Samares Pal
Department of Mathematics
University of Kalyani
INDIA
E-mail: samaresp@yahoo.co.in

Based on a joint work with Anal Chatterjee

BIOMAT 2013
The dynamics of a rapid (or massive) increase of plankton populations is an important subject in marine plankton ecology and generally termed as a 'bloom'. There has been global increase in harmful plankton in last two decades and considerable scientific attention towards harmful plankton has been paid in recent years.

The planktonic blooms may be categorized into spring blooms and red tides. Spring blooms occur seasonally due to changes in temperature or nutrient availability. Red tides are the result of localized outbreaks associated with water temperature (Truscot and Brindley, 1994, *Bull. Math Biol.*).
The adverse effects of harmful plankton species on human health, commercial fisheries, subsistence fisheries, recreational fisheries, tourism and coastal recreation, ecosystem and environment are well established. Nevertheless, despite the attention towards this issue, the nature of harmful plankton and its possible control mechanism are not yet well established and required special attention.
Plankton Bloom

Phytoplankton Bloom in the Baltic Sea
(Courtesy of NASA Visible Earth, http://visibleearth.nasa.gov/)
A group of researchers is in the favor of viral infection and the other groups are using toxin producing phytoplankton (TPP) for controlling the algal bloom.

Figure 1: Map of Coastal Region of West Bengal and part of Orissa, India. (Source: CIFRI, Barrackpore, India.)

Geographical Situation
21°37’ Northern Latitude
87°31’ Eastern Longitude

Region Investigated →
Figure 2: Collection Region of marine plankton samples in the NorthWest Coastal Region of Bay of Bengal.
Fig. 1. Representation of field data. The abundance of *Paracalanus* sp. is low when the *chaetocerous* sp. is at high abundance.
Fig. 2. Average biomass distribution of Chaetocerous sp. (TPP) and Paracalanus sp. (zooplankton) when only TPP present
Fig. 3 Average biomass distribution of NTP and zooplankton for experimental data when only NTP present.
Fig. 4 Average biomass distribution of TPP, NTP and zooplankton for experimental data when both NTP and TPP present in the system.
Field Observation

- In this context we like to mention the same results of Hulot and Huisman (Nature) and Sole et al. (Ecol. Mod.) in consistence of our findings.

- TPP has a negative effect on the growth of zooplankton. This observation resembles the results obtained earlier from field (Nielsen et al., Mar. Ecol. Prog.) and laboratory experiments (Ives, J.Mar. Biol. Ecol.).

- From this point of view we take account the negative effect in the growth equation of zooplankton in formulation of our model.
\[
\frac{dP_1}{dt} = rP_1 \left(1 - \frac{P_1 + \alpha P_2}{K_1}\right) - \frac{\alpha_1 P_1 Z}{1 + \beta_1 P_1 + \beta_2 P_2}
\]
\[
\frac{dP_2}{dt} = sP_2 \left(1 - \frac{P_2 + \beta P_1}{K_2}\right) - \frac{\alpha_2 P_2 Z}{1 + \beta_1 P_1 + \beta_2 P_2}
\]
\[
\frac{dZ}{dt} = \frac{\left(\alpha_1 P_1 - \alpha_2 P_2\right) Z}{1 + \beta_1 P_1 + \beta_2 P_2} - \mu Z
\]
Let $P_1(t)$ be the concentration of the non-toxic phytoplankton at time $t$. Let $P_2(t)$ and $Z(t)$ be the concentration of toxic phytoplankton population and zooplankton respectively at time $t$. Let $r$ and $s$ be the growth rates of non-toxic phytoplankton and toxic phytoplankton respectively. $K_1$ and $K_2$ be the carrying capacities of non-toxic and toxic phytoplankton respectively. Let $\alpha$ and $\beta$ be the competition coefficients. Let $\alpha_1$ and $\alpha_2$ be the attack rates of zooplankton on non-toxic and toxic phytoplankton respectively. $\alpha_1^\prime$ and $\alpha_1^\prime$ be the conversion efficiency of non-toxic and toxic phytoplankton into zooplankton biomass respectively. Let $\mu$ be the death rate of zooplankton. Let $h_1$ and $h_2$ be the product of attack rate and handling time for non-toxic and toxic phytoplankton respectively.
The Mathematical Model \textit{contd.}

\[
\frac{dx_1}{dt} = x_1(1 - x_1 - \mu_1x_2) - \frac{x_1x_3}{1 + \gamma_1x_1 + \gamma_2x_2} = F_1(x_1, x_2, x_3)
\]

\[
\frac{dx_2}{dt} = \gamma_3x_2(1 - x_2 - \mu_2x_1) - \frac{\gamma_4x_2x_3}{1 + \gamma_1x_1 + \gamma_2x_2} = F_2(x_1, x_2, x_3)
\]

\[
\frac{dx_3}{dt} = \frac{(\alpha''_1x_1 - \alpha''_2x_2)x_3}{1 + \gamma_1x_1 + \gamma_2x_2} - \gamma_6x_3 = F_3(x_1, x_2, x_3)
\]
where

\[ \begin{align*}
\mu_1 &= \frac{a_2 K_2}{K_1}, \quad \mu_2 = \frac{\beta K_1}{K_2}, \quad \gamma_6 = \frac{\mu}{r}, \quad \gamma_1 = \beta_1 K_1, \quad \gamma_2 = \beta_2 K_2, \quad \gamma_3 = \frac{\gamma}{r}, \quad \gamma_4 = \frac{a_2}{a_1}, \\
\alpha_1'' &= \frac{a_1' K_1}{r}, \quad \alpha_2'' = \frac{a_2' K_2}{r}
\end{align*} \]  \quad (3.4)

