

Competing Effects of Toxin-Producing Phytoplankton on Overall Plankton Populations in the Bay of Bengal

Shovonlal Roy^a, S. Alam^b, J. Chattopadhyay^{a,*}

^a*Agricultural and Ecological Research Unit, Indian Statistical Institute, 203 B. T. Road, Kolkata 700108, India*

^b*Department of Mathematics, Bengal Engineering and Science University, Shibpur, Howrah 711103, India*

Abstract The coexistence of a large number of phytoplankton species on a seemingly limited variety of resources is a classical problem in ecology, known as 'the paradox of the plankton'. Strong fluctuations in species abundance due to the external factors or competitive interactions leading to oscillations, chaos and short-term equilibria have been cited so far to explain multi-species coexistence and biodiversity of phytoplankton. However, none of the explanations has been universally accepted. The qualitative view and statistical analysis of our field data establish two distinct roles of toxin-producing phytoplankton (TPP): toxin allelopathy weakens the interspecific competition among phytoplankton groups and the inhibition due to ingestion of toxic substances reduces the abundance of the grazer zooplankton. Structuring the overall plankton population as a combination of nontoxic phytoplankton (NTP), toxic phytoplankton, and zooplankton, here we offer a novel solution to the plankton paradox governed by the activity of TPP. We demonstrate our findings through qualitative analysis of our sample data followed by analysis of a mathematical model.

Keywords Paradox of plankton · Toxin-producing phytoplankton · Limit cycle · Equilibria · Non-equilibria · Stability

1. Introduction

In a famous paper '*The Paradox of the plankton,*' Hutchinson (1961) argued that the coexistence of a large number of species in most plankton communities is remarkable in view of the competitive exclusion principle, which suggests that in homogeneous, well-mixed environments species that compete for the same

resource cannot coexist. Indeed, simple competition models and laboratory competition experiments also suggest that the number of species that can co-exist in equilibrium cannot be greater than the number of limiting resources, unless additional mechanisms are involved (Tilman, 1977, 1981; Sommer, 1985, 1986; Rothhaupt, 1988, 1996; Scheffer et al., 1997; Huisman and Weissing, 1999). Hutchinson himself suggested that a probable explanation for this coexistence could be that the plankton communities are not in equilibrium at all because of weather-driven fluctuations in the environment (Hutchinson, 1961). Authors such as Richerson et al. (1970) argued in a fashion similar to Hutchinson (1961) that continuous variation in environmental conditions, due to the seasonal cycle and less predictable factors such as weather, offer the most possible explanation. However, to explain the paradoxical coexistence of many competing phytoplankton species, several possible solutions have been proposed during the last four decades. The proposed mechanisms include spatial and temporal heterogeneity in physical and biological environment (Levins, 1979; Powel and Richerson, 1985), externally imposed or self-generated spatial segregation (Ives and May, 1985; Britton, 1989; Hassel et al., 1994), incomplete vertical mixing (Huisman et al., 1999), horizontal mesoscale turbulence of ocean characterized by coherent vortices (Bracco et al., 2000), oscillation and chaos generated by resource competition among the phytoplankton species (Huisman and Weissing, 1999; review by Scheffer et al., 2003), and stable coexistence and compensatory dynamics under fluctuating temperature in resource competition (Descamps-Julien and Gonzalez, 2005). However, in view of the ever-persisting unpredictability of species abundance, the question as to what drives the non-equilibrium dynamics of plankton community still remains open for further investigation (review by Scheffer et al., 2003).

In contrast to the explanations proposed so far, in this paper, our objective is to introduce a new internal mechanism for regulation of the dynamics of overall plankton population. Monitoring and identification (Tomas, 1997) of marine plankton population has been carried out by our group in the north-west coast of the Bay of Bengal since January 1999. We have found a significant number of species of phytoplankton that have the ability to produce toxic or inhibitory compounds (Hallegraeff, 1993; Steidinger, 1996; Chattopadhyay et al., 2002a,b; Sarkar and Chattopadhyay, 2003a). We call these toxin-producing phytoplankton (TPP), and distinguish them from nontoxic phytoplankton (NTP). In general, TPP group contains (i) planktonic or benthic microalgae that produce toxin (e.g., the motile stage of *Alexandrium*, the benthic *Gambierdiscus*), (ii) other toxic dinoflagellates (e.g., *Pfiesteria*), (iii) macroalgae that results in noxious smells (e.g., *Pilayella*), (iv) a few species of Cynobacteria or blue algae (e.g., *Microcystis*), (v) nontoxic microorganisms that result in hypoxic conditions (e.g., *Chaetoceros*, *Mesodinium*) (for a detailed list of TPP species that have been identified by our group, see Chattopadhyay et al., 2002a). These TPP are entirely different from other phytoplankton in biochemical nature. Inhibitory substances released by TPP reduce the grazing pressure of zooplankton (e.g., Kirk and Gilbert, 1992). Buskey and Stockwell (1993) have demonstrated in their field studies that micro- and mesozooplankton populations are reduced during the blooms of a chrysophyte *Aureococcus anophagefferens* in the southern Texas coast. Toxicity may be a strong mediator of zooplankton feeding rate, as shown in both field studies (Nielsen

et al., 1990) and laboratory studies (Ives, 1987). These observations indicate that the toxic substances play an important role in the growth of the zooplankton population and have a great impact on phytoplankton–zooplankton interactions (Kozłowski-Suzuki et al., 2003).

