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Non-toxic phytoplankton, toxin producing phytoplankton and zooplankton interaction in an open marine system

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Non-toxic phytoplankton, toxin producing phytoplankton and zooplankton interaction in an open marine system-a mathematical study

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Planktonic Bloom

- The dynamics of a rapid (or massive) increase or decrease 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.

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.

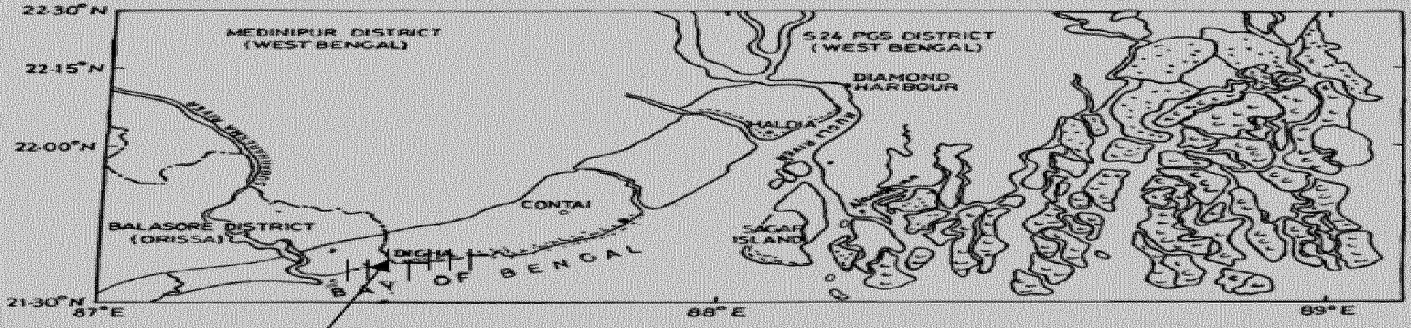
- Recent works suggest that viruses are important regulatory factors in marine ecosystem. Lytic viruses directly control population dynamics by viral lysis (Suttle et al., 1995, *Nature; Brussard et al., 1996, Ecology*). Few mathematical models also suggest that viral infection may be used as a controlling 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*).

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 → ///////

Fig. 1. Representation of field data against the collection dates. The abundance of Paracalanus sp. is low when the chaetocerous sp. Is at high abundance

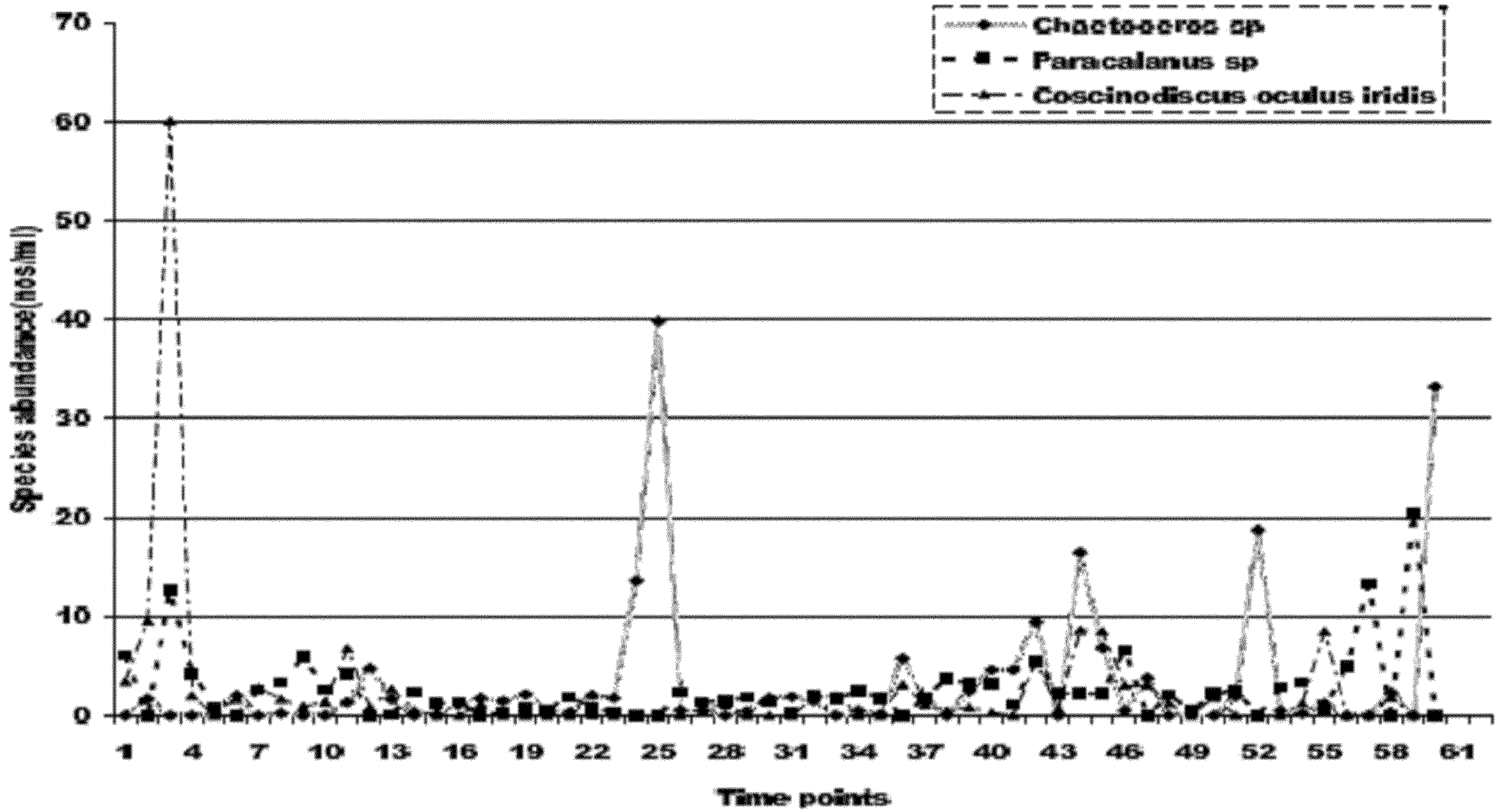


Fig. 2. Average biomass distribution of Chaetocerous sp. (TPP) and Paracalanus sp. (zooplankton) when only TPP present

