

Plankton-Nutrient Interaction in an Open Marine System-A Mathematical Study

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

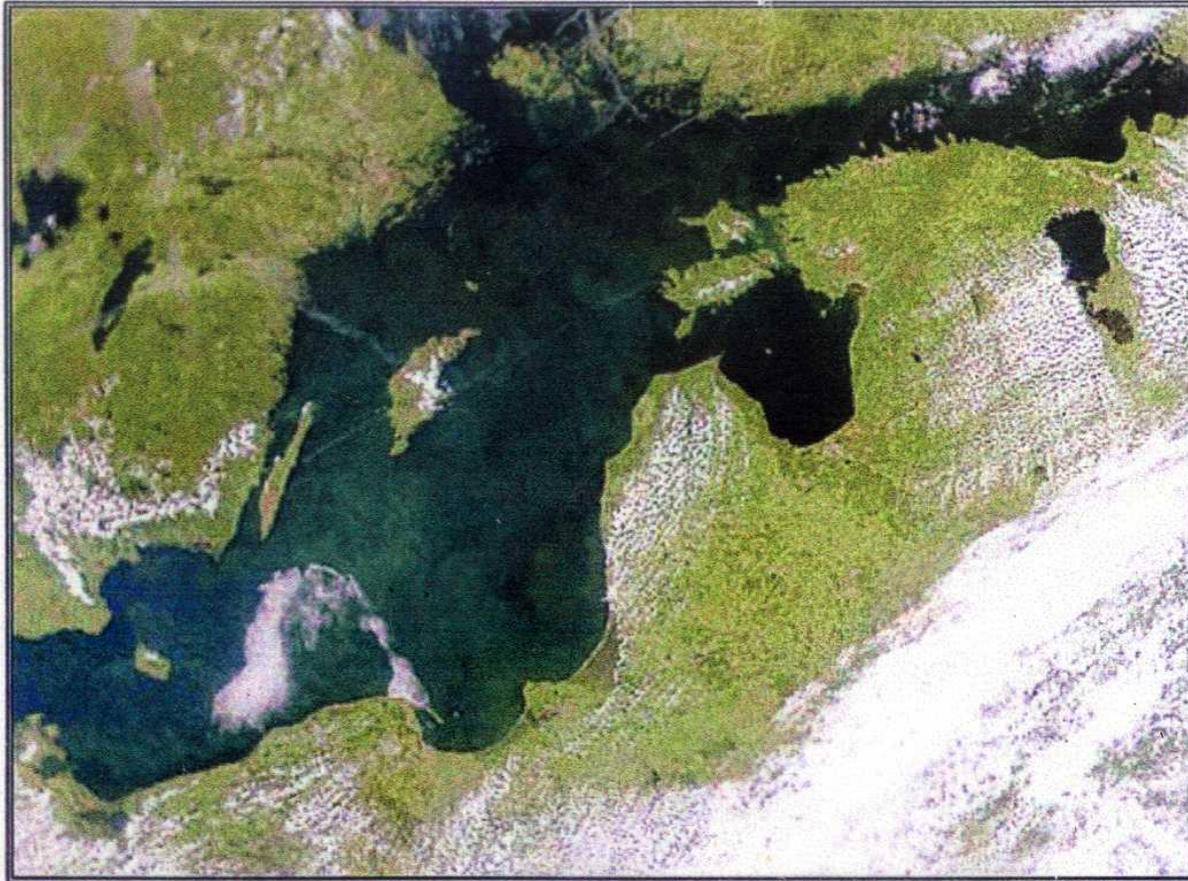
Planktonic Bloom

- **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.*).**

Effect of Harmful Algal Bloom (HAB)

- **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/>)

How to control algal bloom

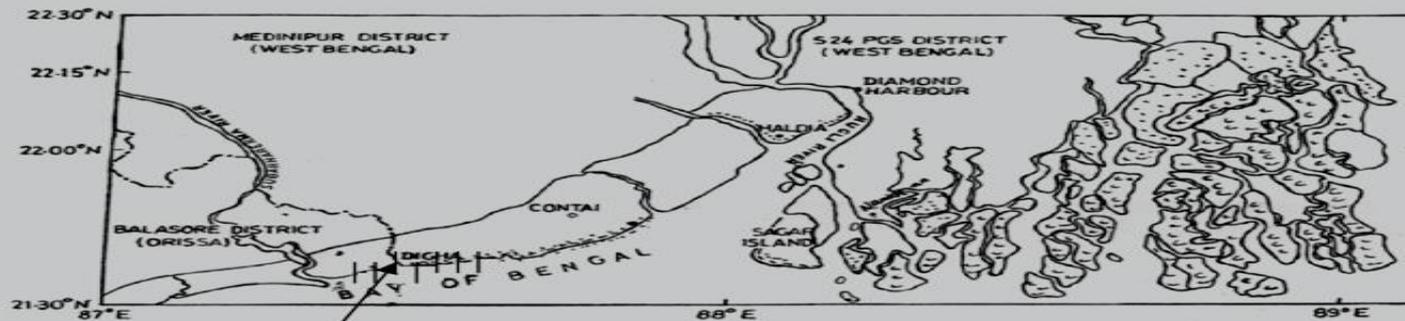
- A group of researchers is in the favor of viral infection and the other groups are using toxin producing phytoplankton (TPP) for controlling the algal bloom.
- Recent works suggest that viruses are important regulatory factors in marine ecosystem. Lytic viruses directly control population dynamics by viral lysis (Suttle et al., 1995, *Nature*; Brussard et al., 1996, *Ecology*). Few mathematical models also suggest that viral infection may be used as a controlling agent for the termination of planktonic blooms (Beltrami and Carroll, 1994, *J.Math.Biol.*; Chattopadhyay and Pal, 2002, *Ecol.Mod.*; Chattopadhyay and Pal, 2003, *BioSystems*).

Toxin Producing Phytoplankton (TPP)

- **Recent studies reveal that some times bloom of certain harmful species leads to release of toxic substances. Toxin producing plankton (TPP) release toxic chemicals and reduce the grazing pressure of zooplankton. As a result TPP may act as biological control for the termination of planktonic blooms (Chattopadhyay et al., 2002, *J. Theo. Biol.*, Chattopadhyay and Pal, 2004, *Ecol. Complexity*, Chatterjee and Pal, 2011, *Journal of Biological Systems*, Chatterjee et al., 2011, *Applied Mathematics and Computation*).**

Study region

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 → // // // //



Collection Zone

Figure 2: Collection Region of marine plankton samples in the NorthWest Coastal Region of Bay of Bengal.

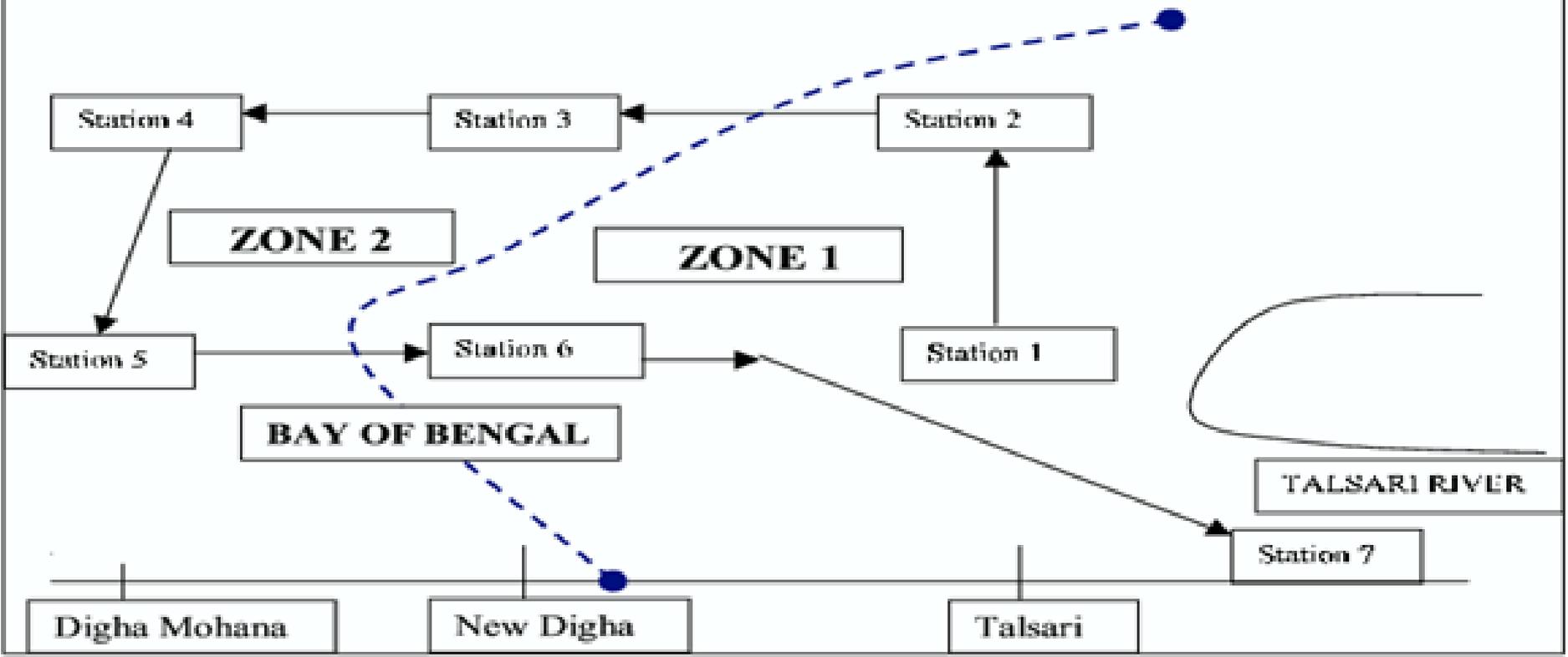


Fig. 1. Representation of field data. The abundance of *Paracalanus* sp. is low when the chaetocerous sp. is at high abundance

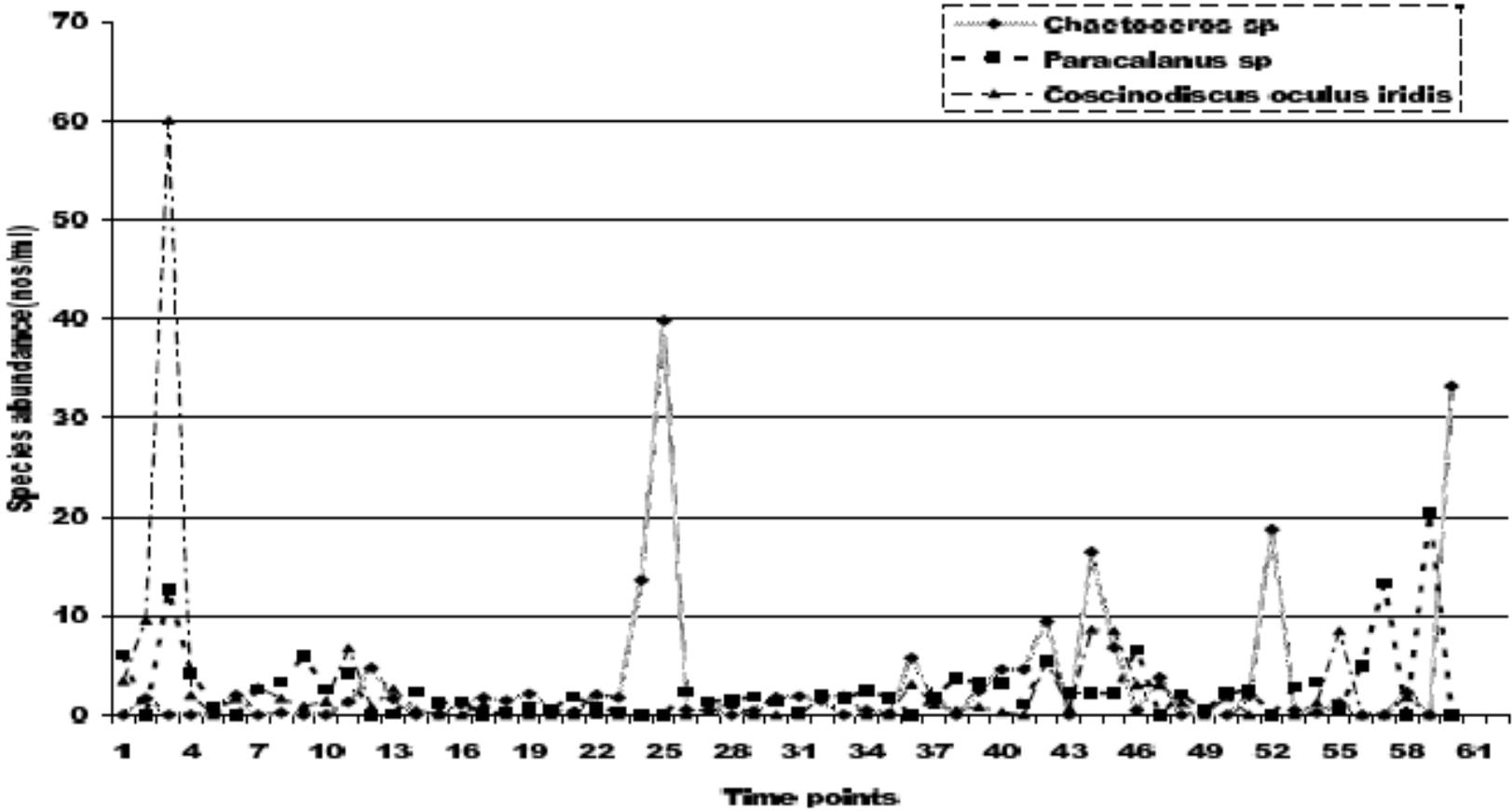


Fig. 2. Average biomass distribution of *Chaetoceros* sp. (TPP) and *Paracalanus* sp. (zooplankton) when only TPP present

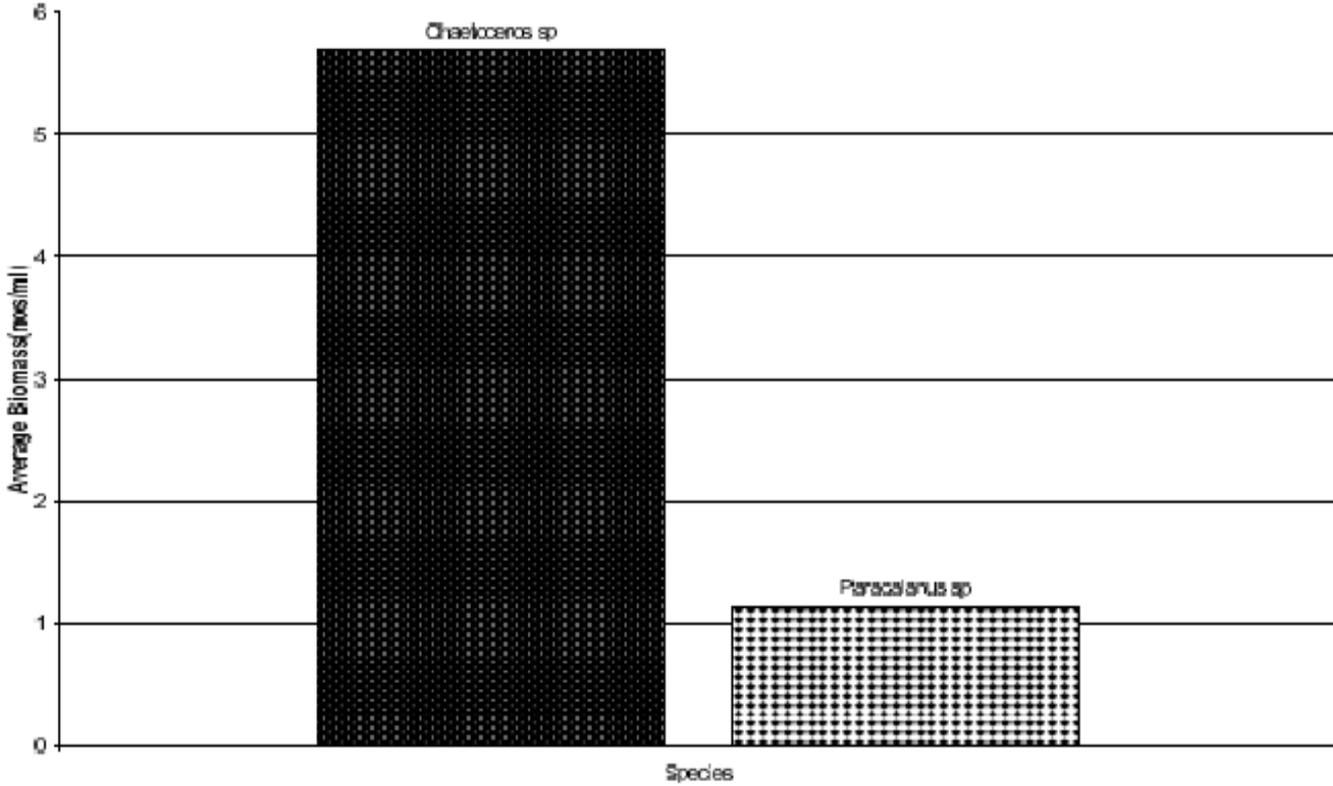


Fig.3 Average biomass distribution of NTP and zooplankton for experimental data when only NTP present