Analysis of our monitoring data shows a regulatory behavior of TPP on zooplankton populations as well as its compensating role for competitive disadvantage among phytoplankton groups. Our observations indicate TPP presence as a significant factor promoting the coexistence of the species. Taking this factor into consideration, we have proposed and analyzed a three-component mathematical model consisting of the NTP, TPP, and zooplankton populations. We have estimated the parameters of the model system from our field data by dynamic estimation methods. We have numerically simulated the model system using estimated parameter values and observed limit-cycle oscillations. We have also found the condition for a Hopf bifurcation in the model. We have assessed, starting from the estimated parameters, the effect of all the parameters on the model system. Throughout, we have observed that TPP provides a mechanism for switching of plankton dynamics from oscillation to stability and vice versa, leading to planktonic-disequilibria. Thus, coexistence and biodiversity of plankton may be maintained.

2. Qualitative view of field data

The study area extends from Talsari (Orissa, India) to Digha Mohana (West Bengal, India). Geographically, the area is situated from $21^{\circ}37'$ northern latitude and $87^{\circ}25'$ eastern longitude to $21^{\circ}42'$ northern latitude and $87^{\circ}31'$ eastern longitude (Fig. 1).

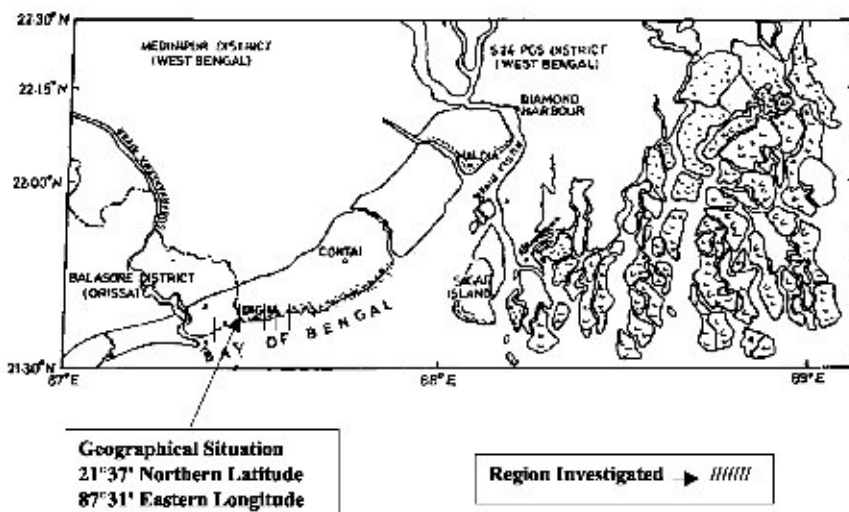


Fig. 1 Map of coastal region of West Bengal and part of Orissa, India (source: CIFRI, Barrackpore, India).

Frequency of sampling was every 2 weeks, except the months of September and October when the sampling program had to be suspended because of bad weather. Moreover, due to local disturbances and financial constrains, we were unable to collect the data every fortnight. Plankton samples were collected both from the surface and subsurface water (1–2 m depth) by a horizontal plankton tow with a 20 μm mesh net 0.3 m in diameter. The collected samples were preserved in 3% formaldehyde in seawater. Counting of phytoplankton was done under microscope using Sedgewick–Rafter counting cell and expressed in number of samples per liter (nos. per liter). Identification of plankton community was done following the method of Tomas (1997). Sample data on populations for the period 2000–2001 have been considered for the present study.

The graphical plot of the observed data for NTP, TPP along with their grazer zooplankton is presented in Fig. 2. In the sample data, the time lag between two consecutive data point is not always constant. Moreover, because of the breaks in data collection (including the months of September and October of each year), some values are missing in our data. The gaps in the axis of date of collection show the missing of data (Fig. 2).

To accommodate the nonuniform spacing of sampling times, in the subsequent analysis, we consider the collection times as discrete time points, the time lag between any two of these points is measured in days.

The graphical representation (Fig. 2) of species' abundance against the discrete time of collection shows fluctuating number of organisms. This plot also depicts that the number of zooplankton is low in those points where TPP is at high abundance. The trend of variation in the abundances of NTP and zooplankton can be

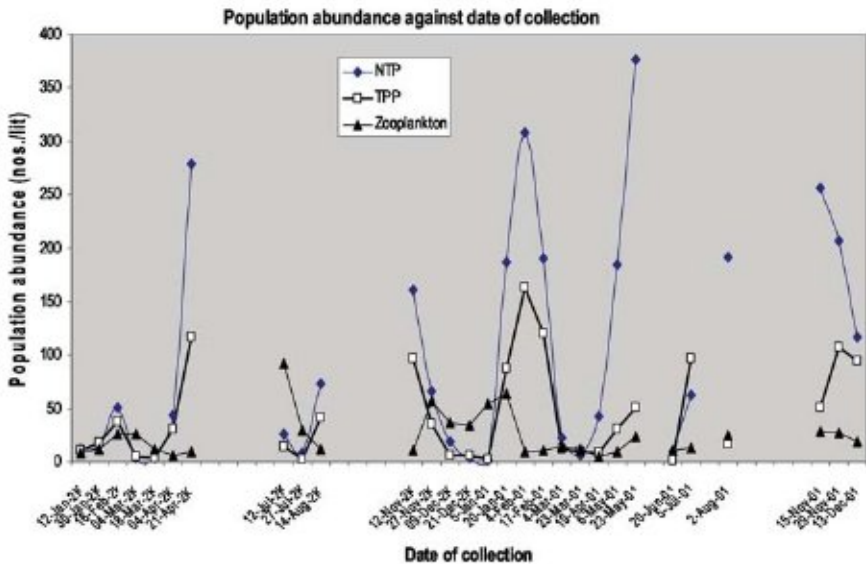


Fig. 2 Representation of the field data against the dates of collection. The gaps indicate the breaks in data collection, the data are missing at those points; all the populations are in fluctuating abundance. The abundance of zooplankton is low when the TPP is at high abundance.