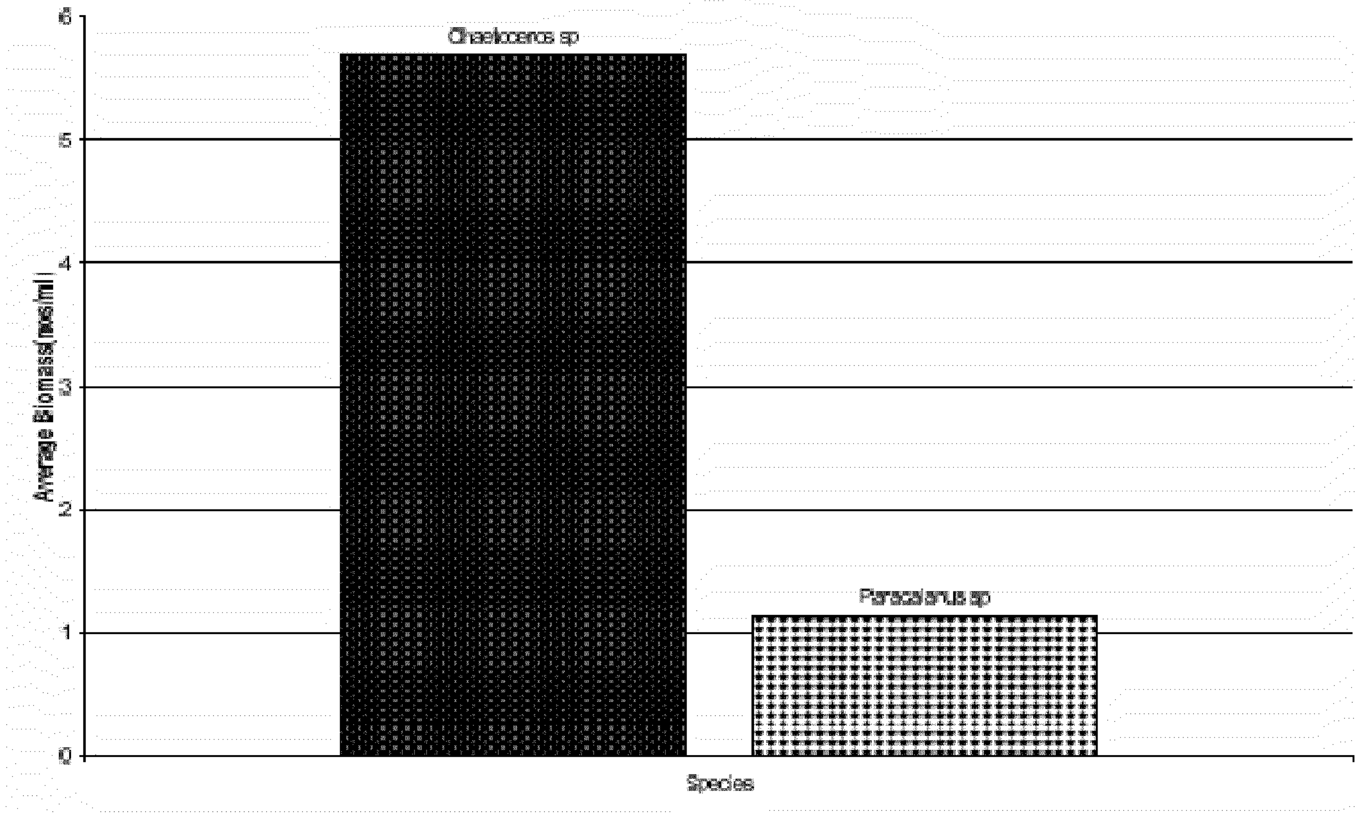


Fig.3 Average biomass distribution of NTP and zooplankton for experimental data when only NTP present

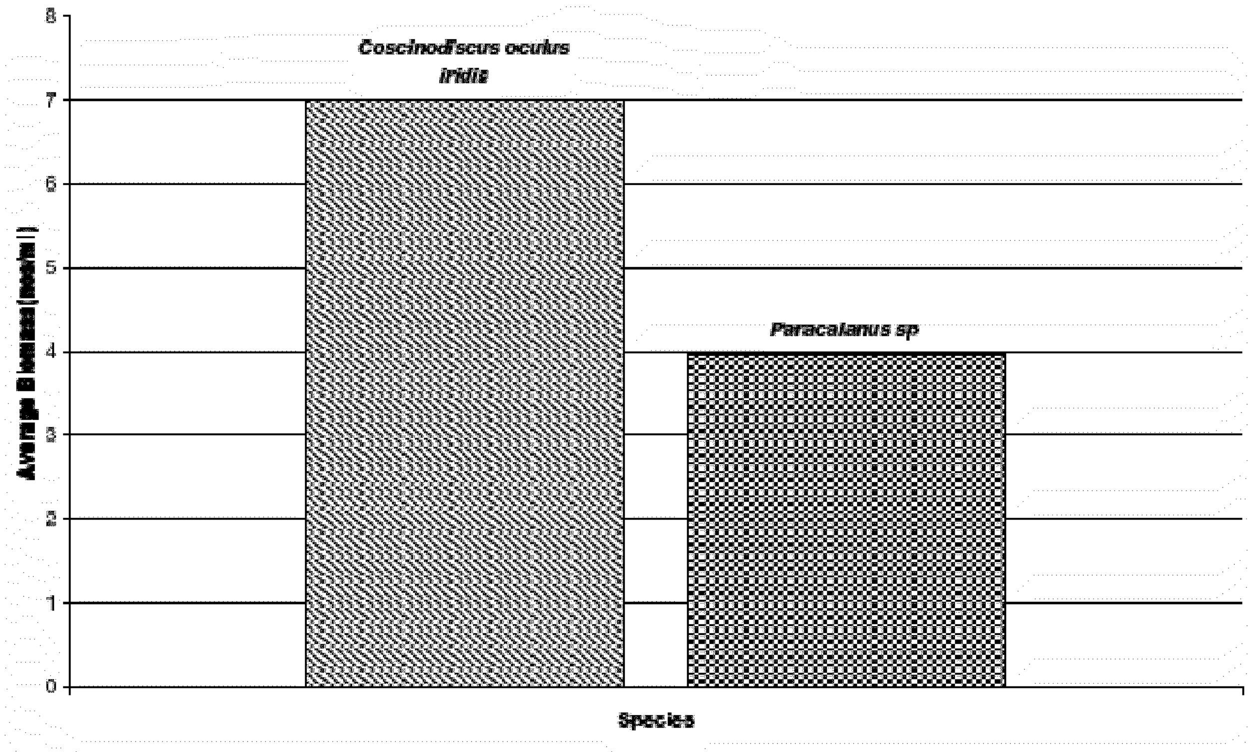
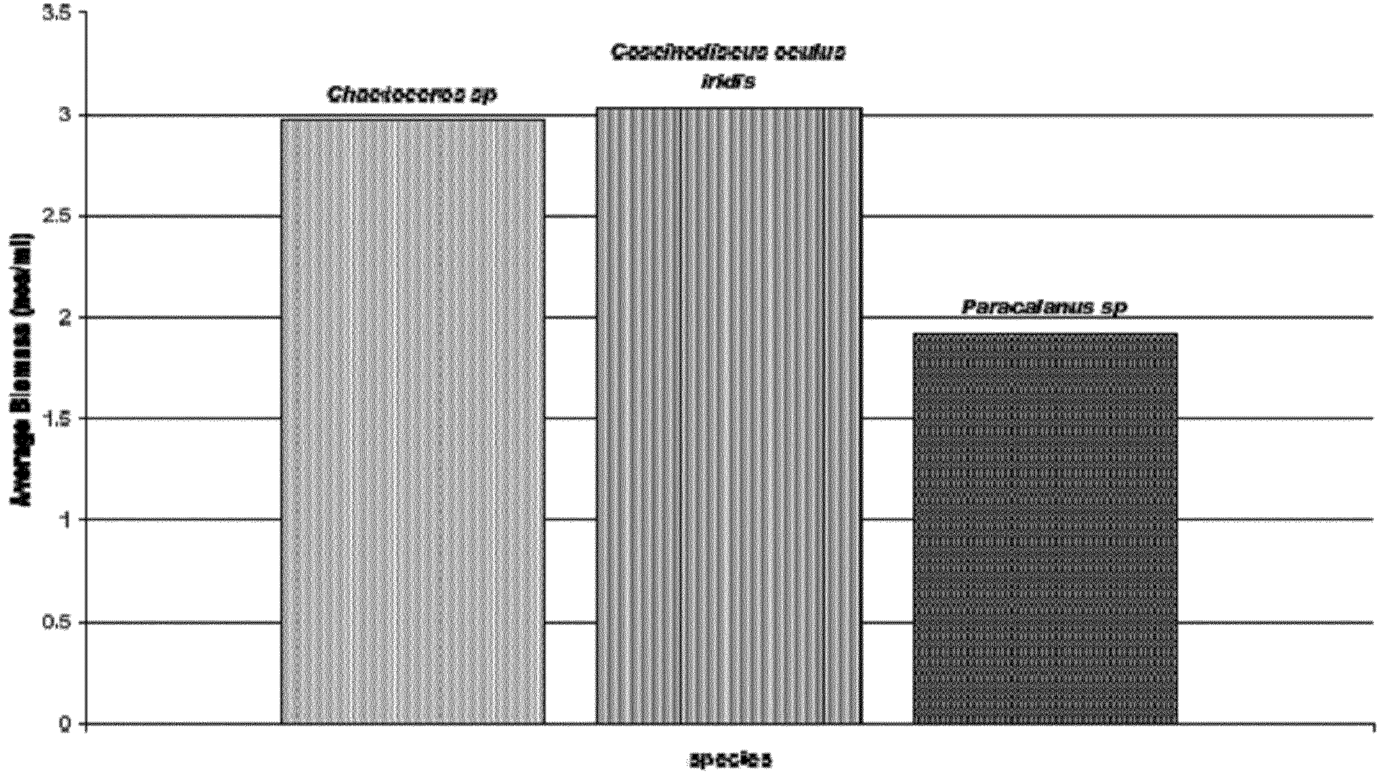
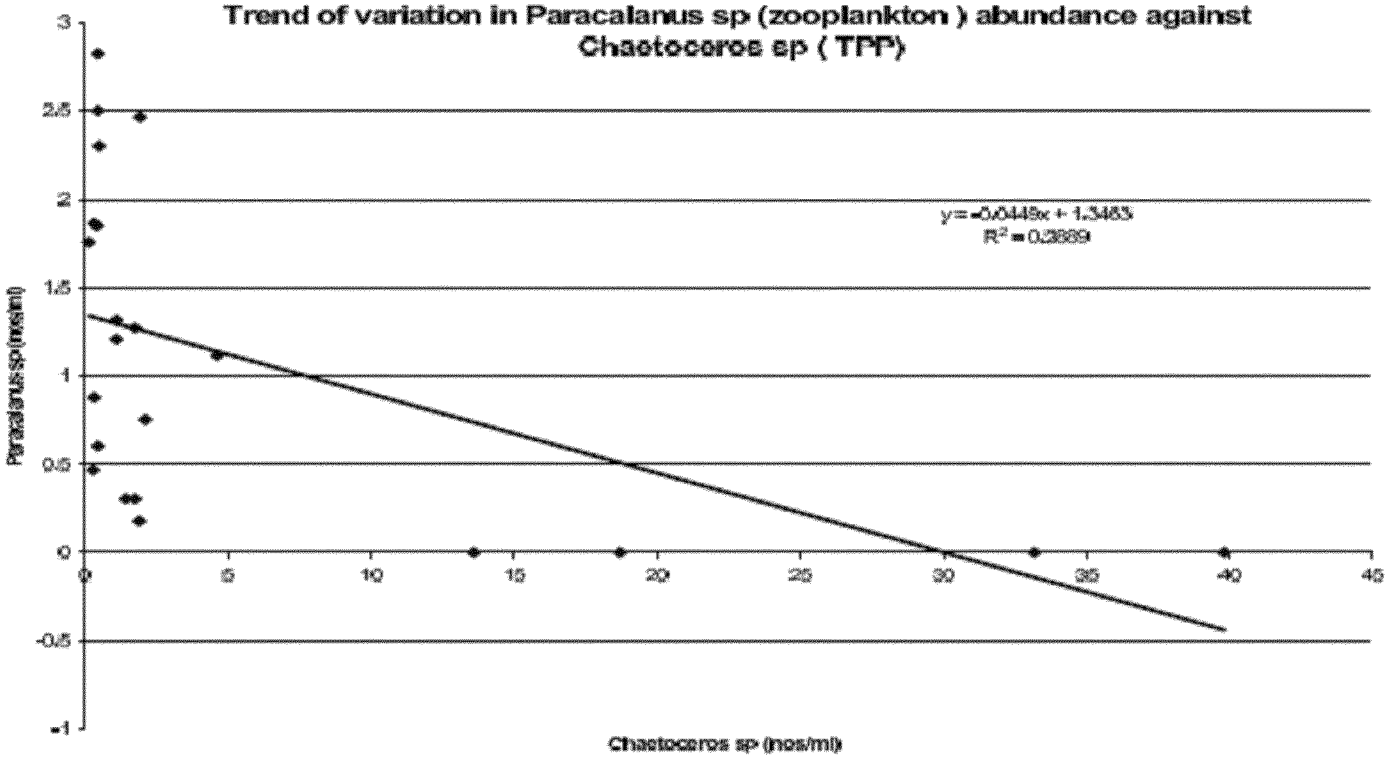


