Article

Understanding of plankton patterns and complex spatial interaction among nontoxic phytoplankton, toxic phytoplankton and zooplankton populations

Rashi Gupta
Department of Mathematics, NIT, Raipur (C.G.), India
E-mail: rashigupta1234@gmail.com

Received 28 December 2019; *Accepted 5 February 2020*; *Published 1 June 2020*

Abstract
In this paper, I have proposed a mathematical model for aquatic ecosystem with three interacting species, toxin-producing phytoplankton (TPP), non-toxin producing phytoplankton (NTP) and zooplankton with Holling type II functional responses. I have carried out a detail study of stability analysis for the non-spatial and spatial model systems and obtained the conditions for diffusive instability. I have also performed the numerical simulation for a particular set of parameter values which is realistic for natural planktonic system. The numerical results revealed the following: (i) dominant TPP population is under control which is essential for aquatic systems, (ii) cyclic behavior of NTP, TPP and zooplankton population in heterogeneous biomass distribution, and (iii) the evolution of patchy non-Turing patterns. The overall result may be useful for sustainability and maintenance of biodiversity of aquatic systems.

Keywords toxin-producing phytoplankton; diffusive instability; turing domain; spatio-temporal pattern.

Computational Ecology and Software
ISSN 2220-721X
URL: http://www.iaees.org/publications/journals/ces/online-version.asp
RSS: http://www.iaees.org/publications/journals/ces/rss.xml
E-mail: ces@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

The construction and study of mathematical models for population dynamics have remained an important area in theoretical ecology since the famous Lotka-Volterra model (Zhang and Zhang, 2018). The study of organism movement and dispersal has become a key element for understanding a series of ecological questions related to the spatiotemporal dynamics of populations (Kareiva, 1990; Levin, 1974). Planktons are extremely variable in abundance, both spatially and temporally. Plankton patchiness depends on biological as well as physical process for the spatial structure. Biological processes includes such as growth, grazing and behavior and physical processes includes such as lateral stirring and mixing, and nonlinearity of ecosystems, all contribute to the spatial structure in plankton distributions. Huisman et al. (2004) have studied the physical processes in the generation and maintenance of patchiness. Phytoplankton takes up CO_2 from the atmosphere and provides the basis of the food chain in the oceans. Many phytoplankton species are toxic to zooplankton. This toxicity influences the distribution of phytoplankton and zooplankton populations. Modeling of plankton population is vital to understanding the dynamics of plankton populations and the feedback of marine phytoplankton on greenhouse effect. Recently, a number of papers focused on harmful algal blooms which reflect the increasing interest for strategies and management (Franks, 1997; Adriana et al., 2000; Anderson et al., 1997; Blaxter et al., 1997; Hallegraeff, 1993; Truscott et al., 1994; Wyatt, 1998), biological stoichiometry (Elser et al., 2012). The mechanism to explain the cyclic nature of bloom dynamics using different forms of toxin liberation process in phytoplankton-zooplankton interaction has been studied by Chattopadhyay et al. (2000). With the help of field observations, the space-time frame for promotion of plankton diversity due to the presence of TPP has been studied by some researchers (Roy et al., 2008; Roy, 2007; Roy et al., 2006). They have explained the role of toxin-producing phytoplankton (TPP) to determine and maintain the diversity of the overall phytoplankton and zooplankton species in the Bay of Bengal. Yang et al. (2008) studied a spatial tritrophic food chain model with Holling type II functional response and the global existence of solutions for the model of cross diffusion type is investigated when the spatial dimension is less than six. A method to monitor, prevent and control harmful algal blooms has been studied by Anderson et al. (2009). Chakraborty et al. (2012) have explained the role of avoidance by zooplankton for survival and dominance of toxic phytoplankton. Using three species Lotka-Volterra reaction–diffusion system, Scotti et al. (2015) investigated the role of toxicity and zooplankton’s predation in the persistence of toxic prey and observed that a toxic prey may destabilize the spatially homogeneous coexistence and trigger spatial pattern formation. Upadhyay et al. (2010) have introduced the mathematical modeling of plankton dynamics and studied the spatiotemporal pattern formation in a minimal model of a spatial aquatic system.

In this work, I have taken three interacting species, non-toxic, toxic phytoplankton and zooplankton for modeling the planktonic dynamics with diffusion. I have considered that the local growth of the phytoplankton is logistic and that the zooplankton shows the Holling type II functional response for non-toxic phytoplankton (NTP) and toxin producing phytoplankton (TPP). I have obtained the conditions for local and global stability of the model system in the absence and the presence of diffusion. I also obtained the criteria for Turing instability. The main aim of this paper is to see the spatial interaction and the selection of spatiotemporal patterns. This paper is organized as follows. In Section 2, the model system and parameters are discussed. The model system is analyzed in the absence as well as in the presence of diffusion in Section 3 and 4. I have discussed the conditions for Turing instabilities in Section 3. In Section 5, I have discussed the numerical simulation results for one and two dimensional spatial domain. Finally, results are discussed in Section 6.

2 Model System

I consider a reaction-diffusion model for non-toxic phytoplankton-toxic phytoplankton-zooplankton system where $u(x, y, t)$ represents the non-toxin producing phytoplankton (NTP), $v(x, y, t)$ represents the toxin producing phytoplankton (TPP) and $w(x, y, t)$ represents the zooplankton populations at any location (x, y) and time t. I follow the following assumptions to construct out mathematical model:

(i) NTP and TPP populations follow the logistic growth in the absence of each other and the zooplankton.
(ii) NTP and TPP exhibit Holling type-II functional response to zooplankton. In absence of NTP, zooplankton go extinct.
(iii) Non-toxic prey does not invest resources into producing toxins, its maximal growth rate is higher than that of the toxic prey.

Based on the above assumptions, non-dimensional diffusive plankton dynamics may be written as follows

(Roy, 2008; Roy et al., 2006; Chakraborty et al., 2012; Scotti et al., 2015):

$$\left.\begin{aligned}\frac{\partial u}{\partial t}&=r_1u\left(1-\frac{u+\xi_1 v}{K_1}\right)-\frac{\alpha_1 uw}{m_1+u}+d_1\nabla^2 u,\\ \frac{\partial v}{\partial t}&=r_2v\left(1-\frac{v+\xi_2 u}{K_2}\right)-\frac{\alpha_2 vw}{m_2+v}+d_2\nabla^2 v,\\ \frac{\partial w}{\partial t}&=\frac{\beta_1 uw}{m_1+u}-\frac{\beta_2 vw}{m_2+v}-cw+d_3\nabla^2 w.\end{aligned}\right\} \tag{1}$$

The parameters r_1 and r_2 are the intrinsic growth rates of NTP and TPP in the absence of predation; K_1 and K_2 are the carrying capacity of NTP and TPP populations; α_1 and α_2 are the rates at which NTP and TPP are grazed by zooplankton; m_1 and m_2 are half-saturation constants for NTP and TPP density ; ξ_1 and ξ_2 measure the competitive effect of TPP on NTP and NTP on TPP; β_1 be the maximum rate of gain in zooplankton growth due to predation of NTP at a rate α_1 and β_2 be the rate of inhibition of (or reduction in) zooplankton growth by toxic material ingested in feeding on TPP; c is the mortality rate of zooplankton, d_1, d_2 and d_3 are the diffusion coefficient of NTP, TPP and zooplankton density respectively. Now I assume that competitive effect of TPP on NTP and NTP on TPP are very small or zero, so I have taken $\xi_1=\xi_2=0$ in the model system (1). So our new model takes the following form:

$$\left.\begin{aligned}\frac{\partial u}{\partial t}&=r_1u\left(1-\frac{u}{K_1}\right)-\frac{\alpha_1 uw}{m_1+u}+d_1\nabla^2 u,\\ \frac{\partial v}{\partial t}&=r_2v\left(1-\frac{v}{K_2}\right)-\frac{\alpha_2 vw}{m_2+v}+d_2\nabla^2 v,\\ \frac{\partial w}{\partial t}&=\frac{\beta_1 uw}{m_1+u}-\frac{\beta_2 vw}{m_2+v}-cw+d_3\nabla^2 w,\end{aligned}\right\} \tag{2}$$

non vanishing initial conditions

$$u(x,\ y,\ 0)>0,\ v(x,y,\ 0)>0,\ w(x,y,\ 0)>0,\ (x,\ y)\in\Omega=[0,\ L]\times[0,\ L], \tag{3}$$

and the zero-flux boundary conditions

$$\frac{\partial u}{\partial n}=\frac{\partial v}{\partial n}=\frac{\partial w}{\partial n}=0,\ \ (x,\ y)\in\partial\Omega\ \text{ for all } t, \tag{4}$$

where n is the outward normal vector on the smooth part of the boundary $\partial\Omega$.