System (3.3) has to be analyzed with the following initial conditions:

\[ x_1(0) \geq 0, \quad x_2(0) \geq 0, \quad x_3(0) \geq 0. \]  \quad (3.5)

For convenience in the following, time \( \tau \) is replaced by \( t \) as the dimensionless time.
Some basic results

- All the solutions of the above system are ultimately bounded.
- The system possesses five equilibria.

The system (2.3) possesses the following equilibria: the plankton free equilibrium $E_0 = (0, 0, 0)$, the toxic phytoplankton and zooplankton free equilibrium $E_1(1, 0, 0)$, non-toxic phytoplankton and zooplankton free equilibrium $E_2(0, 1, 0)$, a feasible zooplankton free equilibrium $E_3\left(\frac{\mu_1-1}{\mu_1\mu_2-1}, \frac{\mu_2-1}{\mu_1\mu_2-1}, 0\right)$. The existence criterion of $E_3$ is $\mu_1 > 1$ and $\mu_2 > 1$. There exists a feasible toxic phytoplankton free equilibrium $E_4\left(\frac{\gamma_6}{\alpha_1'' - \gamma_1\gamma_6}, 0, \frac{\alpha_1''(\alpha_1'' - \gamma_1\gamma_6 - \gamma_6)}{(\alpha_1'' - \gamma_1\gamma_6)^2}\right)$. The equilibrium $E_4$ exists if $\alpha_1'' > \gamma_6(1 + \gamma_1)$. 
The positive interior equilibrium \( E^* = (x_1^*, x_2^*, x_3^*) \), where

\[
x_1^* = \frac{\gamma_6 (\gamma_3 - \mu_1 \gamma_4) + (\gamma_3 - \gamma_4)(a_2'' + \gamma_2 \gamma_6)}{\Delta},
\]

\[
x_2^* = \frac{(\gamma_3 - \gamma_4)(a_1'' - \gamma_1 \gamma_6) - \gamma_6 (\gamma_3 \mu_2 - \gamma_4)}{\Delta},
\]

\[
x_3^* = \frac{\gamma_3 [(\alpha_2'' + \gamma_2 \gamma_6) (\mu_2 - 1) + (\alpha_1'' - \gamma_1 \gamma_6) (1 - \mu_1) + \gamma_6 (\mu_1 \mu_2 - 1)] (\gamma_3 - \gamma_4) (a_1'' + a_2'' \gamma_1) + a_1'' (\gamma_3 - \mu_1 \gamma_4) + a_2'' (\gamma_3 \mu_2 - \gamma_4)}{\Delta^2},
\]

where \( \Delta = (\alpha_2'' + \gamma_2 \gamma_6) (\gamma_3 \mu_2 - \gamma_4) + (\alpha_1'' - \gamma_1 \gamma_6) (\gamma_3 - \mu_1 \gamma_4) \).

The positive interior equilibrium \( E^* \) exists if \( x_1^*, x_2^*, x_3^* > 0 \) and this leads to the following condition: \( a_1'' - \gamma_1 \gamma_6 > 0 \), \( \frac{\gamma_3}{\gamma_4} > \max \{ \mu_1, \frac{1}{\mu_2}, 1 \} \) and \( R_1 = \frac{(\gamma_3 - \gamma_4) (a_1'' - \gamma_1 \gamma_6)}{\gamma_6 (\gamma_3 \mu_2 - \gamma_4)} > 1 \) where \( \mu_2 > 1 \), \( \mu_1 < 1 \) and \( \mu_1 \mu_2 > 1 \).
By computing the variational matrix around the respective biological feasible equilibria, one can easily deduce the following lemmas:

- Lemma 1. The steady state $E_0=(0,0,0)$ of the system (2.3) is a saddle point.
- Lemma 2. There exists a feasible toxic phytoplankton and zooplankton free steady state $E_1=(1,0,0)$ which is saddle.
- Lemma 3. There exists a non-toxic phytoplankton and zooplankton free steady state $E_2=(0,1,0)$ which is saddle.
- Lemma 4. There exists a zooplankton free steady state $E_3=(x_1,x_2,0)$ which is saddle (From the existence criterion of $E_3$).
We observe that the toxic phytoplankton free state $E_4$ is unstable under certain parametric condition.

By computing the variational matrix around the positive interior equilibrium $E^*$ we find that for a certain threshold of the system parameters, the system possesses asymptotic stability around the positive interior equilibrium depicting the coexistence of all the three species.

When the competition coefficient $\mu_2$ crosses a critical value, say $\mu_2^*$ then the system (2.3) enters into Hopf bifurcation around the positive equilibrium and that induces oscillations of the populations.
The Stochastic Model

- In the present study we introduce stochastic perturbation terms into the growth equations of both prey and predator population to incorporate the effect of randomly fluctuating environment (Tapaswi, P.K. and Mukhopadhyay, A. J. Math. Biol.).