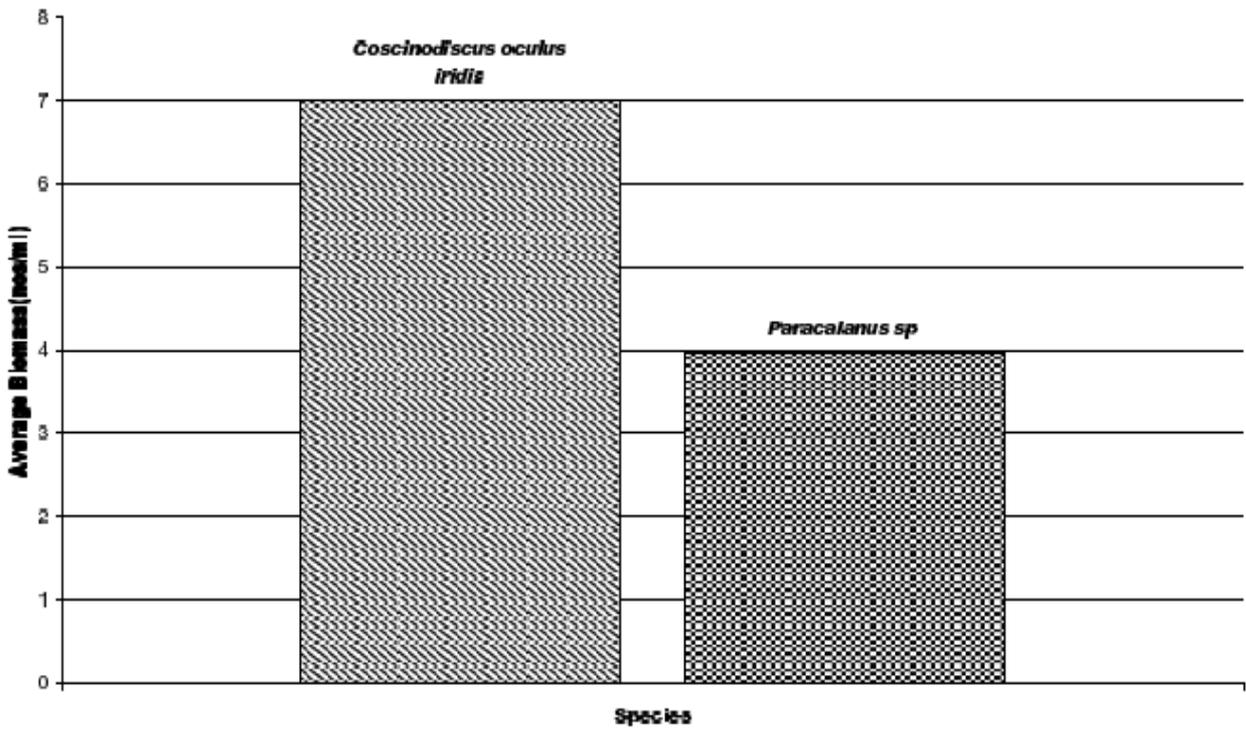
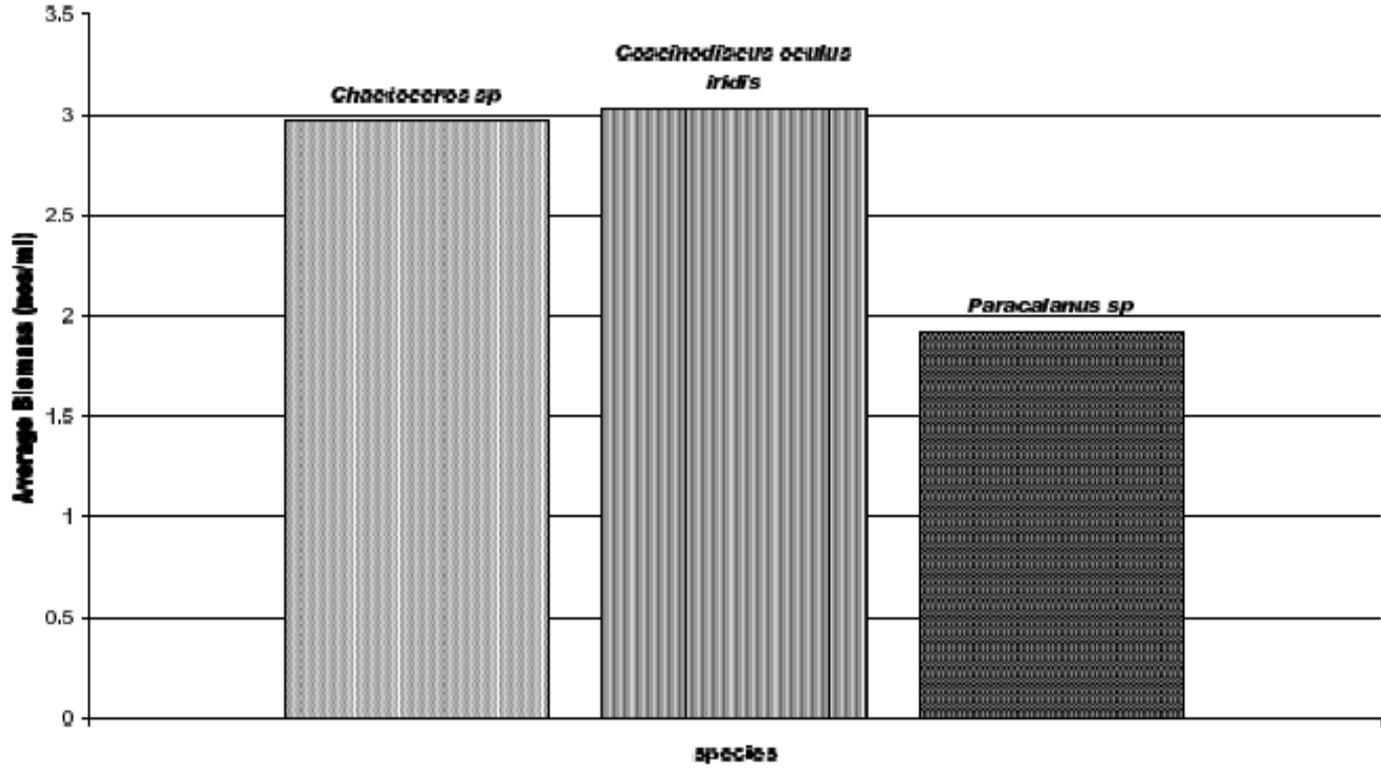


Fig.4 Average biomass distribution of TPP, NTP and zooplankton for experimental data when both NTP and TPP present in the system



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.**

Mathematical Model

$$\frac{dP_1}{dt} = rP_1 \left(1 - \frac{P_1 + \alpha P_2}{K_1}\right) - \frac{\alpha_1 P_1 Z}{1 + \beta_1 P_1 + \beta_2 P_2}$$

$$\frac{dP_2}{dt} = sP_2 \left(1 - \frac{P_2 + \beta P_1}{K_2}\right) - \frac{\alpha_2 P_2 Z}{1 + \beta_1 P_1 + \beta_2 P_2}$$

$$\frac{dZ}{dt} = \frac{(\alpha_1' P_1 - \alpha_2' P_2) Z}{1 + \beta_1 P_1 + \beta_2 P_2} - \mu Z$$

The Mathematical Model contd.

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 α and β be the competition coefficients. Let α_1 and α_2 be the attack rates of zooplankton on non-toxic and toxic phytoplankton respectively. α_1' and α_2' be the conversion efficiency of non-toxic and toxic phytoplankton into zooplankton biomass respectively. Let μ 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.

$$\frac{dx_1}{dt} = x_1(1 - x_1 - \mu_1 x_2) - \frac{x_1 x_3}{1 + \gamma_1 x_1 + \gamma_2 x_2} = F_1(x_1, x_2, x_3)$$

$$\frac{dx_2}{dt} = \gamma_3 x_2(1 - x_2 - \mu_2 x_1) - \frac{\gamma_4 x_2 x_3}{1 + \gamma_1 x_1 + \gamma_2 x_2} = F_2(x_1, x_2, x_3)$$

$$\frac{dx_3}{dt} = \frac{(\alpha_1'' x_1 - \alpha_2'' x_2) x_3}{1 + \gamma_1 x_1 + \gamma_2 x_2} - \gamma_6 x_3 = F_3(x_1, x_2, x_3)$$

The Mathematical Model contd.

where

$$\begin{aligned} \mu_1 &= \frac{\alpha K_2}{K_1}, \quad \mu_2 = \frac{\beta K_1}{K_2}, \quad \gamma_0 = \frac{\mu}{r}, \quad \gamma_1 = \beta_1 K_1, \quad \gamma_2 = \beta_2 K_2, \quad \gamma_3 = \frac{s}{r}, \quad \gamma_4 = \frac{\alpha_2}{\alpha_1}, \\ \alpha_1'' &= \frac{\alpha_1' K_1}{r}, \quad \alpha_2'' = \frac{\alpha_2' K_2}{r} \end{aligned} \quad (3.4)$$

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 τ 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 $E_3(\frac{\mu_1-1}{\mu_1\mu_2-1}, \frac{\mu_2-1}{\mu_1\mu_2-1}, 0)$. The existence criterion of E_3 is $\mu_1 > 1$ and $\mu_2 > 1$. There exists a feasible toxic phytoplankton free equilibrium $E_4(\frac{\gamma_6}{\alpha_1'' - \gamma_1\gamma_6}, 0, \frac{\alpha_1''(\alpha_1'' - \gamma_1\gamma_6 - \gamma_6)}{(\alpha_1'' - \gamma_1\gamma_6)^2})$. The equilibrium E_4 exists if $\alpha_1'' > \gamma_6(1 + \gamma_1)$.

Positive Interior Equilibrium

The positive interior equilibrium $E^* = (x_1^*, x_2^*, x_3^*)$, where

$$x_1^* = \frac{\gamma_8(\gamma_3 - \mu_1\gamma_4) + (\gamma_3 - \gamma_4)(\alpha_2'' + \gamma_2\gamma_8)}{\Delta},$$

$$x_2^* = \frac{(\gamma_3 - \gamma_4)(\alpha_1'' - \gamma_1\gamma_8) - \gamma_8(\gamma_3\mu_2 - \gamma_4)}{\Delta},$$

$$x_3^* = \frac{\gamma_3[(\alpha_2'' + \gamma_2\gamma_8)(\mu_2 - 1) + (\alpha_1'' - \gamma_1\gamma_8)(1 - \mu_1) + \gamma_8(\mu_1\mu_2 - 1)] + (\gamma_3 - \gamma_4)(\alpha_1''\gamma_2 + \alpha_2''\gamma_1) + \alpha_1''(\gamma_3 - \mu_1\gamma_4) + \alpha_2''(\gamma_3\mu_2 - \gamma_4)}{\Delta^2},$$

where $\Delta = (\alpha_2'' + \gamma_2\gamma_8)(\gamma_3\mu_2 - \gamma_4) + (\alpha_1'' - \gamma_1\gamma_8)(\gamma_3 - \mu_1\gamma_4)$.

The positive interior equilibrium E^* exists if $x_1^*, x_2^*, x_3^* > 0$ and this leads to

the following condition: $\alpha_1'' - \gamma_1\gamma_8 > 0$, $\frac{\gamma_3}{\gamma_4} > \max\{\mu_1, \frac{1}{\mu_2}, 1\}$ and $R_1 = \frac{(\gamma_3 - \gamma_4)(\alpha_1'' - \gamma_1\gamma_8)}{\gamma_8(\gamma_3\mu_2 - \gamma_4)} > 1$ where $\mu_2 > 1$, $\mu_1 < 1$ and $\mu_1\mu_2 > 1$

Stability Analysis

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).

Stability Analysis contd.

- *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 μ_2 crosses a critical value, say μ_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*

Stochastic Model contd.

$$\begin{aligned}dx_1 &= F_1(x_1, x_2, x_3)dt + \sigma_1(x_1 - x_1^*)d\xi_t^1 \\dx_2 &= F_2(x_1, x_2, x_3)dt + \sigma_2(x_2 - x_2^*)d\xi_t^2 \\dx_3 &= F_3(x_1, x_2, x_3)dt + \sigma_3(x_3 - x_3^*)d\xi_t^3\end{aligned}\tag{3.1}$$

where σ_1 , σ_2 and σ_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

$$dX_t = f(t, X_t)dt + g(t, X_t)d\xi_t, \quad X_{t_0} = X_0\tag{3.2}$$

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 ξ_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)**

Parameters/ Variable	Default values
γ_1	2
γ_2	3
γ_3	1.5
γ_4	0.9
γ_6	0.102
α_1	0.8
α_2	0.2
μ_1	0.3
μ_2	1.16

Fig. 8. Figure depicting coexistence of all the population

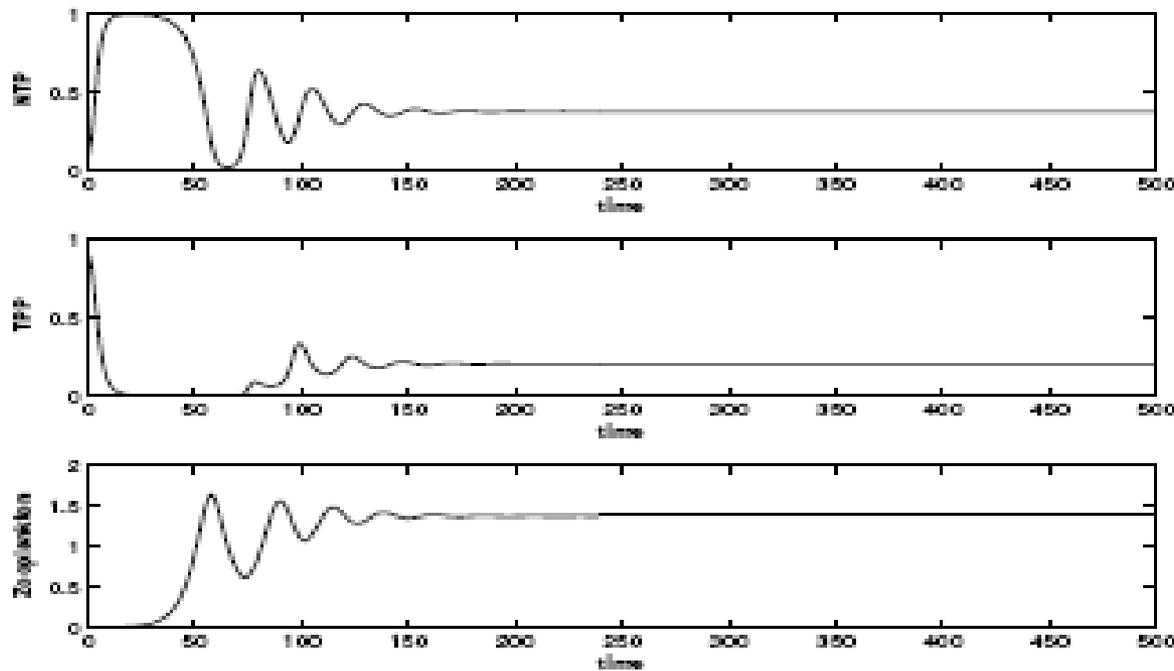


Fig.9-Figure depicting the phase portrait corresponding to Fig.8 and showing that E^* is stable while E_0, E_1, E_2, E_3 are saddle points and E_4 does not exist

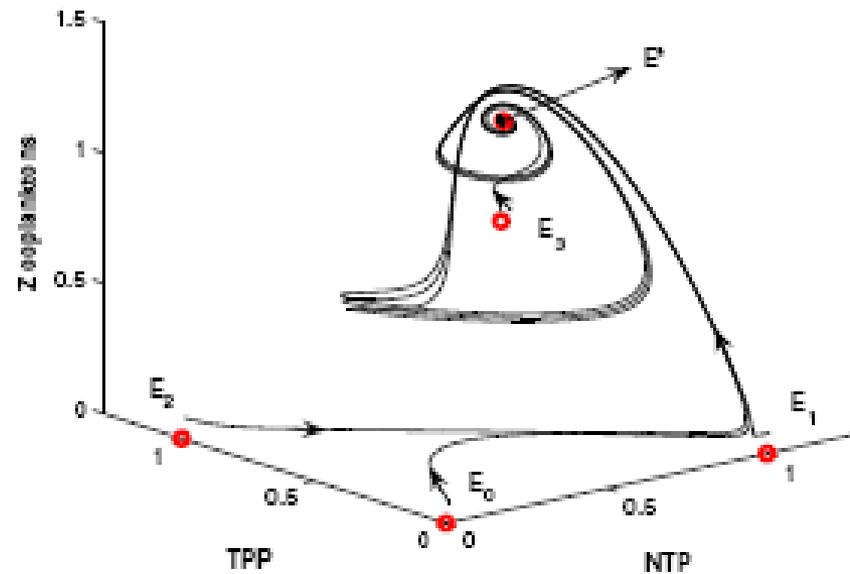


Fig. 10- Figure depicting extinction of the zooplankton population when the competition between NTP and TPP is very low. (We have used different time scale to show the clear dynamics)

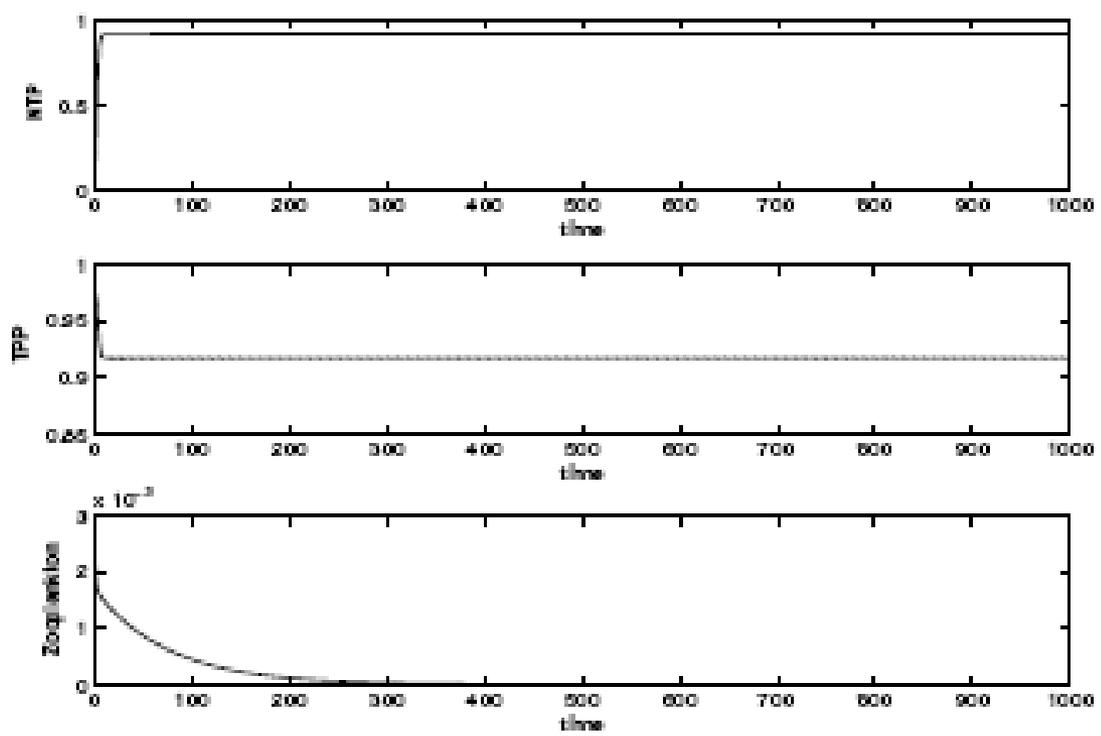


Fig.11-Figure depicting the phase portrait corresponding to Fig.10 and showing that E_3 is stable while E_0, E_1, E_2 are saddle points, E_4 is a spiral source and E^* does not exist