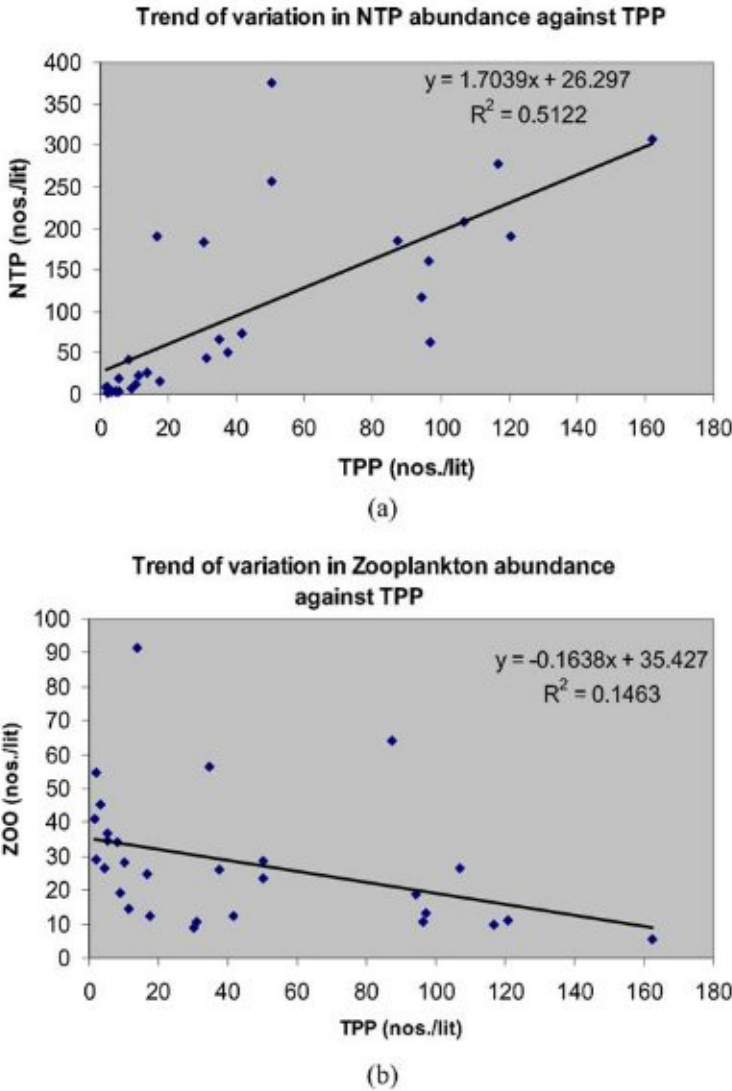


Fig. 3 Linear-regression plot representing the variation in abundance of NTP and zooplankton with respect to variation of TPP; (a) NTP vs. TPP; the regression line has a positive slope, indicating that the presence of TPP reduces the competitive disadvantage. (b) Zooplankton vs. TPP; the regression line has a negative slope, indicating that TPP has an inhibitory effect on zooplankton and high abundance of TPP is not favorable for the persistence of zooplankton.

found from the scatter plot of NTP against TPP and zooplankton against TPP (Fig. 3).

The negative slope of the linear-regression line for zooplankton against TPP (Fig. 3(b)) indicates an antagonistic relationship manifesting that the abundance of zooplankton reduces in the presence of TPP. This observation resembles the

results obtained earlier from field (Nielsen et al., 1990) and laboratory experiments (Ives, 1961) that the grazing pressure of zooplankton decreases in the presence of TPP. This view of data points out that TPP has a significant controlling command on zooplankton and acts as a regulatory factor on plankton dynamics. On the other hand, the positive slope of the linear-regression line for NTP against TPP (Fig. 3(a)) indicates an insignificant competitive disadvantage between these two groups of phytoplankton. Our observation in this context is consistent with the recent studies such as Hulot and Huisman (2004), and Solé et al. (2005).

Further statistical analysis of our field data followed by the estimation of the missing values by expectation maximization algorithm (E–M algorithm) and vector auto-regressive (VAR) modeling also indicate two distinct roles of TPP: the inhibitory role influencing the abundance of zooplankton and compensation of competitive disadvantage among phytoplankton groups by toxin allelopathy. We would like to point out here that the qualitative behavior of the dynamics remains unaltered even if we include the missing values estimated by E–M algorithm. The detail of this analysis can be found in Roy et al. (manuscript in preparation). Additionally, a study on the interaction among two NTP and a toxic phytoplankton suggests that toxin allelopathy (i.e., toxic materials released by TPP) weakens the interspecific competition among phytoplankton species that allows several species to coexist in a stable equilibrium. In other words, in the absence of the predator zooplankton, toxin allelopathy acts as a stabilizing factor for the dynamics of competitive phytoplankton species (see Roy and Chattopadhyay, 2006). However, in reality, the dynamics of phytoplankton are not stable but fluctuating and unpredictable. And the presence of the predator zooplankton influences the overall dynamics. In the following section, taking into account the inhibitory role of TPP on zooplankton, we consider a mathematical model that describes the interaction among NTP–TPP–zooplankton. And in the subsequent analysis, we explore how toxin inhibition on the predator zooplankton influences the overall dynamics.