- We assume that stochastic perturbations of the state variables around their steady-state values $E^*$ are of Gaussian white noise type which are proportional to the distances of $x_1, x_2, x_3$ from their steady-state values $x_1^*, x_2^*, x_3^*$ respectively [Beretta et al., Math. Comp. Simul.]. Gaussian white noise is extremely useful to model rapidly fluctuating phenomena. So the deterministic model system (2.2) results in the following stochastic model system
\[ dx_1 = F_1(x_1, x_2, x_3)dt + \sigma_1(x_1 - x_1^*)d\xi_t^1 \]
\[ dx_2 = F_2(x_1, x_2, x_3)dt + \sigma_2(x_2 - x_2^*)d\xi_t^2 \]
\[ dx_3 = F_3(x_1, x_2, x_3)dt + \sigma_3(x_3 - x_3^*)d\xi_t^3 \]

(3.1)

where \( \sigma_1, \sigma_2 \) and \( \sigma_3 \) are real constants and known as intensity of environmental fluctuation, \( \xi_t^i = \xi_i(t), i = 1, 2, 3 \) are standard Wiener processes independent from each other [see, Gikhman and Skorokhod, (1979)].

In rest of the work we consider (3.1) as an Ito stochastic differential system of the type
\[ dX_t = f(t, X_t)dt + g(t, X_t)d\xi_t, \quad X_{t0} = X_0 \]

(3.2)

where the solution \((X_t, t > 0)\) is a Ito process, ‘\( f \)’ is slowly varying continuous component or drift coefficient and ‘\( g \)’ is the rapidly varying continuous random component or diffusion coefficient and \( \xi_t \) is a three-dimensional stochastic process having scalar Wiener process components with increments \( \Delta \xi_t^j = \xi_j(t + \Delta t) - \xi_j(t) \) are independent Gaussian random variables \( N(0, \Delta t) \).
Stochastic Stability

- Conditions for the deterministic stability of the interior equilibrium point \( E^* \) along with some other conditions are the necessary conditions for stochastic stability of the interior equilibrium point \( E^* \) under environmental fluctuation (see Bandyopadhyay and Chattopadhyay (Nonlinearity)).

- Thus the internal parameters of the model system and the intensities of environmental fluctuation have the ability to maintain the stability of the stochastic model system and exhibit a balanced dynamics at any future time within a bounded domain of the parametric space.
Table 1: The estimated Parameter values for our numerical calculation (best fit estimation of the parameters consistence with the behavior of ODE developed by SAS Institute)

<table>
<thead>
<tr>
<th>Parameters/Variable</th>
<th>Default values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\gamma_1$</td>
<td>2</td>
</tr>
<tr>
<td>$\gamma_2$</td>
<td>3</td>
</tr>
<tr>
<td>$\gamma_3$</td>
<td>1.5</td>
</tr>
<tr>
<td>$\gamma_4$</td>
<td>0.9</td>
</tr>
<tr>
<td>$\gamma_6$</td>
<td>0.102</td>
</tr>
<tr>
<td>$\alpha_1$</td>
<td>0.8</td>
</tr>
<tr>
<td>$\alpha_2$</td>
<td>0.2</td>
</tr>
<tr>
<td>$\mu_1$</td>
<td>0.3</td>
</tr>
<tr>
<td>$\mu_2$</td>
<td>1.16</td>
</tr>
</tbody>
</table>
Fig. 8. Figure depicting coexistence of all the population
Fig. 9 - Figure depicting the phase portrait corresponding to Fig. 8 and showing that $E'$ is stable while $E_0$, $E_1$, $E_2$, $E_3$ are saddle points and $E_4$ does not exist.
Fig. 10- Figure depicting extinction of the zooplankton population when the competition between NTP and TPP is very low. (We have used different time scale to show the clear dynamics)
Fig. 11 - Figure depicting the phase portrait corresponding to Fig. 10 and showing that $E_3$ is stable while $E_0$, $E_1$, $E_2$, are saddle points, $E_4$ is a spiral source and $E^*$ does not exist.
Fig. 12- Figure depicting coexistence of all population through oscillation when we increase the competition coefficient $\mu_2$ from 1.18 to 1.38 (remaining parameter values same as in figure 10)
Fig. 13 - Figure depicting the phase portrait corresponding to Fig. 12 and showing that $E^*$ is stable limit cycle while $E_0$, $E_1$, $E_2$, $E_4$ are saddle points and $E_3$ does not exist.
Fig. 14. Coexistence of all population in the presence of environmental fluctuation ($\sigma_i=0.05$, $i=1,2,3$), (here we have used the scheme given by Carletti, Math. Biosc.)
Fig. 15: Figure depicting aperiodic oscillation of all population in the presence of environmental fluctuation for $\mu_1=0.1$, $\mu_2=1.5$ (when we increase the competition coefficient). (In absence of environmental fluctuation for the same parametric values the system shows regular oscillation).
Fig. 16: Figure depicting stable population distribution in the presence of environmental fluctuation for $\mu_1=1$, $\mu_2=1.56$. (In absence of environmental fluctuation for the same parametric values the system shows chaotic bloom).
We observe that in the absence of the environmental disturbances, high competition may take the system to chaos.

