutrient, phytoplankton can switch over to other sources. But its growth will be limited due to the fact that its most favorite source, nutrients, is not available in abundance. This can be incorporated by adding a positive constant to the denominator, and hence, the growth function is considered to be modified Leslie–Gower type. Grazing of zooplankton on phytoplankton is parametrized using the Ivlev function. Further, we have considered the impact of fish on plankton dynamics without taking into account the effect of plankton on the population dynamics of fish.

Again, it is reasonable to consider a sigmoid functional response which explains the fact that, at low densities of zooplankton population, the effect of predation is low, but if the zooplankton population size increases, predation is then more intensive, i.e., the predator (fish) is considered to be generalist. It is to be noted that the loss term $\sigma Z^2(t)/(a^2+Z^2(t))$ represents the impact of fish community as a whole.

Therefore, at any given location (X, Y) and time T, let us assume that the phytoplankton $P(X, Y, T)$ and zooplankton $Z(X, Y, T)$ populations satisfy the reaction–diffusion equations given below:

$$\begin{aligned}\frac{\mathrm{d}P}{\mathrm{d}t} &= rP(t)\left[1-\frac{P(t)}{mN+K}\right]\\ &\quad -\beta[1-e^{-\alpha P(t)}]Z(t)+D_P\Delta P(t), \qquad (2.1)\\ \frac{\mathrm{d}Z}{\mathrm{d}t} &= \gamma\beta\left[1-e^{-\alpha P(t)}\right]Z(t)\\ &\quad -\delta Z(t)-\frac{\sigma Z^2(t)}{a^2+Z^2(t)}+D_Z\Delta Z(t). \qquad (2.2)\end{aligned}$$

where D_P and D_Z are the diffusion coefficients of the phytoplankton and zooplankton, respectively. α is the Ivlev constant, and β is the rate of consumption of zooplankton to the phytoplankton population. γ represents the conversion efficiency of the consumed phytoplankton into new zooplanktons, and a is the half capturing saturation constant. m is the nutrient phytoplanktons' conversion factor. K represents the residual loss in phytoplankton due to severe scarcity of nutrient N. The mortality rate of the predator is denoted by δ, and σ is the predation rate of the zooplankton by the fish population.

We consider a domain in which the system is bounded. We assume that the system has zero-flux boundary condition, which means that the species cannot leave the domain under consideration. We also assume appropriate initial conditions. Without the effect of diffusion, the system would be:

$$\frac{\mathrm{d}P}{\mathrm{d}t}=rP(t)\left[1-\frac{P(t)}{mN+K}\right]-\beta[1-e^{-\alpha P(t)}]Z(t), \qquad (2.3)$$

$$\frac{\mathrm{d}Z}{\mathrm{d}t}=\gamma\beta\left[1-e^{-\alpha P(t)}\right]Z(t)-\delta Z(t)-\frac{\sigma Z^2(t)}{a^2+Z^2(t)}. \qquad (2.4)$$

The model contains many parameters such as α and β, all of which are positive. We write Eqs. (2.3) and (2.4) in a dimensionless form by taking $P(t)=(mN+K)u(t)$, $Z(t)=\frac{r(mN+K)}{\beta}v(t)$ and $rt=T$.

For the sake of simplicity, let us assume that

$$b=\frac{\gamma\beta}{r},\quad c=\frac{\delta}{r},\quad h=mN+K,\quad \theta=\frac{\sigma\beta}{h}.$$

By applying these assumptions to the system, the system gets reduced to:

$$\begin{aligned}\frac{\mathrm{d}u}{\mathrm{d}T} &= u(1-u)-v(1-e^{-\alpha' u}),\\ \frac{\mathrm{d}v}{\mathrm{d}T} &= b(1-e^{-\alpha' u})v-cv-\theta\frac{h^2v^2}{a^2\beta^2+r^2h^2v^2},\end{aligned}$$

where $\alpha'=\alpha(mN+K)$. The phytoplankton and zooplankton populations are denoted by $u(x, y, T)$ and $v(x, y, T)$, respectively. c is the per capita death rate of zooplankton. Again, for simplicity, we drop the tildas and the equations become:

$$\frac{\mathrm{d}u}{\mathrm{d}T} = u(1-u)-v(1-e^{-\alpha u}), \qquad (2.5)$$

$$\frac{\mathrm{d}v}{\mathrm{d}T} = b(1-e^{-\alpha u})v-cv-f\theta, \qquad (2.6)$$

where $f=\dfrac{h^2v^2}{a^2\beta^2+r^2h^2v^2}$.

The zero isoclines of the equations above are:

$$u(1-u)-v(1-e^{-\alpha u})=0, \qquad (2.7)$$

$$b(1-e^{-\alpha u})-c-\frac{f}{v}\theta=0. \qquad (2.8)$$

3 Stability analysis

It would be appropriate to consider the local dynamics of the system before moving on to numerical analysis and spatio-temporal pattern formation. In this section, we present the analytical analysis of the model system without the effect of diffusion. This analysis would help us estimate the parameter ranges required for numerical analysis.

3.1 Linear stability analysis

The system has the following equilibrium states:

1. Total extinction $E_0=(0,0)$
2. Extinction of the zooplankton $E_1=(P_1,0)$
3. Non-trivial coexistence point $E_*=(P_*, Z_*)$

The final state, the non-trivial equilibrium state E_* in which both zooplankton and phytoplankton coexist, is the state we are most interested in.

From Eq. (2.3), we get

$$rP_*\left[1-\frac{P_*}{mN+K}\right]=\beta(1-e^{-\alpha P_*})Z_*.$$

This can be simplified to get an equation in terms of Z_*,

$$Z_*=\frac{rP_*\left[1-\frac{P_*}{mN+K}\right]}{\beta\left(1-e^{-\alpha P_*}\right)}. \tag{3.1}$$

We apply Taylor expansion to the exponential term in Eq. (3.1),

$$Z_*=\frac{rP_*\left[1-\frac{P_*}{mN+K}\right]}{\beta\left(\alpha P_*-\frac{\alpha^2P_*^2}{2}\right)}. \tag{3.2}$$

Substituting (3.2) in Eq. (2.4), we get a polynomial for P.

$$A_1P^3+A_2P^2+A_3P+A_4=0, \tag{3.3}$$

where

$$A_1=\frac{-\gamma r^3}{(mN+K)^3},$$
$$A_2=\frac{3\gamma r^3}{(mN+K)^2},$$
$$A_3=\frac{3a^2\beta^2\gamma r\alpha^2}{(mN+K)},\ A_4=\gamma r^3+a^2\beta^2\gamma r\alpha^2.$$

P_* is the real positive root of the polynomial. Since all the parameters are positive, we can conclude that $A_1<0$ and $A_2, A_4>0$. Also, if $a\beta\alpha>r$, then A_3 is positive. Similarly, if $a\beta\alpha=r$ or $a\beta\alpha<r$, then $A_3=0$ or $A_4<0$, respectively. Therefore, the coexistence equilibria exist conditionally. We now look into the local behavior of the system of Eqs. (2.3) and (2.4) at each of the three equilibrium points. The variational matrix V at any point $E(P,Z)$ is given by

$$V(P,Z)=\begin{bmatrix} r-\frac{2rP}{mN+K}-\alpha\beta ze^{-\alpha P} & \beta(e^{-\alpha P}-1)\\ \alpha\beta\gamma ze^{-\alpha P} & \gamma\beta(1-e^{-\alpha P})-\delta-\frac{2\sigma a^2z}{(z^2+a^2)^2}\end{bmatrix}$$

The eigenvalues of the variational matrix V at E_0 are $\lambda_1=r$ and $\lambda_2=-\delta$. Thus, the equilibrium point E_0 is a saddle point with unstable manifold along the X-axis and stable manifold along the Y-axis.