3. Analysis of mathematical model and results

In this section, we develop a mathematical model of those interacting groups: NTP, TPP, and zooplankton under the following assumptions:

- (i) Each of NTP and TPP population follow logistic growth in the absence of the other and the grazer (Odum, 1971).
- (ii) Both the groups of phytoplankton exhibit Holling type-II functional response (Ludwig, 1978) to the grazer zooplankton.
- (iii) Toxic materials ingested on predation of TPP cause a significant inhibitory effect on zooplankton growth.

The assumption of independent predation of TPP and NTP by zooplankton follows from the literature dealing with the modeling of interaction among toxic, non-toxic, and zooplankton (e.g., Sarkar and Chattopadhyay, 2003b, Chattopadhyay et al., 2004).

Let $P_1(t)$, $P_2(t)$, and $Z(t)$ be the concentrations of NTP, TPP, and zooplankton population, respectively, at time t . Let K be the environmental carrying capacity of phytoplankton which is shared by NTP and TPP; where α_1 and α_2 be the competition coefficients among them respectively, arising from the resource competition for the common resource of the shared environment. Let r_1 and r_2 be the constant intrinsic growth rates of NTP and TPP population respectively. Let w_1 and w_2 be the rates at which NTP and TPP are consumed by zooplankton. Let ξ_1 be the maximum rate of gain in zooplankton growth due to predation of NTP at a rate w_1 and ξ_2 be the rate of inhibition of (or reduction in) zooplankton growth by toxic material ingested in feeding on TPP. Let D_1 and D_2 be half saturation constants for NTP and TPP respectively, and c be the mortality rate of zooplankton due to natural death.

Based on the earlier assumptions, plankton dynamics may be written in the form of simple differential equations as follows:

$$\begin{aligned}\frac{dP_1}{dt} &= P_1 \left\{ r_1 \left(1 - \frac{P_1 + \alpha_1 P_2}{K} \right) - \frac{w_1 Z}{D_1 + P_1} \right\}, \\ \frac{dP_2}{dt} &= P_2 \left\{ r_2 \left(1 - \frac{P_2 + \alpha_2 P_1}{K} \right) - \frac{w_2 Z}{D_2 + P_2} \right\}, \\ \frac{dZ}{dt} &= Z \left\{ \frac{\xi_1 P_1}{D_1 + P_1} - \frac{\xi_2 P_2}{D_2 + P_2} - c \right\}.\end{aligned}\tag{1}$$

with the initial conditions $P_1(0) \geq 0$, $P_2(0) \geq 0$, $Z(0) \geq 0$.

3.1. Equilibria analysis

All the solutions of system (1) which initiate in \mathcal{R}_+^3 are uniformly bounded. (*the proof is obvious.*)

The system (1) possesses the following equilibria: (i) the plankton-free equilibrium, $E_0 = (0, 0, 0)$; (ii) TPP- and zooplankton-free equilibrium, $E_1 = (K, 0, 0)$; (iii) NTP- and zooplankton-free equilibrium, $E_2 = (0, K, 0)$; (iv) zooplankton-free equilibrium, $E_3 = (\hat{p}_1, \hat{p}_2, 0)$, where

$$\hat{p}_1 = \frac{K(\alpha_1 - 1)}{\alpha_1 \alpha_2 - 1}, \quad \hat{p}_2 = \frac{K(\alpha_2 - 1)}{\alpha_1 \alpha_2 - 1};$$

(v) TPP-free equilibrium, $E_4 = (\bar{p}_1, 0, \bar{z}_1)$, where

$$\bar{p}_1 = \frac{cD_1}{\xi_1 - c},$$

$$\bar{z}_1 = \frac{\xi_1 r_1 D_1 (K \xi_1 - c(K + D_1))}{w_1 K (\xi_1 - c)^2};$$

(vi) the interior equilibrium $E^* = (P_1^*, P_2^*, Z^*)$, where

$$P_1^* = \frac{D_1 (\xi_2 P_2^* + cD_2 + cP_2^*)}{\xi_1 D_2 + \xi_1 P_2^* - \xi_2 P_2^* - cD_2 - cP_2^*},$$

$$Z^* = \frac{r_2(D_2 + P_2^*)(c - \xi_1 + \xi_2)P_2^{*2} + [(\xi_1 - \xi_2 - c)K - \alpha_2 D_1 \xi_2 + cD_2 - \alpha_2 D_1 c - \xi_1 D_2]P_2^* + D_2(K\xi_1 - Kc - \alpha_2 D_1 c)}{w_2(\xi_1 D_2 + \xi_1 P_2^* - \xi_2 P_2^* - cD_2 - cP_2^*)K},$$

and P_2^* is given by

$$\theta_1(P_2^*)^3 + \theta_2(P_2^*)^2 + \theta_3 P_2^* + \theta_4 = 0,$$

with

$$\theta_1 = w_1 r_2 (\xi_1 - \xi_2 - c)^2,$$

$$\theta_2 = -(\xi_1 - \xi_2 - c) \{-r_2 w_1 (K + D_1 \alpha_2) \xi_2 + (-2r_2 w_1 D_2 + r_2 w_1 K + r_1 w_2 D_1 \alpha_1) \xi_1 - r_2 w_1 c (D_1 \alpha_2 + K - 2D_2)\},$$