More the effect of competition on the TPP population more there is a chance of occurrence of planktonic bloom. This may be because of the TPP population as already identified as a controlling agent for the termination of planktonic blooms and increase in the competition between NTP and TPP decreases the growth rate of TPP population.

But under environmental disturbances, which is common in marine system, high competition helps the system to remain stable around coexistence equilibrium point.
Algal blooms in the presence nutrient and toxic substances

From our field study we observe the following two situations:

- Phytoplankton population fluctuates irregularly in the collection zone 1, nearer to the river due to the input of high nutrient concentration and the presence of zooplankton in this region is very low due to high abundance of phytoplankton population. This phenomenon is also comparable to the fact that high concentration of phytoplankton population suppress the abundance of zooplankton population and thus triggers algae bloom.

- Further in the collection zone 2, which is far from the riverside, the irregular fluctuations are less likely occur due to low concentration of nutrient and a sustained existence of the zooplankton population has been observed. This establishes the fact input of nutrient concentration play an important role in the occurrence of planktonic blooms (see figures).
Different Grazing functions

- We know that phytoplankton population competes for the same limiting resources, including nutrient and light. For the exploitation of the same limiting resources, various species have indirect or direct competition through the release of chemicals, known as allelopathy.

- Fristol et al. (Environ. Microbiol. 2004) showed that stronger allelopathic effects would cause a higher mortality, while mild allelopathic effects could cause non-lethal effects. Thus we have considered two types of grazing functions to represent the grazing dynamics.
Dilution Rate

- Dilution rate is referred to as the water exchange rate or flushing rate when referring to open marine system (Ecological effects of wastewater: applied limnology and pollution effects By Eugene B. Welch, T. Lindell).

- The rate of nutrient exchange rate is referred to as Dilution rate. When the dilution rate is very low, the cells reach a high density as the nutrients are leaving the system at a very slow rate and the cells get ample timed to use the substrate. Thus the nutrient concentration is maintained at a low level in the system. On the other hand, if the dilution rate of nutrient is high, the cell density is low as they have a little time to use the substrate.
The mathematical model for Nutrient - Phytoplankton - Zooplankton

\[
\frac{dN}{dt} = D(N^0 - N) - \alpha_1 PN + \mu_3 P + \mu_4 Z \\
\frac{dP}{dt} = \alpha_2 PN - \gamma_1 PZ - (\mu_1 + D_1) P \\
\frac{dZ}{dt} = \gamma_2 PZ - (\mu_2 + D_2) Z - \frac{\theta PZ}{\gamma + P}
\]
The behavior of phytoplankton and zooplankton for different values of $D$:
(a) $D=0.02$, (b) $D=0.08$, (c) $D=0.1$, (d) $D=0.65$ (other parameter values are kept fixed)
From this figure we observe that as $D$ increases, the system bifurcates from a stable focus to limit cycle periodic solution. This observation indicates that there is a level of $D$, below which the system shows no excitability and above which the system enters into excitable state.
Behavior of Phytoplankton population: For different values of $\theta$ (a) $\theta = 0$, (b) $\theta = 0.01$, (c) $\theta = 0.03$, (d) $\theta = 0.07$.
Behavior of Zooplankton population: For different values of $\theta$ (a) $\theta = 0$, (b) $\theta = 0.01$, (c) $\theta = 0.03$, (d) $\theta = 0.07$
Thus we observe that increasing the value of $\theta$ gradually from 0 to 0.07, the system comes back to a stable focus solution (with decaying oscillations) from a stable limit cycle periodic solution.

It was observed that chance of planktonic bloom is high, when the nutrient concentration is high and in that case the toxin produced by phytoplankton species plays an important role in the termination of bloom.
Nutrient – Non-toxic Phytoplankton – Toxic Phytoplankton – Zooplankton

\[
\frac{dN}{dt} = D(N^0 - N) - \alpha_1 P_1 N - \alpha_2 P_2 N + \eta_1 P_1 + \eta_2 P_2 + \eta_3 Z \\
\equiv F_1(N, P_1, P_2, Z),
\]

\[
\frac{dP_1}{dt} = \theta_1 P_1 N - \beta_1 P_1 Z - e_1 P_1 P_2 - \mu_1 P_1 - D_1 P_1 \equiv F_2(N, P_1, P_2, Z),
\]

\[
\frac{dP_2}{dt} = \theta_2 P_2 N - \beta_2 P_2 Z - e_2 P_1 P_2 - \mu_2 P_2 - D_2 P_2 \equiv F_3(N, P_1, P_2, Z),
\]

\[
\frac{dZ}{dt} = \gamma_1 P_1 Z - \gamma_2 P_2 Z - \mu_3 Z - D_3 Z \equiv F_4(N, P_1, P_2, Z).
\]

This system of ordinary differential equations is subject to the initial conditions

\[N(0) > 0, \ P_1(0) > 0, \ P_2(0) > 0 \ \text{and} \ Z(0) > 0.\]
## Set of Parameter Values

