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Dynamics of three species plankton model with Holling type-IV functional responses and control of toxic phytoplankton

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Abstract
In this paper we proposed a minimal model of non-toxic phytoplankton - toxic phytoplankton - zooplankton dynamics with Holling type-II and Holling type-IV functional responses. We carried out the analytical study of spatial and non-spatial model for one dimensional system in detail and found out the condition for diffusive instability of a locally stable equilibrium. With the help of numerical simulations, we have observed that when the rate of inhibition of zooplankton growth by toxic material ingested in feeding on toxic phytoplankton is very large, then because of high toxic effect, the zooplankton goes to extinction.

keywords plankton; planktonic bloom; diffusion; spatio-temporal pattern.

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1 Introduction

Phytoplankton are photo-synthesizing microscopic organisms of the plankton community and a key part of oceans, seas and freshwater basin ecosystems. The phytoplankton communities consist of accumulation of species with different morphological (size, shape) and physiological (nutrition mode, reproduction) characteristics and whose organization is a key to understand the dynamics of any ecosystem. A significant number of species of phytoplankton has been found that have the ability to produce toxic or inhibitory compounds (Chattopadhyay, 2002; Hallegrae, 1993; Sarkar, 2003; Steidinger, 1996). These are called toxin-producing phytoplankton (TPP), and distinguish them from non-toxic phytoplankton (NTP). These TPP are entirely different from other phytoplankton in biochemical nature.

Reduction in zooplankton density due to release of toxic substances by phytoplankton is one of the most indispensable parameters in this context (Fay, 1983; Keating, 1976; Kirk, 1992; Lefevre, 1952). Buskey and Stockwell (1993) have demonstrated in their field studies that micro- and meso-zooplankton populations are reduced during the blooms of a chrysophyte *Aureococcus anophagefferens* on the southern Texas coast. Toxicity may be a strong mediator of zooplankton feeding rate, as shown in both field studies (Estep, 1990; Hansen and Nielsen, 1990) and laboratory studies (Buskey, 1995; Huntley, 1986; Ives, 1987; Nejstgaard, 1996). With the help of field observation and mathematical modelling, Roy et al. (2006, 2007) discovered the role of TPP in determining the dynamics and main-taining diversity of the overall phytoplankton and zooplankton species in the Bay of Bengal. Roy (2008) also studied the space-time framework for promo-tion of plankton diversity due to the presence of TPP. These observations indicate that the toxic substance as well as toxic phyto-plankton plays an important role in the growth of the zooplankton population and has a great impact on phytoplankton-zooplankton interactions. He investigated the effects of spatial interaction on plankton populations in the presence of toxic species.

In this paper, we propose and analyze a three-component mathematical model consisting of the NTP, TPP, and zooplankton populations for modelling the plankton dynamics in spatially distributed population with local diffusion. Here, we assume that the local growth of the prey is logistic and that the predator shows the Holling type II functional response for non-toxin-producing (NTP) and Holling type IV functional for TPP. We obtained the conditions for local stability of the model system in the absence and presence of diffusion. We also obtained the criteria for turing in-stability. We numerically simulated the model system using estimated parameter values. TPP provides a mechanism for switching of plankton dynamics from limit cycle to stability. Our observation indicates that TPP has a significant controlling command on zooplankton.

2 Model System

We formulate a mathematical model of those interacting groups: non-toxic phytoplankton, toxic phytoplankton and zooplankton under the following assumptions:

(i) Each of non-toxic phytoplankton and toxic phytoplankton population follow logistic growth.

(ii) The groups of phytoplankton exhibit Holling type-II and Holling type-IV functional response to the grazer zooplankton.

(iii) Toxic materials ingested on predation of Toxic Phytoplankton cause a significant inhibitory effect on zooplankton growth.

We consider a reaction-diffusion model for non-toxic phytoplankton, toxic phytoplankton and zooplankton system.

Table 1 Definition of parameters and variables.

Parameter	Definition
$P_N(x,t)$	Concentrations of non-toxic phytoplankton at any location x and time t .
$P_T(x,t)$	Concentrations of toxic phytoplankton at any location x and time t .
$Z(x,t)$	Concentrations of zooplankton at any location x and time t .
k_1	Carrying capacity of phytoplankton which is shared by non-toxic phytoplankton.
k_2	Carrying capacity of phytoplankton which is shared by toxic phytoplankton.
r_1	Constant intrinsic growth rate of non-toxic phytoplankton population.
r_2	Constant intrinsic growth rate of toxic phytplankton population.
w_1	Rate at which non-toxic phytoplankton are consumed by zooplankton.
w_2	Rate at which toxic phytoplankton are consumed by zooplankton.

ξ_1	The maximum rate of gain in zooplankton growth due to predation of non-toxic phytoplankton at a rate w_1.
ξ_2	The rate of inhibition of (or reduction in) zooplankton growth by toxic material ingested in feeding on toxic phytoplankton.
m	Half saturation constant for non-toxic phytoplankton.
α	Half saturation constant for toxic phytoplankton.
c	Mortality rate of zooplankton due to natural death.
D_1	Diffusion coefficient of non-toxic phytoplankton.
D_2	Diffusion coefficient of toxic phytoplankton.
D_3	Diffusion coefficient of zooplankton.