$$\begin{aligned} \theta_3 = & \{r_2 w_1 D_2^2 + (-2r_2 w_1 K - r_1 w_2 D_1 \alpha_1) D_2 + r_1 w_2 D_1 K\} \xi_1^2 \\ & + [-r_1 w_2 (c + \xi_2) D_1^2 + \{(-r_1 w_2 K + r_2 w_1 D_2 \alpha_2) \xi_2 - r_1 w_2 Kc \\ & + 2r_2 w_1 \alpha_2 c D_2 + r_1 w_2 \alpha_1 D_2 c\} D_1 + 2r_2 w_1 D_2 K (\xi_2 + 2c) \\ & - 2r_2 w_1 D_2^2 c] \xi_1 - r_2 w_1 D_2 c \{(2\alpha_2 c + 2\alpha_2 \xi_2) D_1 \\ & - cD_2 + K(2\xi_2 + 2c)\}, \end{aligned}$$

and

$$\begin{aligned} \theta_4 = & D_2 \{K(-r_2 w_1 D_2 + r_1 w_2 D_1) \xi_1^2 - c(r_1 w_2 D_1^2 \\ & - 2r_2 w_1 D_2 K - r_2 w_1 \alpha_2 D_1 D_2 + r_1 w_2 D_1 K) \xi_1 - r_2 w_1 c^2 D_2 (K + D_1 \alpha_2)\}. \end{aligned}$$

The equilibria E_0 , E_1 , and E_2 always exist. The zooplankton-free equilibrium E_3 exists if either $\alpha_1 > 1, \alpha_2 > 1$, or $\alpha_1 < 1, \alpha_2 < 1$. The TPP-free equilibrium E_4 exists if $\xi_1 > c(1 + \frac{D_1}{K})$. The positivity of the interior equilibrium point leads to following conditions

$$(i) \quad \xi_1 > \max \left\{ c, \frac{r_2 w_1}{r_1 w_2 \alpha_1} \left(2 \frac{D_2}{D_1} + (1+c)\alpha_2 \right) \right\},$$

$$(ii) \quad \xi_2 < \frac{1}{K + D_1 \alpha_2} \left\{ (\xi_1 - c)(K - 2D_2) + \left(\frac{r_1 w_2 \alpha_1}{r_2 w_1} \xi_1 - \alpha_2 c \right) D_1 \right\}.$$

The following theorem (which is obvious and thus stated only) summarizes the results of local stability of system (1) around each biologically feasible equilibria.

Theorem 3.1 *The plankton-free equilibrium $E_0 = (0, 0, 0)$, TPP- and zooplankton-free equilibrium $E_1 = (K, 0, 0)$, and NTP- and zooplankton-free equilibrium $E_2 = (0, K, 0)$ are unstable saddles. The zooplankton-free equilibrium $E_3 = (\hat{p}_1, \hat{p}_2, 0)$ is an unstable saddle under the conditions (i) $\xi_1 > \xi_2 + c$, (ii)*

$$\hat{P}_1 > \max \left\{ \frac{D_1(\xi_2 + c)}{\xi_1 - \xi_2 - c}, \frac{cD_1}{\xi_1 - c} \right\}.$$

The TPP-free equilibrium $E_4 = (\bar{p}_1, 0, \bar{z}_1)$ is locally unstable if

$$\frac{\alpha_2}{K} \bar{p}_1 + \frac{w_2}{r_2 D_2} \bar{z}_1 < 1.$$

The interior equilibrium $E^(P_1^*, P_2^*, Z^*)$ is locally asymptotically stable if*

$$(i) \quad Z^* < \min \left\{ \frac{r_1 D_1^2}{w_1 K}, \frac{r_2 D_2^2}{w_2 K} \right\},$$

$$(ii) \quad \left(\frac{r_1}{K} - \frac{d_1^2 Z^*}{w_1} \right) \left(\frac{r_2}{K} - \frac{d_2^2 Z^*}{w_2} \right) > \frac{\alpha_1 \alpha_2 r_1 r_2}{K^2}$$

and

$$(iii) \quad \frac{\xi_1}{\xi_2} > \frac{D_2 P_2 w_1^3 d_2^2}{D_1 P_1 w_2^3 d_1^2} \left\{ \frac{d_2 P_2^* (r_2 w_2 - d_2^2 K Z^*) + r_2 \alpha_2 w_2 d_1 P_1^*}{d_1 P_1^* (r_1 w_1 - d_1^2 K Z^*) + r_1 \alpha_1 w_1 d_2 P_2^*} \right\},$$

where

$$d_1 = \frac{w_1}{D_1 + P_1^*}, \quad d_2 = \frac{w_2}{D_2 + P_2^*}.$$

Due to the complexity of the expressions, we are unable to see the effect of system parameters analytically. To see this, we shall take the help of numerical analysis.

3.2. Hopf bifurcation

The dynamical behavior of system (1) around the positive interior equilibrium (where all of the three species coexist) depends on the system parameters. We find from standard analysis that the system is locally asymptotically stable in some region of parameter space, and that the dynamics of the system changes for different