3 Stability Analysis of Non-Spatial Model System

In this section, I study the stability analysis of the model system (2) in the absence of diffusion. Therefore I consider only the interaction part of the model system. I find the non-negative equilibrium point of the model system and discuss their stability analysis with respect to variation of several parameters. I first analyzed model system (2) without diffusion (i.e., $d_1 = 0, d_2 = 0, d_3 = 0$) the spatial uniform version of (2). In this case, the model system takes the form as:

$$\left.\begin{aligned}\frac{du}{dt} &= r_1 u\left(1-\frac{u}{K_1}\right)-\frac{\alpha_1 uw}{m_1+u},\\ \frac{dv}{dt} &= r_2 v\left(1-\frac{v}{K_2}\right)-\frac{\alpha_2 vw}{m_2+v},\\ \frac{dw}{dt} &= \frac{\beta_1 uw}{m_1+u}-\frac{\beta_2 vw}{m_2+v}-cw,\end{aligned}\right\} \tag{5}$$

with $u(0)>0,\ v(0)>0,\ w(0)>0.$

The model system (5) possesses six nonnegative real equilibrium points:

(i) Plankton-free equilibrium point $E_0(0,\ 0,\ 0)$ always exits.

(ii) TPP and zooplankton-free equilibrium point $E_1(K_1,\ 0,\ 0)$ exists on the boundary of the first octant.

(iii) NTP and zooplankton-free equilibrium point $E_2(0,\ K_2,\ 0)$ exists on the boundary of the first octant.

(iv) Zooplankton-free equilibrium point $E_3(\hat{u},\ \hat{v},\ 0)$ is the planer equilibrium point on the *uv*-plane, where $\hat{u} = K_1$ and $\hat{v} = K_2$.

(v) TPP-free equilibrium point $E_4(\bar{u},\ 0,\ \bar{w})$ is the planer equilibrium point on the *uw*-plane, where

$$\bar{u} = \frac{cm_1}{\beta_1 - c},\ \ \bar{w} = \frac{r_1}{\alpha_1}\left(m_1 + \frac{cm_1}{\beta_1 - c}\right)\left(1-\frac{cm_1}{K_1(\beta_1 - c)}\right) \text{ if } K_1(\beta_1 - c)/c > m_1 \text{ and } \beta_1 > c.$$

(vi) The existence of interior equilibrium point $E_5(u^*,\ v^*,\ w^*)$.

In this case, u^*, v^* and w^* are the positive solutions of the following three equations:

$$r_1\left(1-\frac{u}{K_1}\right)-\frac{\alpha_1 w}{m_1+u} = 0, \tag{6a}$$

$$r_2\left(1-\frac{v}{K_2}\right)-\frac{\alpha_2 w}{m_2+v} = 0, \tag{6b}$$

$$\frac{\beta_1 u}{m_1+u}-\frac{\beta_2 v}{m_2+v}-c=0. \tag{6c}$$

Solving Eqs. (6a) and (6b) I get an equation in *u* and *v*. Also from Eq. (6c), I get an equation in *u* and *v* as follows:

$$F_1(u,\, v)=r_1\alpha_2(1-u/K_1)(m_1+u)-r_2\alpha_1(1-v/K_2)(m_2+v)=0, \tag{7a}$$

$$F_2(u,\, v)=\frac{\beta_1 u}{(m_1+u)}-\frac{\beta_2 v}{(m_2+v)}-c=0. \tag{7b}$$

From Eq. (7a) when $v \to 0$ then $u \to u_{1a}$ where

$$u_{1a}=\frac{-(m_1-K_1)+\sqrt{(m_1-K_1)^2-4(K_1/r_1\alpha_2)(\alpha_1 r_2 m_2-\alpha_2 r_1 m_1)}}{2}. \tag{8}$$

We note that $u_{1a}>0,$ if

$$\frac{\alpha_1 r_2 m_2}{\alpha_2 r_1}<m_1<K_1. \tag{9}$$

Let $\dfrac{du}{dv}=-\dfrac{F_{1v}}{F_{1u}}$ where $F_{1u}\neq 0$ with

$$F_{1v}=r_2\alpha_1[-(1-v/K_2)+(m_2+v)/K_2],\ \ F_{1u}=r_1\alpha_2[(1-u/K_1)+(m_1+u)/K_1].$$

It may be noted that $du/dv<0$ if

$$\left.\begin{array}{l}\text{either }\ (i)\ F_{1u}>0\ \text{ and }\ F_{1v}>0,\\ \text{or }\quad\ (ii)\ F_{1u}<0\ \text{ and }\ F_{1v}<0.\end{array}\right\} \tag{10}$$

From Eq. (7b) when $v \to 0$ then $u \to u_{1b}$ where

$$u_{1b}=\frac{cm_1}{\beta_1-c}>0 \text{ if } \ \beta_1>c \tag{11}$$

Let $\frac{du}{dv} = -\frac{F_{2v}}{F_{2u}}$ where $F_{2u} \neq 0$ with $F_{2v} = -\beta_2 m_2 /(m_2 + v)^2$, $F_{2u} = \beta_1 m_1 /(m_1 + u)^2$.

It may be noted that $du/dv > 0$ because $F_{2v} < 0$ and $F_{2u} > 0$.

From above analysis, I note that the isoclines (7a) and (7b) intersect at a unique point $\left(u^*, v^*\right)$ if in addition to conditions (7a)-(7b), the following condition holds:

$u_{1b} < u_{1a}$.

This completes the existence of equilibrium point E_5.

Now, I study the local behavior of the model system (5) at each equilibrium points. To study the local stability behavior each equilibrium point of the model system, I compute the variational matrices corresponding to each equilibrium point. From these matrices, the following results are obtained.

(i) $E_0(0, 0, 0)$ is a saddle point with unstable manifold in *uv*-direction and stable manifold in *w*-direction.

(ii) $E_1(K_1, 0, 0)$ is a saddle point with stable manifold in *uw*-direction provided $\beta_1 K_1 < c(m_1 + K_1)$ and unstable manifold in *v*-direction.

(iii) $E_2(0, K_2, 0)$ is a saddle point with stable manifold in *vw*-direction and unstable manifold in *u*-direction.

(iv) $E_3(\bar{u}, \bar{v}, 0)$ is stable or unstable in the positive direction orthogonal to *uv*-direction depending on whether $\lambda_3 = - c + (\beta_1(\bar{u}(m_1 + \bar{u})) - (\beta_2(\bar{v}(m_1 + \bar{v}))$ is negative or positive, provided $\bar{u} > K_1 / 2$, $\bar{v} > K_2 / 2$.

(v) $E_4(\bar{u}, 0, \bar{w})$ is stable in the positive direction orthogonal to *uw*-direction if $\bar{w} > (r_2 m_2 / \alpha_2)$ provided

(a) $K_1 \left\{\beta_1 \bar{u}(m_1 + \bar{u}) - \alpha_1 m_1 \bar{w}\right\} < (m_1 + \bar{u})^2 \left\{2 r_1 \bar{u} - K_1 (r_1 + c)\right\}$,

(b) $\left\{r_1 (1 - 2\bar{u} / K_1)(m_1 + \bar{u})^2 - \alpha_1 m_1 \bar{w}\right\} < \alpha_1 \beta_1 m_1 \bar{u}\bar{w} / \left\{c(m_1 + \bar{u}) - \beta_1 \bar{u}\right\}$.

In the following theorem, I propose the necessary and sufficient conditions for the positive equilibrium $E_5(u^*, v^*, w^*)$ to be locally asymptotically stable.