Here, $\nabla^2 = \dfrac{\partial^2}{\partial x^2}$

Based on earlier assumptions, plankton dynamics may be written as follows:

$$\frac{\partial P_N}{\partial t} = r_1 P_N\left(1-\frac{P_N+\alpha_1 P_T}{k_1}\right)-\frac{w_1 P_N Z}{m+P_N}+D_1\nabla^2 P_N,$$

$$\frac{\partial P_T}{\partial t} = r_2 P_T\left(1-\frac{P_T+\alpha_2 P_N}{k_2}\right)-\frac{w_2 P_T Z}{\frac{P_T^{\,2}}{\alpha}+P_T+1}+D_2\nabla^2 P_T,$$

$$\frac{\partial Z}{\partial t} = \frac{\xi_1 P_N Z}{m+P_N}-\frac{\xi_2 P_T Z}{\frac{P_T^{\,2}}{\alpha}+P_T+1}-cZ+D_3\nabla^2 Z,$$

(1)

with non-zero initial conditions:

$$P_N(x,0)>0, P_T(x,0)>0, Z(x,0)>0, x\in[0,R].$$

(2)

and the zero-flux boundary conditions

$$\frac{\partial P_N}{\partial x}=\frac{\partial P_T}{\partial x}=\frac{\partial Z}{\partial x}=0, x\in[0,R].$$

(3)

The zero flux boundary conditions are used for modeling the dynamics of spatially bounded aquatic ecosystem. Here, r_1 and r_2 are the intrinsic growth rate of non toxic phytoplankton and toxic phytoplankton in the absence of predation respectively; α_1 and α_2 are the interspecific competition coefficient for non toxic phytoplankton and toxic phytoplankton; k_1 and k_2 are the carrying capacity of phytoplankton populations; w_1 and w_2 are maximum rate of predation; m and α are half-saturation constant for non toxic phytoplankton and toxic phytoplankton density respectively; ξ_1 is the rate at which non toxic phytoplankton is grazed and ξ_2 is the reduction rate in the growth of zooplankton due to toxic material ingested in feeding on toxic phytoplankton ; c is the mortality rate of zooplankton, D_1, D_2 and D_3 are the diffusion coefficients of non toxic phytoplankton, toxic phytoplankton and zooplankton density respectively.

3 Stability Analysis of Non-Spatial Model System

In this section, we restrict ourselves to the stability analysis of the model system in the absence of diffusion ($D_1 = 0, D_2 = 0, D_3 = 0$) in which only the interaction part of the model system is taken into account. We find the non-negative equilibrium states of the model system and discuss their stability properties with respect to variation of several parameters. In this case, the model system reduces to the form

$$\begin{aligned}
\frac{dP_N}{dt} &= r_1 P_N\left(1-\frac{P_N+\alpha_1 P_T}{k_1}\right)-\frac{w_1 P_N Z}{m+P_N},\\
\frac{dP_T}{dt} &= r_2 P_T\left(1-\frac{P_T+\alpha_2 P_N}{k_2}\right)-\frac{w_2 P_T Z}{\frac{P_T{}^2}{\alpha}+P_T+1},\\
\frac{dZ}{dt} &= \frac{\xi_1 P_N Z}{m+P_N}-\frac{\xi_2 P_T Z}{\frac{P_T{}^2}{\alpha}+P_T+1}-cZ,
\end{aligned} \tag{4}$$

Lemma 1: $\theta = \left\{(P_N(t), P_T(t), Z(t)) : 0 \le P_N(t) \le k_1, 0 \le P_T(t) \le k_2, 0 \le P_N(t) + \frac{w_1}{\xi_1} z(t) \le k_1\left(1+\frac{r_1}{\delta}\right)\right\}$ is a region of attraction for all solutions initiating in the interior of the positive octant, where $0 < \delta \le c$.

The model system (4) possesses six non-negative real equilibrium points:

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

(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 $E_3(\hat{P}_1, \hat{P}_2, 0)$ is the planar equilibrium point on the $P_N P_T$ -plane where $\hat{P}_N = \frac{k_1-\alpha_1 k_2}{1-\alpha_1\alpha_2}$ and $\hat{P}_T = \frac{k_2-\alpha_2 k_1}{1-\alpha_1\alpha_2}$ if $\alpha_1 < \frac{k_1}{k_2} < \frac{1}{\alpha_2}$.

(v) TPP-free equilibrium point $E_4(\hat{P}_N, 0, \hat{Z})$ is the planar equilibrium point on the $P_N Z$ - plane where

$\overline{P_N} = \frac{cm}{\xi_1 - c}$ and $\bar{z} = \frac{r_1}{w_1}\left(1-\frac{P_N}{k_1}\right)(m+P_N)$ if $\xi_1 > c$, $k_1(\xi_1 - c) > cm$.

(vi) The existence of interior equilibrium point $E_5(P_N{}^*, P_T{}^*, Z^*)$.

In this case, P_N^*, P_T^* and Z^* are the positive solutions of the following three equations:

$$r_1\left(1-\frac{P_N+\alpha_1 P_T}{k_1}\right)-\frac{w_1 Z}{m+P_N}=0 \tag{5}$$

$$r_2\left(1-\frac{P_T+\alpha_2 P_N}{k_2}\right)-\frac{w_2 Z}{\frac{P_T^{\,2}}{\alpha}+P_T+1}=0 \tag{6}$$

$$\frac{\xi_1 P_N}{m+P_N}-\frac{\xi_2 P_T}{\frac{P_T^{\,2}}{\alpha}+P_T+1}-c=0 \tag{7}$$

From Eq.(5) ,we get

$$Z=\frac{r_1}{w_1}\left(1-\frac{P_N+\alpha_1 P_T}{k_1}\right)(\alpha+P_N) \tag{8}$$

Clearly, $Z>0$ if $k_1>(P_N+\alpha_1 P_T)$.