The eigenvalues of the variational matrix V at E_1 are $\lambda_1=-r$ and $\lambda_2=\gamma\beta(1-e^{-\alpha(mN+K)})-\delta$. Hence, the stationary point E_1 is asymptotically stable if $\delta>\gamma\beta(1-e^{-\alpha(mN+K)})$.

The characteristic equation corresponding to variational matrix V at E_* is

$$\lambda^2-A\lambda+B=0$$

where

$$A=\left[r-\frac{2rP_*}{(mN+K)}-\frac{r\alpha e^{-\alpha P_*}P_*\left(1-\frac{P_*}{(mN+K)}\right)}{(1-e^{-\alpha P_*})}+\gamma\beta(1-e^{-\alpha P_*})-\delta-\frac{\sigma a^2z}{(a^2+z^2)}\right],$$

$$B=a_{11}a_{22}+\beta\alpha\gamma rP_*\left[1-\frac{P_*}{(mN+K)}\right]e^{-\alpha P_*},$$

$$a_{11}=\left[r-\frac{2rP_*}{(mN+K)}-\frac{r\alpha e^{-\alpha P_*}P_*\left(1-\frac{P_*}{(mN+K)}\right)}{(1-e^{-\alpha P_*})}\right],$$

$$a_{22}=\left[\gamma\beta(1-e^{-\alpha P_*})-\delta-\frac{\sigma a^2z}{(a^2+z^2)}\right].$$

For the coexisting equilibrium point E_* to be asymptotically stable, $A<0$ and $B>0$.

4 Plankton dynamics with diffusion

4.1 Constant diffusion

Let us now consider the effect of constant diffusion of the plankton populations on the system. By adding diffusion terms to the dimensionless Eqs. (2.5) and (2.6), we get

$$\frac{\mathrm{d}u}{\mathrm{d}T}=u(1-u)-v(1-e^{-\alpha u})+D_u\frac{\partial^2u}{\partial x^2}, \tag{4.1}$$
$$\frac{\mathrm{d}v}{\mathrm{d}T}=b(1-e^{-\alpha u})v-cv-f\theta+D_v\frac{\partial^2v}{\partial x^2}. \tag{4.2}$$

D_u and D_v represent the diffusion coefficients of phytoplankton and zooplankton, respectively. For this one-dimensional model system, we take the following boundary conditions for the phytoplankton $u(x,t)$ and zooplankton $v(x,t)$ populations in the interval $0\le x\le L$, $L>0$:

$$\frac{\partial u(0,t)}{\partial t}=\frac{\partial u(L,t)}{\partial t}=\frac{\partial v(0,t)}{\partial t}=\frac{\partial v(L,t)}{\partial t}=0.$$

The linearized system of the above equations is:

$$\frac{\mathrm{d}u}{\mathrm{d}T}=f_uX+f_vY+D_u\frac{\partial^2u}{\partial s^2},$$
$$\frac{\mathrm{d}v}{\mathrm{d}T}=g_uX+g_vY+D_v\frac{\partial^2v}{\partial s^2},$$

where $X = X(s, T)$ and $Y = Y(s, T)$ and

$$\begin{aligned} f_u &= 1 - 2u_* - \alpha v e^{-\alpha u_*}, \\ f_v &= -(1 + e^{-\alpha u_*}), \\ g_u &= b v_* \alpha e^{-\alpha u_*}, \\ g_v &= b(1 - e^{-\alpha u_*}) - c - \frac{\theta}{v_*} f. \end{aligned}$$

We now choose a solution for this set of equations:

$$\begin{aligned} u(x, t) &= \alpha_1 e^{\lambda T + ikx}, \\ v(x, t) &= \alpha_2 e^{\lambda T + ikx}. \end{aligned}$$

α_1 and α_2 are the amplitudes, while k is the wave number of the solution. The characteristic equation of the model system is:

$$\lambda^2 + A\lambda + B = 0, \tag{4.3}$$

where

$$\begin{aligned} A &= f_u + g_v - k^2(D_u + D_v), \\ B &= \left[f_u - D_u k^2\right]\left[g_v - k^2 D_v\right]. \end{aligned}$$

The roots of Eq. (4.3) are

$$\lambda = \frac{-A \pm \sqrt{A^2 - 4B}}{2}.$$

Our aim was to derive the criteria for diffusive instability of the model given by Eqs. (4.1) and (4.2). The system is unstable if one of the roots of the characteristic Eq. (4.3) is positive. A necessary condition for one of the roots to be positive is $A > 0$. So,

$$\begin{aligned} & f_u + g_v > k^2(D_u + D_v) \\ & \Rightarrow k^2 < \frac{f_u + g_v}{D_u + D_v}. \end{aligned}$$

From Eq. (3.8), we know that $g_v = 0$. Hence,

$$k^2 < \frac{f_u}{D_u + D_v}$$

As mentioned earlier, k is the wave number, and hence, k has to be real and positive. We know that D_u and D_v are positive and real. Hence, the above equation is feasible only if $f_u > 0$. Thus, the necessary condition for instability of the system reduces to $f_u > 0$. In terms of parameters, the necessary condition reduces to

$$\beta > \beta_* = \frac{\alpha r u_* e^{-\alpha u_*}\left[1 - \frac{u_*}{(mN+K)}\right]}{(1 - 2u_*)(1 - e^{-\alpha u_*})}. \tag{4.4}$$

The necessary condition for one of the roots to be positive is $F(k^2) < 0$, i.e,

$$\begin{aligned} & \left[f_u - D_P k^2\right]\left[g_v - D_v k^2\right] - f_v g_u < 0 \\ & \Rightarrow k^2 < \frac{f_u D_v + g_v D_u}{2 D_u D_v}. \end{aligned}$$