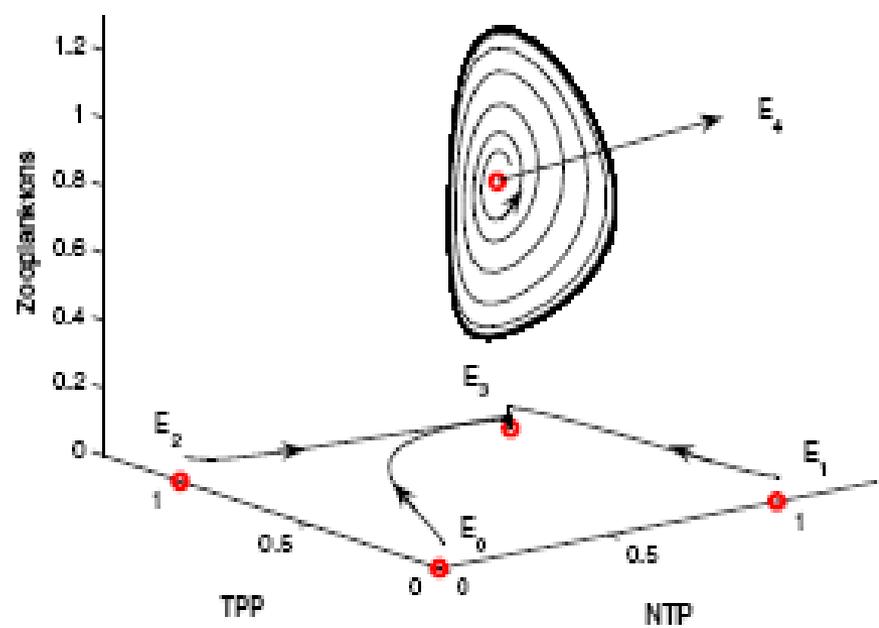


Fig. 12- Figure depicting coexistence of all population through oscillation when we increase the competition coefficient μ_2 from 1.18 to 1.38 (remaining parameter values same as in figure 10)

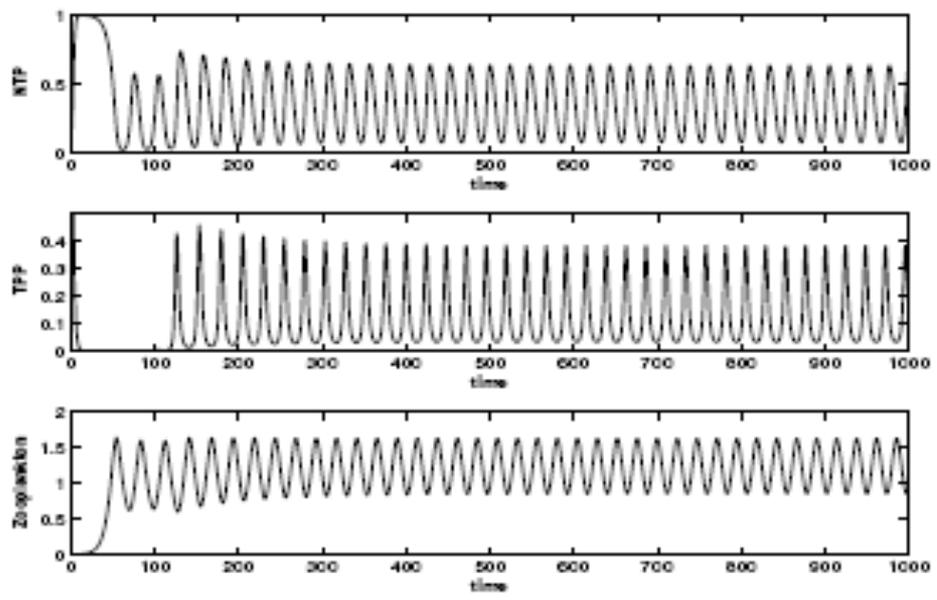


Fig.13-Figure depicting the phase portrait corresponding to Fig.12 and showing that E^* is stable limit cycle while E_0, E_1, E_2, E_4 are saddle points and E_3 does not exist

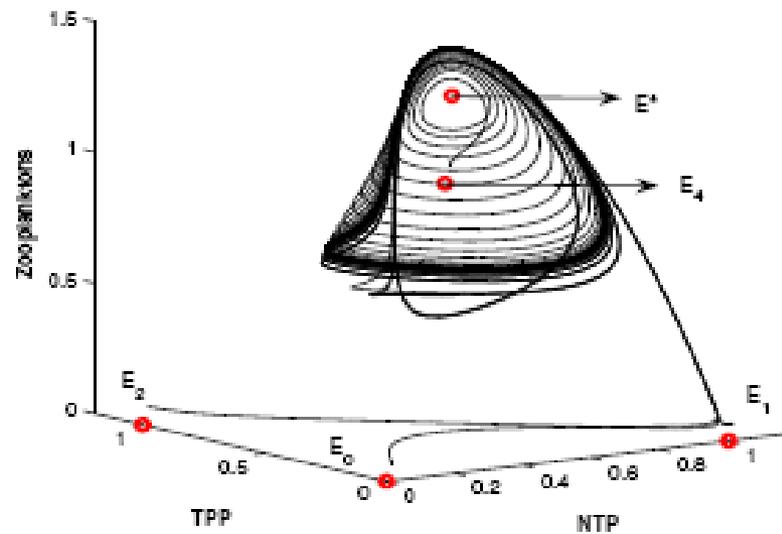


Fig.14. Coexistence of all population in the presence of environmental fluctuation ($\sigma_i=0.05, i=1,2,3$), (here we have used the scheme given by Carletti , Math. Biosc.)

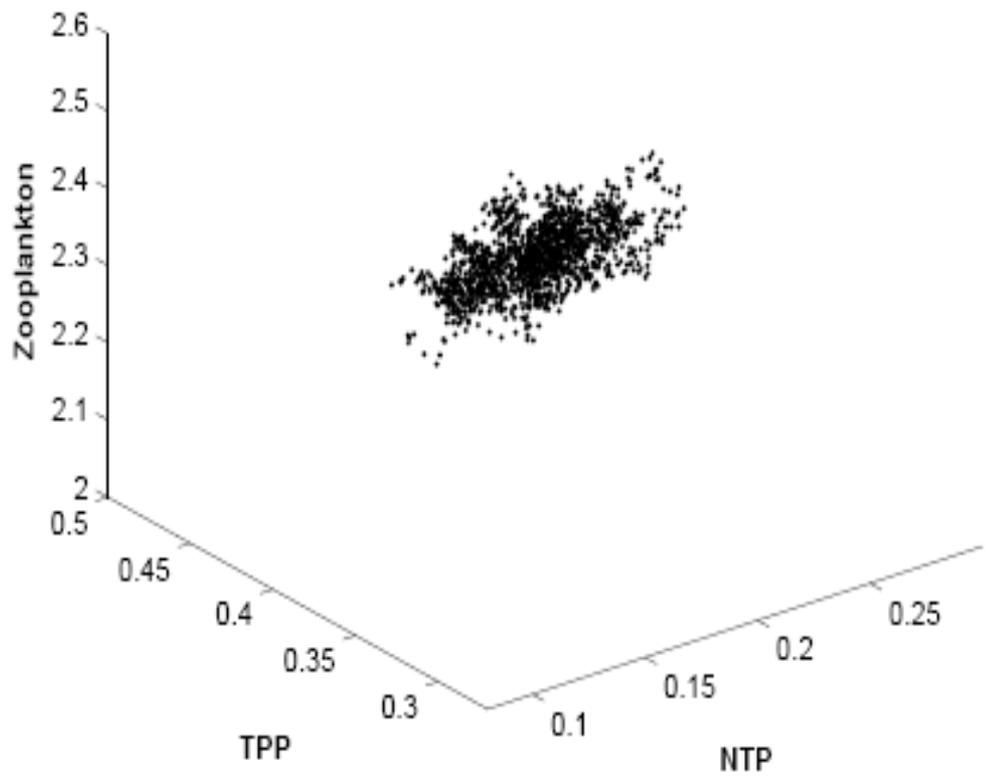


Fig.15: Figure depicting aperiodic oscillation of all population in the presence of environmental fluctuation for $\mu_1=0.1$, $\mu_2=1.5$ (when we increase the competition coefficient). (In absence of environmental fluctuation for the same parametric values the system shows regular oscillation).

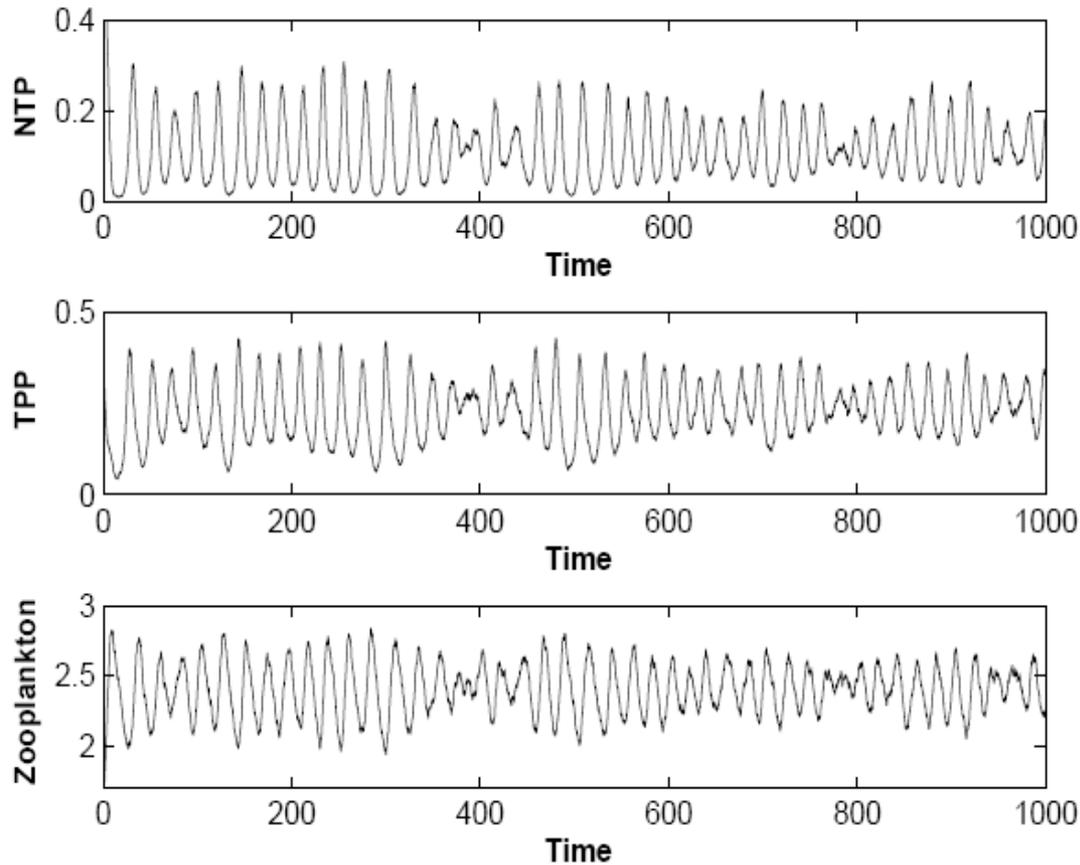
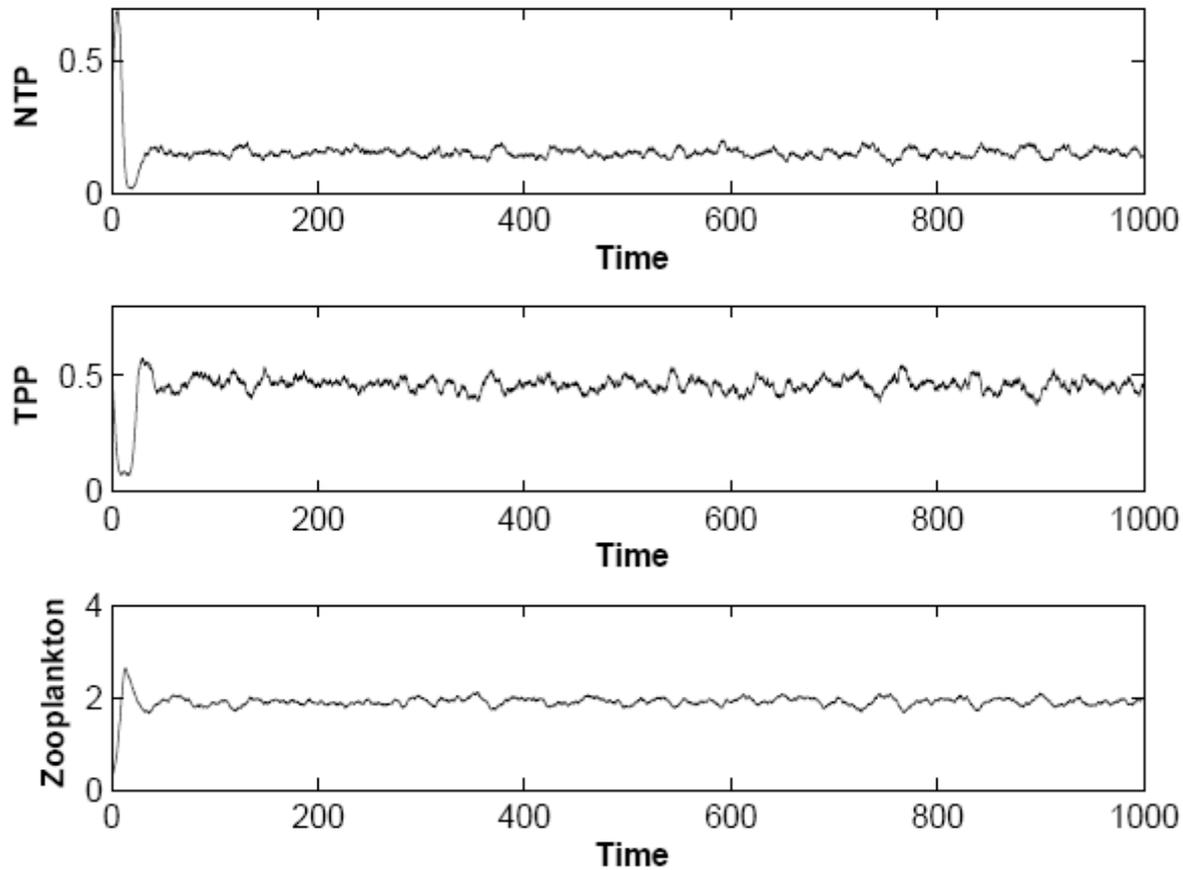


Fig.16: Figure depicting stable population distribution in the presence of environmental fluctuation for $\mu_1=1$, $\mu_2=1.56$. (In absence of environmental fluctuation for the same parametric values the system shows chaotic bloom).



Observations

- **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 time 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.**

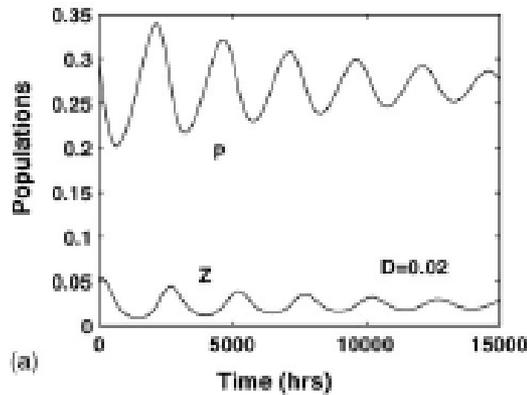
The mathematical model for Nutrient - Phytoplankton - Zooplankton

$$\frac{dN}{dt} = D(N^0 - N) - \alpha_1 PN + \mu_3 P + \mu_4 Z$$

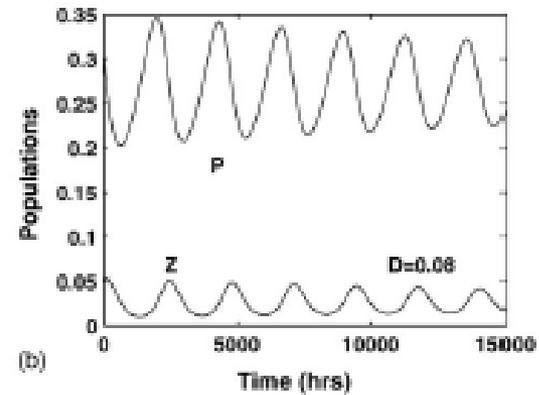
$$\frac{dP}{dt} = \alpha_2 PN - \gamma_1 PZ - (\mu_1 + D_1)P$$

$$\frac{dZ}{dt} = \gamma_2 PZ - (\mu_2 + D_2)Z - \frac{\theta PZ}{\gamma + P}$$

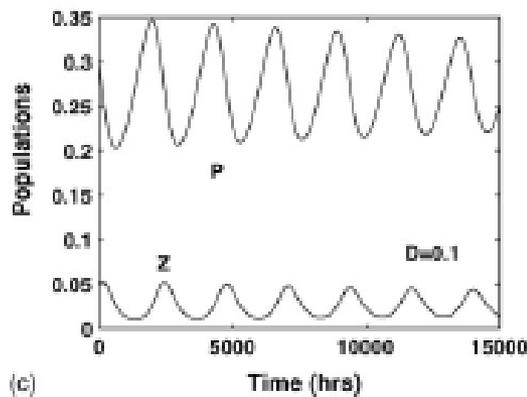
The behavior of phytoplankton and zooplankton for different values of D : (a) $D=0.02$, (b) $D=0.08$, (c) $D=0.1$, (d) $D=0.65$ (other parameter values are kept fixed)



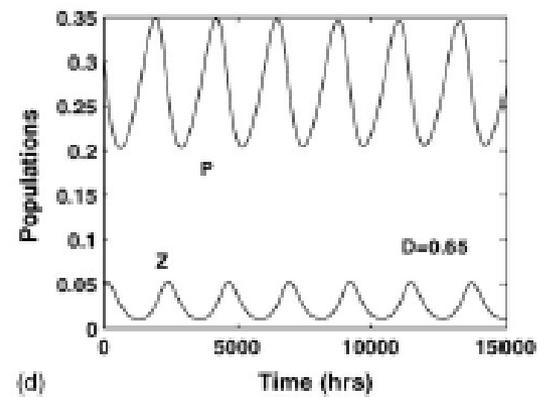
(a)



(b)



(c)