Putting the value of Z from Eq.(8) in Eqs.(6) and (7), we obtain:

$$F_1(P_N,P_T)=r_2\left(1-\frac{P_T+\alpha_2 P_N}{k_2}\right)-\frac{r_1 w_2}{w_1\left(\frac{P_T^{\,2}}{\alpha}+P_T+1\right)}\left(1-\frac{P_N+\alpha_1 P_T}{k_1}\right)(m+P_N)=0, \tag{9}$$

$$F_2(P_N,P_T)=\frac{\xi_1 P_N}{m+P_N}-\frac{\xi_2 P_T}{\frac{P_T^{\,2}}{\alpha}+P_T+1}-c=0 \tag{10}$$

From Eq.(9), when $P_T=0$ then $P_N=P_{N_a}$ where

$$P_{N_a}>0,\ \text{if}\Rightarrow r_2 w_1<r_1 w_2 \tag{11}$$

Putting $P_N=0$ in Eq.(9), we note that $F_1(0,P_T)$ has a unique positive root P_{T_a}, which is the solution of the following equation:

$$r_2 P_2^{\,3} - (r_2 k_2 + r_2 d_2 k_2) P_2^{\,2} - (k_2 d_2 r_2 + r_2 d_2 - \frac{r_1 w_2 k_2 d_1 d_2 \alpha_1}{k_1 w_1}) P_2 - r_2 d_2 k_2 + \frac{r_1 w_2 d_1 d_2 k_2}{w_1} = 0 \tag{12}$$

It may be noted here that Eq.(12) has one or three positive roots. Eq. (12) can be re-written as

$$P_2^{\,3} + q_1 P_2^{\,2} + q_2 P_2 + q_3 = 0 \tag{13}$$

where $q_1 = (-k_2 + \alpha k_2), q_2 = (-\alpha k_2 - \alpha + \frac{r_1 w_2 m \alpha \alpha_1 k_2}{k_1 w_1 r_2}), q_3 = \left(-k_2 \alpha + \frac{k_2 w_2 m \alpha r_1}{w_1 r_2}\right)$.

Thus Eq.(12) has a unique real positive root P_{N_a} (other roots will be complex conjugate) if

$$\frac{a_2^{\,2}}{4} + \frac{a_1^{\,3}}{27} > 0 \tag{14}$$

where $a_1 = \frac{1}{3}(3q_2 - q_1^{\,2}), a_2 = \frac{1}{27}(2q_1^{\,3} - 9q_1 q_2 + 27q_3)$.

Let $F_{1_{P_N}}$ and $F_{1_{P_T}}$ are the partial derivatives of F_1 with respect to P_N and P_T respectively. Now we have

$\frac{dP_N}{dP_T} = \frac{-F_{1_{P_T}}}{F_{1_{P_N}}}$, where $F_{1_{P_N}} \neq 0$.

It may be noted that $\frac{dP_N}{dP_T} < 0$ if

either $(i) F_{1_{P_N}} > 0$ and $F_{1_{P_T}} > 0,$

or $(ii) F_{1_{P_N}} < 0$ and $F_{1_{P_T}} < 0,$

(15)

From Eq.(10), when $P_T = 0$ then $P_N = P_{N_b}$ where:

$$P_{N_b} = \frac{cm}{\xi_1 - c} \tag{16}$$

$$P_{N_b} > 0 \text{ if } \xi_1 > c \tag{17}$$

Let $F_{2_{P_N}}$ and $F_{2_{P_T}}$ are the partial derivatives of F_2 with respect to P_N and P_T respectively. Now we have

$\frac{dP_N}{dP_T}=\frac{-F_{2_{P_T}}}{F_{2_{P_N}}}$, where $F_{2_{P_N}} \neq 0$. It may be noted that $\frac{dP_N}{dP_T}>0$ because

$$F_{2_{P_N}} = \frac{m\xi_1}{(m+P_1)^2} > 0, F_{2_{P_T}} = \frac{-P_2\xi_2\alpha(P_2+\alpha-2)}{(P_2{}^2+\alpha P_2+\alpha)^2} < 0 \tag{18}$$

From the above analysis, we note that the isoclines (9) and (10) intersect at a unique point $(P_N{}^*, P_T{}^*)$, if in addition to conditions (14), (15) and (17) the following condition holds:

$P_{N_b} < P_{N_a}$.

Knowing the values of P_N and P_T, the value of Z^* can be calculated from Eq.(8). This completes the existence of equilibrium point $E_5\left(P_N{}^*, P_T{}^*, Z^*\right)$.

Now, in order to investigate local behavior of the model system (1)-(3) at each equilibrium points, the variational matrix of the point is $\left(P_N, P_T, Z\right)$ computed as

$$\begin{pmatrix} P_N\frac{\partial f_1}{\partial P_N}+f_1 & P_N\frac{\partial f_1}{\partial P_T} & P_N\frac{\partial f_1}{\partial Z} \\ P_T\frac{\partial f_2}{\partial P_N} & P_T\frac{\partial f_2}{\partial P_T}+f_2 & P_T\frac{\partial f_2}{\partial Z} \\ Z\frac{\partial f_3}{\partial P_N} & Z\frac{\partial f_3}{\partial P_T} & Z\frac{\partial f_3}{\partial Z}+f_3 \end{pmatrix} \tag{19}$$

Let $V_j, j=0,1,2,3,4,5$ denotes the variational matrix at $E_j, j=0,1,2,3,4,5$ respectively.

For $E_0(0,0,0)$ we have

$$V_0=\begin{pmatrix} r_1 & 0 & 0 \\ 0 & r_2 & 0 \\ 0 & 0 & -c \end{pmatrix}$$

The eigenvalues of matrix V_0 are $r_1, r_2, -c$. There is unstable manifold along P_N, P_T direction and stable manifold along Z direction. Therefore, the equilibrium point E_0 is a saddle point.