Theorem 1. *The unique non-trivial positive equilibrium point* $E_5(u^*, v^*, w^*)$ *is locally asymptotically stable if and only if the following inequalities hold*:

$$\left\{\frac{\alpha_1 u^*}{(m_1 + u^*)^2} + \frac{\alpha_2 v^*}{(m_2 + v^*)^2}\right\} < \frac{1}{w^*}\left(\frac{r_1 u^*}{K_1} + \frac{r_2 v^*}{K_2}\right), \tag{12a}$$

$$\left\{\frac{\alpha_1 u^* w^*}{(m_1+u^*)^2}-\frac{r_1 u^*}{K_1}\right\}\left\{\frac{\alpha_2 v^* w^*}{(m_2+v^*)^2}-\frac{r_2 v^*}{K_2}\right\}>\left\{\frac{\alpha_2\beta_2 m_2 v^* w^*}{(m_2+v^*)^3}-\frac{\alpha_1\beta_1 m_1 u^* w^*}{(m_1+u^*)^3}\right\}, \tag{12b}$$

$$\left\{\frac{\alpha_2 v^* w^*}{(m_2+v^*)^2}-\frac{r_2 v^*}{K_2}\right\}\left\{\frac{\alpha_1\beta_1 m_1 u^*}{(m_1+u^*)^3}\right\}<\left\{-\frac{r_1 u^*}{K_1}+\frac{\alpha_1 u^* w^*}{(m_1+u^*)^2}\right\}\left\{\frac{\alpha_2\beta_2 m_2 v^*}{(m_2+v^*)^3}\right\}. \tag{12c}$$

In order to study the global stability behavior of the positive equilibrium $E_5(u^*, v^*, w^*)$,I assumed that $E_5(u^*, v^*, w^*)$ is locally asymptotically stable. In the following theorem, I able to write down the sufficient conditions under which the positive equilibrium point $E_5(u^*, v^*, w^*)$ is globally asymptotically stable.

Theorem 2. *Let the following inequalities hold*:

$$\alpha_1 K_1 w^* < r_1 m_1 (m_1+u^*), \tag{13a}$$

$$\alpha_2 K_2 w^* < r_2 m_2 (m_2+v^*), \tag{13b}$$

$$\beta_1 M_1 < c\left(m_1+M_1\right), \tag{13c}$$

$$\left\{\frac{\alpha_1\beta_2 m_2 (m_1+u^*)}{\beta_1 m_1 (m_2+M_2)(m_2+v^*)}+\frac{\alpha_2}{(m_2+M_2)}\right\}^2>\frac{\alpha_1(m_1+u^*)}{\beta_1 m_1}\left\{\frac{r_2}{K_2}-\frac{\alpha_2 w^*}{m_2(m_2+v^*)}\right\}\left\{c+\frac{\beta_2 M_1}{m_2}\right\}, \tag{13d}$$

where $M_1=\max u$ and $M_2=\max v$. Then, the positive equilibrium point $E_5(u^*, v^*, w^*)$ is globally asymptotically stable.

Proof: Consider the following positive definite function,

$$V_1(t)=\left[u-u^*-u^*\ln\left(\frac{u}{u^*}\right)\right]+\left[v-v^*-v^*\ln\left(\frac{v}{v^*}\right)\right]+\frac{m\left(w-w^*\right)^2}{2}, \tag{14}$$

where m is a positive constant to be chosen suitably.

Now, differentiating V_1 with respect to time t along the solutions of the model system (5), a little algebraic manipulation yields,

$$\frac{dV_1}{dt} = -\left\{\frac{r_1}{K_1} - \frac{\alpha_1 w^*}{(m_1+u)(m_1+u^*)}\right\}(u-u^*)^2 - \left\{\frac{r_2}{K_2} - \frac{\alpha_2 w^*}{(m_2+v)(m_2+v^*)}\right\}(v-v^*)^2$$
$$-m\left\{c - \frac{\beta_1 u}{(m_1+u)} + \frac{\beta_2 v}{(m_2+v)}\right\}(w-w^*)^2 + \left\{\frac{m\beta_1 m_1}{(m_1+u)(m_1+u^*)} - \frac{\alpha_1}{(m_1+u)}\right\}(u-u^*)(w-w^*)$$
$$-\left\{\frac{m\beta_2 m_2}{(m_2+v)(m_2+v^*)} + \frac{\alpha_2}{(m_2+v)}\right\}(v-v^*)(w-w^*).$$

The above equation can be written as sum of quadratics,

$$\frac{dV_1}{dt} = -\frac{1}{2}m_{11}(u-u^*)^2 + m_{12}(u-u^*)(v-v^*) - \frac{1}{2}m_{22}(v-v^*)^2$$
$$-\frac{1}{2}m_{22}(v-v^*)^2 + m_{23}(v-v^*)(w-w^*) - \frac{1}{2}m_{33}(w-w^*)^2$$
$$-\frac{1}{2}m_{11}(u-u^*)^2 + m_{13}(u-u^*)(w-w^*) - \frac{1}{2}m_{33}(w-w^*)^2,$$

where

$$m_{11} = \left\{\frac{r_1}{K_1} - \frac{\alpha_1 w^*}{(m_1+u)(m_1+u^*)}\right\},\ \ m_{22} = \left\{\frac{r_2}{K_2} - \frac{\alpha_2 w^*}{(m_2+v)(m_2+v^*)}\right\},$$
$$m_{33} = m\left\{c - \frac{\beta_1 u}{(m_1+u)} + \frac{\beta_2 v}{(m_2+v)}\right\},\ \ m_{12} = 0,$$
$$m_{13} = \left\{\frac{m\beta_1 m_1}{(m_1+u)(m_1+u^*)} - \frac{\alpha_1}{(m_1+u)}\right\},\ \ m_{23} = -\left\{\frac{m\beta_2 m_2}{(m_2+v)(m_2+v^*)} + \frac{\alpha_2}{(m_2+v)}\right\}.$$

Sufficient conditions for dV_1/dt to be negative definite are that the following inequalities hold:

$$m_{11} > 0, \tag{15a}$$

$$m_{22} > 0, \tag{15b}$$

$$m_{33} > 0, \tag{15c}$$

$$m_{12}^2 < m_{11}m_{22}, \tag{15d}$$

$$m_{13}^2 < m_{11}m_{33},$$

(15e)

$m_{23}^2 < m_{22}m_{33}$.

(15f)

Under the conditions (13a), (13b) and (13c) the condition (15a), (15b) and (15c) holds. I note that $m_{12} = 0$, therefore (15d) holds. By choosing $m = \alpha_1\left(m_1 + u^*\right)/\beta_1 m_1$, I obtain $m_{13} = 0$, and thus condition (15e) is automatically satisfied. Finally, under the condition (13d) the condition (15f) holds.

4 Stability Analysis of Spatial Model System

In this section, I study the effect of diffusion on the model system (2)-(4) about the interior equilibrium point $E_5(u^*, v^*, w^*)$ for one dimensional case. In order to derive the condition for stability, we have considered the lineralized form of the model system (2) about $E_5(u^*, v^*, w^*)$ with small perturbations $U\left(x, t\right)$, $V\left(x, t\right)$ and $W\left(x, t\right)$ as follows:

$$\frac{\partial U}{\partial t} = a_{11}U + a_{12}V + a_{13}W + d_1\frac{\partial^2 U}{\partial x^2},$$
$$\frac{\partial V}{\partial t} = a_{21}U + a_{22}V + a_{23}W + d_2\frac{\partial^2 V}{\partial x^2},$$
$$\frac{\partial W}{\partial t} = a_{31}U + a_{32}V + a_{33}W + d_3\frac{\partial^2 W}{\partial x^2}.$$