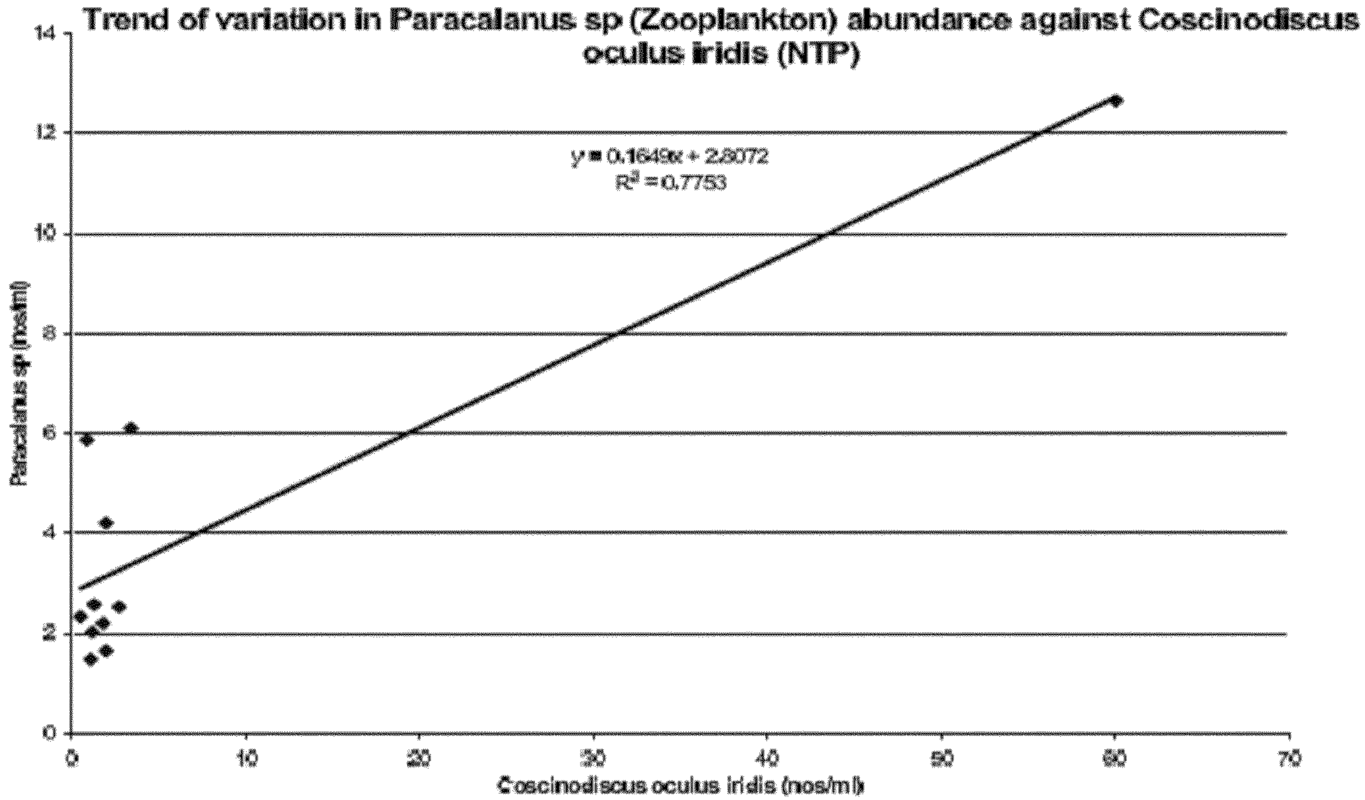
Fig.3 Average biomass distribution of TPP, NTP and zooplankton for experimental data when both NTP and TPP present in the system