The variational matrix for $E_1(k_1,0,0)$ is given by

$$V_1 = \begin{pmatrix} -r_1 & -\alpha_1 r_1 & -\frac{w_1 k_1}{k_1+m} \\ 0 & r_2\left(1-\frac{\alpha_2 k_1}{k_2}\right) & 0 \\ 0 & 0 & -c+\frac{k_1\xi_1}{k_1+m} \end{pmatrix}$$

The eigenvalues of the matrix V_1 are $-r_1, r_2\left(1-\frac{\alpha_2 k_1}{k_2}\right), \left(\frac{\xi_1 k_1}{k_1+m}-c\right)$.There is a stable manifold along P_N direction and unstable manifold along $P_T, Z-$ direction provided $\frac{k_2}{\alpha_2} < k_1 < \frac{cm}{(\xi_1 - c)}, \xi_1 > c$. It is a saddle point if the inequality opposes.

The variational matrix for $E_2(0,k_2,0)$ is given by

$$V_2 = \begin{pmatrix} r_1\left(1-\frac{\alpha_1 k_2}{k_1}\right) & 0 & 0 \\ -r_2\alpha_2 & -r_2 & -\frac{w_2\alpha k_2}{k_2^{\ 2}+k_2\alpha+\alpha} \\ 0 & 0 & -c-\frac{\xi_2 k_2\alpha}{k_2^{\ 2}+k_2\alpha+\alpha} \end{pmatrix}$$

The eigen values of the matrix V_2 are $r_1\left(1-\frac{\alpha_1 k_2}{k_1}\right), -r_2$ and $-c-\frac{\xi_2 k_2\alpha}{k_2^{\ 2}+k_2\alpha+\alpha}$. There is unstable manifold along P_N direction if $k_1 > \alpha_1 k_2$ and stable mani-fold along P_T and Z direction. E_2 is a saddle point.

The variational matrix for $E_3(P_N, P_T, 0)$ is given by

$$V_3 = \begin{pmatrix} -\frac{r_1 P_N}{k_1} & -\frac{\alpha_1 r_1 P_N}{k_1} & -\frac{w_1 P_N}{m+P_N} \\ -\frac{r_2\alpha_2 P_T}{k_2} & -\frac{r_2 P_2}{k_2} & -\frac{w_2\alpha P_T}{P_T^{\ 2}+P_T\alpha+\alpha} \\ 0 & 0 & -c-\frac{\xi_1 P_N}{m+P_N}-\frac{\xi_2 P_2\alpha}{P_T^{\ 2}+P_T\alpha+\alpha} \end{pmatrix}$$

The equilibrium point $E_3(P_N, P_T, 0)$ is stable or unstable in the positive di-rection orthogonal to the P_N P_T plane, i.e. Z-direction depending on whether $\lambda_3 = c + \frac{\xi_1 P_N}{m+P_N} - \frac{\xi_2 P_T \alpha}{P_T^{\,2} + P_T\alpha + \alpha}$ is negative or positive respectively.

The variational matrix about the equilibrium point $E_4(P_N, 0, Z)$ is given by

$$V_4 = \begin{pmatrix} P_N\left(-\frac{r_1}{k_1} + \frac{w_1 Z}{(P_N+m)^2}\right) & -\frac{\alpha_1 r_1 P_N}{k_1} & -\frac{w_1 P_N}{m+P_N} \\ 0 & r_2\left(1-\frac{\alpha_2 P_N}{k_2}\right) - w_2 Z & 0 \\ \frac{m\xi_1 Z}{(P_N+m)^2} & -\xi_2 Z & 0 \end{pmatrix}$$

The equilibrium point $E_4(P_N, 0, Z)$ is stable or unstable in the positive di-rection orthogonal to the $P_N Z$ plane, i.e. P_T - direction depending on whether $r_2\left(1-\frac{\alpha_2 P_N}{k_2}\right) - w_2 Z$ is negative or positive respectively, if $w_1 k_1 Z < r_1 (P_N + m)^2$.

The variational matrix about the equilibrium point $E_5(P_N*, P_T*, Z*)$ is given by

$$V_5 = \begin{pmatrix} P_N*\left(-\frac{r_1}{k_1} + \frac{w_1 Z*}{(P_N*+m)^2}\right) & -\frac{\alpha_1 r_1 P_N*}{k_1} & -\frac{w_1 P_N*}{m+P_N*} \\ -\frac{r_2\alpha_2 P_T*}{k_2} & -\frac{r_2 P_T*}{k_2} - \frac{(w_2 Z*\alpha^2 - w_2 Z^* \alpha P_T^{*2})}{(P_T^{*2} + P_T^*\alpha + \alpha)^2} & -\frac{w_2 \alpha P_T^*}{P_T^{*2} + P_T^*\alpha + \alpha} \\ \frac{m\xi_1 Z*}{(P_N*+m)^2} & \frac{\xi_2 Z^* \alpha P_T^{*2} - \xi_2 Z^* \alpha^2}{(P_T^{*2} + P_T^*\alpha + \alpha)^2} & \frac{\xi_1 P_N^*}{m+P_N^*} - \frac{\xi_2 P_T^* \alpha}{P_T^{*2} + P_T^*\alpha + \alpha} - c \end{pmatrix}$$

$$= \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}$$

In the following theorem, we are able to find conditions for the positive equilibrium point $E_5(P_N*, P_T*, Z*)$ to be locally asymptotically stable.