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Default value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N^0$</td>
<td>Constant input of nutrient</td>
<td>1.58</td>
<td>$h^{-1}$</td>
</tr>
<tr>
<td>$D$</td>
<td>Dilution rate of nutrient</td>
<td>0.3</td>
<td>$h^{-1}$</td>
</tr>
<tr>
<td>$\alpha_1$</td>
<td>Nutrient uptake rate of NTP</td>
<td>0.03</td>
<td>$ml.\ h^{-1}$</td>
</tr>
<tr>
<td>$\alpha_2$</td>
<td>Nutrient uptake rate of TPP</td>
<td>0.022</td>
<td>$ml.\ h^{-1}$</td>
</tr>
<tr>
<td>$\theta_1$</td>
<td>Conversion rate of NTP</td>
<td>0.02</td>
<td>$ml.\ h^{-1}$</td>
</tr>
<tr>
<td>$\theta_2$</td>
<td>Conversion rate of TPP</td>
<td>0.02</td>
<td>$ml.\ h^{-1}$</td>
</tr>
<tr>
<td>$\mu_1$</td>
<td>Death rate of NTP</td>
<td>0.006</td>
<td>$h^{-1}$</td>
</tr>
<tr>
<td>$\mu_2$</td>
<td>Death rate of TPP</td>
<td>0.006</td>
<td>$h^{-1}$</td>
</tr>
<tr>
<td>$\mu_3$</td>
<td>Death rate of zooplankton</td>
<td>0.005</td>
<td>$h^{-1}$</td>
</tr>
<tr>
<td>$\eta_1$</td>
<td>Nutrient recycling rate of NTP</td>
<td>0.004</td>
<td>$mg.\ h^{-1}$</td>
</tr>
<tr>
<td>$\eta_2$</td>
<td>Nutrient recycling rate of TPP</td>
<td>0.004</td>
<td>$mg.\ h^{-1}$</td>
</tr>
<tr>
<td>$\eta_3$</td>
<td>Nutrient recycling rate of zoopl.</td>
<td>0.0035</td>
<td>$mg.\ h^{-1}$</td>
</tr>
<tr>
<td>$\epsilon_1$</td>
<td>Competition coefficient</td>
<td>0.02</td>
<td>$ml.\ h^{-1}$</td>
</tr>
<tr>
<td>$\epsilon_2$</td>
<td>Competition coefficient</td>
<td>0.02</td>
<td>$ml.\ h^{-1}$</td>
</tr>
<tr>
<td>$\beta_1$</td>
<td>Predation rate of NTP</td>
<td>0.02</td>
<td>$ml.\ h^{-1}$</td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>Predation rate of TPP</td>
<td>0.01</td>
<td>$ml.\ h^{-1}$</td>
</tr>
<tr>
<td>$\gamma_1$</td>
<td>Conversion rate for NTP</td>
<td>0.01</td>
<td>$ml.\ h^{-1}$</td>
</tr>
<tr>
<td>$\gamma_2$</td>
<td>Death rate due to consumption of TPP</td>
<td>0.008</td>
<td>$ml.\ h^{-1}$</td>
</tr>
<tr>
<td>$D_1$</td>
<td>Dilution rate of NTP</td>
<td>0.0004</td>
<td>$h^{-1}$</td>
</tr>
<tr>
<td>$D_2$</td>
<td>Dilution rate of TPP</td>
<td>0.0004</td>
<td>$h^{-1}$</td>
</tr>
<tr>
<td>$D_3$</td>
<td>Dilution rate of zooplankton</td>
<td>0.0003</td>
<td>$h^{-1}$</td>
</tr>
</tbody>
</table>
Effect of Nutrient: Periodic solution of the system for the parameters as given in Table-II

\(N^0=1.58\) (Fig 1)

(a) For \(N^0=1.5\) the system is stable at \(E^*\)
(b) For \(N^0=1.4\) the system is stable at \(E_4 (N,P_1, 0, Z_4)\) (Fig 2)
(a) For $N^0=0.321$ the system is stable at $E_1 (N, P_1, 0, 0)$
(b) For $N^0=0.3$ the system is stable at $E_0 (N, 0, 0, 0)$ (Fig 3)

$E_2$ is locally asymptotically stable with high biomass of TPP for $N^0=1.6$ (Fig 4)
(a) \( E^* \) is stable when \( \mu_2 = 0.007 \) and \( N^0 = 1.6 \) (Increase the death rate of TPP)

(b) \( E_4 \) is stable when \( \mu_2 = 0.008 \) and \( N^0 = 1.6 \) (Fig 5)

For high biomass of TPP with \( \mu_1 = 0.008 \) (the death rate of NTP)\& \( N^0 = 1.6 \) the system is asymptotically stable at \( E_2 \) (Fig 6)
Effect of Competition: If NTP is a stronger competitor than TPP
(a) System is stable $e_2=0.0215$  
(b) Increase $e_2=0.025$ (stable around $E_4$) (Fig 7)

Effect of Competition: If TPP is a stronger competitor than NTP i.e. $e_1 > e_2$ then the system is stable around $E_2$ with a high TPP biomass  (Fig 8)
Combined effects of nutrient and competition (a) $E^*$ is stable when $e_2 = 0.0215$ and $N^0=1.6$ (b) $E_4$ is stable when $e_2 = 0.025$ and $N^0=1.6$ (Fig 9)