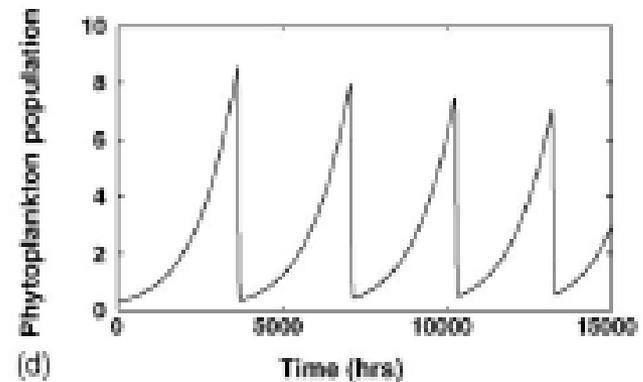
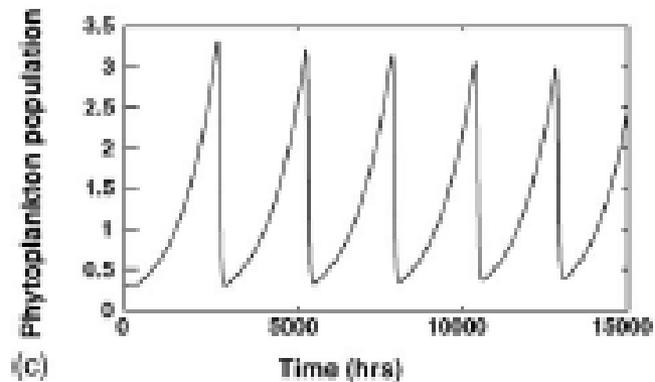
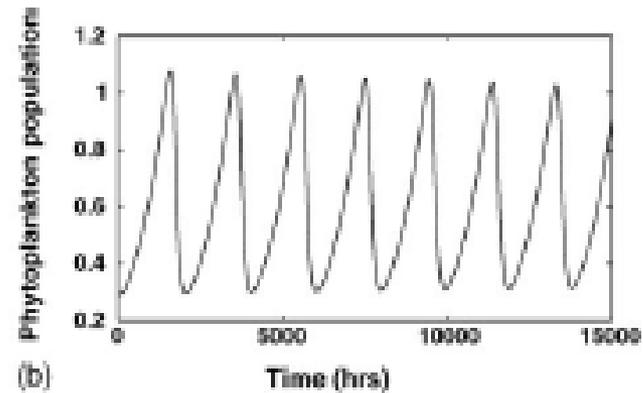
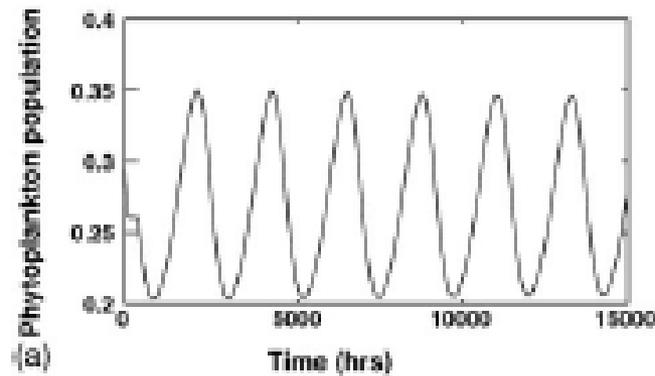


(d)

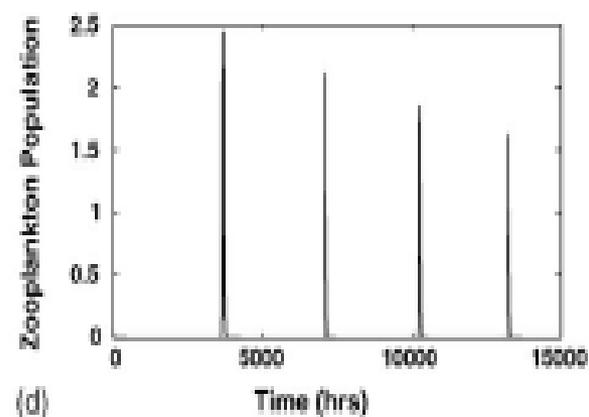
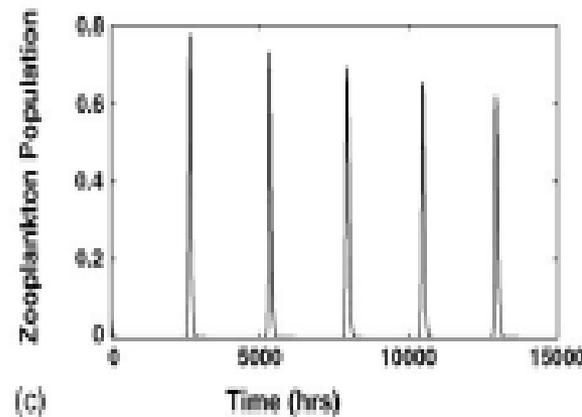
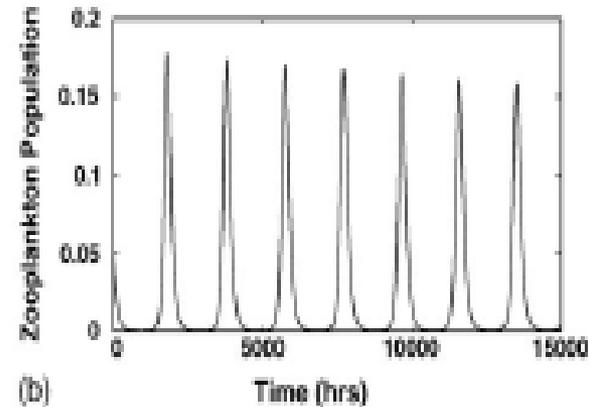
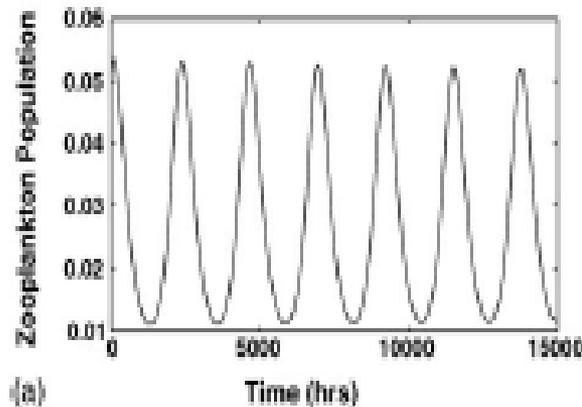
Effect of Dilution rate

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 θ (a) $\theta=0$, (b) $\theta=0.01$, (c) $\theta=0.03$, (d) $\theta=0.07$



Behavior of Zooplankton population: For different values of θ (a) $\theta=0$, (b) $\theta=0.01$, (c) $\theta=0.03$, (d) $\theta=0.07$



Effect of Nutrient and toxin

- Thus we observe that increasing the value of θ 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

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 - N) - \alpha_1 P_1 N - \alpha_2 P_2 N + \eta_1 P_1 + \eta_2 P_2 + \eta_3 Z \\ &\equiv F_1(N, P_1, P_2, Z),\end{aligned}$$

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

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

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

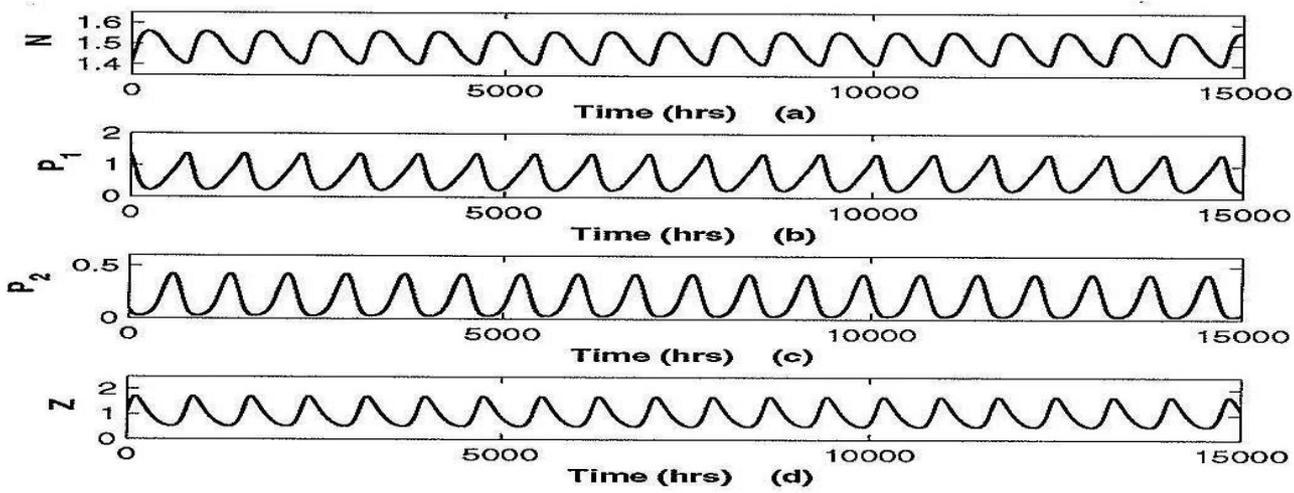
This system of ordinary differential equations is subject to the initial conditions

$$N(0) > 0, P_1(0) > 0, P_2(0) > 0, Z(0) > 0.$$

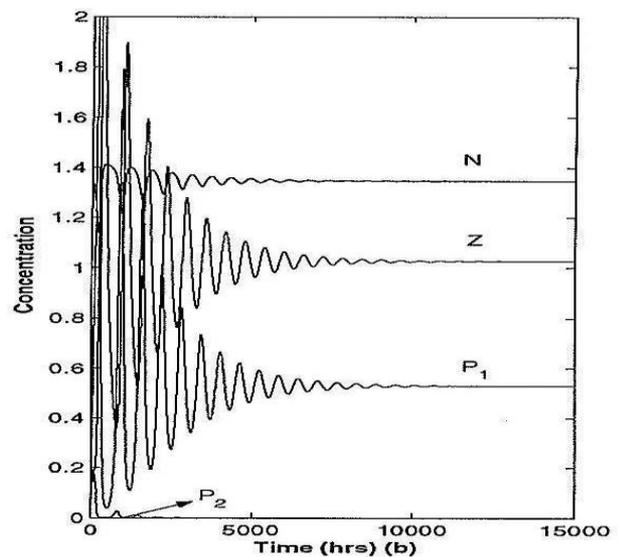
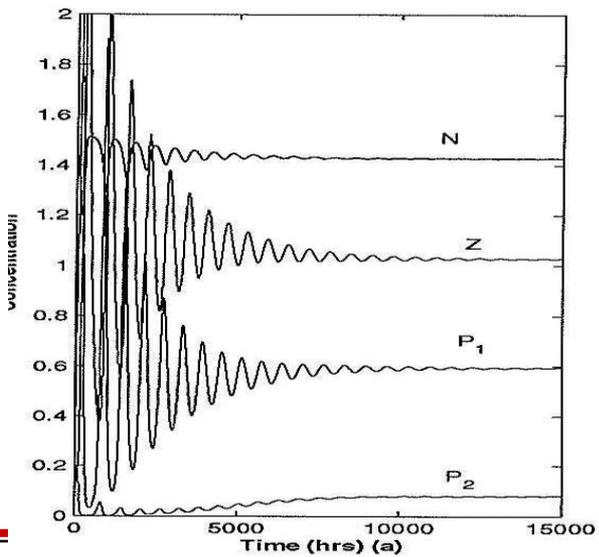
Set of Parameter Values

Parameter	Definition	Default value	Unit
N^0	Constant input of nutrient	1.58	h^{-1}
D	Dilution rate of nutrient	0.3	h^{-1}
α_1	Nutrient uptake rate of NTP	0.03	$ml. h^{-1}$
α_2	Nutrient uptake rate of TPP	0.022	$ml. h^{-1}$
θ_1	Conversion rate of NTP	0.02	$ml. h^{-1}$
θ_2	Conversion rate of TPP	0.02	$ml. h^{-1}$
μ_1	Death rate of NTP	0.006	h^{-1}
μ_2	Death rate of TPP	0.006	h^{-1}
μ_3	Death rate of zooplankton	0.005	h^{-1}
η_1	Nutrient recycling rate of NTP	0.004	$mg. h^{-1}$
η_2	Nutrient recycling rate of TPP	0.004	$mg. h^{-1}$
η_3	Nutrient recycling rate of zoopl.	0.0035	$mg. h^{-1}$
e_1	Competition coefficient	0.02	$ml. h^{-1}$
e_2	Competition coefficient	0.02	$ml. h^{-1}$
β_1	Predation rate of NTP	0.02	$ml. h^{-1}$
β_2	Predation rate of TPP	0.01	$ml. h^{-1}$
γ_1	Conversion rate for NTP	0.01	$ml. h^{-1}$
γ_2	Death rate due to consumption of TPP	0.008	$ml. h^{-1}$
D_1	Dilution rate of NTP	0.0004	h^{-1}
D_2	Dilution rate of TPP	0.0004	h^{-1}
D_3	Dilution rate of zooplankton	0.0003	h^{-1}

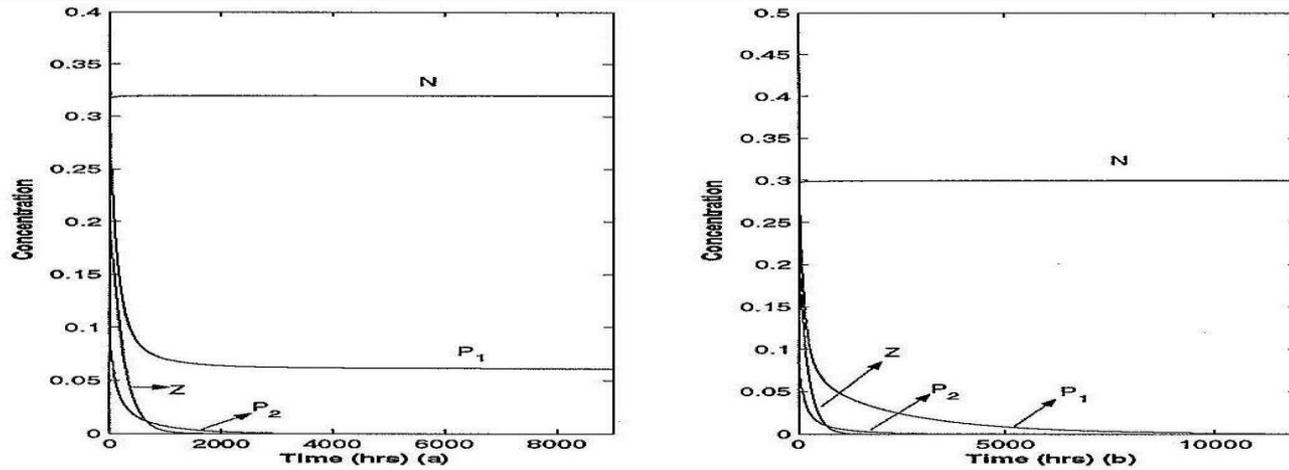
Effect of Nutrient: Periodic solution of the system for the parameters as given in Table-II $N^0=1.58$ (Fig 1)



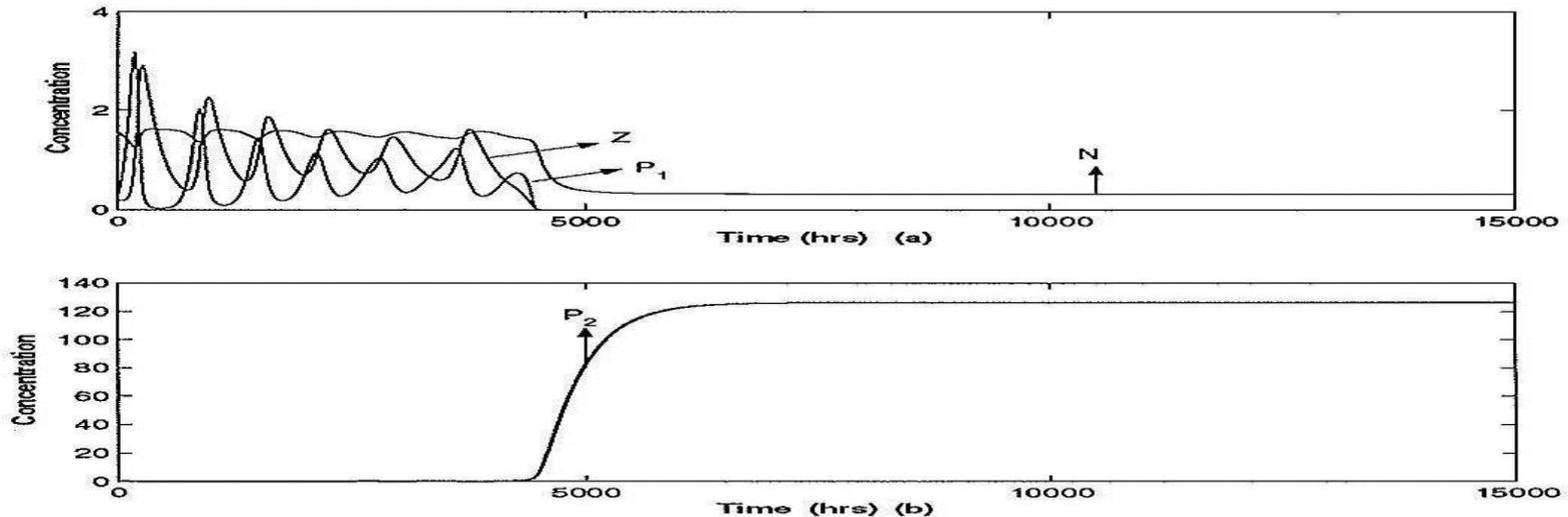
- (a) For $N^0=1.5$ the system is stable at E^*
- (b) For $N^0=1.4$ the system is stable at $E_4 (N, P_1, 0, Z_4)$ (Fig 2)



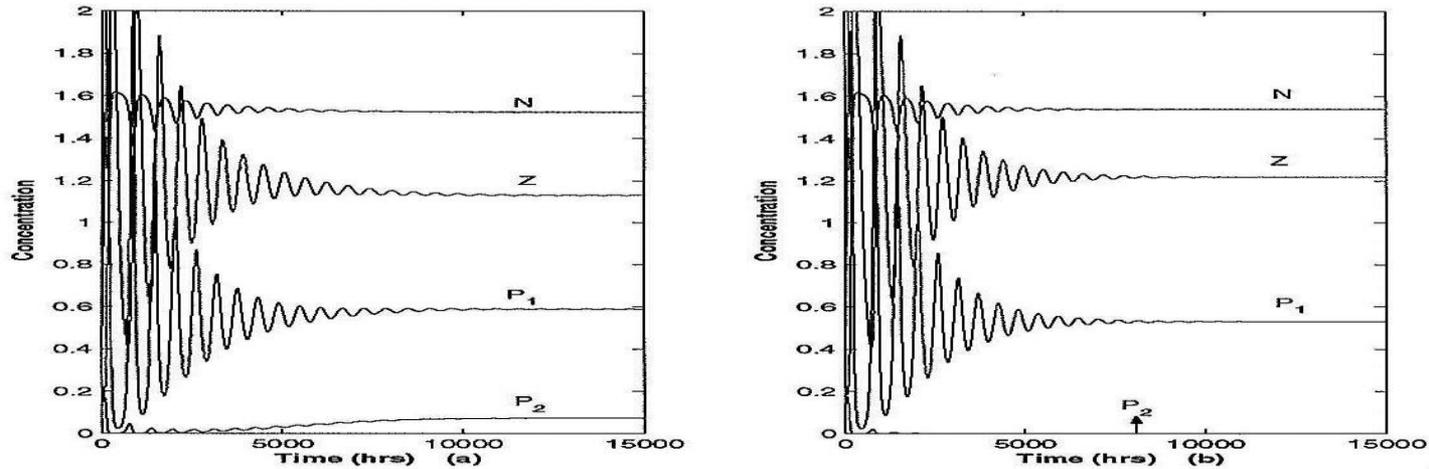
(a) For $N^0=0.321$ the system is stable at $E_1 (N, P_1, 0, 0)$
(b) For $N^0=0.3$ the system is stable at $E_0 (N, 0, 0, 0)$ (Fig 3)