Theorem 2.1. Suppose that the positive equilibrium point $E_5(P_N*, P_T*, Z*)$ of the model system (4) exists. The equilibrium point $E_5(P_N*, P_T*, Z*)$ is locally asymptotically stable if the following conditions hold:

$$(i) r_1(P_N*+m)^2 > w_1 k_1 Z^*, r_2 P_T^*(P_T^{*2} + P_T^*\alpha + \alpha)^2 > k_2(w_2 Z^*\alpha P_T^{*2} - w_2 Z^*\alpha^2)$$

$$(ii) \frac{r_2 P_T^*}{k_2} + \frac{\left(w_2 Z^*\alpha^2 - w_2 Z^*\alpha P_T^{*2}\right)}{(P_T^{*2} + P_T^*\alpha + \alpha)^2} > \frac{\alpha_1 r_1 \alpha w_2 P_T^*(m + P_N^*)}{k_1 w_1 (P_T^{*2} + P_T^*\alpha + \alpha)}, P_N^*\left(-\frac{r_1}{k_1} + \frac{w_1 Z^*}{(P_N^* + m)^2}\right) > \frac{w_1 r_2 \alpha_2 P_N^* P_T^*}{k_2(m + P_N^*)},$$

$$(iii) \alpha_1 \alpha_2 r_1 r_2 (P_N^* + m)^3 > m w_1 \xi_1 k_1 k_2, \frac{m\xi_1 Z^* w_2 \alpha \alpha_1 r_1}{k_1(P_N^* + m)} > \frac{w_1 r_2 \alpha_2}{k_2} \frac{\left[\xi_2 Z^*\alpha P_N^{*2} - \xi_2 Z^*\alpha^2\right]}{k_2(P_T^{*2} + P_T^*\alpha + \alpha)},$$

$$\left[P_N^*\left(-\frac{r_1}{k_1} + \frac{w_1 Z^*}{(P_N^* + m)^2}\right)\right]\left[-\frac{r_2 P_T^*}{k_2} - \frac{(w_2 Z^*\alpha^2 - w_2 Z^*\alpha P_T^{*2})}{(P_T^{*2} + P_T^*\alpha + \alpha)^2}\right] + \left[P_N^*\left(-\frac{r_1}{k_1} + \frac{w_1 Z^*}{(P_N^* + m)^2}\right)\right]^2 +$$

$$\frac{w_2 \alpha P_T^*(\xi_2 Z^*\alpha P_N^{*2} - \xi_2 Z^*\alpha^2)}{(P_T^{*2} + P_T^*\alpha + \alpha)^3} < \frac{\alpha_1 \alpha_2 r_1 r_2 P_N^* P_T^*}{k_1 k_2}$$

3 Stability Analysis of Spatial Model System

In this section, we study the effect of diffusion on the model system about the interior equilibrium point. In order to derive the condition of stability for the equilibrium point with diffusion, we have considered the linearized form of the model system (1) about $E_5(P_N*, P_T*, Z*)$ with small perturbations $U(x;t)$, $V(x;t)$ and $W(x;t)$ as $P_N = P_N^* + U, P_T = P_T^* + V, Z = Z^* + W$.

The linearized form of the equations is obtained as

$$\frac{\partial U}{\partial t} = a_{11}U + a_{12}V + a_{13}W + D_1\frac{\partial^2 U}{\partial x^2}$$
$$\frac{\partial V}{\partial t} = a_{21}U + a_{22}V + a_{23}W + D_2\frac{\partial^2 V}{\partial x^2}$$
$$\frac{\partial W}{\partial t} = a_{31}U + a_{32}V + a_{33}W + D_3\frac{\partial^2 W}{\partial x^2} \tag{20}$$

where

$$a_{11} = -\frac{w_1 Z^* P_N^*}{(\alpha + P_N^*)^2} - \frac{r_1 P_N^*}{k_1}, a_{12} = -\frac{\alpha_1 r_1 P_N^*}{k_1}, a_{13} = -\frac{w_1 P_N^*}{m + P_N^*},$$

$$a_{21} = -\frac{r_2 \alpha_2 P_T^*}{k_2}, a_{22} = -\frac{(w_2 Z^*\alpha^2 - w_2 Z^*\alpha P_T^{*2})}{(P_T^{*2} + P_T^*\alpha + \alpha)^2} - \frac{r_2 P_T^*}{k_2}, a_{23} = -\frac{w_2 P_T^*\alpha}{(P_T^{*2} + P_T^*\alpha + \alpha)},$$

$$a_{31} = \frac{m\xi_1 Z^*}{(m + P_N^*)^2}, a_{32} = \frac{\xi_2 Z^*\alpha P_T^{*2} - \xi_2 Z^*\alpha^2}{(P_T^{*2} + P_T^*\alpha + \alpha)^2}, a_{33} = \frac{\xi_1 P_N^*}{\alpha + P_N^*} - \frac{\xi_2 P_T^*\alpha}{P_T^{*2} + P_T^*\alpha + \alpha} - c$$

Let us suppose that the model system (20) has the solution which is of the form

$$\begin{pmatrix} U \\ V \\ W \end{pmatrix} = \begin{pmatrix} A \\ B \\ C \end{pmatrix} \exp(\lambda t)\cos(n\pi x / R), \tag{21}$$

where *A*, *B* and *C* are sufficiently small constants. $R/n\pi$ is the critical wave-length and $k = n\pi / R$ is wave number, *R* is the length of the system, $2\pi / n$ is the period of cosine and λ is the frequency respectively. The characteristic equation of the linearized system is given by

$$\lambda^3 + \rho_1\lambda^2 + \rho_2\lambda + \rho_3 = 0 \tag{22}$$

where

$$\rho_1 = -Tr(M) + (D_1 + D_2 + D_3)k^2$$

$$\rho_2 = R(M) + (D_1D_2 + D_1D_3 + D_3D_2)k^4 - \left[a_{11}(D_2 + D_3) + a_{22}(D_1 + D_3) + a_{33}(D_1 + D_3)\right]k^2, \tag{23}$$