If k^2_{min} is the corresponding value of k^2 for the minimum value of $F(k^2)$, then:

$$k^2_{\text{min}} = \frac{f_u D_v + g_v D_u}{2 D_u D_v}.$$

Therefore,

$$\begin{aligned} & F(k^2_{\text{min}}) = \left[f_u - D_P k^2_{\text{min}}\right]\left[g_v - D_v k^2_{\text{min}}\right] - f_v g_u \\ & \Rightarrow F(k^2_{\text{min}}) = -\frac{(f_u D_v - g_v D_u)^2}{4 D_u D_v} - f_v g_u. \end{aligned}$$

From Eq. (2.8), we know that $g_v = 0$. So, the equation reduces to:

$$F(k^2_{\text{min}}) = -\frac{f_u^2 D_v}{4 D_u} - f_v g_u.$$

Thus, the sufficient condition reduces to $-\frac{f_u^2 D_v}{4D_u} - f_v g_u < 0$ which gives

$$\tau + 4\frac{f_v g_u}{f_u^2} > 0,$$

where $\tau = \frac{D_v}{D_u}$. Therefore, the necessary condition in terms of parameters reduces to

$$\begin{aligned} & \tau > \tau_* \\ & \quad = \frac{4\alpha\beta b r u_* e^{(-\alpha u_*)}\left(1 - e^{-2\alpha u_*}\right)\left(1 - \frac{u_*}{mN+K}\right)}{\left[\beta(1 - 2u_*)(1 - e^{-\alpha u_*}) + \alpha r u_* e^{-\alpha u_*}\left(\frac{u_*}{mN+K} - 1\right)\right]^2}. \end{aligned} \tag{4.5}$$

We have derived the conditions for diffusive instability of the system. The conditions are described by Eqs. (4.4) and (4.5). The diffusion of the phytoplankton drives the plankton system to an instable state when $\beta > \beta_*$ and when $\tau > \tau_*$. Ecologically, this translates to the fact that instability will continue to prevail if the zooplankton diffusion rate is more than phytoplankton diffusion rate, satisfying $\tau > \tau_*$.

4.2 Variable diffusion

In the diffusive system Eqs. (4.1) and (4.2), we have considered a constant diffusion coefficient for phytoplankton and zooplankton. Instead, we now assume that the diffusion coefficient of phytoplankton is constant, while the diffusion coefficient of zooplankton is periodic with time. Such periodic change in the diffusion coefficient could occur due to the movement of predator population for the hunt of food in different seasons. Availability of prey is a factor that is responsible for the periodicity in the diffusion of predator. Similar to the case of constant diffusion, we take D_u and D_u to be the diffusion coefficients of the prey and predator, respectively. D_v is a periodic function of time, given by:

$$D_v(T) = D_u(\zeta + \rho \sin(\omega T)). \tag{4.6}$$

In the above equation, $\zeta > 1$, ρ is small and $\zeta > |\rho|$. Since the period of oscillation is assumed to be small, the angular frequency ω will be large, i.e., $\omega \gg 1$. The model system can be written as:

$$\frac{\mathrm{d}u}{\mathrm{d}T} = u(1-u) - v(1 - e^{-\alpha u}) + D_u \frac{\partial^2 u}{\partial s^2}, \tag{4.7}$$

$$\frac{\mathrm{d}v}{\mathrm{d}T} = b(1 - e^{-\alpha u})v - cv - f\theta + D_v(\omega T)\frac{\partial^2 v}{\partial s^2}. \tag{4.8}$$

The boundary conditions are the same as those considered in Sect. (4.1). To obtain a dimensionless system, we assume $\omega T = \tau$. We want to study the diffusive stability of the system around the interior equilibrium point E_*, when the diffusion coefficient is periodic with time. We choose time-dependent solutions to the equations:

$$X(s, T) = \phi_1(T)e^{iks}, \quad Y(s, T) = \phi_2(T)e^{iks}.$$

In this equations, ϕ_1 and ϕ_2 are dependent on time T, and k is the wave number of perturbation. The linearized system around the equilibrium point E_* in terms of ϕ_1 and ϕ_2 is:

$$\frac{\mathrm{d}\phi_1}{\mathrm{d}\tau} = \Theta_1\phi_1 + \Theta_2\phi_2, \tag{4.9}$$

$$\frac{\mathrm{d}\phi_2}{\mathrm{d}\tau} = \Theta_3\phi_1 + \Theta_4(\tau)\phi_2, \tag{4.10}$$

where $\Theta_1 = \frac{f_u - k^2 D_u}{\omega}$, $\Theta_2 = \frac{f_v}{\omega}$, $\Theta_3 = \frac{g_u}{\omega}$ and $\Theta_4(\tau) = \Theta_5 + \Theta_6(\tau)$ where $\Theta_5 = \frac{g_v - \zeta k^2 D_u}{\omega}$ and $\Theta_6(\tau) = -\frac{k^2 D_u \rho}{\omega}\sin(\tau)$.

We solve the Eqs. (4.9) and (4.10) by taking the following transformation:

$$\psi(\tau) = \exp\left(-\frac{1}{2}\int [\Theta_1 + \Theta_4(\tau)]d\tau)\phi_1(\tau)\right). \tag{4.11}$$

Substituting Eq. (4.11) in (4.9) and (4.10), we get:

$$\frac{\mathrm{d}^2\psi}{\mathrm{d}\tau^2} + P(\tau)\psi(\tau) = 0, \tag{4.12}$$

where $P(\tau) = \frac{1}{2}\frac{\mathrm{d}}{\mathrm{d}\tau}(\Theta_4(\tau)) - \frac{1}{4}(\Theta_1 + \Theta_4(\tau))^2 + (\Theta_1\Theta_4(\tau) - \Theta_2\Theta 3)$.

Let $\tau = 2\eta$, then substituting the values of Θs from above into Eq. (4.12), we get the Hill's equation.

$$\frac{\mathrm{d}^2\psi}{\mathrm{d}\eta^2} + [l_1 + l_2(-2\cos(2\eta) + 2l_3\sin(2\eta)) + l_4 \cos 4\eta]\,\psi(\eta) = 0, \tag{4.13}$$

where

$$l_1 = -\frac{1}{\omega^2}\left[f_u - (1+\zeta)k^2 {D_u}^2 + \frac{1}{2}\rho^2 k^4 D_u^2 + 4\zeta k^2 D_u(f_u - k^2 D_u) + 4 f_v g_u\right],$$

$$l_2 = \frac{\rho k^2 D_u}{\omega},$$

$$l_3 = -\frac{1}{\omega}\left[f_u + (\zeta - 1)k^2 D_u\right],$$

$$l_4 = \frac{\rho^2 k^4 D_u^2}{2\omega^2}.$$

If Eq. (4.13) is solved, we can find ϕ_1 and ϕ_2 from Eqs. (4.9) and (4.10). Using ϕ_1 and ϕ_2, we can determine the stability of the system. From Eq. (4.11), we have the time-dependent solution

$$\phi_1 = \exp\left(\frac{1}{2}\int [\Theta_1 + \Theta_4]d\tau\right)\psi(\tau). \tag{4.14}$$

Earlier, we had assumed that the period of oscillation and the amplitude of variability of the diffusion coefficient were small. So, $l_2 \ll 1$. Then, l_4 becomes very small, and the Eq. (4.13) reduces to

$$\frac{\mathrm{d}^2\psi}{\mathrm{d}\eta^2} + [l + l_2(-2\cos(2\eta) + 2l_3\sin(2\eta))]\psi(\eta) = 0, \tag{4.15}$$

where $l = -\frac{1}{\omega^2}[f_u - (1+\zeta)k^2 {D_u}^2 + 4\zeta k^2 D_u(f_u - k^2 D_u) + 4 f_v g_u]$.