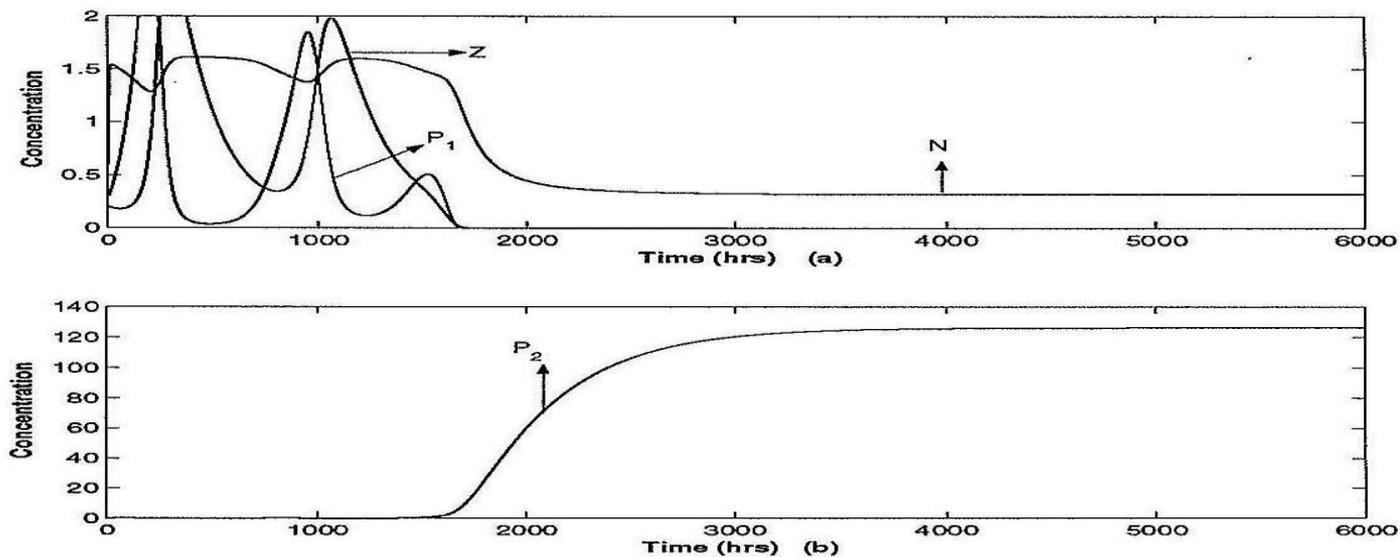
E_2 is locally asymptotically stable with high biomass of TPP for $N^0=1.6$ (Fig 4)



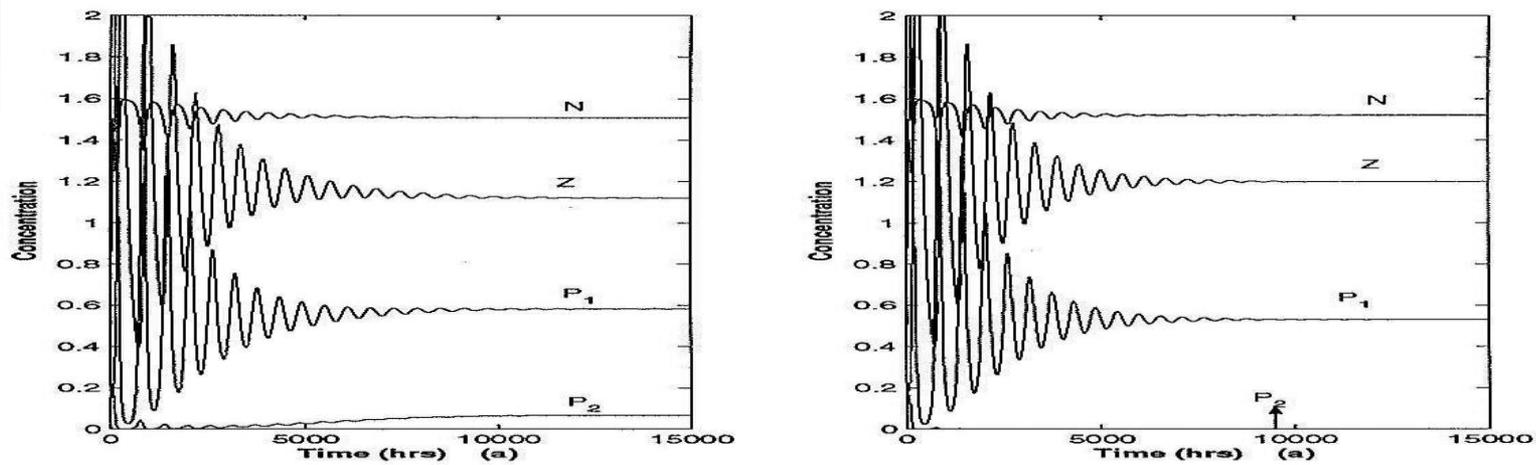
(a) E^* is stable when $\mu_2 = 0.007$ and $N^0 = 1.6$ (Increase the death rate of TPP)
 (b) E_4 is stable when $\mu_2 = 0.008$ and $N^0 = 1.6$ (Fig 5)



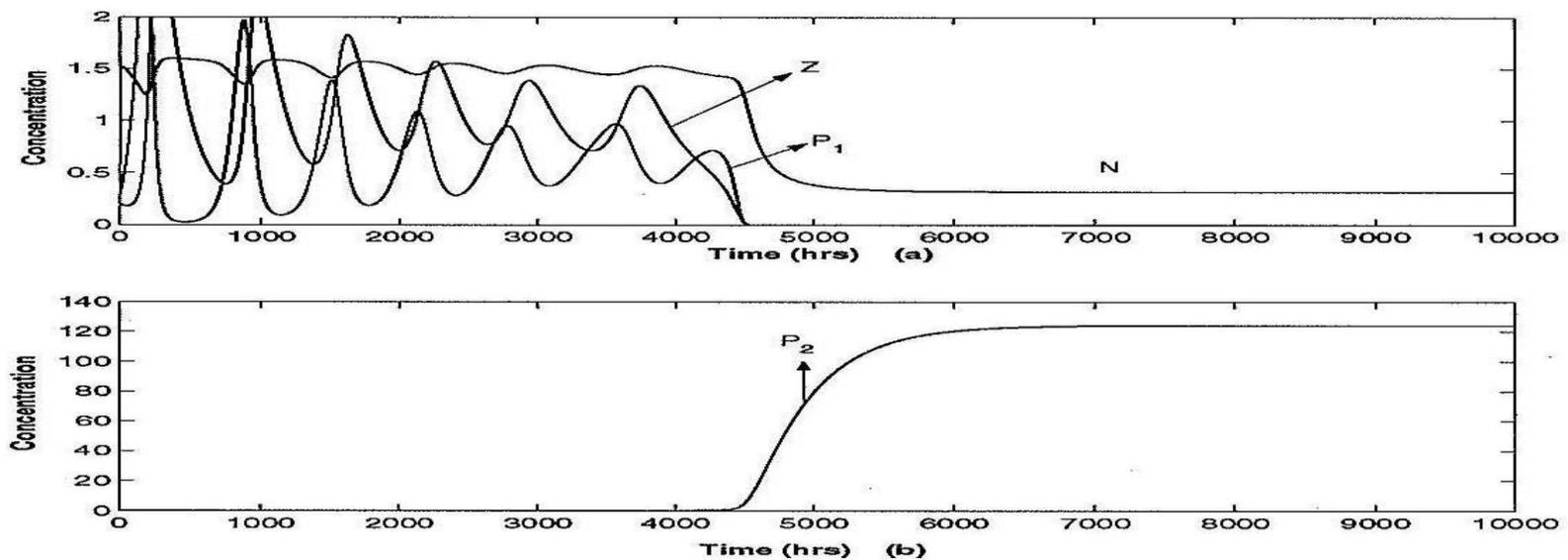
For high biomass of TPP with $\mu_1 = 0.008$ (the death rate of NTP) & $N^0 = 1.6$ the system is asymptotically stable at E_2 (Fig 6)



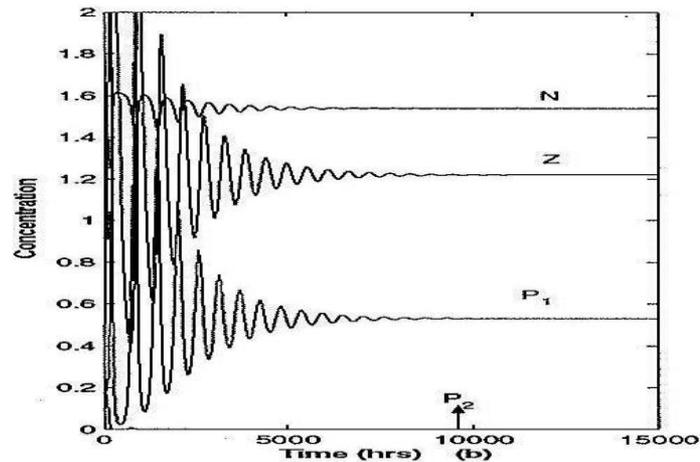
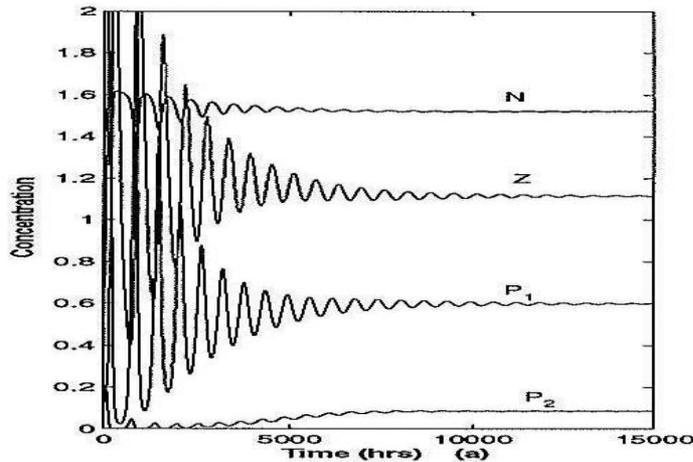
Effect of Competition: If NTP is a stronger competitor than TPP
(a) System is stable $e_2=0.0215$ (b) Increase $e_2=0.025$ (stable around E_1) (Fig 7)



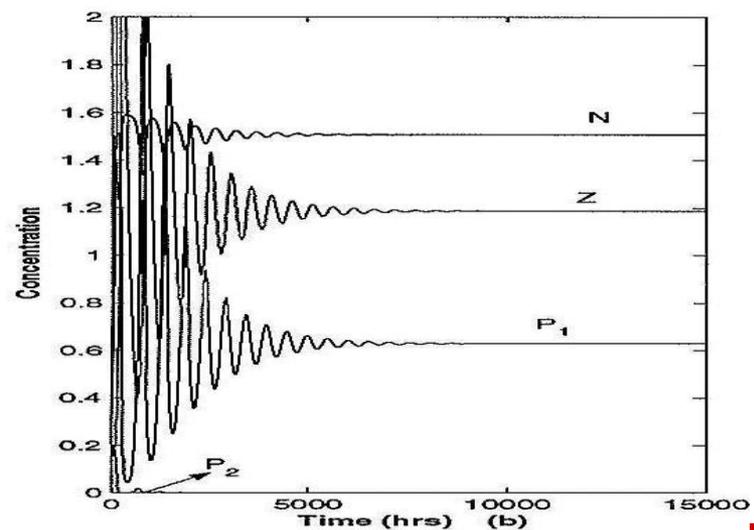
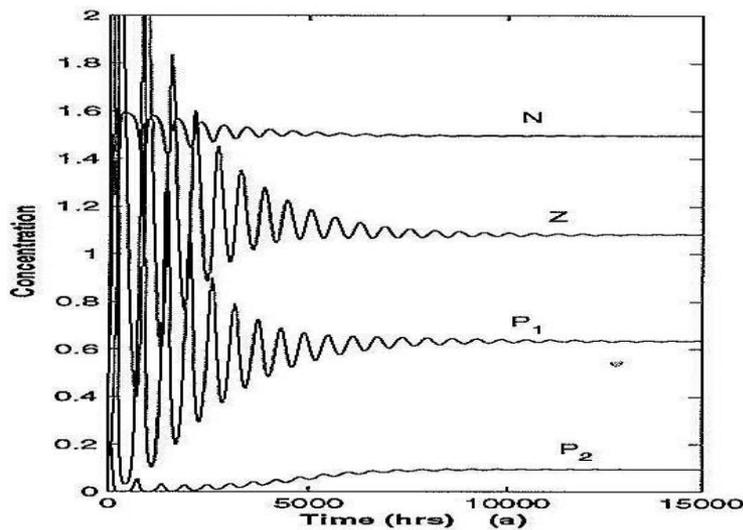
Effect of Competition: If TPP is a stronger competitor than NTP i.e. $e_1 > e_2$ then the system is stable around E_2 with a high TPP biomass (Fig 8)



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 μ_3 then the system is stable at E_{11}]



Mathematical Model

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

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

$$\frac{dZ}{dt} = \frac{(\beta_2 - \theta) P^2 Z}{K_2 + P^2} - \mu_2 Z - \frac{h_2 Z}{E_2 + Z} \equiv F_3(N, P, Z).$$

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

$$N(0) > 0, P(0) > 0, Z(0) > 0.$$

The Mathematical Model contd.

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 α_1 and α_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 μ_1 be the mortality rate of the phytoplankton population and μ_2 be the mortality rate of the zooplankton population.

The Mathematical Model contd.

Let μ_3 ($\mu_3 \leq \mu_1$) be the nutrient recycle rate after the death of phytoplankton population and μ_4 ($\mu_4 \leq \mu_2$) be the nutrient recycle rate after the death of zooplankton population. Let β_1 be the maximal zooplankton ingestion rate and β_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 catchability 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

The Mathematical Model contd.

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 $\lim_{H_1 \rightarrow \infty} \frac{h_1 H_1}{E_1 + H_1} = h_1$

and $\lim_{H_2 \rightarrow \infty} \frac{h_2 H_2}{E_2 + H_2} = h_2$, so that the harvesting level is close to h_1 and h_2 respec-

tively, the catchability constant. It is assumed θ is the rate of zooplankton decay

due to toxin producing phytoplankton.

The table representing thresholds and stability of steady states

Thresholds(R_0, R_1)	$(N^0, 0, 0)$	$(N_1, P_1, 0)$	(N^*, P^*, Z^*)
$R_0 < 1$	Asymptotically stable	Not feasible	Not feasible
$R_0 > 1, R_1 < 1$	Unstable	Asymptotically stable	Not feasible
$R_1 > 1$	Unstable	Not feasible	Asymptotically stable

Direction of Hopf-Bifurcation

Theorem: 4. Here μ_{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 $\theta > \theta^*$; β_{22} determines the stability of the bifurcating periodic solutions: the solutions are orbitally stable (unstable) if $\beta_{22} < 0 (> 0)$; and τ_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

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 - N) - \frac{\alpha_1 P N}{K_1 + N} + \mu_3 P + \mu_4 Z \equiv F_1(N, P, Z), \\ \frac{dP}{dt} &= \frac{\alpha_2 P N}{K_1 + N} - \frac{\beta_1 P^2 Z}{K_2 + P^2} - \mu_1 P - \frac{h_1 P}{E_1 + P} \equiv F_2(N, P, Z), \\ \frac{dZ}{dt} &= \frac{(\beta_2 - \theta) P^2 (t - \tau) Z (t - \tau)}{K_2 + P^2 (t - \tau)} - \mu_2 Z - \frac{h_2 Z}{E_2 + Z} \equiv F_3(N, P, Z).\end{aligned}\quad (2)$$

Table 2 (Set of parameter values)

Parameter	Definition	Default value	Unit
N^0	Constant input of nutrient	2	mgml ⁻¹
D	Dilution rate of nutrient	1	day ⁻¹
α_1	Nutrient uptake rate for the phytoplankton	3.2	mlmg ⁻¹ day ⁻¹
α_2	Nutrient conversion rate for the phytoplankton	2.4	mlmg ⁻¹ day ⁻¹
β_1	Phytoplankton uptake rate for the zooplankton	2.1	mlmg ⁻¹ day ⁻¹
β_2	Phytoplankton conversion rate for the zooplankton	1	mlmg ⁻¹ day ⁻¹
μ_1	Mortality rate of phytoplankton	.1	day ⁻¹
μ_2	Mortality rate of zooplankton	.1	day ⁻¹
μ_3	Nutrient Recycle rate due to the death phytoplankton	.06	mgday ⁻¹
μ_4	Nutrient Recycle rate due to the death of zooplankton	.06	mgday ⁻¹
K_1	Half saturation constant	.6	mlday ⁻¹
K_2	Half saturation constant	.1	mlday ⁻¹
h_1	Harvesting rate of phytoplankton population	.4	day ⁻¹
E_1	Effort required to harvest the phytoplankton.	1	day ⁻¹
h_2	Harvesting rate of zooplankton population	.4	day ⁻¹
E_2	Effort required to harvest the zooplankton	1	day ⁻¹
θ	Rate of zooplankton decay due to toxin production phytoplankton	0	mlday ⁻¹

The equilibrium point E^* is stable for the parametric values as given in the Table 2

Fig-1

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.