$$\rho_3 = P(k^2)$$

With

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

where

$$\begin{aligned} b_0 &= D_1D_2D_3, \\ b_1 &= a_{11}D_2D_3 + a_{22}D_1D_3 + a_{33}D_1D_2 \\ b_2 &= D_1(a_{22}a_{33} - a_{23}a_{32}) + D_2(a_{11}a_{33} - a_{13}a_{31}) + D_3a_{11}a_{22}, \end{aligned} \tag{24}$$

and

$$M = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}, Tr(M) = a_{11} + a_{22} + a_{33},$$

$$\begin{aligned} R(M) &= a_{11}(a_{22} + a_{33}) - a_{13}a_{31} + a_{22}a_{33} - a_{23}a_{32}, \\ Det(M) &= a_{11}(a_{22}a_{33} - a_{23}a_{32}) - a_{22}a_{13}a_{31} \end{aligned} \tag{25}$$

Theorem 3.1 The positive equilibrium point $E_5(P_N{*}, P_T{*}, Z{*})$ is locally asymptotically stable in the presence of diffusion if and only if:

$$\rho_1 > 0 \tag{26}$$

$$\rho_3 > 0 \tag{27}$$

$$\rho_1\rho_2 - \rho_3 > 0 \tag{28}$$

From Eq. (22) and using the Routh-Hurwitz criterion, the above theorem follows immediately.

4 Turing Instability

The Turing instability occurs if at least one of the roots of the above Eq.(22) has a positive root or positive real part or in other words, $\mathrm{Re}(\lambda) > 0$ for some k > 0. Irrespective of the sign of ρ_1 and ρ_2, the diffusion-driven instability occurs when $\rho_3 = P(k^2) < 0$. Hence the condition for diffusive instability is given by

$$P(k^2) = b_0k^6 - b_1k^4 + b_2k^2 - Det(M) < 0 . \tag{29}$$

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

$$k_{cr}{}^2 = \frac{b_1 \pm \sqrt{b_1{}^2 - 3b_0b_2}}{3b_0} \tag{30}$$

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

$$b_1{}^2 - 3b_0b_1 > 0 \text{ and } b_1 > 0 \text{ or } b_2 < 0 \tag{31}$$

$$\begin{gathered} r_1 = 0.4632;\ r_2 = 0.4425;\ \alpha_1 = 0.002;\ \alpha_2 = 0.001;\ k_1 = 505;\ k_2 = 505; \\ w_1 = 0.6625; w_2 = 0.435;\ \xi_1 = 0.516;\ \xi_2 = 0.198;\ m = 45;\ \alpha = 30;\ c = 0.109 \end{gathered} \tag{32}$$

For this set of parameter values given in Eq.(32), we have obtained the equi-librium point $(P_N{}^*, P_T{}^*, Z^*)$ =(37.2907; 15.6704; 53.2830). For $D_1 = D_2 = 0.0001, D_3 = 10$, and the above set of parameter values given in Eq.(32), we have obtained the critical values $k_{cr}{}^2 =$ (-17.01; 8.798) and corresponding $P(k_{cr}{}^2) =$ (6.497;-2.441) (cf. Fig. 1). The graph of $P(k^2)$ versus k^2 has been plotted for different values of D_3. The positive values of k^2 for which $\rho_3 = P(k^2) < 0$, the plankton system (1) is unstable.

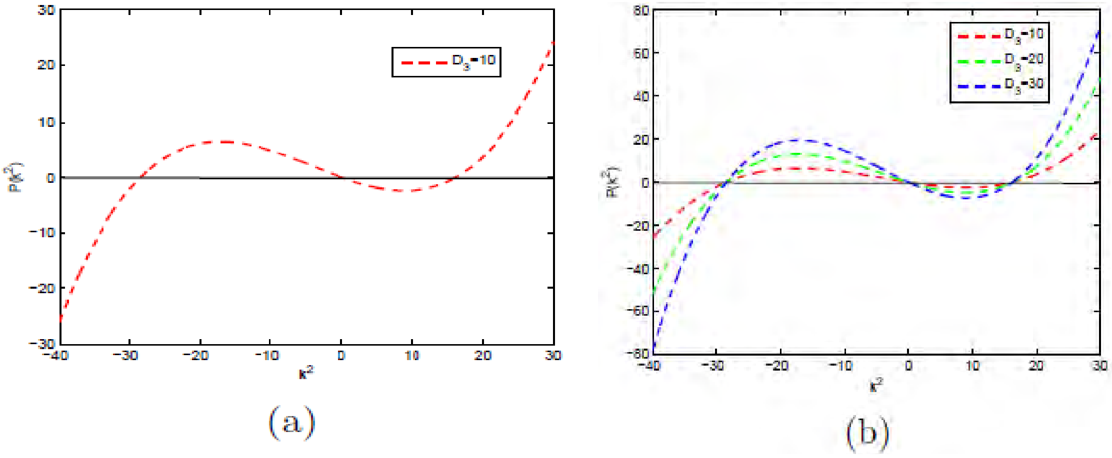


Fig. 1 The graph of the function $P(k^2)$ verses k^2 for the set of parametric values given in Eq.(32) With $D_1 = D_2 = 0.0001$ for (a) $D_3 = 10$ and (b) $D_3 = 10, 20, 30$