We solve Eq. (4.15) using the power series expansion of $\psi(\tau)$ upto the first degree. We substitute this into Eq. (4.15) and then equate the coefficients of the like powers of l_2 to get the following two equations:

$$\frac{\mathrm{d}^2\psi_0}{\mathrm{d}\eta^2} + l\psi_0(\eta) = 0, \tag{4.16}$$

$$\frac{\mathrm{d}^2\psi_1}{\mathrm{d}\eta^2} + l\psi_1(\eta) + (-2\cos(2\eta) + 2n\sin(2\eta))\psi_0(\eta) = 0. \tag{4.17}$$

If $l < 0$, let $l = -\theta^2$. The solution of Eq. (4.16) is

$$\psi_0(\eta) = A_{\psi_0}e^{\theta\eta} + B_{\psi_0}e^{-\theta\eta}, \tag{4.18}$$

where A_{ψ_0} and B_{ψ_0} are arbitrary constants which do not depend on η. Substituting Eq. (4.18) into Eq. (4.17), we get

$$\frac{\mathrm{d}^2\psi_1}{\mathrm{d}\eta^2} + l\psi_1(\eta) = A_{\psi_0}e^{\theta\eta}[2\cos(2\eta) - 2n\sin(2\eta)] + B_{\psi_0}e^{\theta\eta}[2\cos(2\eta) - 2n\sin(2\eta)]. \tag{4.19}$$

Thus, both $\psi_0(\eta)$ and $\psi_1(\eta)$ can be solved using the above equations, and the solutions are bounded. Thus, from Eq. (4.14), we get

$$\phi_1 = \exp\left[\frac{1}{\omega}f_u - (1+\zeta)k^2 D_u\eta + \frac{1}{2\omega}\rho k^2 D_u\cos(2\eta)\right](\psi_o(\eta) + m\psi_1(\eta)). \tag{4.20}$$

We follow Bhattacharyya et al. [30] to conclude that the system is stable if

$$\Theta_1 + \Theta_5 + \sqrt{(\Theta_1 - \Theta_5)^2 + 4\Theta_2\Theta_3} < 0.$$

This reduces to $\Theta_1\Theta_5 > \Theta_2\Theta_3$, or

$$\zeta k^4 - \zeta f_u D_u k^2 - f_v g_u > 0. \tag{4.21}$$

Here, we know that $f_v < 0$ and $g_u > 0$. Hence, we can conclude that $-f_v g_u > 0$. So, the criterion is met if $f_u > 0$. In terms of parameters, this reduces to:

$$\beta > \beta_* = \frac{\alpha r u_* e^{-\alpha u_*}\left[1 - \frac{u_*}{(mN+K)}\right]}{(1-2u_*)(1-e^{-\alpha u_*})}. \tag{4.22}$$

Also, we know that Eq. (4.21) is positive for all k. This criterion is met if

$$[f_u\zeta D_u]^2 - 4\zeta f_v g_u < 0.$$

Hence, in terms of parameters, this reduces to

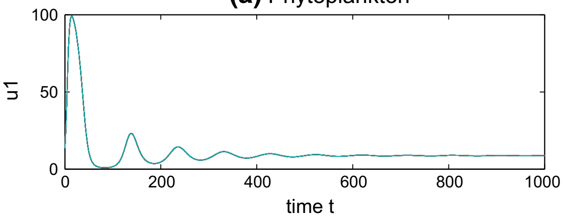
$$\zeta < \zeta_* = \frac{4\alpha b r u_* e^{-\alpha u_*}\left(1 - \frac{u_*}{mN+K}\right)}{\beta(1-e^{-\alpha u_*})(1-2u_*) + \alpha r u_* e^{-\alpha u_*}\left(\frac{u_*}{mN+K} - 1\right)}. \tag{4.23}$$

Hence, Eqs. (4.22) and (4.23) are the conditions for diffusive instability in the presence of variable diffusion coefficient of the predator.

5 Numerical analysis

The reaction–diffusion system has very interesting dynamics depending on the parameters of the system. The system with constant diffusion coefficients shows that the equilibrium point E_* is conditionally stable. The system becomes unstable when $\beta > \beta_*$ and $\tau > \tau_*$. We have verified the results numerically. The numerical analysis is performed with the help of the software MATLAB. We show three states of the system with the effect of diffusion. At $t = 1000$, we observe that for parameter values $\alpha = 0.01, b = 0.42, D = 0.5, \gamma = 0.3, \beta = 0.4, m = 0.5, N = 20, K = 110, a = 3, c = 0.02, \epsilon = 10^{-7}, r = 0.5, \delta = 0.01$ and $\sigma = 0.001$, the system is in stable state (Fig. 1). When α is increased to 0.012, γ is increased to 0.6 and β is increased to 0.7, the population of the system is showing large amplitude oscillations. However, this oscillation does not sustain, and with $t > 5000$, a stable solution is observed. Instead, when $\alpha = 0.015$, $\beta = 0.9$ and $\gamma = 0.6$ is considered, a clear periodic oscillation can be observed which corresponds to an unstable solution.

(a) Phytoplankton



(b) Zooplankton

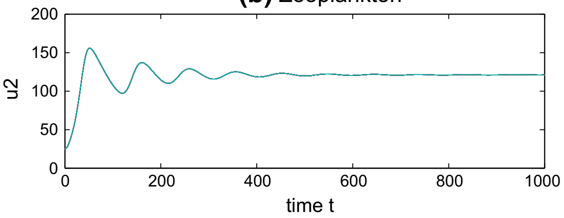


Fig. 1 Stable solution of phytoplankton and zooplankton of the system at $\alpha = 0.01, b = 0.42, D = 0.5, \gamma = 0.3, \beta = 0.4, m = 0.5, N = 20, K = 110, a = 3, c = 0.02, \epsilon = 10^{-7}, r = 0.5, \delta = 0.01$, and $\sigma = 0.001$

The phase graphs of the stable solution with the same parameter values mentioned for the two-dimensional plot are depicted (Figs. 2, 3).

The evolution of oscillatory behavior get into the system can be observed from Fig. 4. We can see that the amplitude of the graph is steadily reducing. This shows that the system will become stable with time.

Figures 5 and 6 are showing phase plots corresponding to intermediate state (stable to unstable) of the system.