Fig-2

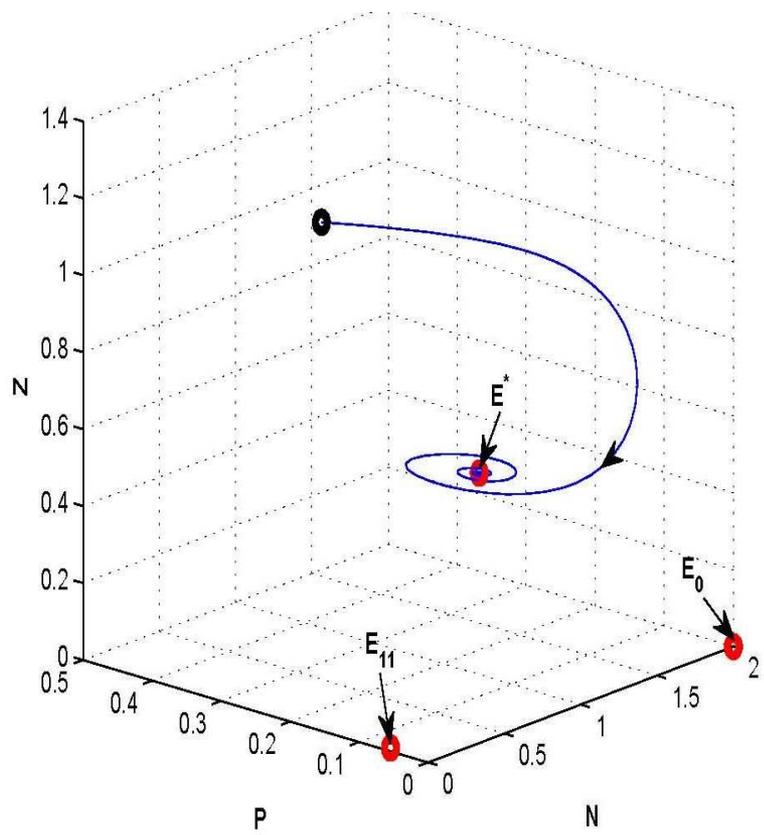


Fig-1

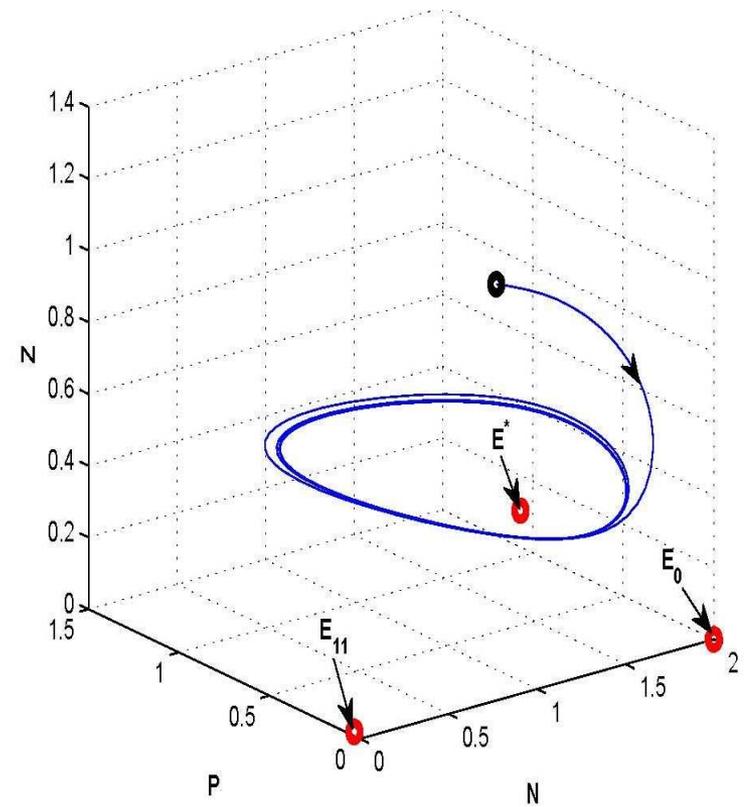


Fig-2

The figure depicts stable behavior at E^* of the system (1) for $\theta = .3$ 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 $\theta = .3$ and $N^0 = 1$ (from $N^0 = 2$) with same set of parametric values as given in the Table 2. (FIG-4)

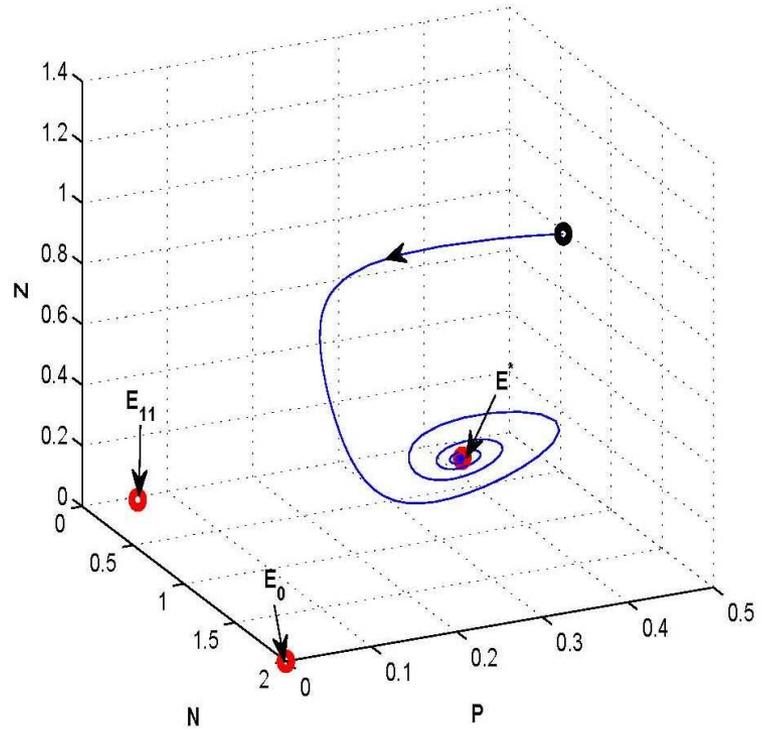


Fig-3

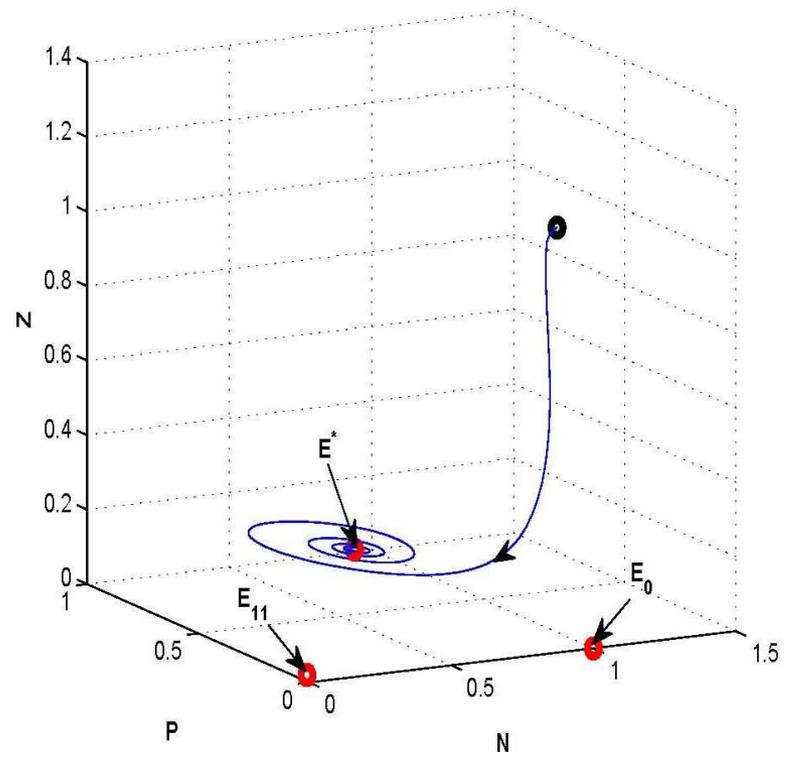


Fig-4

The figure depicts stable behavior at E^* of the system (1) for $\theta = .3$ and $D = .5$ (from $D=1$) with same set of parametric values as given in the Table 2. *Fig-5*

The figures depicts oscillatory behavior around the positive interior equilibrium E^* of the system (1) for increasing h_1 from .4 to 1.2 and other parametric values as given in the Table 2. *Fig-6*

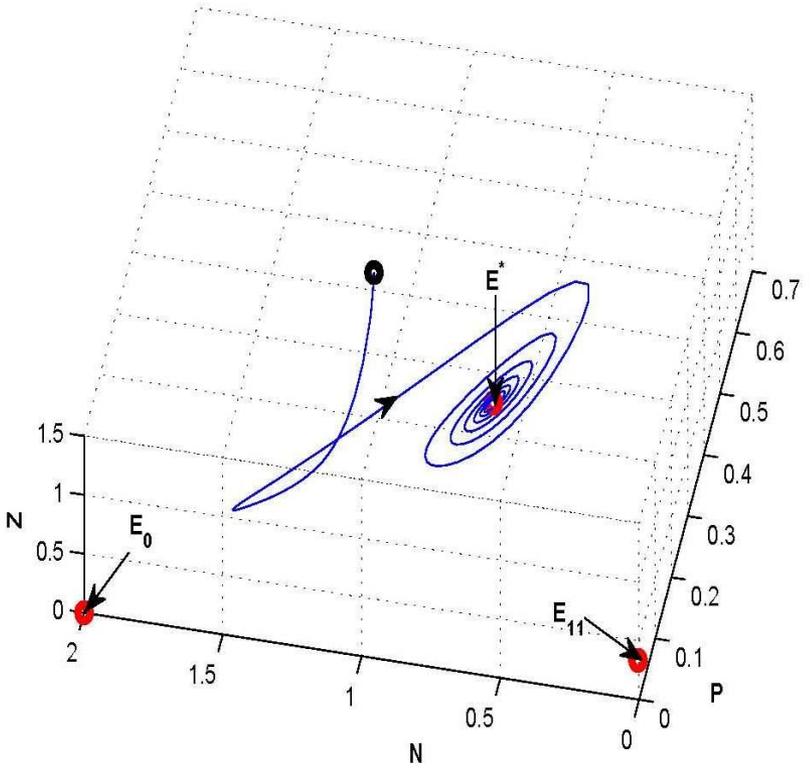


Fig-5

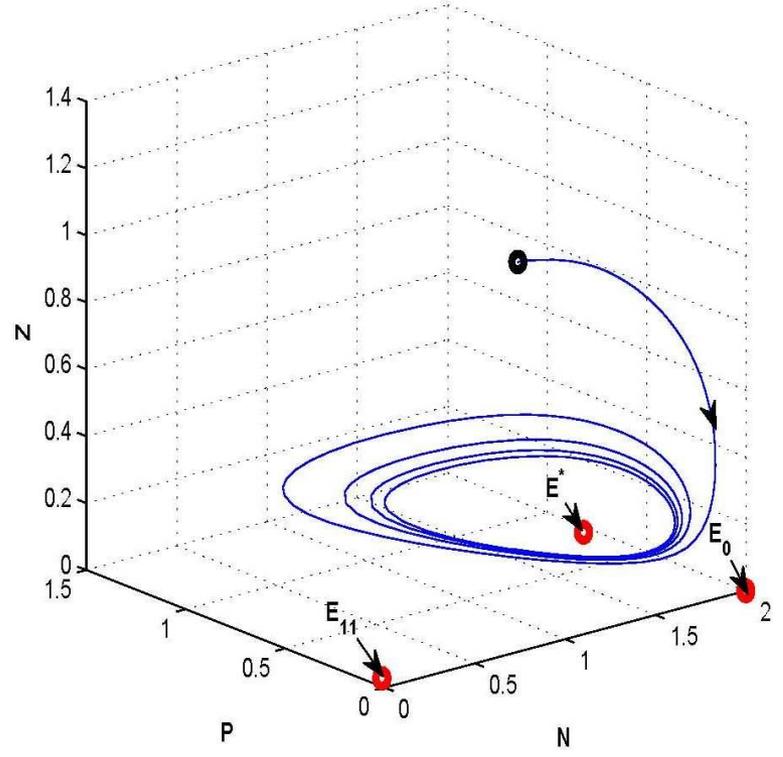


Fig-6

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

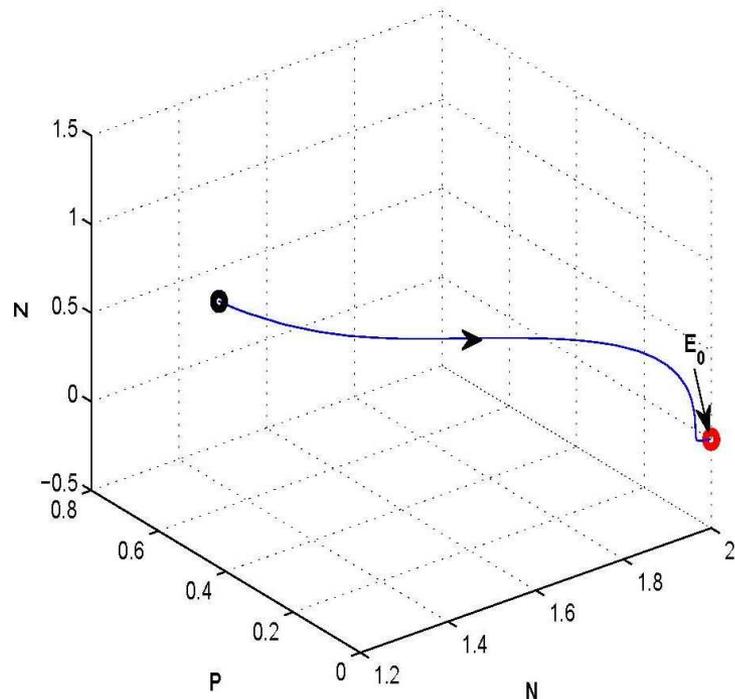


Fig-7

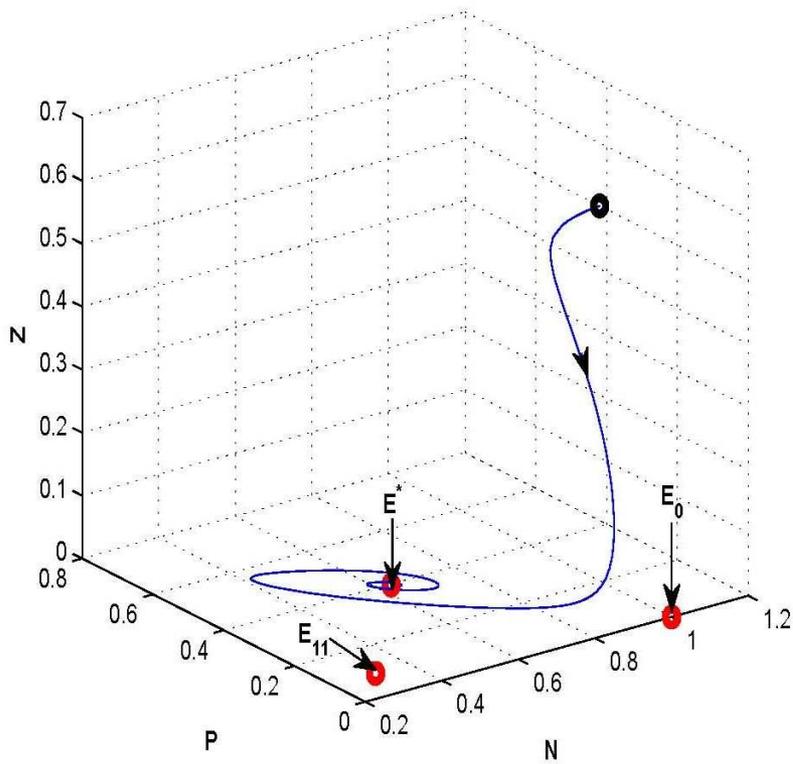


Fig-8

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 depicts 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

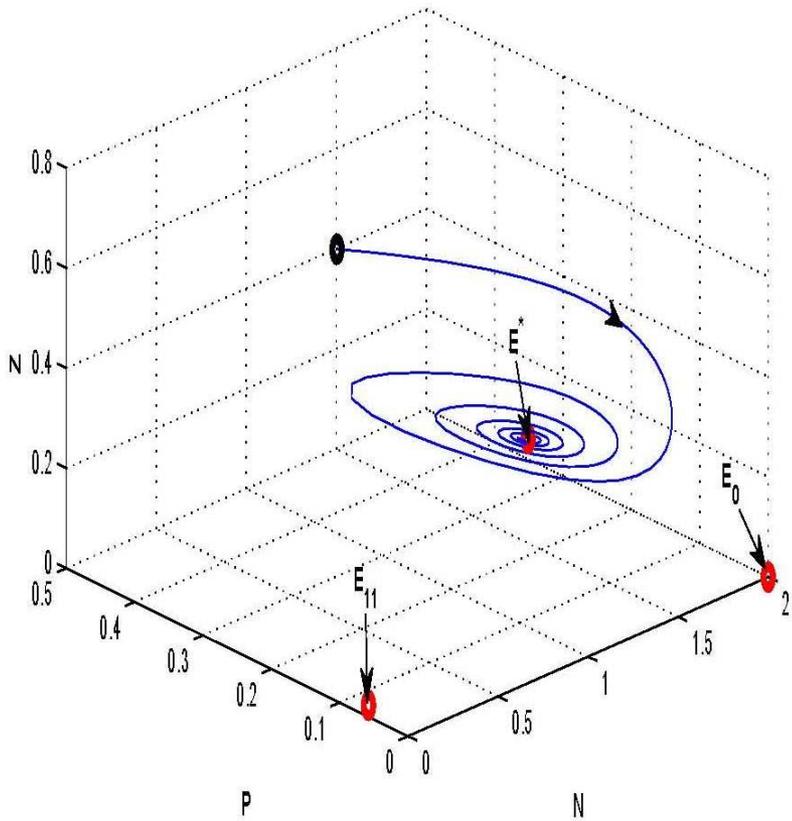


Fig-9

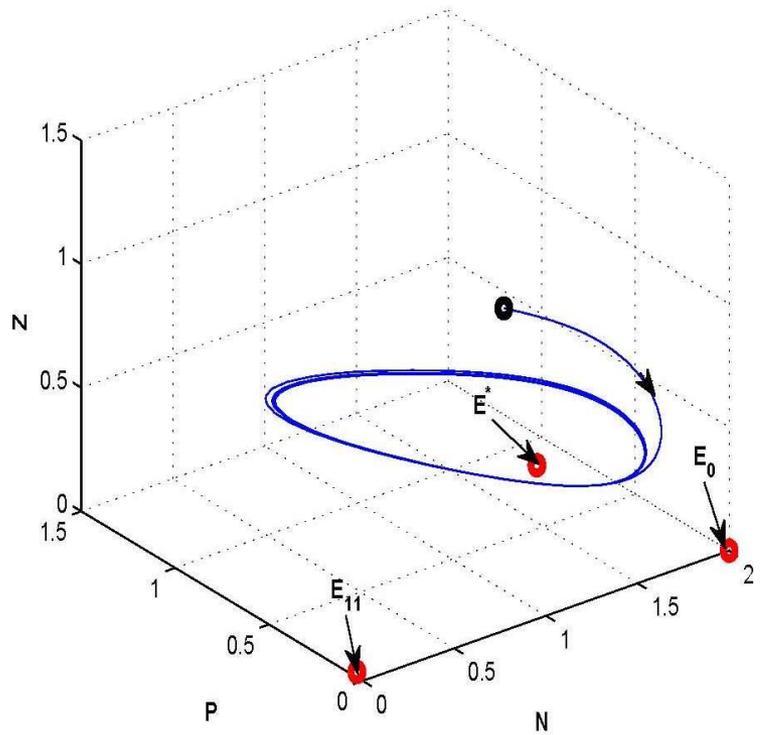


Fig-10

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.

Fig 11

The bifurcation diagram for θ with all parametric values as given in Table 2.