(16)

where $u = u^* + U,\ v = v^* + V,\ W = w^* + W,$

and

$$a_{11} = r_1\left(1 - \frac{2u^*}{K_1}\right) - \frac{\alpha_1 m_1 w^*}{(m_1 + u^*)^2}, \qquad a_{12} = 0, \qquad a_{13} = -\frac{\alpha_1 u^*}{m_1 + u^*},$$
$$a_{21} = 0, \qquad a_{22} = r_2\left(1 - \frac{2v^*}{K_2}\right) - \frac{\alpha_2 m_2 w^*}{(m_2 + v^*)^2}, \qquad a_{23} = -\frac{\alpha_2 v^*}{m_2 + v^*}, \qquad (17)$$
$$a_{31} = \frac{\beta_1 m_1 w^*}{(m_1 + u^*)^2}, \qquad a_{32} = -\frac{\beta_2 m_2 w^*}{(m_2 + v^*)^2}, \qquad a_{33} = \frac{\beta_1 u^*}{m_1 + u^*} - \frac{\beta_2 v^*}{m_2 + v^*} - c.$$

It may be noted that (U, V, W) are small perturbations of (u, v, w) about the equilibrium point (u^*, v^*, w^*). In this case I look for eigen functions of the form

$$\sum_{n=0}^{\infty}\begin{pmatrix} a_n \\ b_n \\ c_n \end{pmatrix}\exp(\lambda t + ikx),$$

and thus solution of system (16) of the form

$$\begin{pmatrix} U \\ V \\ W \end{pmatrix} = \sum_{n=0}^{\infty} \begin{pmatrix} a_n \\ b_n \\ c_n \end{pmatrix} \exp(\lambda t + ikx), \tag{18}$$

where λ and k are the frequency and wave number respectively. The characteristic equation of the linearized system is given by

$$\lambda^3 + \rho_1\lambda^2 + \rho_2\lambda + \rho_3 = 0, \tag{19}$$

where

$$\begin{aligned} \rho_1 &= -Tr(M) + k^2\left(d_1 + d_2 + d_3\right), \\ \rho_2 &= R(M) + k^4\left(d_1d_2 + d_1d_3 + d_2d_3\right) - k^2\left(a_{11}\left(d_2 + d_3\right) + a_{22}\left(d_1 + d_3\right) + a_{33}\left(d_1 + d_2\right)\right), \\ \rho_3 &= P\left(k^2\right), \end{aligned} \tag{20}$$

with

$$P\left(k^2\right) = b_0k^6 - b_1k^4 + b_2k^2 - Det(M),$$

where

$$\begin{aligned} b_0 &= d_1d_2d_3, \\ b_1 &= a_{11}d_2d_3 + a_{22}d_1d_3 + a_{33}d_1d_2, \\ b_2 &= d_1(a_{22}a_{33} - a_{23}a_{32}) + d_2(a_{11}a_{33} - a_{13}a_{31}) + d_3a_{11}a_{22}, \end{aligned} \tag{21}$$

and

$$\begin{aligned} M &= \begin{pmatrix} a_{11} & 0 & a_{13} \\ 0 & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}, \; Tr(M) = a_{11} + a_{22} + a_{33}, \\ R(M) &= a_{11}(a_{22} + a_{33}) - a_{13}a_{31} + a_{22}a_{33} - a_{23}a_{32}, \\ Det(M) &= a_{11}(a_{22}a_{33} - a_{23}a_{32}) - a_{22}a_{13}a_{31}. \end{aligned} \tag{22}$$

From Eqs. (19)-(22) and using the Routh-Hurwitz criteria, the following theorem follows immediately.

Theorem 3. *(i) The positive equilibrium* $E_5(u^*, v^*, w^*)$ *is locally asymptotically stable in the presence of diffusion if and only if*

$$\rho_1 > 0, \tag{23}$$
$$\rho_3 > 0, \tag{24}$$
$$\rho_1\rho_2 - \rho_3 > 0. \tag{25}$$

(ii) *If the inequalities in Eq.* (11) *are satisfied, then the positive equilibrium* $E_5(u^*, v^*, w^*)$ *is locally asymptotically stable in the presence as well as absence of diffusion.*

(iii) *Suppose that any one or all of the inequalities in Eqs.* (23)-(25) *are not satisfied, then* (22)-(24) *can be made positive by increasing* d_1, d_2 *and* d_3 *to a sufficiently large value, and hence* $E_5(u^*, v^*, w^*)$ *can be made locally asymptotically stable.*

The Turing instability occurs if at least one of the roots of Eq. (19) has a positive real part or in other words, $\text{Re}\,(\lambda) > 0$ for some $k \neq 0$. Irrespective of the sign of ρ_1 and ρ_2 the equation has a positive root if $\rho_3 < 0$. Therefore, diffusion driven instability occurs when $\rho_3 = P(k^2) < 0$. Hence the condition for diffusive instability is given by

$$P\left(k^2\right) = b_0k^6 - b_1k^4 + b_2k^2 - Det(M) < 0. \tag{26}$$

P is a cubic polynomial in k^2. The critical values of $P(k^2)$ occurs at $k^2 = k_{cr}^2$, where

$$k_{cr}^2 = \frac{b_1 \pm \sqrt{b_1^2 - 3b_0b_2}}{3b_0}. \tag{27}$$

For positive value of critical points $k^2 = k_{cr}^2$ we require

$$b_1^2 - 3b_0b_2 > 0 \text{ and } b_1 > 0 \text{ or } b_2 < 0. \tag{28}$$

Now, I consider the model system (2)-(4) for two dimensional cases. In order to study the stability behavior of this complete system, I define a positive function $V_2(t)$ given by

$$V_2(t) = \iint_{\Omega} V_1(u(t), v(t), w(t))dA,$$

where $V_1(t)$ is defined in Eq. (14). Differentiating $V_2(t)$ along the solution of model system (2), we get

$$\frac{dV_2}{dt} = \iint_{\Omega}\left(\frac{\partial V_1}{\partial u}\frac{\partial u}{\partial t} + \frac{\partial V_1}{\partial v}\frac{\partial v}{\partial t} + \frac{\partial V_1}{\partial w}\frac{\partial w}{\partial t}\right) dA = I_1 + I_2,$$

where

$$I_1 = \iint_\Omega \frac{dV_1}{dt} dA, \qquad I_2 = \iint_\Omega \left(d_1 \frac{\partial V_1}{\partial u} \nabla^2 u + d_2 \frac{\partial V_1}{\partial v} \nabla^2 v + d_3 \frac{\partial V_1}{\partial w} \nabla^2 w \right) dA.$$

Using the zero-flux boundary condition (4), we obtain the following:

(i) $\dfrac{\partial V_1}{\partial u} = 0,\ \dfrac{\partial V_1}{\partial v} = 0,\ \dfrac{\partial V_1}{\partial w} = 0,$ on $\partial\Omega$,

(ii) $\dfrac{\partial^2 V_1}{\partial u^2} > 0,\ \dfrac{\partial^2 V_1}{\partial v^2} > 0,\ \dfrac{\partial^2 V_1}{\partial w^2} > 0,\ \dfrac{\partial^2 V_1}{\partial u \partial v} = \dfrac{\partial^2 V_1}{\partial u \partial w} = \dfrac{\partial^2 V_1}{\partial v \partial w} = 0.$

Using the similar analysis [21], we have

$$\iint_\Omega \frac{\partial V_1}{\partial u} \nabla^2 u \ dA = -\iint_\Omega \frac{\partial^2 V_1}{\partial u^2} \left[\left(\frac{\partial u}{\partial x} \right)^2 + \left(\frac{\partial u}{\partial y} \right)^2 \right] \le 0,$$

$$\iint_\Omega \frac{\partial V_1}{\partial v} \nabla^2 v \ dA = -\iint_\Omega \frac{\partial^2 V_1}{\partial v^2} \left[\left(\frac{\partial v}{\partial x} \right)^2 + \left(\frac{\partial v}{\partial y} \right)^2 \right] \le 0,$$

$$\iint_\Omega \frac{\partial V_1}{\partial w} \nabla^2 w \ dA = -\iint_\Omega \frac{\partial^2 V_1}{\partial w^2} \left[\left(\frac{\partial w}{\partial x} \right)^2 + \left(\frac{\partial w}{\partial y} \right)^2 \right] \le 0.$$

This shows that $I_2 \le 0$.

Since $\dfrac{dV_2}{dt} = I_1 + I_2$ and $I_2 \le 0$, hence $\dfrac{dV_2}{dt} \le 0$ if $I_1 \le 0$. If $I_1 \le 0$ then $\dfrac{dV_1}{dt} \le 0$.