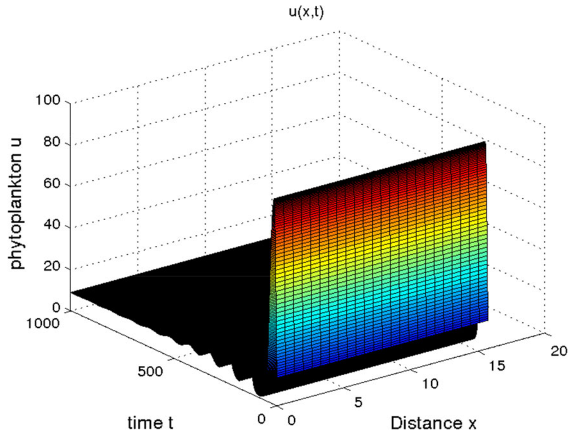


Fig. 2 Three-dimensional stable solution of phytoplankton at $\alpha = 0.01, b = 0.42, D = 0.5, \gamma = 0.3, \beta = 0.4, m = 0.5, N = 20, K = 110, a = 3, c = 0.02, \epsilon = 10^{-7}, r = 0.5, \delta = 0.01$ and $\sigma = 0.001$

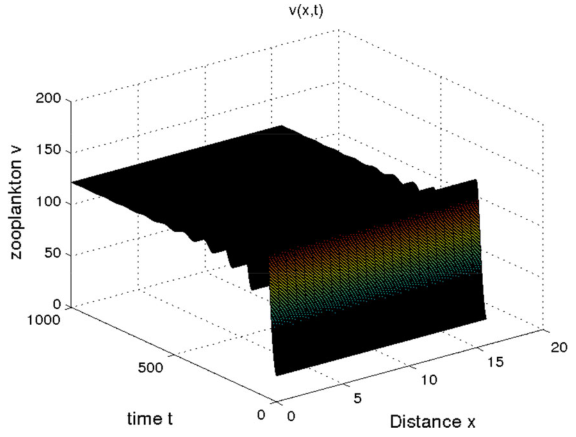


Fig. 3 Three-dimensional stable solution of zooplankton at $\alpha = 0.01, b = 0.42, D = 0.5, \gamma = 0.3, \beta = 0.4, m = 0.5, N = 20, K = 110, a = 3, c = 0.02, \epsilon = 10^{-7}, r = 0.5, \delta = 0.01$ and $\sigma = 0.001$

The reaction–diffusion system becomes unstable in the presence of diffusion when $\beta > \beta_*$ and $\tau > \tau_*$. We verified the unstable state numerically. Figure 7 depicts the unstable state of the system.

Figures 8 and 9 are showing the phase plots for periodic oscillations of the plankton populations.

The spatio-temporal dynamics of a chaotic system largely depends upon the choice of initial conditions. The initial distribution of the species considered is a two-dimensional initial condition of the following form:

$$u = 1 - \exp(-150((X - \lambda/2)^2 + (Y - \lambda/2)^2)),$$
$$v = \exp(-150((X - \lambda/2)^2 + 2(Y - \lambda/2)^2)).$$

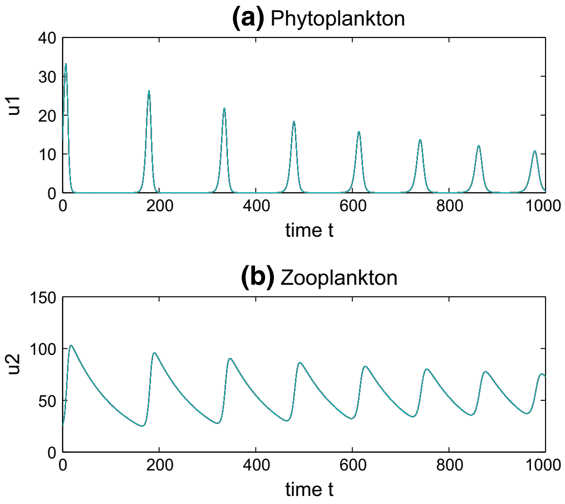


Fig. 4 Intermediate state of the system with parameter values, $\alpha = 0.012, b = 0.42, D = 0.5, \gamma = 0.6, \beta = 0.7, m = 0.5, N = 20, K = 110, a = 3, c = 0.02, \epsilon = 10^{-7}, r = 0.5, \delta = 0.01$ and $\sigma = 0.001$

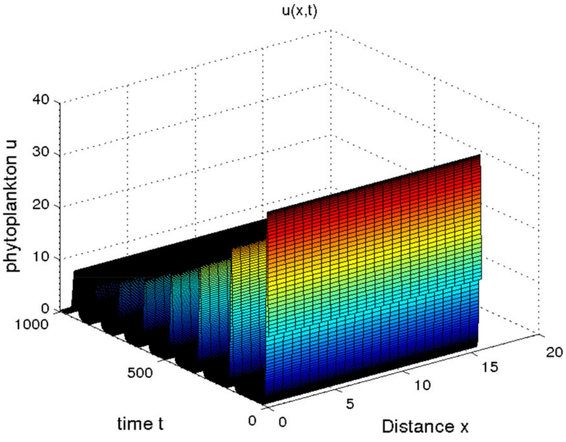


Fig. 5 Three-dimensional intermediate state of phytoplankton at $\alpha = 0.012, b = 0.42, D = 0.5, \gamma = 0.6, \beta = 0.7, m = 0.5, N = 20, K = 110, a = 3, c = 0.02, \epsilon = 10^{-7}, r = 0.5, \delta = 0.01$, and $\sigma = 0.001$

The numerical results obtained using semi-implicit numerical techniques of two-dimensional phytoplankton–zooplankton system are presented in Figs. 10, 11, and 12. Initial condition (as described above) with zero-flux boundary conditions (as explained in stability analysis) in two dimension is used to perform simulations of two-dimensional spatio-temporal system. The parameter values taken are $\alpha = 1.175$, $\gamma = 0.6$, $\beta = 0.75$, $m = 0.5$, $N = 25$, $K = 110$, $a = 3$, $r = 7.5$, $\delta = 0.01$, $\sigma = .001$, $Du = 3 * 10^{-5}$,

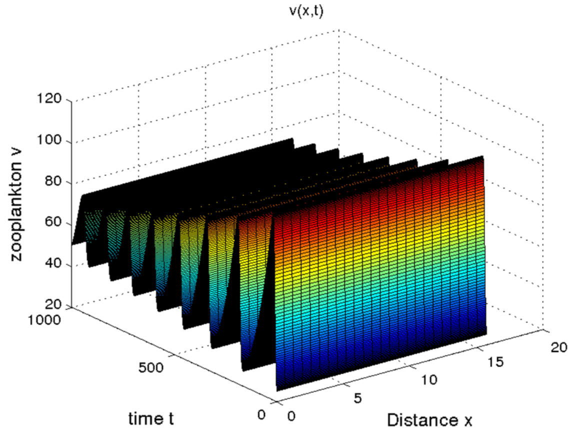
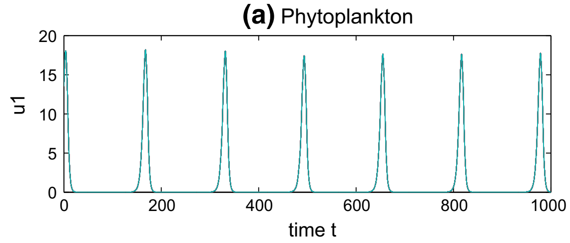