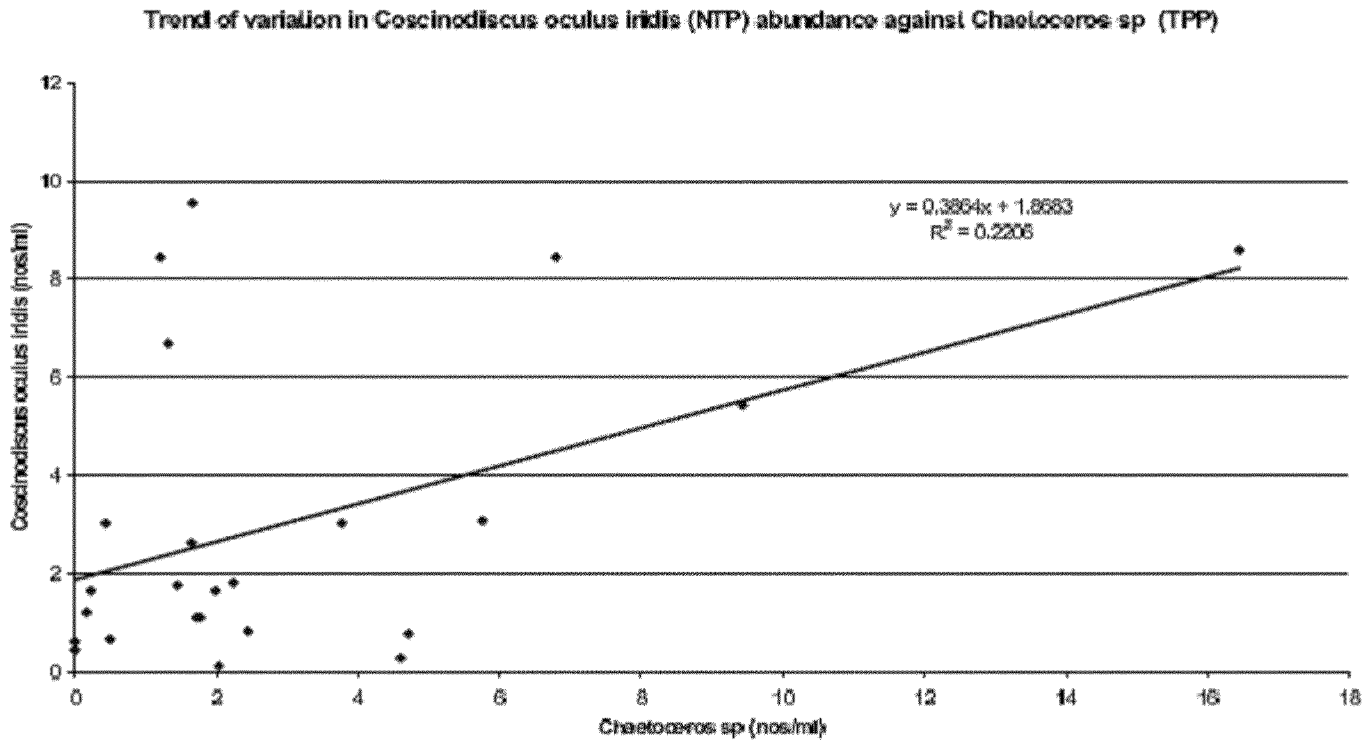
Linear regression plot representing the variation in abundance of zooplankton with respect to variation of TPP and negative slope indicates that TPP has an inhibitory effect on zooplankton and high abundance of TPP is not favorable for the persistence of zooplankton



Linear regression plot representing the variation in abundance of zooplankton with respect to variation of NTP and positive slope indicates that NTP has a positive effect on zooplankton and high abundance of NTP is favorable for the persistence of zooplankton



Linear regression plot representing the variation in abundance of NTP with respect to variation of TPP and positive slope indicates that presence of TPP reduces the competitive disadvantage



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

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

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

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

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. $\alpha_1{}'$ and $\alpha_1{}'$ 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.

The Mathematical Model contd.

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

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

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

The Mathematical Model contd.

where

$$\mu_1 = \frac{\alpha K_2}{K_1},\ \mu_2 = \frac{\beta K_1}{K_2},\ \gamma_6 = \frac{\mu}{r},\ \gamma_1 = \beta_1 K_1,\ \gamma_2 = \beta_2 K_2,\ \gamma_3 = \frac{s}{r},\ \gamma_4 = \frac{\alpha_2}{\alpha_1},$$
$$\alpha_1'' = \frac{\alpha_1' K_1}{r},\ \alpha_2'' = \frac{\alpha_2' K_2}{r} \tag{3.4}$$

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

$$x_1(0) \geq 0,\ x_2(0) \geq 0,\ x_3(0) \geq 0. \tag{3.5}$$

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 $E_4(\frac{\gamma_8}{\alpha_1'' - \gamma_1\gamma_8}, 0, \frac{\alpha_1''(\alpha_1'' - \gamma_1\gamma_8 - \gamma_8)}{(\alpha_1'' - \gamma_1\gamma_8)^2})$. The equilibrium E_4 exists if $\alpha_1'' > \gamma_8(1 + \gamma_1)$.

Positive Interior Equilibrium

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

$$x_1^* = \frac{\gamma_6(\gamma_3-\mu_1\gamma_4)+(\gamma_3-\gamma_4)(\alpha_2'' +\gamma_2\gamma_6)}{\Delta},$$

$$x_2^* = \frac{(\gamma_3-\gamma_4)(\alpha_1'' -\gamma_1\gamma_6)-\gamma_6(\gamma_3\mu_2-\gamma_4)}{\Delta},$$

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

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

The positive interior equilibrium E^* exists if $x_1^*,\ x_2^*, x_3^* > 0$ and this leads to the following condition: $\alpha_1'' - \gamma_1\gamma_6 > 0$, $\frac{\gamma_3}{\gamma_4} > \max\{\mu_1, \frac{1}{\mu_2}, 1\}$ and $R_1 = \frac{(\gamma_3-\gamma_4)(\alpha_1'' -\gamma_1\gamma_6)}{\gamma_6(\gamma_3\mu_2-\gamma_4)} > 1$ where $\mu_2 > 1$, $\mu_1 < 1$ and $\mu_1\mu_2 > 1$

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 E0=(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 E1=(1,0,0) which is saddle.
- Lemma 3. There exists a non-toxic phytoplankton and zooplankton free steady state E2=(0,1,0) which is saddle.
- Lemma 4. There exists a zooplankton free steady state E3=(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.

$$dx_1 = F_1(x_1, x_2, x_3)dt + \sigma_1(x_1 - x_1^*)d\xi_t^1$$
$$dx_2 = F_2(x_1, x_2, x_3)dt + \sigma_2(x_2 - x_2^*)d\xi_t^2 \qquad (3.1)$$
$$dx_3 = F_3(x_1, x_2, x_3)dt + \sigma_3(x_3 - x_3^*)d\xi_t^3$$

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

$$dX_t = f(t, X_t)dt + g(t, X_t)d\xi_t, \quad X_{t0} = X_0 \qquad (3.2)$$

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 $\mathrm{N}(0, \Delta t)$.