Effects of Zooplankton death rate (a) $E^*$ is stable when $\mu_3 = 0.0053$ (b) Further increase in zooplankton death rate the system stabilizes to $E_4$ ($\mu_3 = 0.006$) (Fig 10) [However if we further increase $\mu_3$ then the system is stable at $E_1$]
Mathematical Model

\[
\begin{align*}
\frac{dN}{dt} &= D(N^0 - N) - \frac{\alpha_1 PN}{K_1 + N} + \mu_3 P + \mu_4 Z = F_1(N, P, Z) \\
\frac{dP}{dt} &= \frac{\alpha_2 PN}{K_1 + N} - \frac{\beta_1 P^2 Z}{K_2 + P^2} - \mu_1 P - \frac{h_1 P}{E_1 + P} = F_2(N, P, Z) \\
\frac{dZ}{dt} &= \frac{(\beta_2 - \theta) P^2 Z}{K_2 + P^2} - \mu_2 Z - \frac{h_2 Z}{E_2 + Z} = F_3(N, P, Z).
\end{align*}
\]

The system (1) has to be analyzed with the following initial conditions,

\[N(0) > 0, \ P(0) > 0, \ Z(0) > 0.\]
Let $N(t)$ be the concentration of the nutrient at time $t$. Let $P(t)$ and $Z(t)$ be the concentration of phytoplankton and zooplankton population respectively at time $t$.

Let $N^0$ be the constant input of nutrient concentration, $D$ is the dilution rate of nutrient [18]. The constant $\frac{1}{D}$ has the physical dimension of a time and represents the average time that nutrient and waste products spend in the system [19]. Let $\alpha_1$ and $\alpha_2$ be the nutrient uptake rate for the phytoplankton population and conversion rate of nutrient for the growth of phytoplankton population respectively ($\alpha_2 \leq \alpha_1$). Let $\mu_1$ be the mortality rate of the phytoplankton population and $\mu_2$ be the mortality rate of the zooplankton population.
Let $\mu_3 (\mu_3 \leq \mu_1)$ be the nutrient recycle rate after the death of phytoplankton population and $\mu_4 (\mu_4 \leq \mu_2)$ be the nutrient recycle rate after the death of zooplankton population. Let $\beta_1$ be the maximal zooplankton ingestion rate and $\beta_2 (\beta_2 \leq \beta_1)$ be the maximal zooplankton conversion rate. A more common choice is of the Holling type II and type III functional form to describe the grazing phenomena with $K_1$ and $K_2$ as half saturation constant. Here harvesting are represented by a Holling type-II function with $h_1$ and $h_2$ as the harvest rate (also known as catch-ability constant) of phytoplankton and zooplankton respectively. Here $E_1$ and $E_2$ are the measure of the effort required to harvest the phytoplankton and zooplankton population respectively. This type of harvest function implies that when fewer
planktons are available, it is harder to find them and so the daily catch drops. On the other hand when there are sufficiently many planktons, then $\lim_{H_1 \to \infty} \frac{h_1 H_1}{E_1 + H_1} = h_1$ and $\lim_{H_2 \to \infty} \frac{h_2 H_2}{E_2 + H_2} = h_2$, so that the harvesting level is close to $h_1$ and $h_2$ respectively, the catchability constant. It is assumed $\theta$ is the rate of zooplankton decay due to toxin producing phytoplankton.
The table representing thresholds and stability of steady states

<table>
<thead>
<tr>
<th>Thresholds ($R_0$, $R_1$)</th>
<th>($N^0$, 0, 0)</th>
<th>($N_1$, $P_1$, 0)</th>
<th>($N^<em>$, $P^</em>$, $Z^*$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_0 &lt; 1$</td>
<td>Asymptotically stable</td>
<td>Not feasible</td>
<td>Not feasible</td>
</tr>
<tr>
<td>$R_0 &gt; 1$, $R_1 &lt; 1$</td>
<td>Unstable</td>
<td>Asymptotically stable</td>
<td>Not feasible</td>
</tr>
<tr>
<td>$R_1 &gt; 1$</td>
<td>Unstable</td>
<td>Not feasible</td>
<td>Asymptotically stable</td>
</tr>
</tbody>
</table>
**Direction of Hopf-Bifurcation**

**Theorem:** 4. Here $\mu_{22}$ determines the direction of the Hopf-bifurcation. If $\mu_{22} > 0 (< 0)$ then the Hopf-bifurcation is supercritical (subcritical) and the bifurcating periodic solutions exists for $\theta > \theta^*$; $\beta_{22}$ determines the stability of the bifurcating periodic solutions: the solutions are orbitally stable (unstable) if $\beta_{22} < 0 (> 0)$; and $\tau_2$ determines the period of the bifurcating periodic solutions: the period increases (decreases) if $\tau_2 > 0 (< 0)$. 
Mathematical Model In Presence of Time Delay

\[
\frac{dN}{dt} = D(N^0 - N) - \frac{\alpha_1 PN}{K_1 + N} + \mu_3 P + \mu_4 Z \equiv F_1(N, P, Z),
\]

\[
\frac{dP}{dt} = \frac{\alpha_2 PN}{K_1 + N} - \frac{\beta_1 P^2 Z}{K_2 + P^2} - \mu_1 P - \frac{h_1 P}{E_1 + P} \equiv F_2(N, P, Z),
\]