Fig. 6 Three-dimensional intermediate state of zooplankton at $\alpha = 0.012, b = 0.42, D = 0.5, \gamma = 0.6, \beta = 0.7, m = 0.5, N = 20, K = 110, a = 3, c = 0.02, \epsilon = 10^{-7}, r = 0.5, \delta = 0.01$, and $\sigma = 0.001$


(a) Phytoplankton

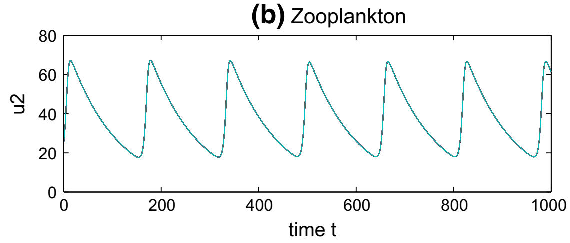

(b) Zooplankton

Fig. 7 Periodic oscillation of phytoplankton and zooplankton at $\alpha = 0.015, b = 0.42, D = 0.5, \gamma = 0.6, \beta = 0.9, m = 0.6, N = 25, K = 120, a = 3, c = 0.02, \epsilon = 10^{-7}, r = 0.5, \delta = 0.01$, and $\sigma = 0.001$

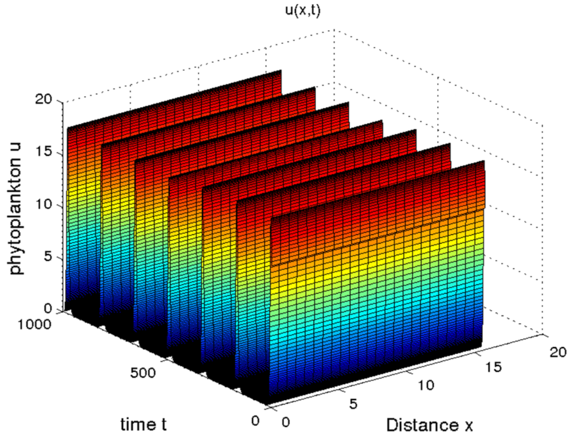


Fig. 8 Three-dimensional periodic oscillations of phytoplankton at $\alpha = 0.015, b = 0.42, D = 0.5, \gamma = 0.6, \beta = 0.9, m = 0.6, N = 25, K = 120, a = 3, c = 0.02, \epsilon = 10^{-7}, r = 0.5, \delta = 0.01$, and $\sigma = 0.001$

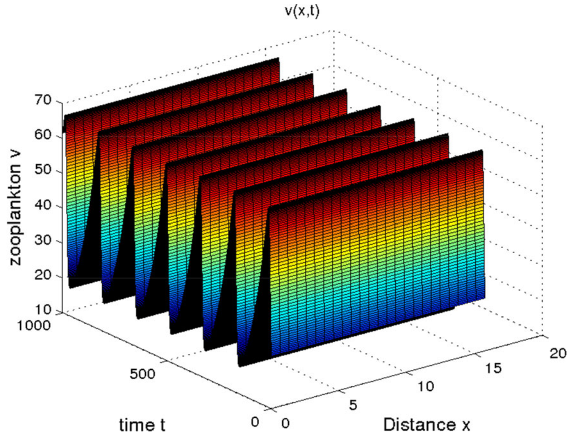


Fig. 9 Three-dimensional periodic oscillations of zooplankton at $\alpha = 0.015, b = 0.42, D = 0.5, \gamma = 0.6, \beta = 0.9, m = 0.6, N = 25, K = 120, a = 3, c = 0.02, \epsilon = 10^{-7}, r = 0.5, \delta = 0.01$, and $\sigma = 0.001$

$Dv = 5 * 10^{-5}, \lambda = 2.5, N = 128$ and $h = 2$. The system is solved, and graphs are generated in MATLAB.

Phytoplankton population density is plotted in left-hand side column and zooplankton population density in the right-hand side column of Figs. 10, 11, and 12 at times t = 1000, 10,000 and 20,000 respectively. The figures depict how the concentration of phytoplankton and zooplankton changes due to local reactions and diffusion in the system. An irregular pattern prevails over the entire square domain. Although choice of the initial condition drastically affects the dynamics of the system, the spatial dynamics observed in the figures is not induced by the initial condition. The chaotic nature of the diffusion model has been studied, and it is observed that spatio-temporal chaotic dynamics of this diffusion system is self-organized.

6 Conclusion

The discovery of spatio-temporal chaos, in the early 90s, has applications in Engineering and Physiology. There exist many mechanisms which cause spatio-

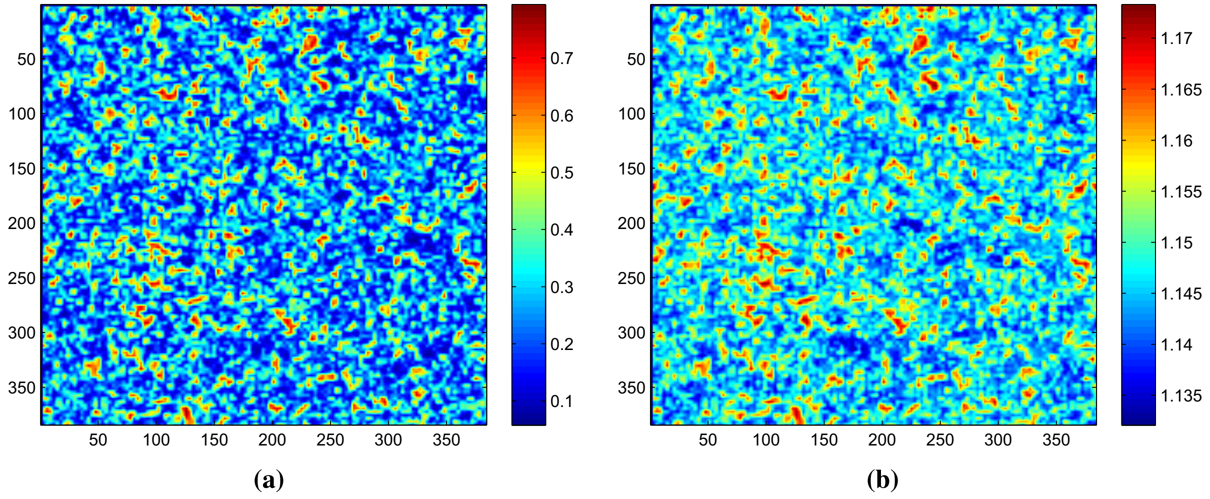


Fig. 10 Spatial plot patterns at time t = 1000 with parameter values mentioned above. **a** Phytoplankton. **b** Zooplankton