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

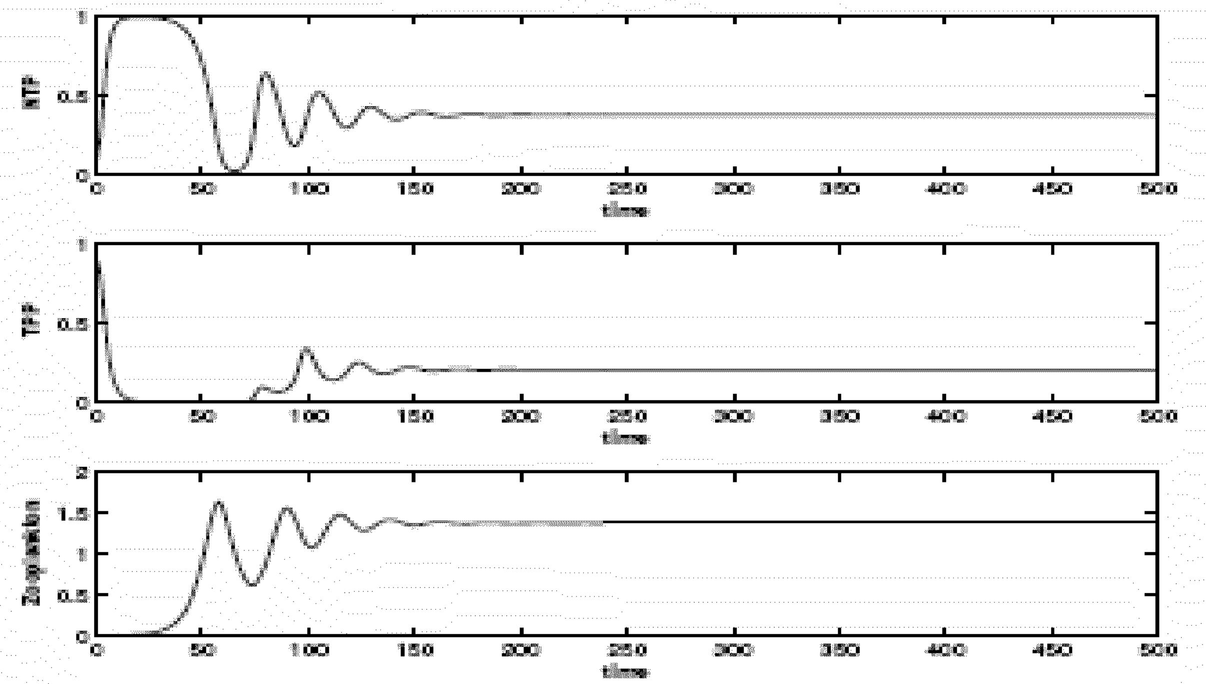


Fig.9-Figure depicting the phase portrait corresponding to Fig.8 and showing that E^* is stable while E_0, E_1, E_2, E_3 are saddle points and E_4 does not exist

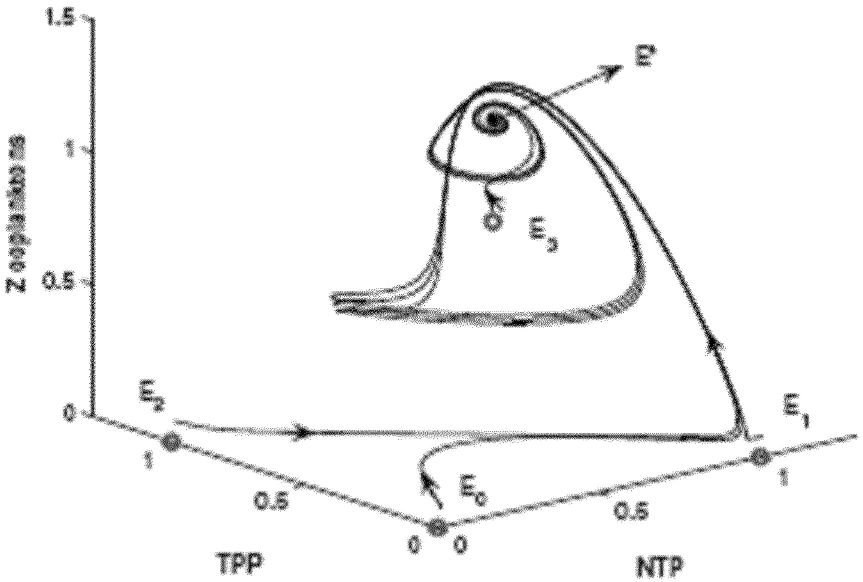


Fig. 10- Figure depicting extinction of the zooplankton population when the competition between NTP and TPP is very low. (We have used different time scale to show the clear dynamics)

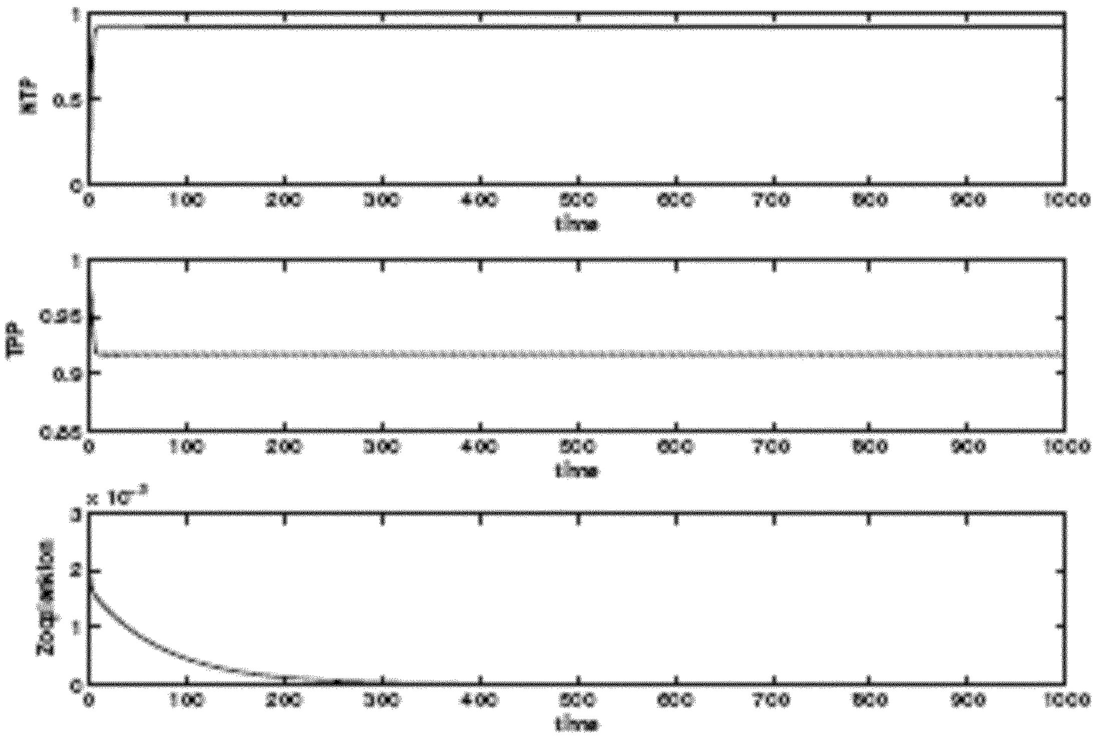


Fig.11-Figure depicting the phase portrait corresponding to Fig.10 and showing that E_3 is stable while E_0, E_1, E_2, are saddle points, E_4 is a spiral source and E^* does not exist