If $dV_1 / dt > 0$ i.e. if $I_1 > 0$, then the positive equilibrium point $E_5(u^*,\ v^*,\ w^*)$ of the model system (5) is unstable. However, by increasing $d_i\ (i = 1,\ 2,\ 3)$ to a sufficiently large values, dV_2 / dt can be made negative definite even if $I_1 > 0$. Thus I can state the following theorem.

Theorem 4.

(i) *If the positive equilibrium* $E_5(u^*,\ v^*,\ w^*)$ *of model* (5) *is globally asymptotically stable, then the corresponding uniform steady state of model* (2) *remains globally asymptotically stable.*

(ii) *If the positive equilibrium* $E_5(u^*,\ v^*,\ w^*)$ *of model* (5) *is unstable, then corresponding uniform steady state of model* (2)-(4) *can be made stable by increasing the diffusion coefficients appropriately*.

5 Numerical Simulations

In this section, I perform numerical simulations to understand the dynamics of the model system (2) for one and two dimensional cases. For this purpose I have plotted the time series, spatiotemporal pattern for one dimensional case and snapshots for two dimensional cases. To investigate the spatiotemporal dynamics of the model system (2), I have used semi implicit (in time) finite difference method. The step lengths of Δx and Δt are chosen sufficiently small. The finite difference method gives rise to a sparse, banded linear system of algebraic equations. The resulting linear system is solved by using the GMRES algorithm for the two-dimensional case (Garvie, 2007). The temporal dynamics is studied by observing the effect of time on space versus density plot of prey and predator populations.

Table 1 The set of fixed parameter values for the model system (2) taken from Roy et al. (2006).

Parameter name	Definition	Value	Unit
r_1	Intrinsic growth rate of NTP	0.4632	d^{-1}
r_2	Intrinsic growth rate of TPP	0.4425	d^{-1}
K_1	Carrying capacity of NTP	305	mgc/m^3
K_2	Carrying capacity of TPP	200	mgc/m^3
α_1	NTP consumption rate	0.6625	d^{-1}
α_2	TPP consumption rate	0.435	d^{-1}
m_1	Half saturation constant for NTP	45	mgc/m^3
m_2	Half saturation constant for TPP	30	mgc/m^3
β_1	Maximum NTP conversion rate	0.516	d^{-1}
β_2	Maximum rate of toxin inhibition	0.198	d^{-1}
c	Zooplankton mortality rate	0.109	d^{-1}

Time t and length $x \in [0, L]$ is measured in days [d] and meters [m] respectively. The diffusion coefficients d_1, d_2 and d_3 are measured in [$m^2 d^{-1}$]. For the parameter values:

$$
\begin{aligned}
&r_1 = 0.4632,\ r_2 = 0.4425, K_1 = 305,\ K_2 = 200,\ \alpha_1 = 0.6625,\\
&\alpha_2 = 0.435, m_1 = 45,\ m_2 = 30,\ \beta_1 = 0.516,\ \beta_2 = 0.198,\ c = 0.109,
\end{aligned}
\tag{29}
$$

I have obtained $(u^*, v^*, w^*) = (25.2811, 18.9343, 45.0654)$. With the above set of parameter values (29) and $d_1 = d_2 = 0.01, d_3 = 0.5,$ I have obtained the critical values k_{cr}^2 are ($5.0823, 19.5017$) and corresponding $P(k_{cr}^2)$ are (0.02381, -0.05114) (Fig. 1). The graph of $P(k^2)$ vs. k^2 has been plotted for different values of d_3 in Fig. 1. The value of k^2 for which $\rho_3 = P(k^2) < 0$ the model system (2) is unstable and the region under the curve for which $P(k^2) < 0$ is known as Turing instability region.

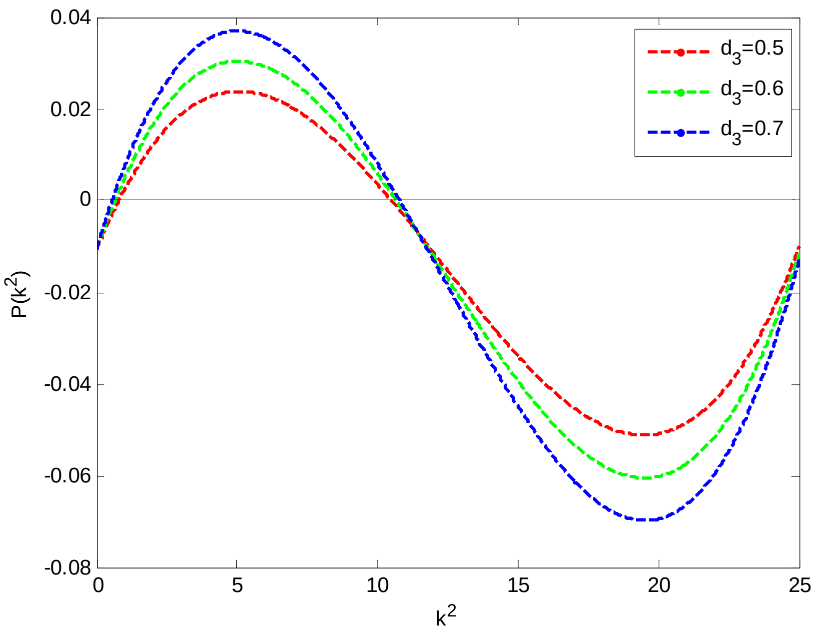


Fig. 1 The graph of the function $P(k^2)$ vs k^2 for the parameter set (29) with $d_1 = d_2 = 0.01$ and $d_3 = 0.5,\ 0.6,\ 0.7.$

To obtain the time series and non-trivial spatiotemporal pattern, we have chosen the same set of parameters as in (29) (one can take other set of parameters also) for the model system (2) and I have perturbed the homogenous initial distribution about the equilibrium point. I consider the following initial condition.

$$u(x,\ 0) = u^* + \varepsilon_1 \sin\left(\frac{2\pi(x - x_0)}{0.2}\right),\ v(x,\ 0) = v^* + \varepsilon_1 \sin\left(\frac{2\pi(x - x_0)}{0.2}\right),$$
$$w(x,\ 0) = w^* + \varepsilon_1 \sin\left(\frac{2\pi(x - x_0)}{0.2}\right), \tag{30}$$

where $\varepsilon_1 = 5\times 10^{-4},\ x_0 = 0.1,\ (u^*,\ v^*,\ w^*) = (25.2811,\ 18.9343,\ 45.0654)$.

To obtain the snapshots of the model system (2) first I have perturbed the homogenous initial distribution about the equilibrium point (Fig. 5) and then I have taken random perturbation about $(u_0,\ v_0,\ w_0) = (0.4,\ 0.2,\ 0.4)$ (Fig. 6 and 7). With the above initial condition (30), time series of the model system (2) shows limit cycle behavior (Fig. 2) for different values of time $t = 300,\ 500,\ 700$.