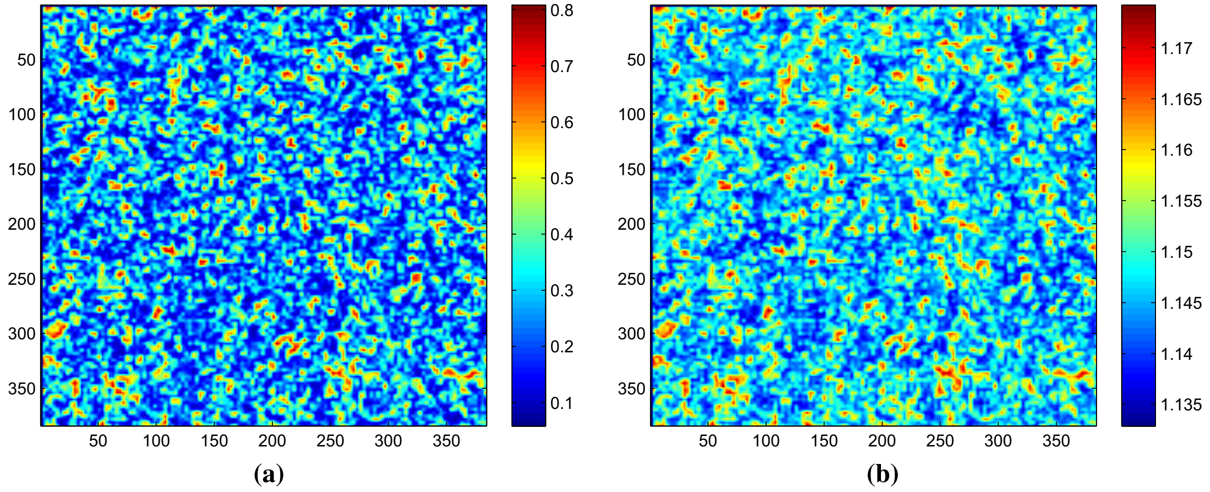


Fig. 11 Spatial plot patterns at time t = 10,000 with parameter values mentioned above. **a** Phytoplankton. **b** Zooplankton

temporal chaos in a given system. It is imperative to assess their potential to solve problems in Physics, Biology, and Engineering. Here, we attempt to do the same in a model ecological system.

Our study is on a plankton system and the interactions of plankton species when the functional response for zooplankton grazing is Ivlev type. In the homogeneous system, we have seen that the maximum phytoplankton consumption rate β can control the system behavior. There is a critical value ($\beta = \beta_*$) of the maximum phytoplankton consumption rate for which the system bifurcates (Hopf type) from stable oscillation into an unstable periodic oscillation. If β exceeds the critical value, then the system becomes unstable leading to periodic oscillation of the plankton population. Also, the system shows that it becomes unstable around coexisting equilibrium point E_*, when the ratio of the diffusion coefficients of the zooplankton to the phytoplankton species (τ) exceeds a critical value τ_*. The reaction–diffusion system with variable diffusion coefficients also has interesting dynamics on the plankton system. The study shows that if the maximum consumption rate (β) of the phytoplankton species exceeds the critical value β_*, the system is stable about the equilibrium point E_*. Also, if the ratio of the diffusion coefficients of zooplank-

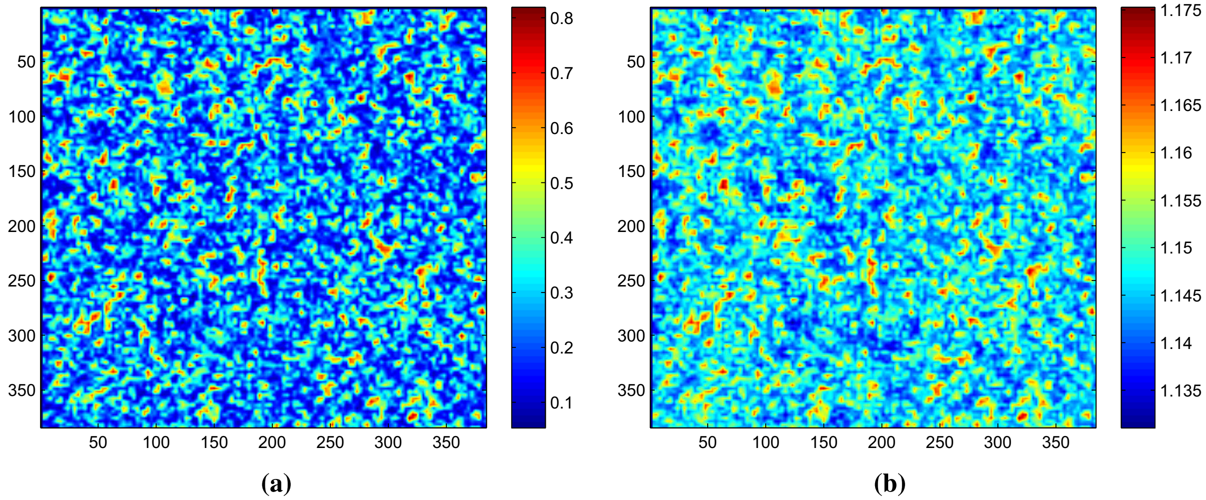


Fig. 12 Spatial plot patterns at time t = 20,000 with parameter values mentioned above. **a** Phytoplankton. **b** Zooplankton

ton to phytoplankton is less than a critical value ζ_* , then the system is stable about the equilibrium point E_*.

It is observed that there is not much noticeable change in the spatial patterns after a specific time. Thus, we can conclude that the patterns are time-independent. The spatio-temporal chaos generated is unaffected by changes in the system parameters. The spatio-temporal patterns obtained show that chaotic behavior spreads over the entire domain. The formation of patterns corresponds to a chaotic dynamics, and thus, it leads to the conclusion that spatio-temporal chaos is an intrinsic property of population dynamics. The results suggest that patchiness is one of the basic characteristics of the functioning of an ecological system. Two-dimensional spatial patterns of phytoplankton–zooplankton dynamics are self-organized and therefore can be considered to provide a theoretical framework to understand patchiness in marine environments.

Throughout this report, we have made certain assumptions about plankton populations and the physical environment, making our system idealized to a certain degree. We have assumed the growth of phytoplankton to be a modified Leslie-Gower type, and this model is based on the assumption that reduction in zooplankton population is inversely related to per capita availability of its preferred food [29]. In the real world, this may not be a perfect inverse relation. Also, we have not accounted for the effect of the plankton population on the fish population dynamics. Thus, our model does not truly replicate nature. Introducing stochastic variations into the model would improve its accuracy. A spatio-temporal model with stochastic variation can be used to assess various sources of uncertainty [31].