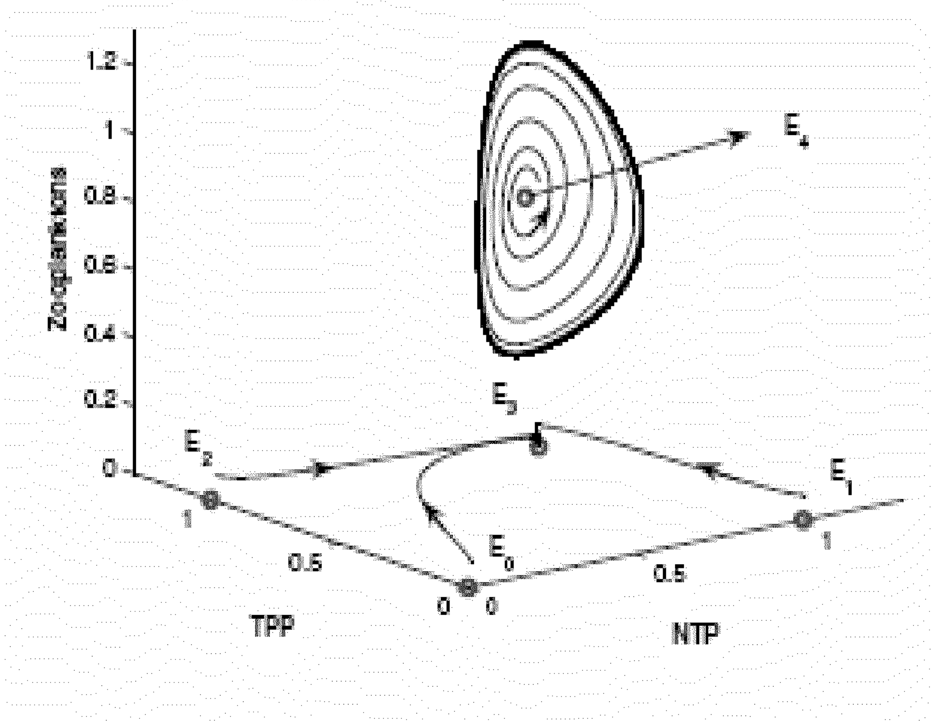


Fig. 12- Figure depicting coexistence of all population through oscillation when we increase the competition coefficient μ_2 from 1.18 to 1.38 (remaining parameter values same as in figure 10)

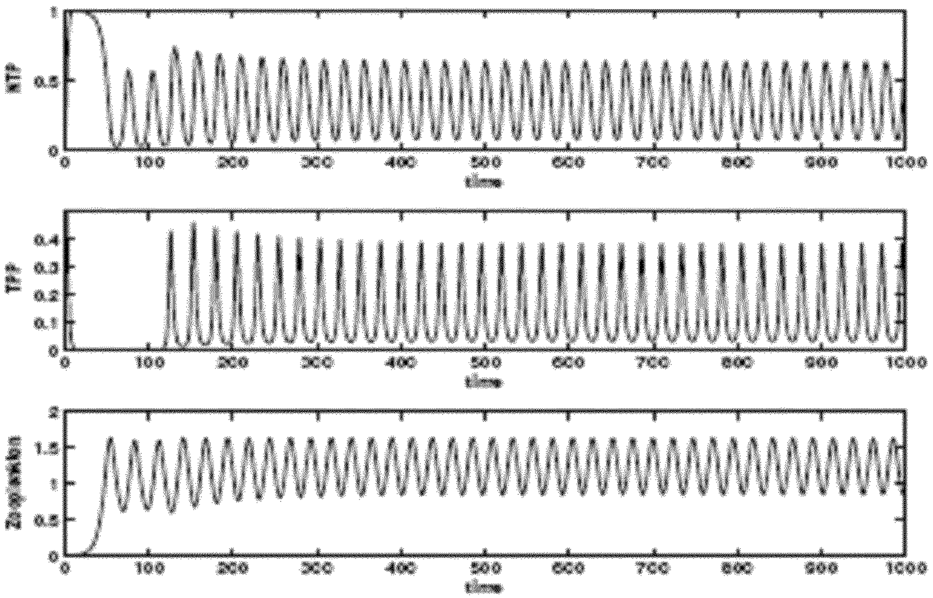


Fig.13-Figure depicting the phase portrait corresponding to Fig.12 and showing that E^* is stable limit cycle while E_0, E_1, E_2, E_4 are saddle points and E_3 does not exist

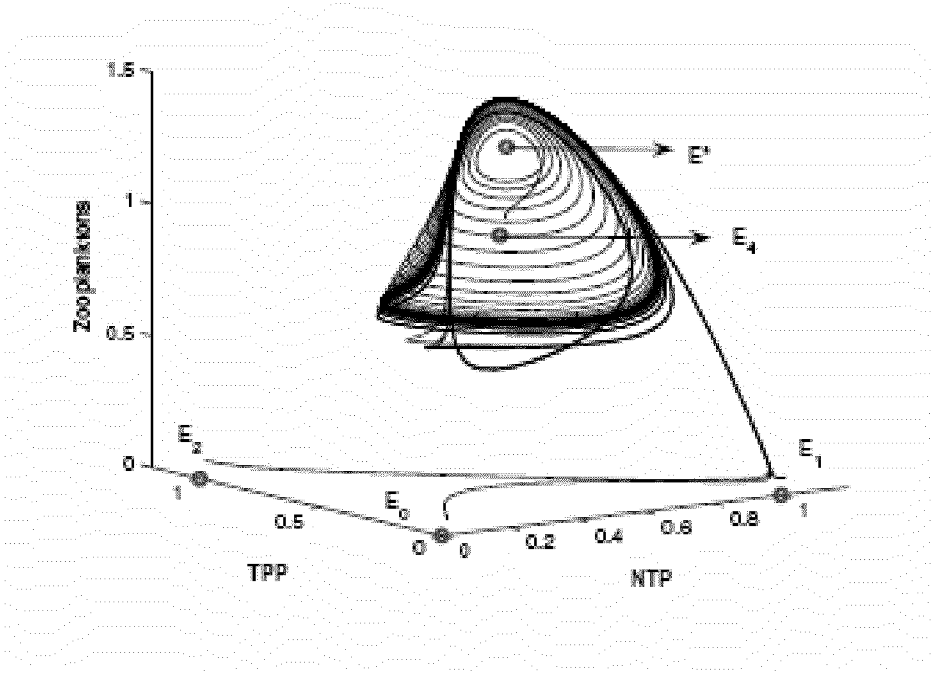


Fig.14. Strange attractor at μ_1=1, μ_2=1.56 (increased from 1.38) with other parameters given in Table 1