\[
\frac{dZ}{dt} = \frac{(\beta_2 - \theta) P^2(t - \tau) Z(t - \tau)}{K_2 + P^2(t - \tau)} - \mu_2 Z - \frac{h_2 Z}{E_2 + Z} \equiv F_3(N, P, Z). \quad (2)
\]
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Default value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N^0$</td>
<td>Constant input of nutrient</td>
<td>2</td>
<td>mg ml$^{-1}$</td>
</tr>
<tr>
<td>$D$</td>
<td>Dilution rate of nutrient</td>
<td>1</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>$\alpha_1$</td>
<td>Nutrient uptake rate for the phytoplankton</td>
<td>3.2</td>
<td>ml mg$^{-1}$ day$^{-1}$</td>
</tr>
<tr>
<td>$\alpha_2$</td>
<td>Nutrient conversion rate for the phytoplankton</td>
<td>2.4</td>
<td>ml mg$^{-1}$ day$^{-1}$</td>
</tr>
<tr>
<td>$\beta_1$</td>
<td>Phytoplankton uptake rate for the zooplankton</td>
<td>2.1</td>
<td>ml mg$^{-1}$ day$^{-1}$</td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>Phytoplankton conversion rate for the zooplankton</td>
<td>1</td>
<td>ml mg$^{-1}$ day$^{-1}$</td>
</tr>
<tr>
<td>$\mu_1$</td>
<td>Mortality rate of phytoplankton</td>
<td>0.1</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>$\mu_2$</td>
<td>Mortality rate of zooplankton</td>
<td>0.1</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>$\mu_3$</td>
<td>Nutrient Recycle rate due to the death phytoplankton</td>
<td>0.06</td>
<td>mg day$^{-1}$</td>
</tr>
<tr>
<td>$\mu_4$</td>
<td>Nutrient Recycle rate due to the death of zooplankton</td>
<td>0.06</td>
<td>mg day$^{-1}$</td>
</tr>
<tr>
<td>$K_1$</td>
<td>Half saturation constant</td>
<td>0.6</td>
<td>ml day$^{-1}$</td>
</tr>
<tr>
<td>$K_2$</td>
<td>Half saturation constant</td>
<td>0.1</td>
<td>ml day$^{-1}$</td>
</tr>
<tr>
<td>$h_1$</td>
<td>Harvesting rate of phytoplankton population</td>
<td>0.4</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>$E_1$</td>
<td>Effort required to harvest the phytoplankton</td>
<td>1</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>$h_2$</td>
<td>Harvesting rate of zooplankton population</td>
<td>0.4</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>$E_2$</td>
<td>Effort required to harvest the zooplankton</td>
<td>1</td>
<td>day$^{-1}$</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Rate of zooplankton decay due to toxin production phytoplankton</td>
<td>0</td>
<td>ml day$^{-1}$</td>
</tr>
</tbody>
</table>
The equilibrium point $E^*$ is stable for the parametric values as given in the Table 2.

The figure depicts oscillatory behavior around the positive interior equilibrium $E^*$ for $\theta = .3$ (increased from $\theta = 0$) with other parametric values as given in the Table 2.
The figure depicts stable behavior at $E^*$ of the system (1) for $\theta = 0.3$ and $\beta_2 = 1.2$ (from $\beta_2 = 1$) with same set of parametric values as given in the Table 2. (Fig-3)

The figure depicts stable behavior at $E^*$ of the system (1) for $\theta = 0.3$ and $N^0 = 1$ (from $N^0 = 2$) with same set of parametric values as given in the Table 2. (Fig-4)
The figure depicts stable behavior at $E^*$ of the system (1) for $\theta = 0.3$ and $D = 0.5$ (from $D=1$) with same set of parametric values as given in the Table 2.

The figures depict oscillatory behavior around the positive interior equilibrium $E^*$ of the system (1) for increasing $h_1$, from 0.4 to 1.2 and other parametric values as given in the Table 2.
The figure depicts stable behavior at $E_0$ of the system (1) for increasing $h_1$ from .4 to 1.8 with same set of parametric values as given in the Table 2.

Fig 7

The figure depicts stable behavior at $E^*$ of the system (1) for $h_1 = 1.2$ and $N^0 = 1$ with same set of parametric values as given in the Table 2.

Fig-8
The figure depicts stable behavior at $E^*$ of the system (1) for $h_1 = 1.2$ and $\beta_2 = 1.3$ (from $\beta_2 = 1$) with same set of parametric values as given in the Table 2.

Fig-9

The figures depict oscillatory behavior around the positive interior equilibrium $E^*$ of the system (1) for increasing $h_2$ from .4 to .6 and other parametric values as given in the Table 2.

Fig-10
The figure depicts stable behavior at $E^*$ of the system (1) for $h_2 = .6$ and $N^0 = 1$ (from $N^0 = 2$) with same set of parametric values as given in the Table 2.

The bifurcation diagram for $\theta$ with all parametric values as given in Table 2.
The bifurcation diagram for $h_1$ with all parametric values as given in Table 2.

The bifurcation diagram for $h_2$ with all parametric values as given in Table 2.
The two parameters bifurcation diagram for $\theta-h_1$ with all parametric values as given in Table 2. Fig-15

The two parameters bifurcation diagram for $\theta-h_2$ with all parametric values as given in Table 2. Fig-16
The figure depicts oscillatory behavior around the positive interior equilibrium at $E^*$ of the system (2) for $\tau=1.3$ with same set of parametric values as given in the Table 2. 