A more complicated model than the one described in the report would provide more mechanisms of pattern formation. Distinguishing between patterns arising from the differences in the complexity of models is a very interesting and important problem. However, it is beyond the scope of this report.

Acknowledgments We are grateful to the anonymous reviewers for their careful reading, constructive comments and helpful suggestions, which have helped us to improve the presentation of this work significantly. First author gratefully acknowledges Director, INCOIS for his encouragement and unconditional help. This is INCOIS contribution number 219. The internship work would have been impossible without Joint Science Academies Summer Fellowship Programme 2013. Second author gladly acknowledges the Joint Science Academies for providing financial support.

References

1. Zhao, J., Zhao, M., Yu, H.: Effect of prey refuge on the spatiotemporal dynamics of a modified Leslie–Gower predator–prey system with Holling type III schemes. Entropy **15**, 2431–2447 (2013)
2. Malchow, H., Petrovskii, S.V., Venturino, E.: Spatiotemporal Patterns in Ecology and Epidemiology: Theory, Models and Simulation. Chapman and Hall/CRC, Florida (2008)
3. Garvie, M.R.: Finite-difference schemes for reaction–diffusion equations modeling predator–prey interactions in MATLAB. Bull. Math. Biol. **69**, 931–956 (2007)

4. Pei, Y., Zhang, G., Chen, L.: Species extinction and permanence in a prey–predator model with two-type functional responses and impulsive biological control. Nonlinear Dyn. **52**, 71–81 (2008)
5. Shi, R., Chen, L.: The study of a ratio-dependent predator–prey model with stage structure in the prey. Nonlinear Dyn. **58**, 443–451 (2009)
6. Xu, C., Tang, X., Liao, M., He, X.: Bifurcation analysis in a delayed Lokta–Volterra predator–prey model with two delays. Nonlinear Dyn. **66**, 169–183 (2011)
7. Chakraborty, K., Jana, S., Kar, T.K.: Effort dynamics of a delay-induced prey–predator system with reserve. Nonlinear Dyn. **70**, 1805–1829 (2012)
8. Chakraborty, K., Haldar, S., Kar, T.K.: Global stability and bifurcation analysis of a delay induced prey-predator system with stage structure. Nonlinear Dyn. **73**, 1307–1325 (2013)
9. Holmes, E.E., Lewis, M.A., Banks, J.E., Veit, R.R.: Partial differential equations in ecology: spatial interactions and population dynamics. Ecology **75**, 17–29 (1994)
10. Yang, W., Li, Y.: Dynamics of a diffusive predator–prey model with modified Leslie–Gower and Holling-type III schemes. Comput. Math. Appl. **65**(11), 1727–1737 (2013)
11. Pascual, M.: Diffusion-induced chaos in a spatial predator–prey system. Proc. Biol. Sci. **251**, 1–7 (1993)
12. Li, J., Gao, W.: A strongly coupled predator–prey system with modified Holling Tanner functional response. Comput. Math. Appl. **60**(7), 1908–1916 (2010)
13. Su, H., Dai, B., Chen, Y., Li, K.: Dynamic complexities of a predator–prey model with generalized Holling type III functional response and impulsive effects. Comput. Math. Appl. **56**, 1715–1725 (2008)
14. Myerscough, M.R., Darwen, M.J., Hogarth, W.L.: Stability, persistence and structural stability in a classical predator–prey model. Ecol. Model. **89**, 31–42 (1995)
15. Kuang, Y., Beretta, E.: Global qualitative analysis of a ratio-dependant predator–prey system. J. Math. Biol. **36**, 389–406 (1998)
16. Aly, S., Kim, I., Sheen, D.: Turing instability for a ratio-dependent predator–prey model with diffusion. Appl. Math. Comput. **217**, 7265–7281 (2011)
17. Wang, J., Qu, X.: Qualitative analysis for a ratio-dependent predator–prey with disease and diffusion. Appl. Math. Comput. **217**, 9933–9947 (2011)
18. Petrovskii, S.V., Malchow, H.: Waves of chaos: new mechanism of pattern formation in spatio-temporal population dynamics. Theor. Popul. Biol. **59**, 157–174 (2001)
19. Zhu, L.-M., Wang, A.-L., Liu, Y.-J., Wang, B.: Stationary patterns of a predator–prey model with spatial effect. Appl. Math. Comput. **216**, 3620–3626 (2010)
20. Sun, G.-Q., Zhang, J., Song, L.-P., Jin, Z., Li, B.-L.: Pattern formation of a spatial predator–prey system. Appl. Math. Comput. **218**, 11151–11162 (2012)
21. Kuwamura, M.: Turing instabilities in preypredator systems with dormancy of predators. J. Math. Biol. (2014). doi:10.1007/s00285-014-0816-5
22. Chakraborty, K., Das, K., Kar, T.K.: Modeling and analysis of a marine Plankton system with nutrient recycling and diffusion. Complexity (2014). doi:10.1002/cplx.21559
23. Chaudhuri, S., Roy, S., Chattopadhyay, J.: Phytoplankton–zooplankton dynamics in the ‘presence’ or ’absence’ of toxic phytoplankton. Appl. Math. Comput. **225**, 102–116 (2013)
24. Rossa, F.D., Fasani, S., Rinaldi, S.: Conditions for patchiness in plankton models. Theor. Popul. Biol. **83**, 95–100 (2013)
25. Jang, S., Baglama, J., Wu, L.: Dynamics of phytoplankton–zooplankton systems with toxin producing phytoplankton. Appl. Math. Comput. **227**, 717–740 (2014)
26. Rao, F.: Spatiotemporal dynamics in a reaction–diffusion toxic-phytoplankton–zooplankton model. J. Stat. Mech. (2013). doi:10.1088/1742-5468/2013/08/P08014
27. Luo, J.: Phytoplankton–zooplankton dynamics in periodic environments taking into account eutrophication. Math. Biosci. **245**, 126–136 (2013)
28. Aziz-Alaoui, M.A., Daher Okiye, M.: Boundedness and global stability for a predator–prey model with modified Leslie–Gower and Holling type II schemes. Appl. Math. Lett. **16**, 1069–1075 (2003)
29. Aziz-Alaoui, M.A.: Study of Leslie–Gower-type tritrophic population model. Chaos Solitons Fractals **14**, 1275–1293 (2002)
30. Bhattacharya, R., Mukhopadhatya, B., Bandopadhaya, M.: Diffusive instability in a prey–predator system with time dependent diffusivity. Int. J. Math. Math. Sci. **66**, 4195–4203 (2003)
31. Leeds, W.B., Wikle, C.K., Fiechter, J., Brown, J., Milliff, R.F.: Modeling 3-D spatio-temporal biogeochemical processes with a forest of 1-D statistical emulators. Environmetrics (2013). doi:10.1002/env.2187