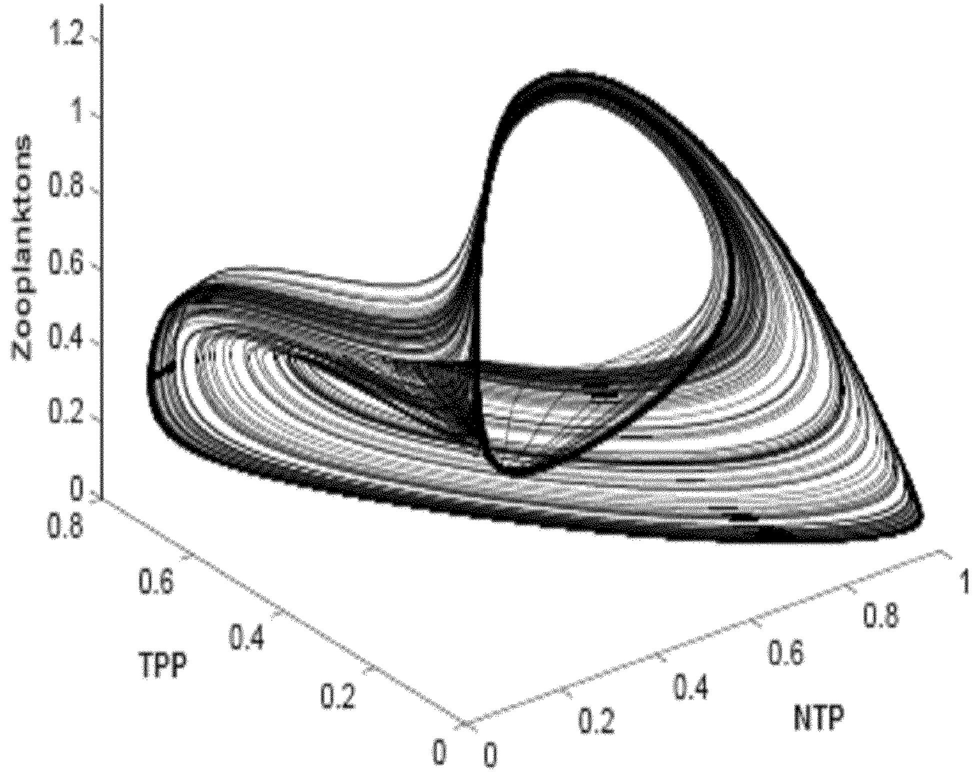


Fig.15. The spectrum of Lyapunov exponent for the system around the strange attractor shown in Figure 14. The largest Lyapunov exponent is positive and this confirm the strange attractor is chaotic in nature, depicting chaotic bloom. (This observation is similar to the observation of Huppert et al. (J.Theo. Biol.) in a different context).

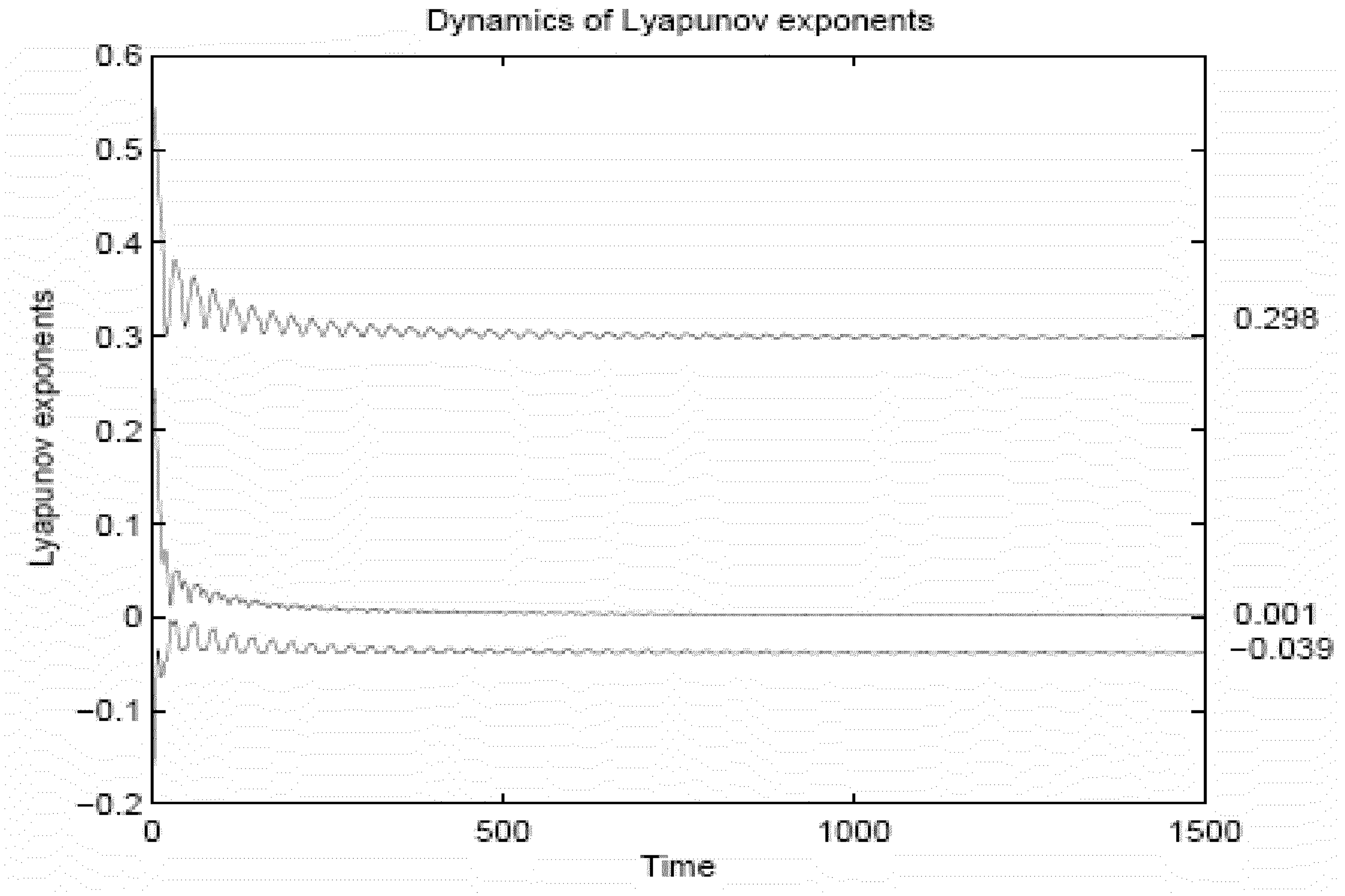


Fig.16. Coexistence of all population in the presence of environmental fluctuation (σi=0.05, i=1,2,3), (here we have used the scheme given by Carletti , Math. Biosc.)

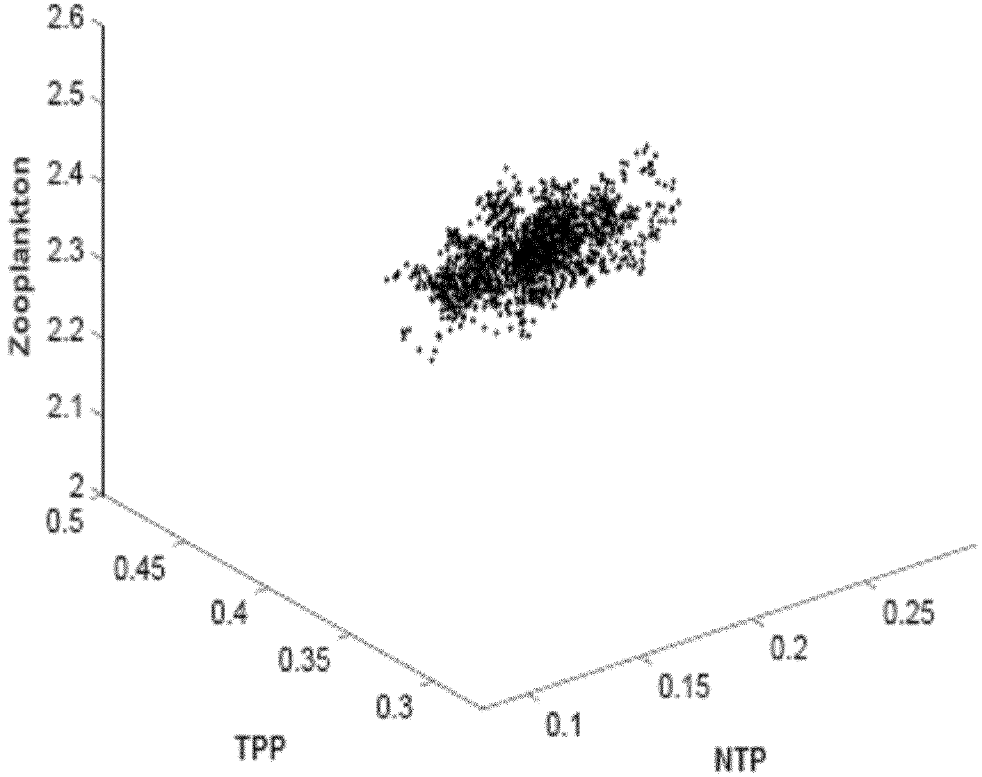


Fig.17: Figure depicting aperiodic oscillation of all population in the presence of environmental fluctuation for μ_1=0.1, μ_2=1.5 (when we increase the competition coefficient). (In absence of environmental fluctuation for the same parametric values the system shows regular oscillation).