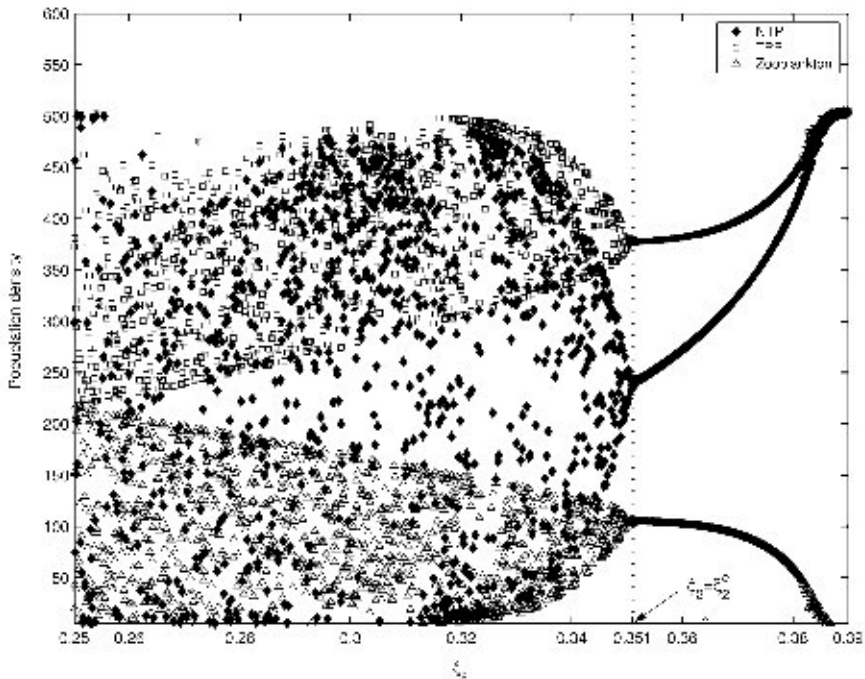


Fig. 4 Bifurcation diagram of the model system with ξ_2 as bifurcation parameter. Hopf bifurcation occurs at a critical value $\xi_2 = \xi_2^c$. Oscillatory dynamics for $\xi_2 < \xi_2^c$, interior equilibrium is locally asymptotically stable for $\xi_2 > \xi_2^c$.

values of ξ_2 . A bifurcation diagram choosing ξ_2 as the bifurcation parameter shows that there exists a critical value ξ_2^c , where a Hopf bifurcation occurs (Fig. 4), and the dynamics show limit-cycle oscillations. The dynamics of the system are oscillatory for the values $\xi_2 < \xi_2^c$. On the other hand, the interior equilibrium is asymptotically stable for $\xi_2 > \xi_2^c$ under the restriction on ξ_2 such as required for the existence of E^* . The bifurcation results suggest that the dynamics of the system are sensitive to the variation of ξ_2 , and that corresponding to different strengths of toxin inhibition, the overall dynamics would show large-amplitude oscillation, small-amplitude oscillation, and stability. In other words, the presence of toxicity of varying strength would allow switching of the overall dynamics through oscillations and stability. The nonuniform fluctuation pattern of the abundance of plankton species (see Fig. 2) suggests that the overall all plankton dynamics change rapidly, and this change might be the result of switching of dynamics from one state to the other. The result of the bifurcation analysis suggest that toxin inhibition might be a potential cause for the switching of plankton dynamics in real world. To confirm this proposition, in the following section, we perform numerical simulations to explore the overall dynamics of the model system over the permissible ranges of the model parameters.

4. Parameter estimation and numerical experiments

For numerical experiments, instead of taking an arbitrary set of parameter values, we approach to find the ‘best-fit’ estimation of the parameters consistent with the behavior of the field data. For this purpose, we follow the dynamic estimation method of ODE developed by SAS Institute Incorporation (see Bryne and Hindmarsh, 1975; Erdman and Morelock, 1996).

From the field data, ‘best-fit estimation’ of the model parameters has been made in the following way.

Estimation procedure starts with an arbitrary set of initial parametric values (say, p_a) chosen on trial basis. We take the first-observed data point, $X(t=0)_{\text{obs}} = (P_1(t=0)_{\text{obs}}, P_2(t=0)_{\text{obs}}, Z(t=0)_{\text{obs}})$ as the initial values for the variables. Next we solve the ODEs numerically with the initial values of parameters and find the solutions of the model at those time points where field data is present. Let these solutions be, $X(t, p_a)_{\text{mod}} = (P_1(t)_{\text{mod}}, P_2(t)_{\text{mod}}, Z(t)_{\text{mod}})$, and the observed data points be $X(t)_{\text{obs}} = (P_1(t)_{\text{obs}}, P_2(t)_{\text{obs}}, Z(t)_{\text{obs}})$. Now the model parameters are estimated from the data by minimizing the following cost function over the parameter space:

$$L(p_a | X_{\text{obs}}) = \sum_{t=t_0}^{t_{\text{max}}} \| X(t)_{\text{obs}} - X(t, p_a) \|^2,$$

where

$$\begin{aligned} & \| X(t)_{\text{obs}} - X(t, p_a) \| \\ &= \sqrt{(P_1(t)_{\text{obs}} - P_1(t)_{\text{mod}})^2 + (P_2(t)_{\text{obs}} - P_2(t)_{\text{mod}})^2 + (Z(t)_{\text{obs}} - Z(t)_{\text{mod}})^2}. \end{aligned}$$

This has been done in the following sequential approach.

Step 1: Calculate the cost function as defined above using the initial parameters.

Step 2: Give a small increment (5.0%) in both direction (positive & negative) to each parameter and calculate the cost function in each case to find minimum value of the cost function and the corresponding parameter for which it is minimum.

Step 3: Preserve this parameter set as the initial value of parameters for the next iteration and carry out the same process.

The whole process was carried out with a special program developed in MATLAB.

A graphical match of parameter estimation is produced (Fig. 5). R^2 -value of estimation is found to be 72.5%.