The figure depicts stable behavior at $E^*$ of the system (2) for $\tau=1.3$ and $\theta = .3$ (from $\theta =0$) with same set of parametric values as given in the Table 2.
The figure depicts stable behavior at $E^*$ of the system (2) for $\tau=1.3$ and $N^0 = 1.6$ (from $N^0 = 2$) with same set of parametric values as given in the Table 2.

The figure depicts stable behavior at $E^*$ of the system (2) for $\tau=1.3$ and $D = .5$ (from $D = 1$) with same set of parametric values as given in the Table 2.
The figure depicts stable behavior at $E^*$ of the system (2) for $\tau = 1.3$ and $h_1 = .2$ (from $h_1 = .4$) with same set of parametric values as given in the Table 2.

The figure depicts stable behavior at $E^*$ of the system (2) for $\tau = 1.3$ and $h_1 = .35$ (from $h_2 = .4$) with same set of parametric values as given in the Table 2.
We observe that increase in toxic level and harvesting rate of both plankton population may lead to instability of the system.

It was observed that to maintain stability around the coexistence equilibrium it is necessary to control the toxic chemicals release by phytoplankton and harvest rate of both plankton population.

It was observed that for the low value of constant nutrient input may lead to stability of the system in presence of toxic chemicals released by the phytoplankton and high harvesting rate of plankton population simultaneously.
Low value of dilution rate of nutrient may also prevents the fluctuating behavior of the system in presence of toxic chemical release by the phytoplankton in the system.

Similar case arise for high value of maximal zooplankton conversion rate.

The system exhibits dynamical instability due to higher gestation delay.

It was observed that increase in toxic level (in presence of delay) induced stability around the positive interior equilibrium.

We observe that low value of harvesting rate of both plankton population may lead to stability of the system in presence of delay.

Similar case arise for low value of constant nutrient input and dilution rate of nutrient.
Additional complications may arise from effects of organisms at higher trophic levels, e.g. the zooplankton grazer. Grazers at higher trophic level may increase the death rate of zooplankton and this type of grazing may affect the qualitative and quantitative behavior of the planktonic ecosystem.

The interspecies competition between NTP and TPP may be an important factor in plankton ecosystem dynamics. The dynamics become more complicated when the effects of nutrient interact with the effects of interspecies competition.

Our overall analysis indicates that the nutrient-phytoplankton-zooplankton interactions are very complex and situations-specific. The nutrient controlled bloom may occur in some favourable conditions. Top-down effects such as predation by higher trophic levels may trigger bloom in some other suitable conditions.

Other mechanisms considered in this model for greater biological realism, such as dilution rate, interspecies competition etc., may also change planktonic dynamics significantly.
References


References


References


Mathematical Model

\[
\frac{dN}{dt} = D(N^0 - N) - \frac{\alpha_1 PN}{K_1 + N} + \mu_4 P + \mu_5 Z + \mu_6 F \equiv G_1(N, P, Z, F)
\]

\[
\frac{dP}{dt} = \frac{\alpha_2 PN}{K_1 + N} - \frac{\alpha_3 PZ}{K_2 + P} - (\mu_1 + D_1) P \equiv G_2(N, P, Z, F)
\]

\[
\frac{dZ}{dt} = \frac{\alpha_4 PZ}{K_2 + P} - \frac{\alpha_5 Z^2 F}{K_3 + Z^2} - (\mu_2 + D_2) Z \equiv G_3(N, P, Z, F)
\]

\[
\frac{dF}{dt} = \frac{\alpha_6 Z^2 F}{K_3 + Z^2} - (\mu_3 + D_3) F \equiv G_4(N, P, Z, F).
\]

(1)

The system (1) has to be analyzed with the following initial conditions,

\[N(0) > 0, \ P(0) > 0, \ Z(0) > 0, \ F(0) > 0.\]
The table representing thresholds and stability of steady states

<table>
<thead>
<tr>
<th>Thresholds ($R_0$, $R_1$, $R_2$)</th>
<th>($N^0$, $0$, $0$, $0$)</th>
<th>($N_1$, $P_1$, $0$, $0$)</th>
<th>($N_2$, $P_2$, $Z_2$, $0$)</th>
<th>($N^<em>$, $P^</em>$, $Z^<em>$, $F^</em>$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_0 &lt; 1$</td>
<td>Asymptotically stable</td>
<td>Not feasible</td>
<td>Not feasible</td>
<td>Not feasible</td>
</tr>
<tr>
<td>$R_0 &gt; 1$, $R_1 &lt; 1$</td>
<td>Unstable</td>
<td>Asymptotically stable</td>
<td>Not feasible</td>
<td>Not feasible</td>
</tr>
<tr>
<td>$R_1 &gt; 1$, $R_2 &lt; 1$,</td>
<td>Unstable</td>
<td>Not feasible</td>
<td>Asymptotically stable</td>
<td>Not feasible</td>
</tr>
<tr>
<td>$R_2 &gt; 1$</td>
<td>Unstable</td>
<td>Not feasible</td>
<td>Not feasible</td>
<td>Asymptotically stable</td>
</tr>
</tbody>
</table>
The bifurcation diagram for \( N^0 \) with all parametric values as in Table 2.

Fig-11
The bifurcation diagram for $D$ with all parametric values as in Table 2.

Fig 12
The bifurcation diagram for $\mu_3$ with all parametric values as in Table 2.