5 Numerical Simulation

In this section, we perform numerical simulations to understand the mechanism that will control the growth of TPP. For that purpose, we have plotted the spatio-temporal patterns and time series to observe the controlling parameters of TPP growth. The dynamics of the model sys-tem (1) is studied with the help of numerical simulation for one-dimensional case. To investigate the spatio-temporal dynamics of the model system (1), we have solved it numerically using semi-implicit (in time) finite difference method. The step lengths Δx and Δt of the numerical grid are chosen sufficiently small so that the results are numerically stable. We choose the following set of parameters (other set of parameters may also exists) for the model system (1):

$$\mathrm{r}_1 = 0.3;\ \mathrm{r}_2 = 0.2;\ \alpha_1 = 0;\ \alpha_2 = 0;\ \mathrm{k}_1 = 300;\ \mathrm{k}_2 = 250; \mathrm{w}_1 = 0.6625; \mathrm{w}_2 = 0.435;$$
$$\xi_1 = 0.516;\ \xi_2 = 0.198;\ \mathrm{m} = 45;\ \alpha = 30;\ \mathrm{c} = 0.109,\ \mathrm{D}_1 = D_2 = 0.001, D_3 = 0.01 \quad (33)$$

with initial condition

$$P_1(x,0) = P_1^* + \varepsilon_1 \sin\left(\frac{2\pi(x-x_0)}{S}\right),$$
$$P_2(x,0) = P_2^* + \varepsilon_1 \sin\left(\frac{2\pi(x-x_0)}{S}\right),$$
$$Z(x,0) = Z^* + \varepsilon_1 \sin\left(\frac{2\pi(x-x_0)}{S}\right), \quad (34)$$

where

$\varepsilon_1 = 5\times10^{-4}, x_0 = 0.1, S = 0.2$ and

(P_N^*, P_T^*, Z^*) = (28.3728, 34.7472,30.0831).

The model system (1) with a fixed set of parameter values given in Eq.(33) and initial condition (34) asserting that the density of TPP remain high in whole domain and system shows the limit cycle behavior (cf. Fig. 2 & 3).

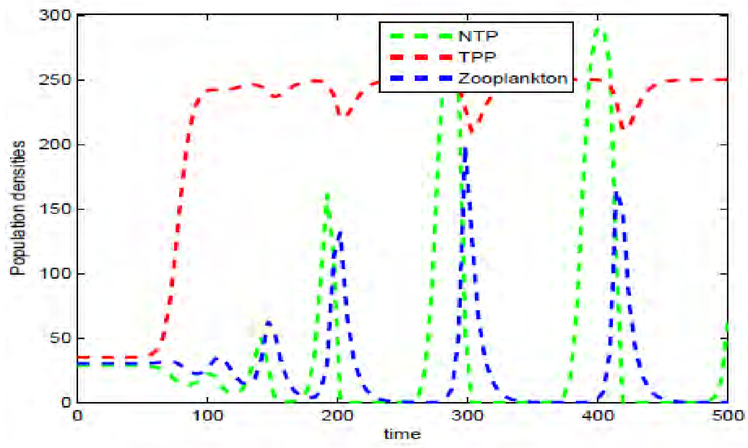
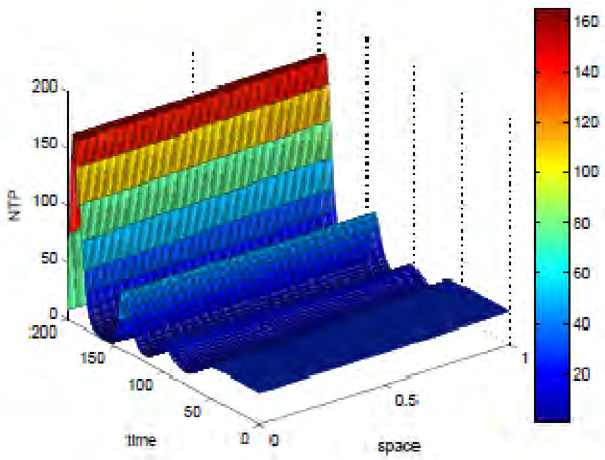
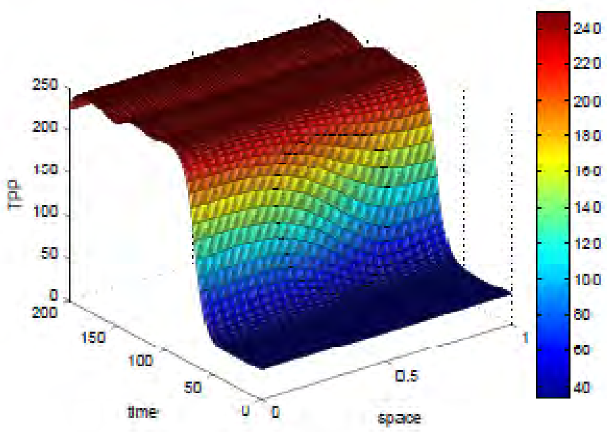


Fig. 2 Time Series of the model system (1) for the fixed set of parameter values given in Eq. (33).



(a)



(b)

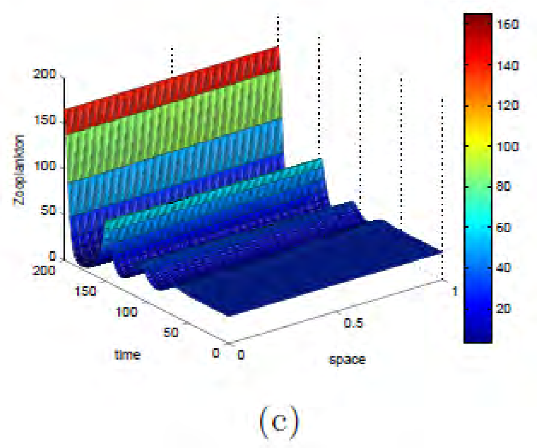


Fig. 3 Spatio-temporal pattern of NTP, TPP and zooplankton of the model system (1) for the fixed set of parameter values given in Eq. (33).