The estimated parameter values are: $r_1 = 0.4632$ per day, $K = 505$ nos. per ml, $w_1 = 0.6625$ per day, $D_1 = 45$ nos. per ml, $r_2 = 0.4425$ per day, $w_2 = 0.435$ per day, $D_2 = 30$ nos. per ml, $\alpha_1 = 0.002$, $\alpha_2 = 0.001$, $\xi_1 = 0.516$ per day, $c = 0.109$ per day, $\xi_2 = 0.198$ per day.

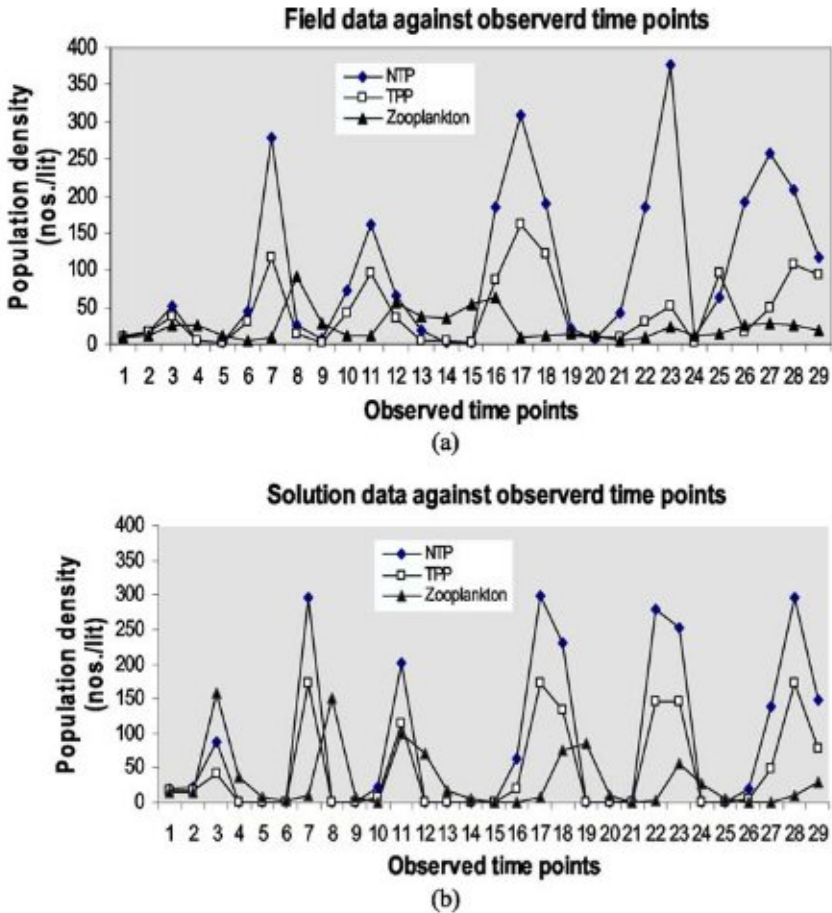


Fig. 5 Graphical match of the parameter estimation. (a) Graphical representation of the field data against the discrete time points at which data is present. (b) Graphical representation of model output with estimated parameters at those discrete points. (Note that, because the figure is intended to provide just a comparison between the observed and estimated data at the discrete time points, the observed points are not separated by a uniform sampling interval as in Fig. 2.)

Very low values of the competition coefficients (α_1, α_2) estimated from the field data resemble that the toxic materials released by TPP weaken the interspecific competition among phytoplankton species. This result supports the qualitative view of the data (Section 2) and is consistent with the previous studies conducted by Hulot and Huisman (2004), and Solé et al. (2005).

The model system with estimated parameter values shows self-sustained oscillations (Fig. 6) asserting that, in general, plankton are in oscillating coexistent state, not in stable equilibrium. However, in reality, plankton dynamics hardly show uniform oscillation; rather, it shows fluctuating coexistence of species (Fig. 2). And these fluctuations indicate that the overall dynamics is frequently changing.

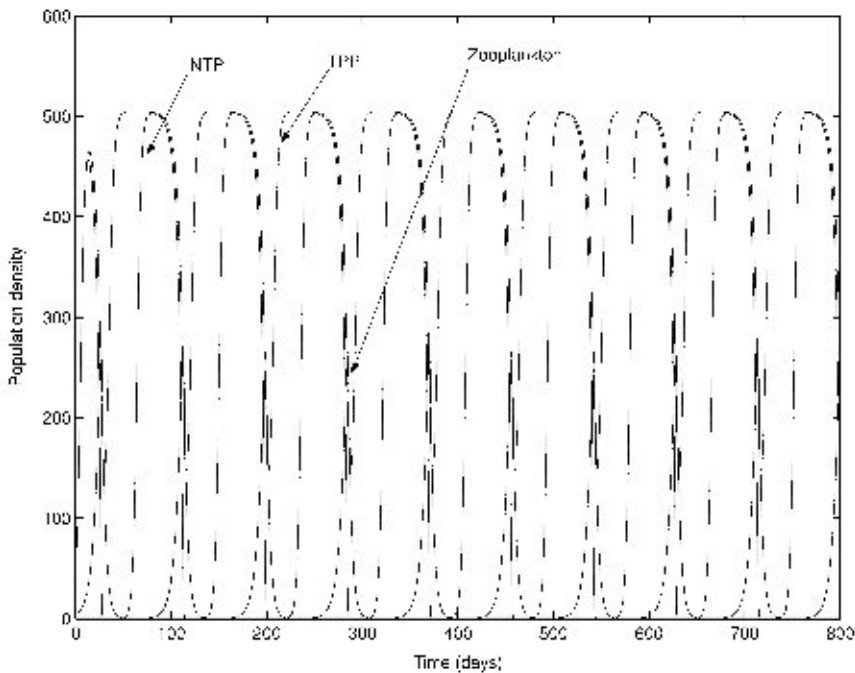


Fig. 6 Limit-cycle oscillations of the model system with estimated parameters; oscillatory coexistence of the plankton population.