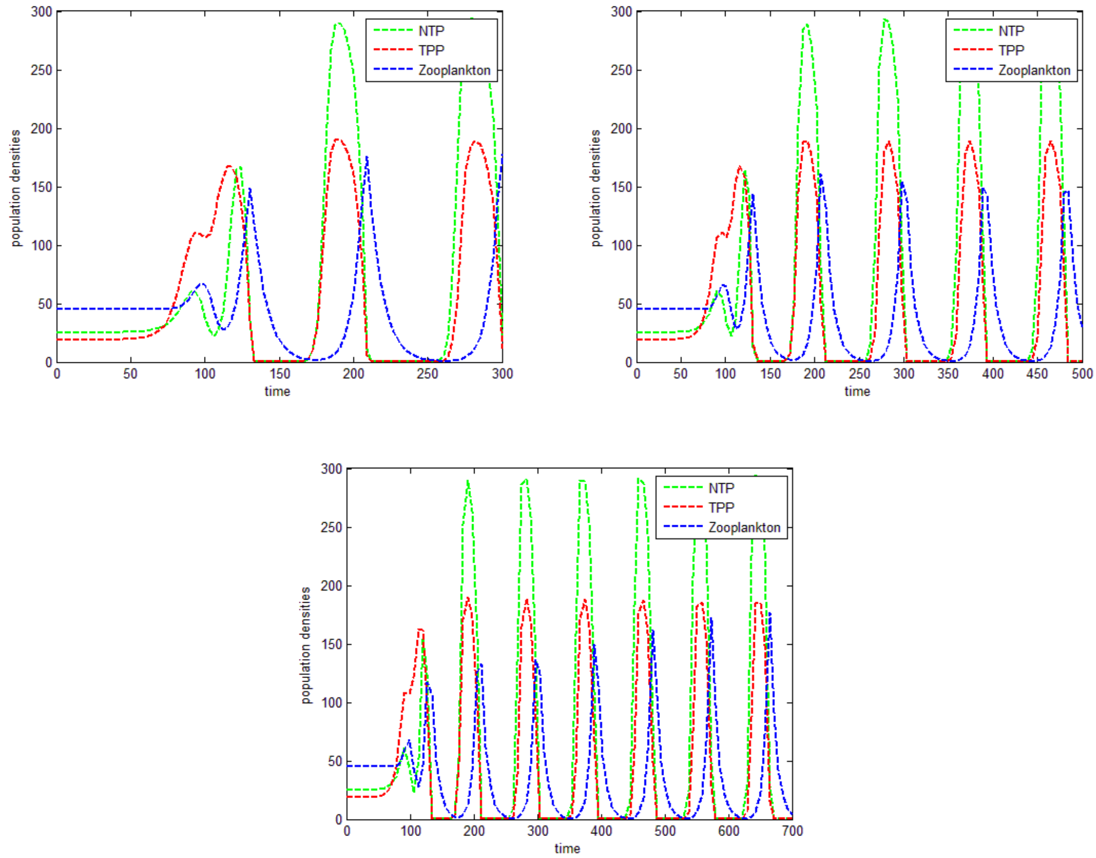
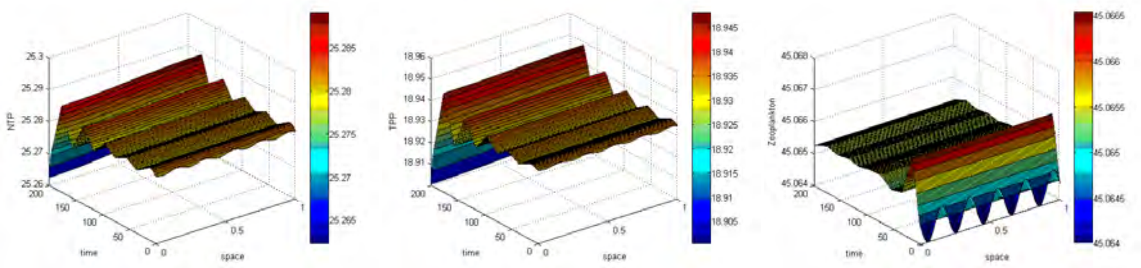


Fig. 2 Time series of the model system (2) for the fixed set of parameter set (29) and $d_1 = d_2 = 0.01,\ d_3 = 0.1$ with $t = 300,\ 500,\ 700$.

In Fig. 3 and 4, I have studied the spatiotemporal dynamics of the model system (2). From Fig. 3 I observed that NTP and TPP show oscillatory behavior in time *t* (first and second column) and zooplankton shows oscillatory behavior in time and space both (third column). Similarly, from Fig. 4 I observed that the system shows oscillatory behavior and oscillation increases with time $t = 100,\ 200,\ 300$.



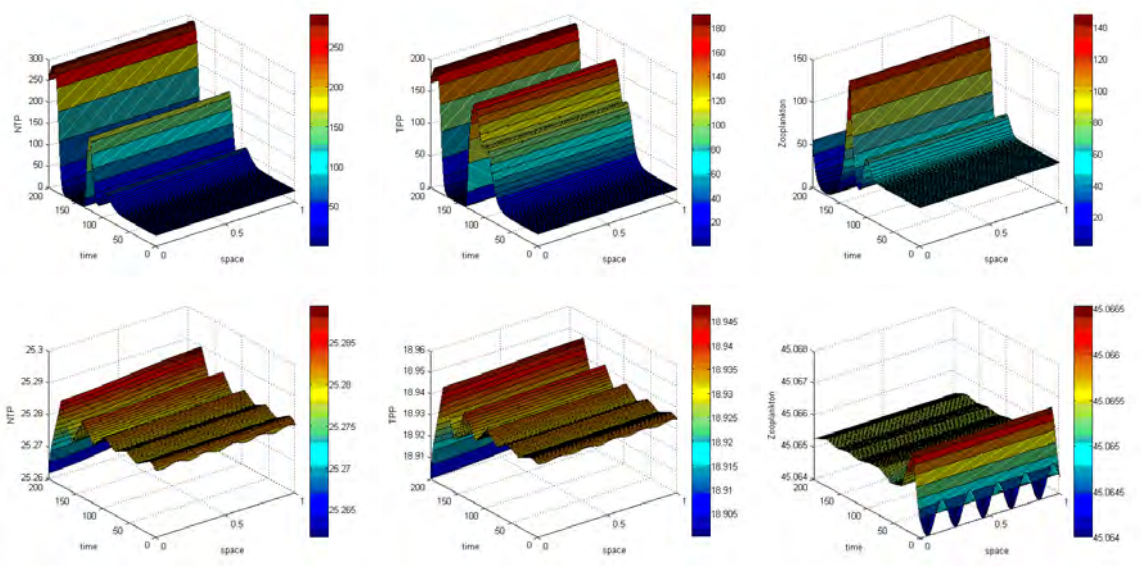


Fig. 3 Spatiotemporal pattern of NTP [*first column figure*], TPP [*second column figure*] and Zooplankton [*third column figure*] of the model System (2) for $t = 200$ with $d_1 = d_2 = 0.01$ and $d_3 = 2, 10, 20$.