When the rate of inhibition of zooplankton growth by toxic material ingested in feeding on TPP is very large $(\xi_2 = 5)$, then because of high toxic effect, the zooplankton goes to extinction.

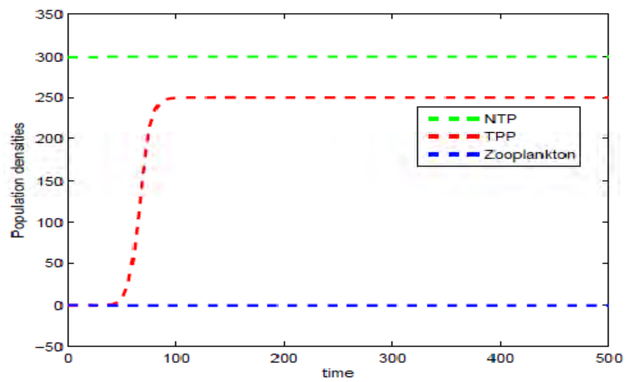


Fig. 4 Time series of the model system (1) when $\xi_2 = 5$ and rest of the parametric values are same as Eq.(33).

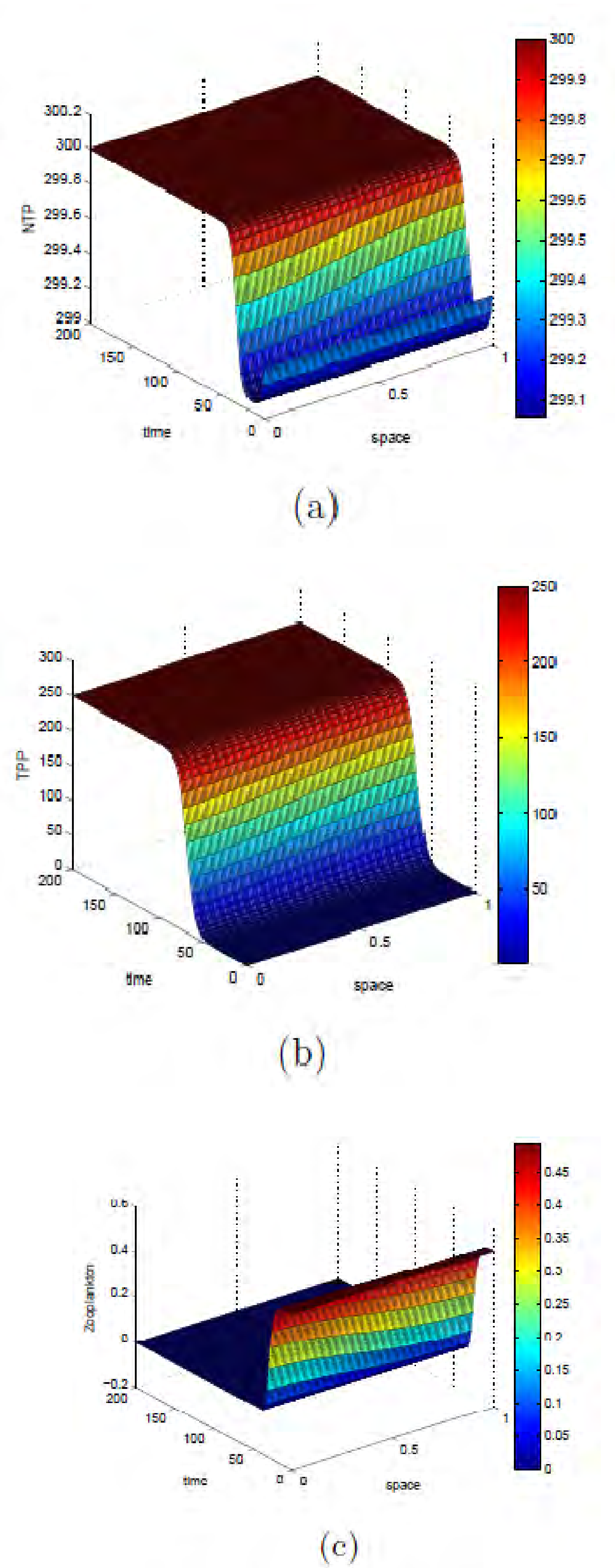


Fig. 5 Spatio-temporal pattern of NTP, TPP and zooplankton of the model system (1) for the fixed set of parameter values given in Eq. (33).

6 Discussions and Conclusions

In this paper, a simple mathematical model of NTP-TPP-zooplankton sys-tem in which zooplankton population reduces due to release of toxic chemical by phytoplankton or due to toxic phytoplankton being eaten by zooplankton has been proposed and analysed. We have investigated the model both analytically and numerically. We have investigated the effects of spatial interaction and spatio-temporal pattern formation. Numerical analysis demonstrates the following conclusions:

(i) The model system (1) with a fixed set of parameter values given in Eq.(33) and initial condition (34) asserting that the density of TPP remain high in whole domain and system shows the limit cycle behaviour.

(ii) When the rate of inhibition of zooplankton growth by toxic material ingested in feeding on TPP is very large $\xi_2 = 5$, then because of high toxic effect the zooplankton goes to extinction.

The results obtained suggest that toxic substances or toxic phytoplankton may serve as a key factor in the termination of planktonic blooms. Here we conclude that TPP has an inhibitory effect on zooplankton and high abundance of TPP is not favorable for the persistence of zooplankton.

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