Fig 12

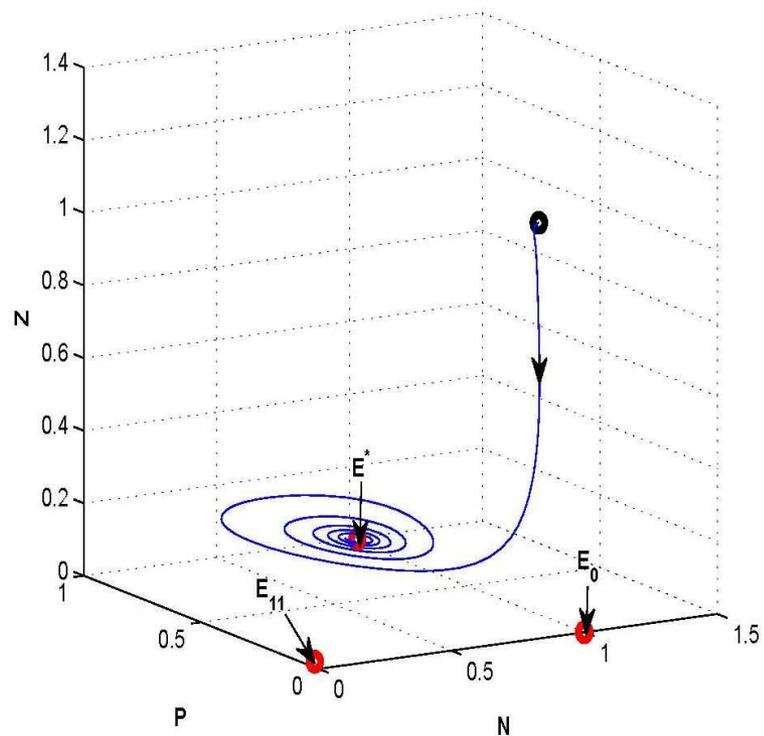


Fig-11

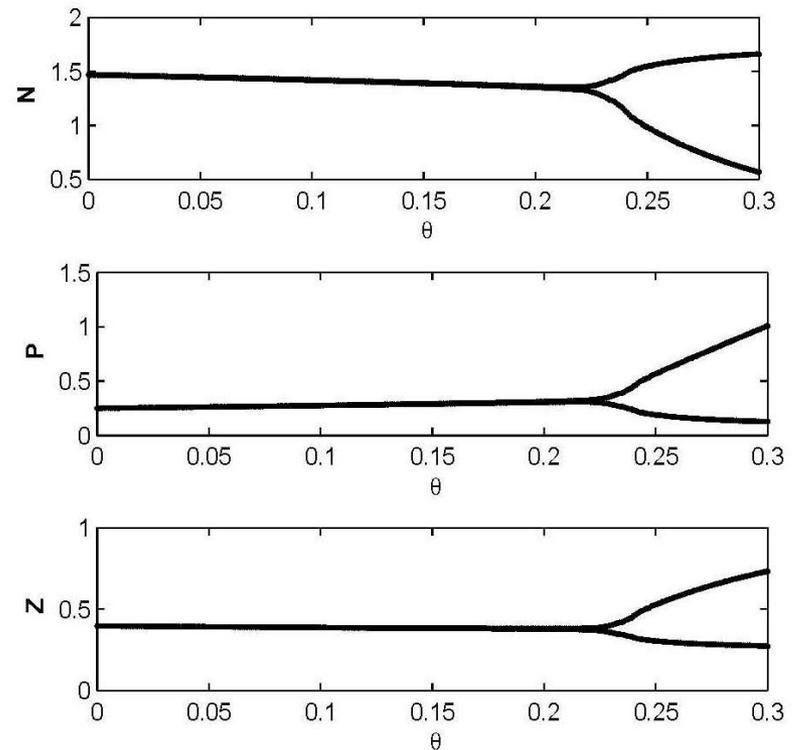


Fig-12

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

Fig-13

The bifurcation diagram for h_2 with all parametric values as given in Table 2.

Fig-14

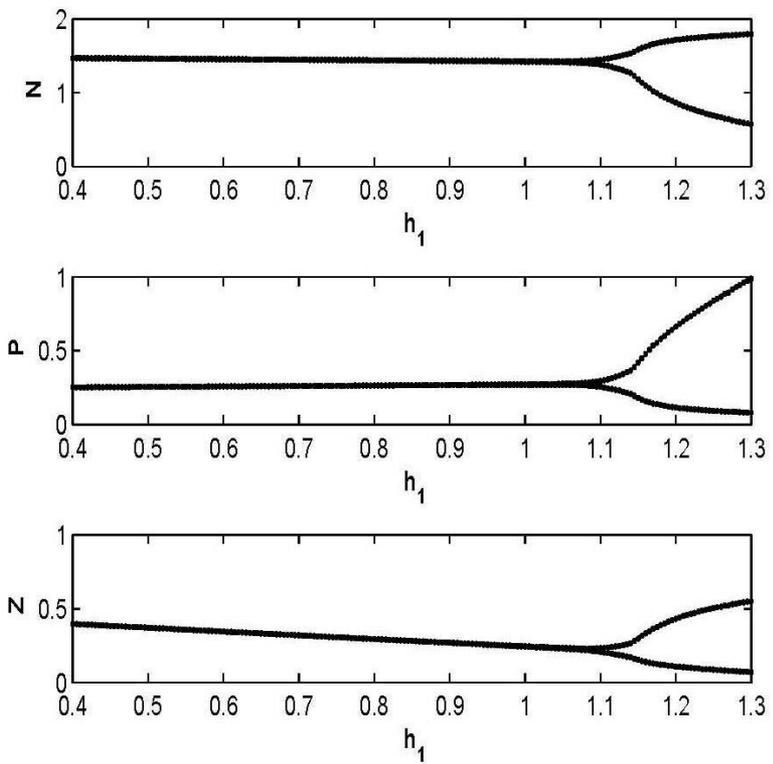


Fig-13

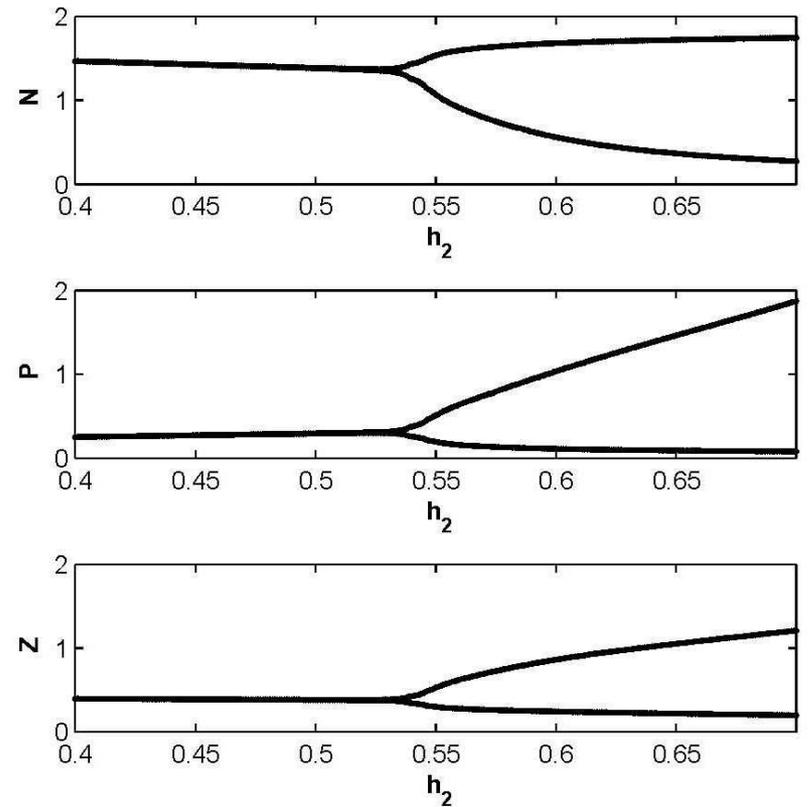


Fig-14

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

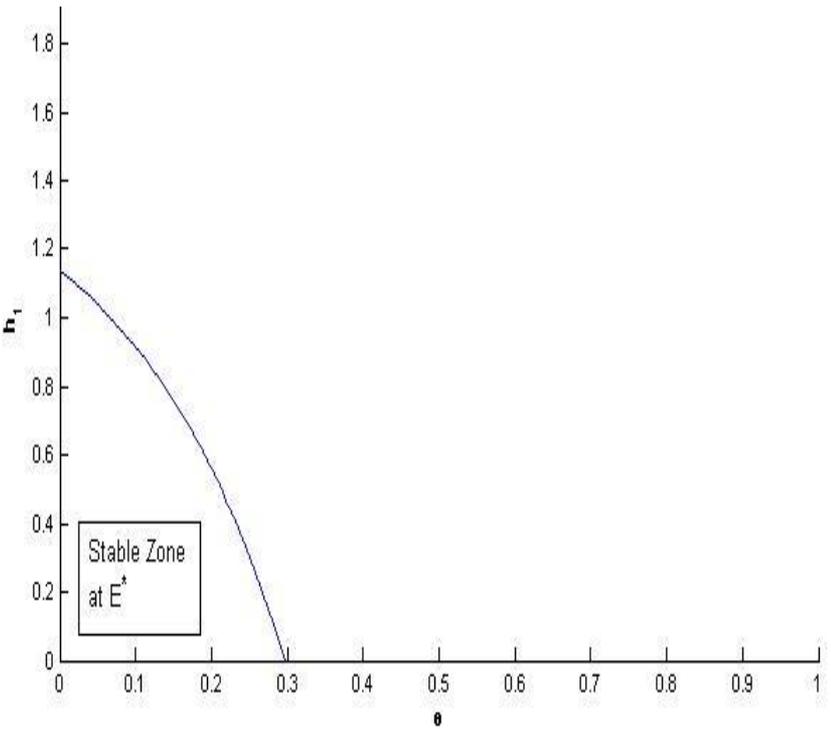


Fig-15

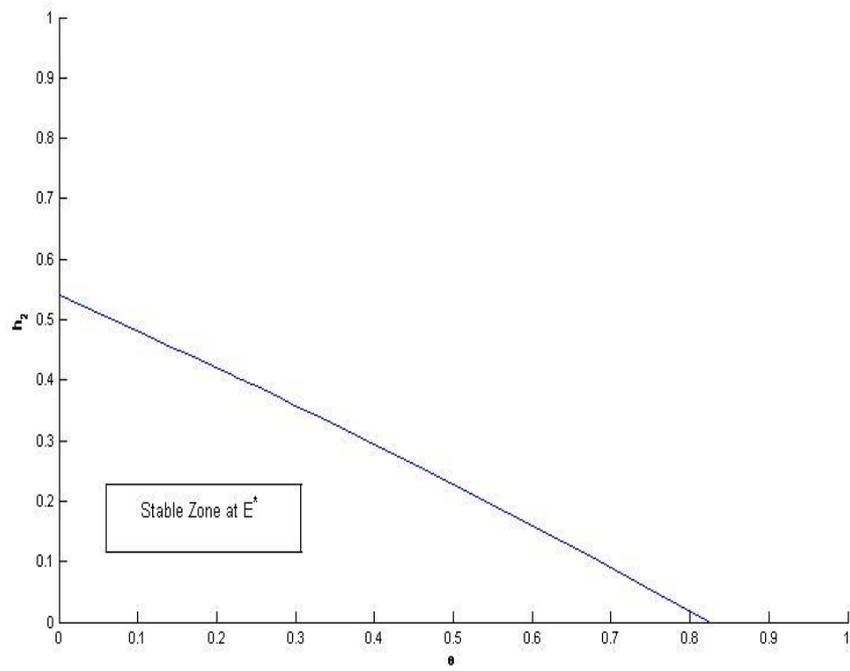


Fig-16

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. Fig-17

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. Fig-18

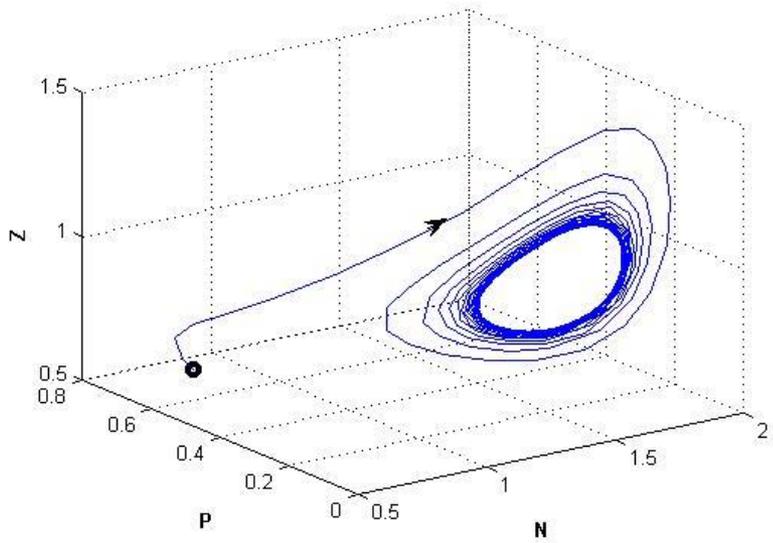


Fig-17

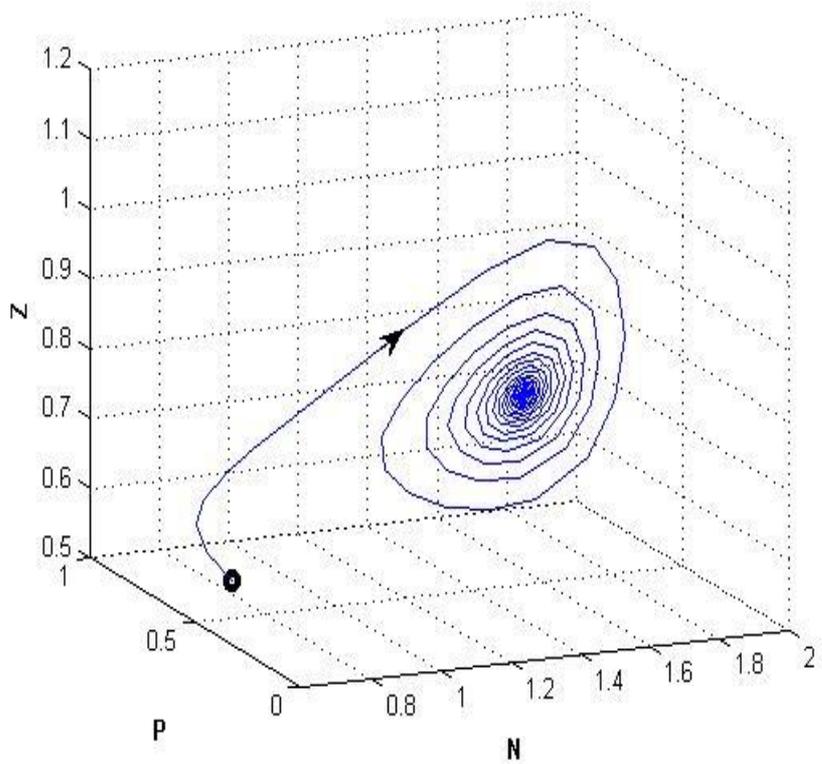


Fig-18

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.

Fig-19

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.

Fig-20

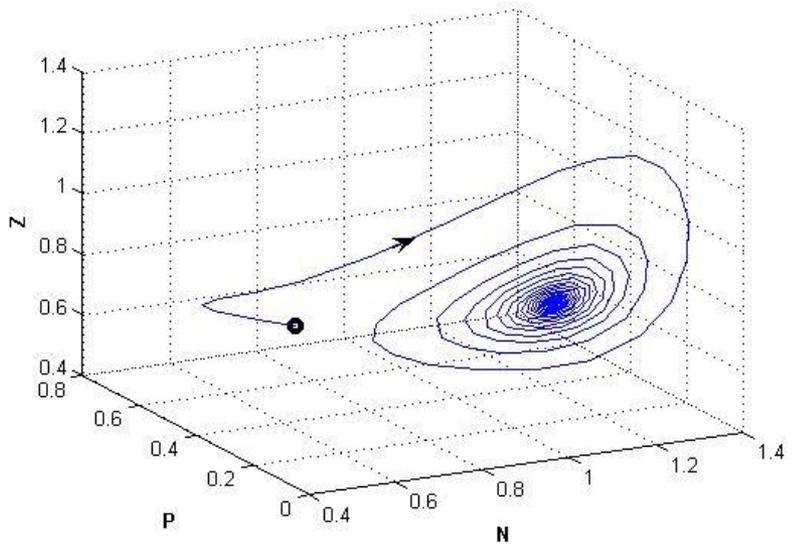


Fig-19

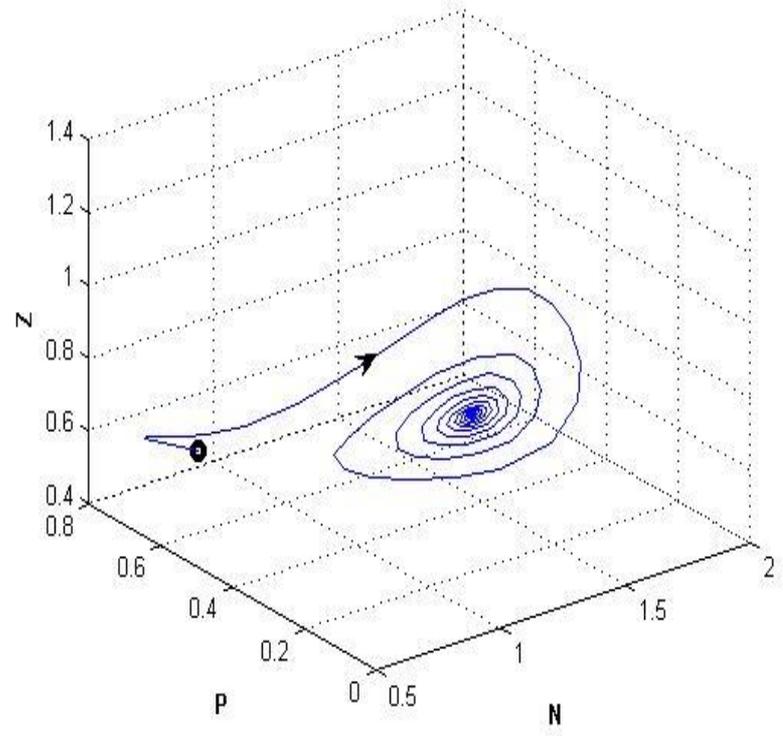


Fig-20

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.

Fig-21

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.