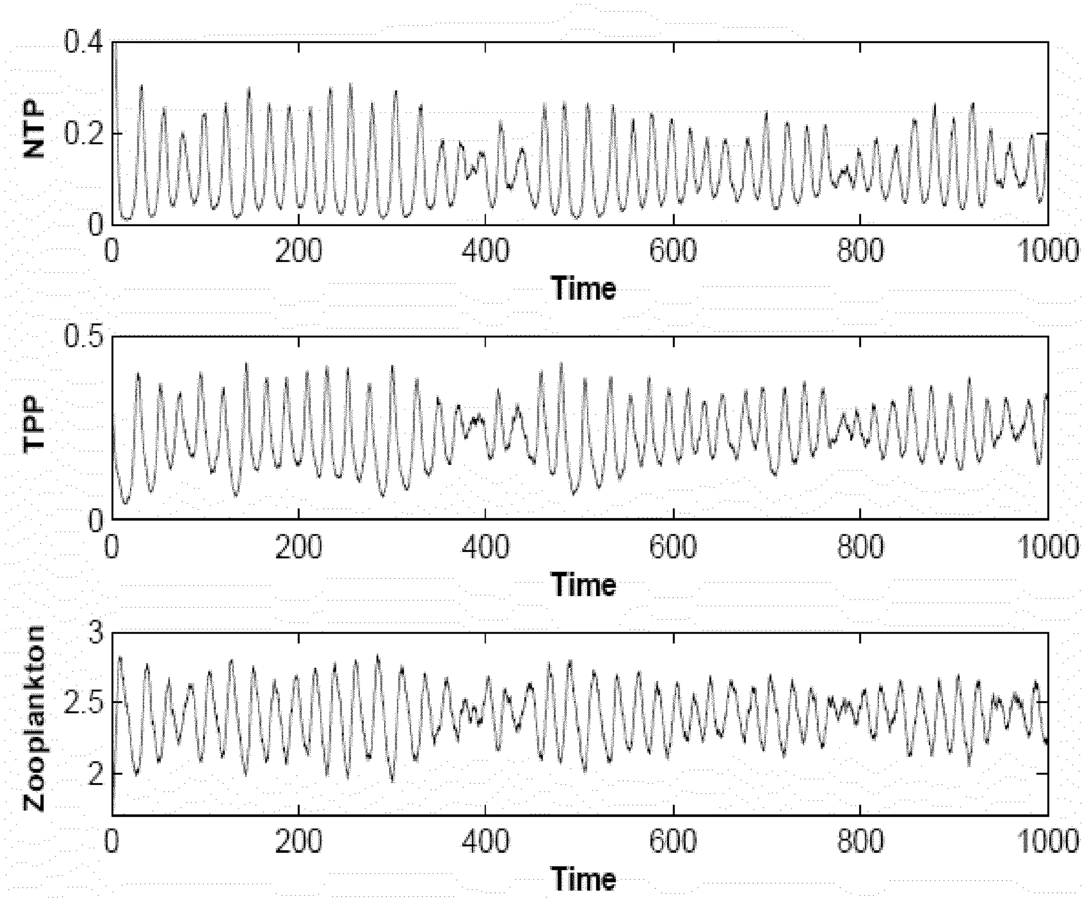
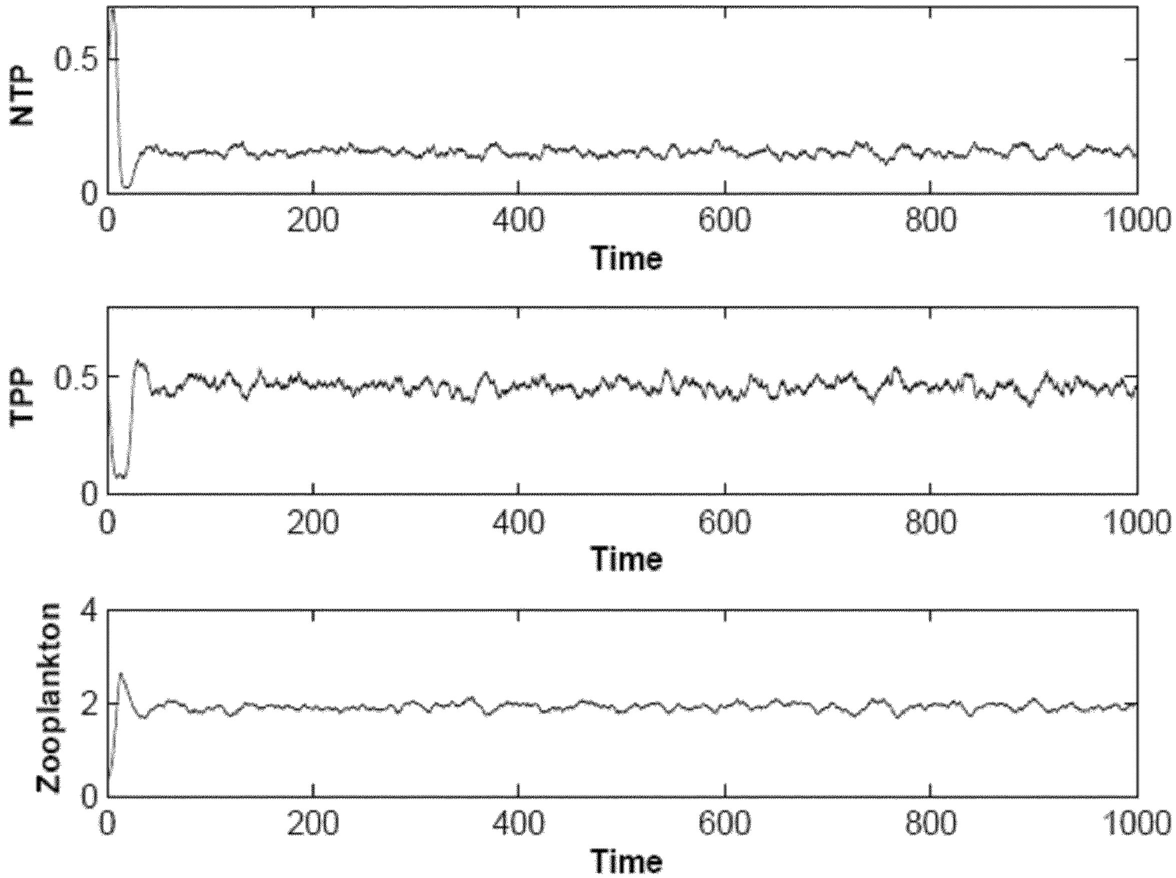


Fig.18: Figure depicting stable population distribution in the presence of environmental fluctuation for μ_1=1, μ_2=1.56. (In absence of environmental fluctuation for the same parametric values the system shows chaotic bloom).



Discussion

- 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.

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