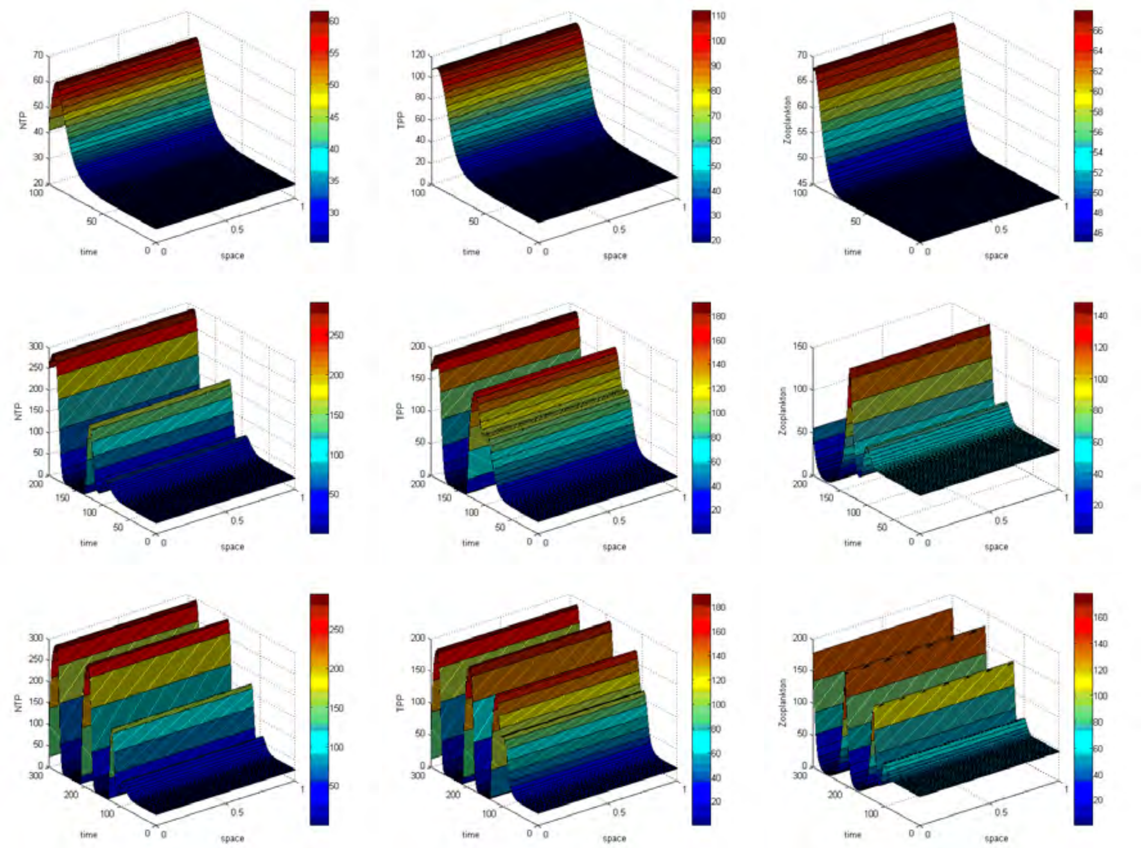


Fig. 4 Spatiotemporal pattern of NTP [*first column figure*], TPP [*second column figure*] and Zooplankton [*third column figure*] of the model System (1) for $d_1 = d_2 = 0.01,\ d_3 = 10$ with $t = 100, 200, 300$.

To understand the patchy distribution and species persistence I have taken the same parameters value (29) and I have perturbed the homogenous initial distribution about the equilibrium point. I consider the following initial condition:

$$u(x,\,0) = u^* + \varepsilon_1 \sin\left(\frac{2\pi(x-x_0)}{0.2}\right) + \varepsilon_1 \sin\left(\frac{2\pi(y-y_0)}{0.2}\right),$$
$$v(x,\,0) = v^* + \varepsilon_1 \sin\left(\frac{2\pi(x-x_0)}{0.2}\right) + \varepsilon_1 \sin\left(\frac{2\pi(y-y_0)}{0.2}\right),$$
$$w(x,\,0) = w^* + \varepsilon_1 \sin\left(\frac{2\pi(x-x_0)}{0.2}\right) + \varepsilon_1 \sin\left(\frac{2\pi(y-y_0)}{0.2}\right), \tag{31}$$

where $\varepsilon_1 = 5\times10^{-4},\ x_0 = 0.1,\ (u^*,\ v^*,\ w^*) = (25.2811,\ 18.9343,\ 45.0654)$.

For the parameters set (29) and initial condition (31) I have not observed any patchy distribution in NTP, TPP and zooplankton dynamics (Fig. 5). Then I have taken the random perturbation about initial point $(u_0,\ v_0,\ w_0) = (0.4,\ 0.2,\ 0.4)$. In Fig. 6, I have plotted the snapshots for fixed value of t =200 with increasing value of $d_3 = 0.05,\ 1,\ 2$ to observe the patchy spatial distribution of NTP, TPP and zooplankton population. Finally, I observed the time evolution of patchy spatial spread of model system (2) for t =200, 500 and 700 (Fig.7).

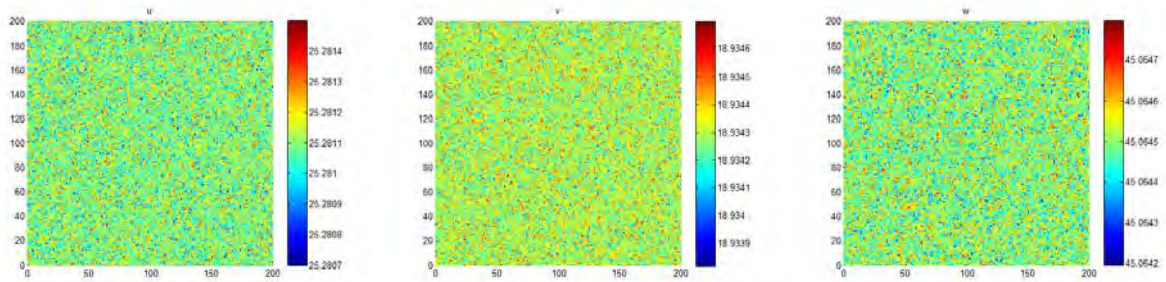
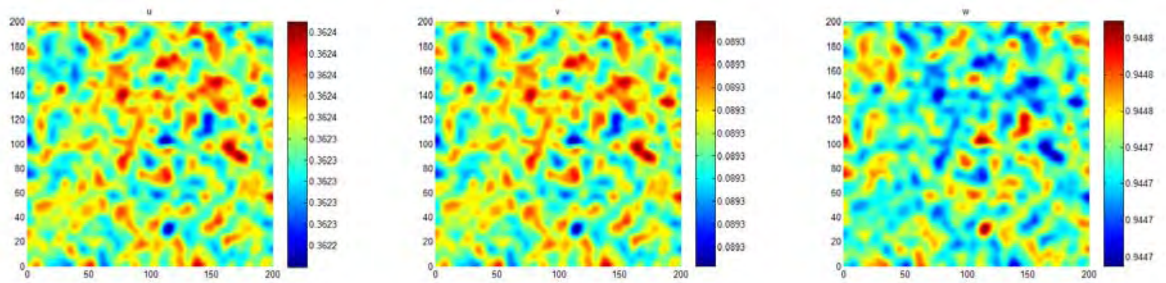


Fig. 5 Snapshots NTP [*first column figure*], TPP [*second column figure*] and Zooplankton [*third column figure*] of the model System (2) for $t = 200$ with $d_1 = d_2 = 0.01$ and $d_3 = 1$.



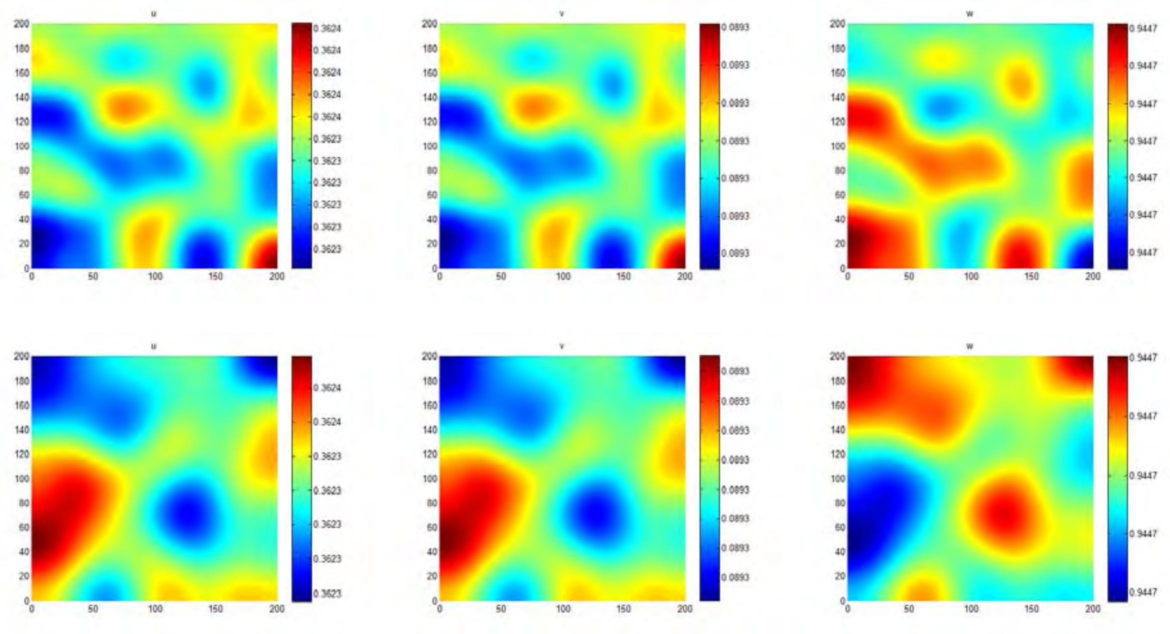


Fig. 6 Snapshots NTP [*first column figure*], TPP [*second column figure*] and Zooplankton [*third column figure*] of the model System (2) for $t = 200$ with $d_1 = d_2 = 0.01$ and $d_3 = 0.05, 1, 2$.