Fig-22

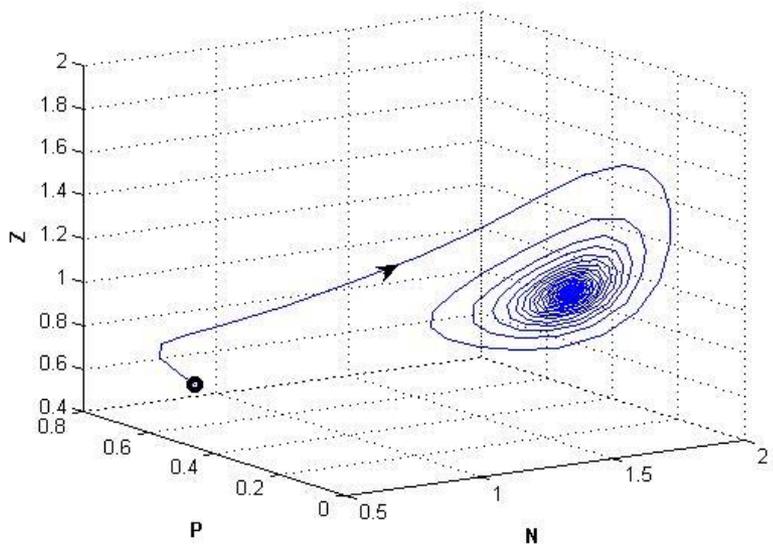


Fig-21

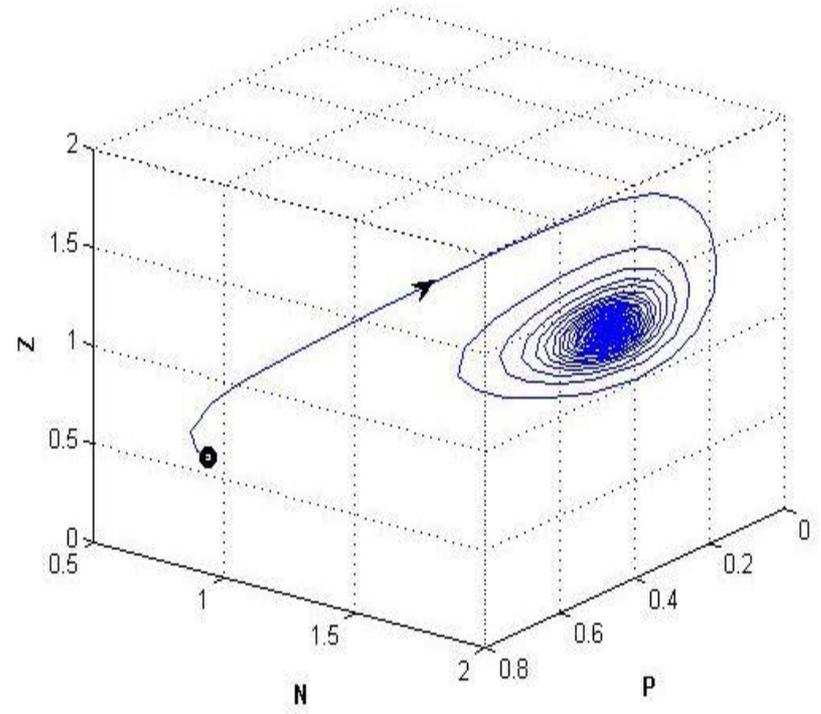


Fig-22

Discussion

- **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.**

Discussion contd.

- **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 .**

Discussion contd.

- ❖ **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

- [1] S. Pal, S. Chatterjee, J. Chattopadhyay, Role of toxin and nutrient for the occurrence and termination of plankton bloom. Results drawn from field observations and a mathematical model, *BioSystems* 90 (2007) 87-100.
- [2] A.Chatterjee, S. Pal, S. Chatterjee, Bottom up and top down effect on toxin producing phytoplankton and its consequence on the formation of plankton bloom, *Applied Mathematics and Comp.* 218 (2011) 3387-3398.
- [3] N. Bairagi, S. Pal, S. Chatterjee, J. Chattopadhyay, Nutrient, non-toxic phytoplankton, toxic phytoplankton and zooplankton interaction in the open marine system, in: R.J. Hosking, E. Venturino (Eds.), *Aspects of Mathematical Modelling, Mathematics and Biosciences in Interaction*, Birkhauser Verlag, Basel, Switzerland, 2008, pp. 4163.
- [4] S. Khare, O.P. Misra, J. Dhar, Role of toxin producing phytoplankton on a plankton ecosystem, *Nonlinear Anal. Hybrid Syst.* 4 (2010) 496-502.
- [5] M. Banerjee, E. Venturino, A phytoplankton-toxic phytoplankton-zooplankton model, *Ecological Comp.* 8(3) (2011) 239-248.
- [6] S. R.-J. Jang, J. Baglama, J. Rick, Nutrient-phytoplankton-zooplankton models with a toxin, *Math. Comput. Model.* 43 (2006) 105-118.

References

- [7] J. Chattopadhyay, R.R. Sarkar, S. Pal, Mathematical modelling of harmful algal blooms supported by experimental findings, *Ecol. Comput.* 1 (2004) 225-235.
- [8] S. Khare, O. P. Misra, C. Singh, J. Dhar, Role of Delay on Planktonic Ecosystem in the Presence of a Toxic Producing Phytoplankton, *International Journal of Differential Equations* Volume 2011, Article ID 603183, 16 pages doi:10.1155/2011/603183 .
- [9] A.Y. Morozov, Emergence of Holling type III zooplankton functional response: bringing together field evidence and mathematical modelling, *J. Theor. Biol.* 265 (2010) 4554.
- [10] C.W.Clark, *The Optimal Management of Renewable Resources*, *Mathematical Bioeconomics*, 2nd edition, Wiley Interscience, (1990).
- [11] W. A. Wurts, Sustainable Aquaculture in the Twenty-First Century, *Reviews in Fisheries Science* 8(2) (2000)141-150.
- [12] M.Omori, Zooplankton Fisheries of the World: A Review, *Marine Biology* 48 (1978) 199-205.
- [13] L.Yunfei, P.Yongzhena, G.Shujing, L.Changguo, Harvesting of a phytoplankton-zooplankton model, *Nonlinear Analysis: Real World Applications* 11(2010) 3608-3619.

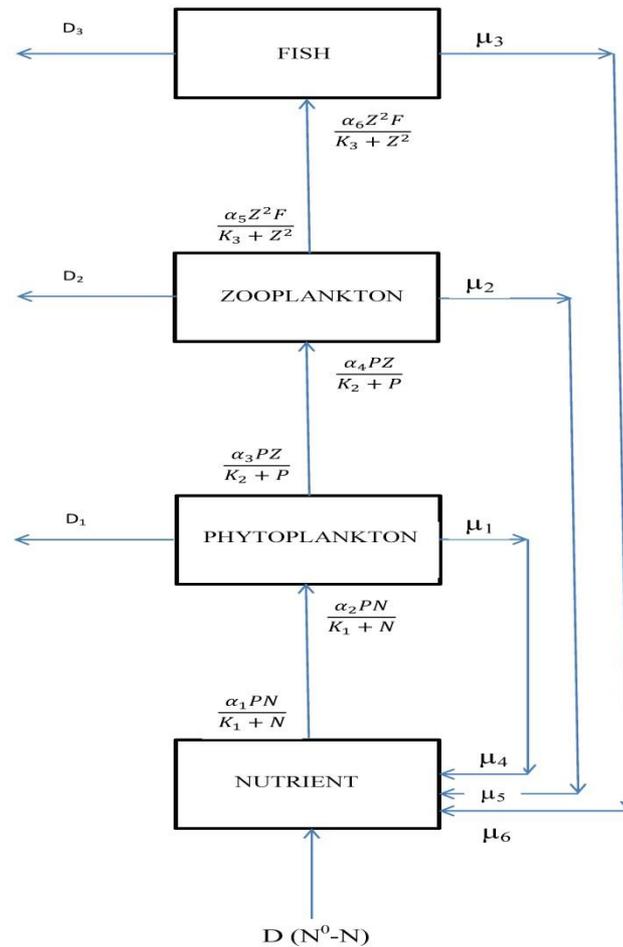
References

- [14] P.Yongzhen, L.Yunfei, L.Changguo, Evolutionary consequences of harvesting for a two-zooplankton one-phytoplankton system, *Appl. Math. Modell.* (2011), doi:10.1016/j.apm.2011.09.015.
- [15] C. A. Price, L.R. Mendiola-Morgenthaler, M. Goldstein, E. N. Breden and R. R. L.Guillard, Harvest of Planktonic Marine Algae by Centrifugation into Gradients of Silica in the CF-6 Continuous -Flow Zonal Rotor, *Biol.Bull.*,147 (1974)136-145.
- [16] C.T.Kuo, Harvesting natural algal blooms for concurrent biofuel production and hypoxia mitigation, *Agricultural & Biological Engineering* (2011).
- [17] K. G. Gravesa & J. C. Morrowa , Method for Harvesting Large Quantities of Zooplankton from Hatchery Ponds, *The Progressive Fish-Culturist* 50(3) (1988) 184-186.
- [18] A.G.Fredrickson, G.Stephanopoulos, Microbial competition, *Science.* 213 (4511) (1981), 972-979.
- [19] H.L.Smith, Competitive coexistence in an oscillating chemostat, *SIAM J. Appl. Math.* 40 (1981), 498-522.

References

- [20] B.Mukhopadhyay, R.Bhattacharyya, On a three -tier ecological food chain model with deterministic and random harvesting: A mathematical study, *Non-linear Analysis: Modelling and Control*, 16(1) (2011), 77-88.
- [21] B.D.Hassard, N.D.Kazarinoff, Y.H.Wan, *Theory and Application of Hopf Bifurcation* Cambridge University Press, Cambridge, (1981).
- [22] A.Sen, D.Mukherjee, B.C.Giri, P.Das, Stability of Limit Cycle in a Prey Predator System with Pollutant, *Applied Mathematical Science*, 5(21) (2011), 1025-1036.

Schematic Diagram



Mathematical Model

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 - N) - \frac{\alpha_1 PN}{K_1 + N} + \mu_4 P + \mu_5 Z + \mu_6 F \equiv G_1(N, P, Z, F) \\ \frac{dP}{dt} &= \frac{\alpha_2 PN}{K_1 + N} - \frac{\alpha_3 PZ}{K_2 + P} - (\mu_1 + D_1)P \equiv G_2(N, P, Z, F) \\ \frac{dZ}{dt} &= \frac{\alpha_4 PZ}{K_2 + P} - \frac{\alpha_5 Z^2 F}{K_3 + Z^2} - (\mu_2 + D_2)Z \equiv G_3(N, P, Z, F) \\ \frac{dF}{dt} &= \frac{\alpha_6 Z^2 F}{K_3 + Z^2} - (\mu_3 + D_3)F \equiv G_4(N, P, Z, F).\end{aligned}\tag{1}$$

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

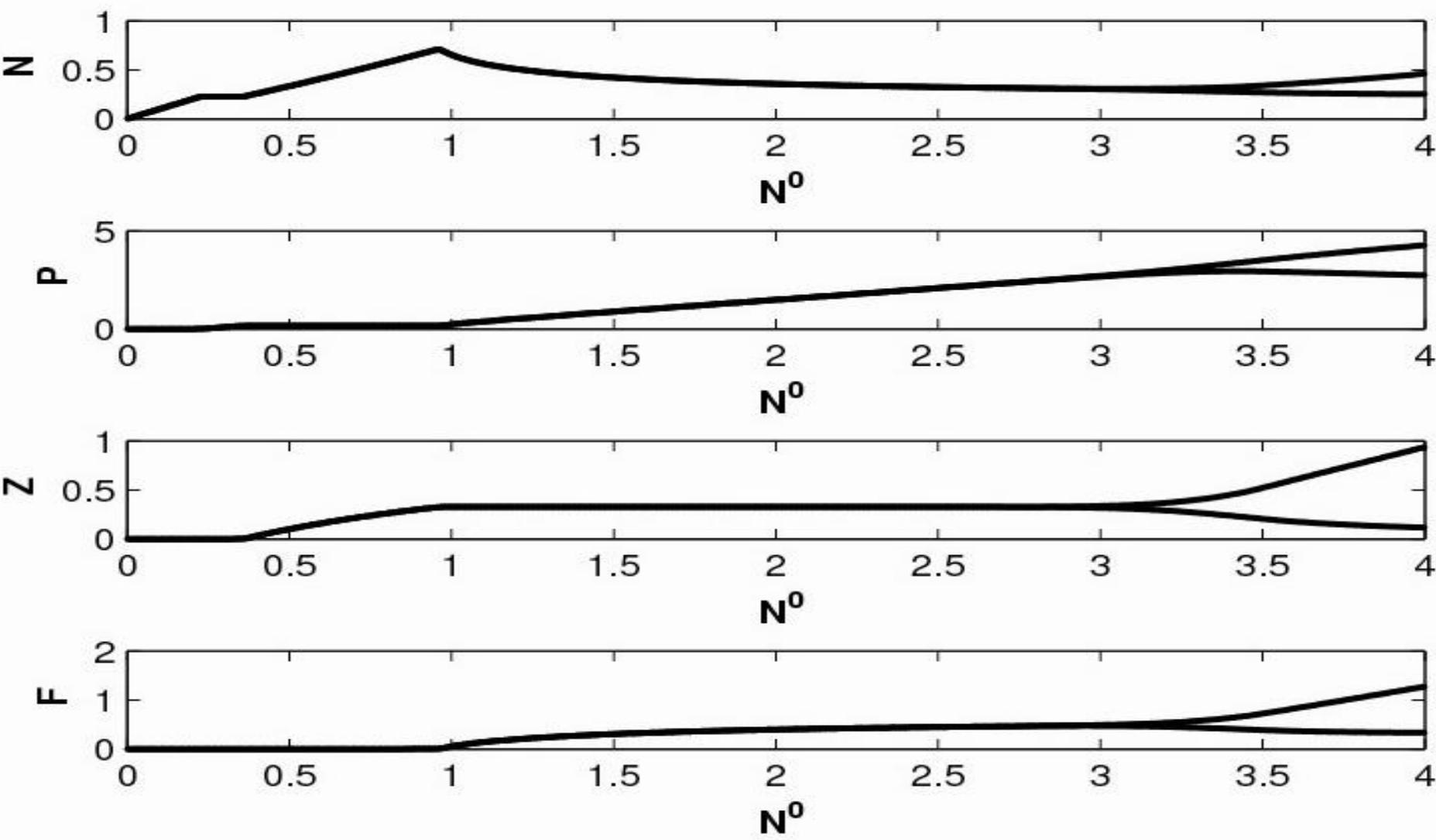
$$N(0) > 0, P(0) > 0, Z(0) > 0, F(0) > 0.$$

The table representing thresholds and stability of steady states

Thresholds(R_0, R_1, R_2)	$(N^0, 0, 0, 0)$	$(N_1, P_1, 0, 0)$	$(N_2, P_2, Z_2, 0)$	(N^*, P^*, Z^*, F^*)
$R_0 < 1$	Asymptotically stable	Not feasible	Not feasible	Not feasible
$R_0 > 1, R_1 < 1$	Unstable	Asymptotically stable	Not feasible	Not feasible
$R_1 > 1, R_2 < 1,$	Unstable	Not feasible	Asymptotically stable	Not feasible
$R_2 > 1$	Unstable	Not feasible	Not feasible	Asymptotically stable

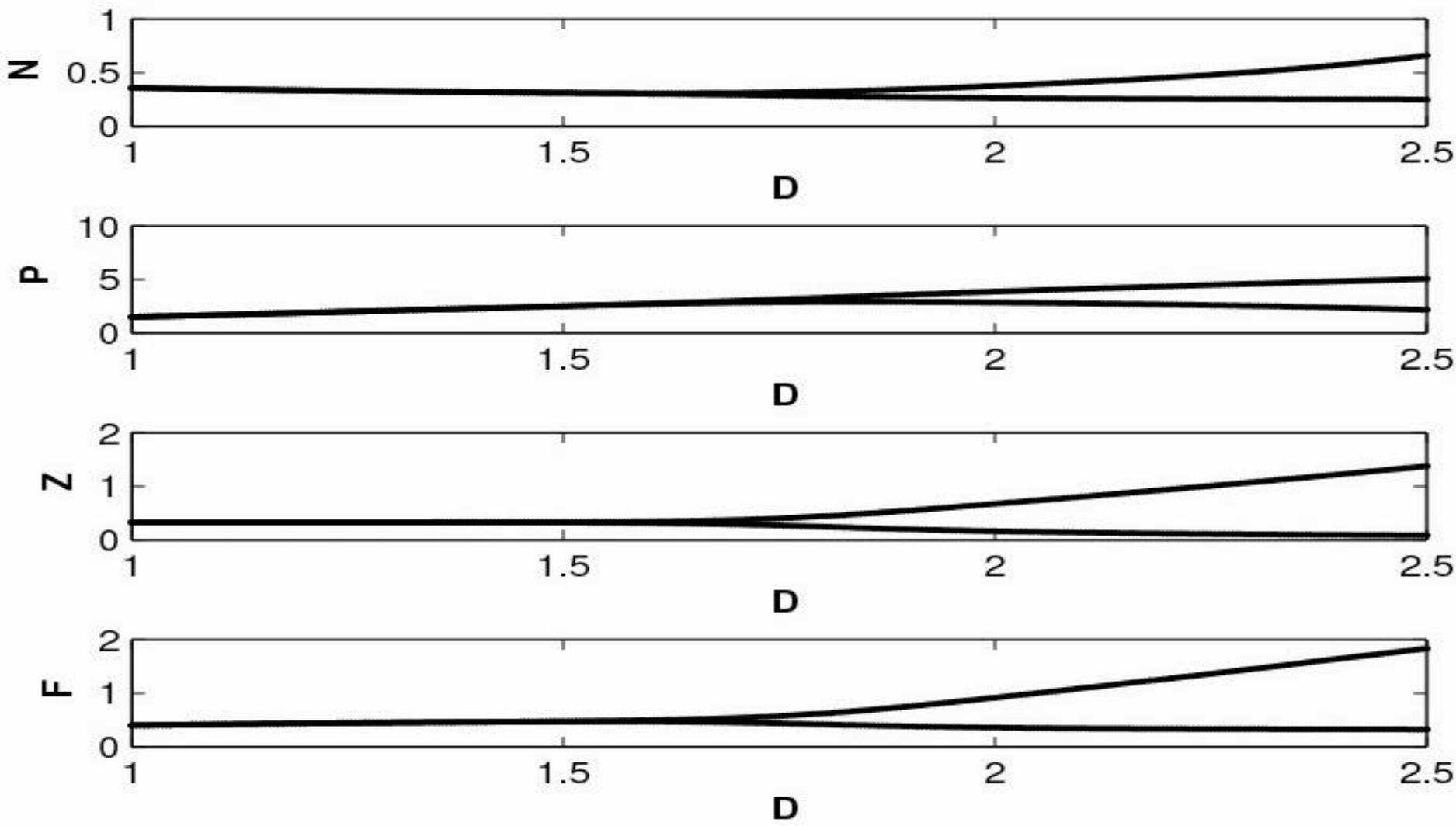
The bifurcation diagram for N^0 with all parametric values as in Table2.

Fig-11



The bifurcation diagram for D with all parametric values as in Table2.

Fig-12



The bifurcation diagram for μ_3 with all parametric values as in Table 2.

Fig-13