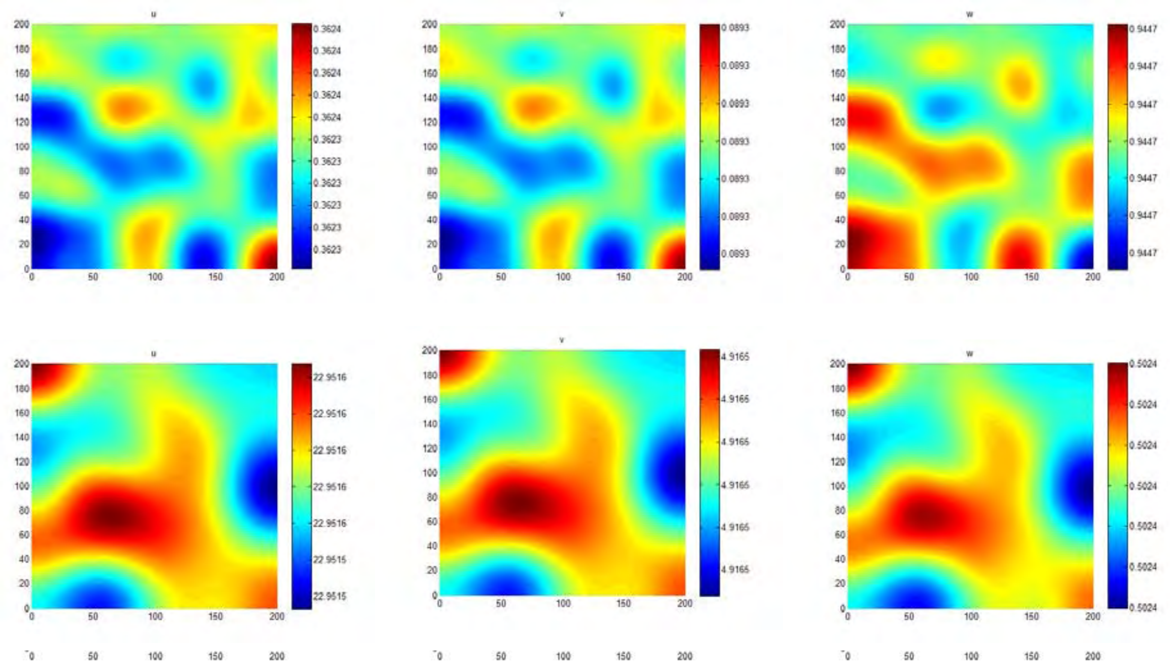


Fig. 7 Snapshots NTP [*first column figure*], TPP [*second column figure*] and Zooplankton [*third column figure*] of the model system (2) with $d_1 = d_2 = 0.01, d_3 = 1$ for $t = 200, 500, 700$.

6 Discussions and Conclusions

In this paper, I have considered a real situation of marine environment with three interacting aquatic species NTP-TPP-zooplankton and investigated their dynamical behavior. A detail study of stability analysis for the model system (2) has been carried out to understand the behavior of the system in presence as well as in the absence of diffusion. For a particular set of parameter values (29) I have plotted the region of Turing instability (Fig. 1). The toxin production by phytoplankton has a great interest both for intrinsic scientific merit and also because of its possible direct effect on fisheries. The TPP blooms in freshwater has severe impact on marine system such as degradation of water quality, habitat alteration and oxygen deficiency in the bottom water. Our goal to control TPP blooms to improve marine ecosystem. For this purpose, I have plotted the time series, spatiotemporal patterns and snap shots of the model system (2) and I observed the following:

(i) For increasing value of time $t = 200, 500 \text{ and } 700,$ the system represent the limit cycle behavior (Fig. 2).
(ii) For increasing value of random movement of zooplankton, the spatiotemporal pattern of the model (2) shows oscillatory behavior in time and stationary in space for $d_3 = 2, 10$ and for $d_3 = 20$ system shows oscillatory behavior in both time and space (Fig. 3).
(iii) For increasing value of random movement of zooplankton, the patchy spatial distribution of NTP, TPP and zooplankton evolved (Fig. 6).
(iv) For increasing value of time $t = 200, 500 \text{ and } 700,$ patchy spatial distribution of NTP, TPP and zooplankton evolved (Fig. 7).

In this work, I demonstrate the non-Turing patch spread of TPP, NTP and zooplankton dynamics for two dimensional cases. To determine patchy spread and species persistence I have taken the same parameter values and initial condition as random perturbation about equilibrium point. With the help of time series, spatiotemporal pattern and snap shot I observed that the TPP blooms under control for a particular set of parameter value. Finally, the overall result may be useful for sustainability and maintenance of biodiversity of aquatic systems.

References

Adriana Z, Enevoldsen HO. 2000. The diversity of harmful algal blooms: a challenge for science and management. Ocean and Coastal Management, 43: 725-748

Anderson DM, Garrison DJ. 1997. The ecology and oceanography of harmful algal blooms. Limnology and Oceanography, 42: 1009-1305

Anderson DM. 2009. Approaches to monitoring, control and management of harmful algal blooms (HABs). Ocean and Coastal Management, 52: 342-347

Blaxter J, Southward A. 1997. Advances in Marine Biology. Academic Press, London, UK

Chattopadhyay J, Sarkar RR, Mandal S. 2000. Toxin producing plankton may act as a biological control for planktonic blooms- field study and mathematical modeling. Journal of Theoretical Biology, 215: 333-344

Chakraborty S, Bhattacharya S, Feudel U, Chattopadhyay J. 2012. The role of avoidance by zooplankton for survival and dominance of toxic phytoplankton. Ecological Complexity, 11: 144-153

Dubey B, Hussain J. 2000. Modelling the interaction of two biological species in polluted environment. Journal of Mathematical Analysis and Applications, 246: 58-79

Elser JJ, Loladze I, Peace AL, Kuang Y. 2012. Modeling trophic interactions under stoichiometric constraints. Ecological Modeling, 245: 3-11

Franks PJS. 1997. Models of harmful algal blooms. Limnology and Oceanography, 42: 1273-1282

Garvie MR. 2007. Finite difference schemes for reaction-diffusion equations modelling predator-prey interactions in MATLAB. Bulletin of Mathematical Biology, 69: 931-956

Huisman J, Sharples J, Stroom, JM, Visser PM, Kardinaal WEA. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology, 85: 2960-2970

Hallegraeff GM. 1993. A review of harmful algal blooms and their apparent global increase. Phycologia, 32, 79-99

Kareiva P. 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Transactions of the Royal Society of London B, 330: 175-190

Levin SA. 1974. Dispersion and population interactions. American Naturalist, 108: 207-228

Roy S, Bhattacharya S, Das P, Chattopadhyay J. 2007. Interaction among nontoxic phytoplankton, toxic phytoplankton and zooplankton: inferences from field observations. Journal of Biological Physics, 33: 1-17

Roy S. 2008. Spatial interaction among nontoxic phytoplankton, toxic phytoplankton, and zooplankton: emergence in space and time. Journal of Biological Physics, 34: 459-474

Roy S, Alam S, Chattopadhyay J. 2006. Competing effects of toxin-producing phytoplankton on the overall plankton populations in the Bay of Bengal. Bulletin of Mathematical Biology, 68: 2303-2320

Scotti T, Mimura M, Wakano JY. 2015. Avoiding toxic prey may promote harmful algal blooms, Ecological Complexity, 21: 157-165

Truscott J, Brindley J. 1994. Ocean plankton populations as excitable media. Bulletin of Mathematical Biology, 56: 981-998

Upadhyay RK, Thakur NK, Dubey B. 2010. Nonlinear non-equilibrium pattern formation in a spatial aquatic system: Effect of fish predation. Journal of Biological Systems, 18: 129-159

Wyatt T. 1998. Harmful algae, marine blooms, and simple population models. Nature and Resources, 34: 40-51

Yang F, Fu S. 2008. Global solutions for a tritrophic food chain model with diffusion. Rocky Mountain Journal of Mathematics, 38: 1-28

Zhang WJ, Zhang GL. 2018. Some dynamic models for development of insecticide resistance in insect population. Computational Ecology and Software, 8(1): 1-6