Now in order to find out the key factors responsible for unpredictable dynamical change, we perform numerical experiments on the estimated parameters. We vary each of the parameters and observe the system behavior of the model in each step. Results demonstrate that oscillations sustain for all possible combinations of parameter values in the respective confidence intervals. We further extend the simulation process up to the permissible range of each of the parameters (i.e., values satisfying the parametric conditions for coexistence obtained from equilibrium and stability analysis). The simulation results show that the dynamics are not sensitive to the magnitudes of the parameters, except for the parameter ξ_2 and c (Fig. 7).

When there is no toxin inhibition (i.e., $\xi_2 = 0$) or the intensity of toxin inhibition is very low, dynamics show self-sustained oscillations (Fig. 8(a) and (b)). On the other hand, if the parameter ξ_2 is very large, then because of high toxic effect, the predator goes to extinction (Fig. 8(d)). The amplitude of the self-sustained oscillations is sensitive to the magnitude of toxin inhibition. Any variation in ξ_2 causes variation in the amplitude of oscillation of the overall dynamics (Fig. 8(b)). However, for a very restricted range of ξ_2 ($0.354 \leq \xi_2 \leq 0.386$), a stable equilibrium is possible. Because of the extreme sensitivity of the stable equilibrium to the magnitude of ξ_2 , we may characterize it as a “fragile-stable state” (Fig. 8(c)). These results demonstrate that the variation in the rate of killing of the grazer zooplankton by toxic materials ingested changes the dynamic behavior of the system. Unless the parameter of toxin inhibition is very large (in that case, zooplankton goes to

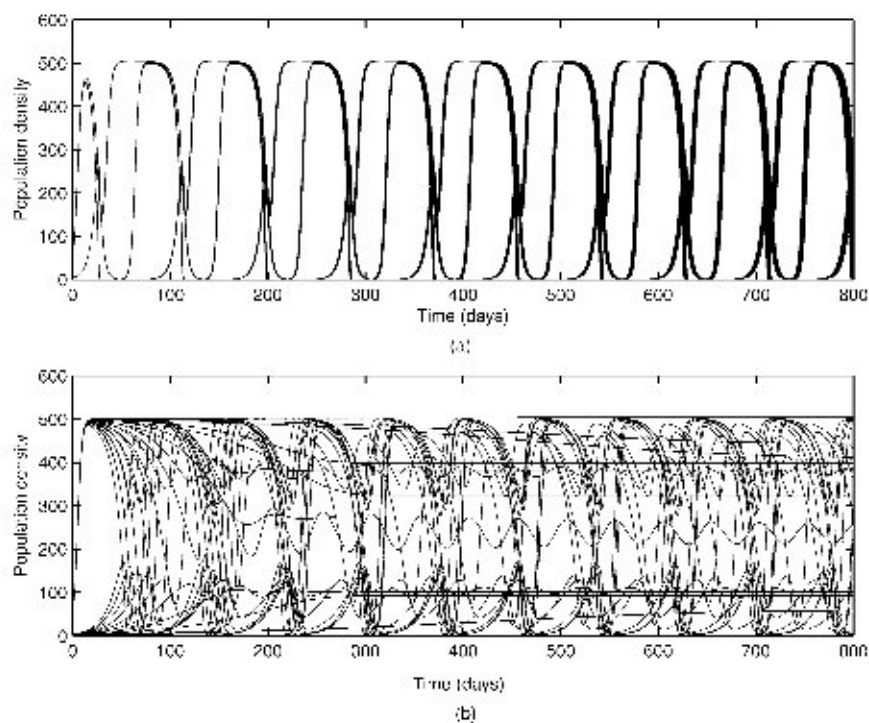


Fig. 7 Effect of different parameter values in the respective permissible range. (a) Self-sustained oscillation due to variation of α_1 in the range $0.0001 \leq \alpha_1 \leq 0.01$; similar results obtained (not shown in figure) for all other parameters except ξ_2 and c . (b) Self-sustained oscillations to fragile stability and vice versa due to variation of ξ_2 ; sustained oscillations obtained for long range and stable focus for short range of values of ξ_2 illustrated the variation of ξ_2 in the range $0.30 \leq \xi_2 \leq 0.39$, which is similar to the results obtained (not shown) for $0.27 \leq c \leq 0.30$.

extinction), all the species coexist either in an oscillating state or in stable equilibrium. However, because the stability is only for a small range of the intensity of toxin inhibition, any variation in the intensity of inhibition will allow switching of the dynamics from stability to oscillation. This phenomenon may be a possible cause for unpredictable plankton dynamics leading to ever-persisting fluctuations in the abundance of phytoplankton. And this result shows that TPP is a possible candidate for determining the nature of plankton dynamics in marine ecosystem.

5. Conclusion

It is well established that non-equilibrium conditions allow the coexistence of many species under limiting resources, and that real-world plankton communities can never be in equilibrium, which is the reason for their coexistence (Hutchinson, 1961; Levins, 1979; Armstrong and McGehee 1980; Sommer 1985; Huisman et al., 2001). Oscillations and chaos in plankton dynamics generated by factors such as

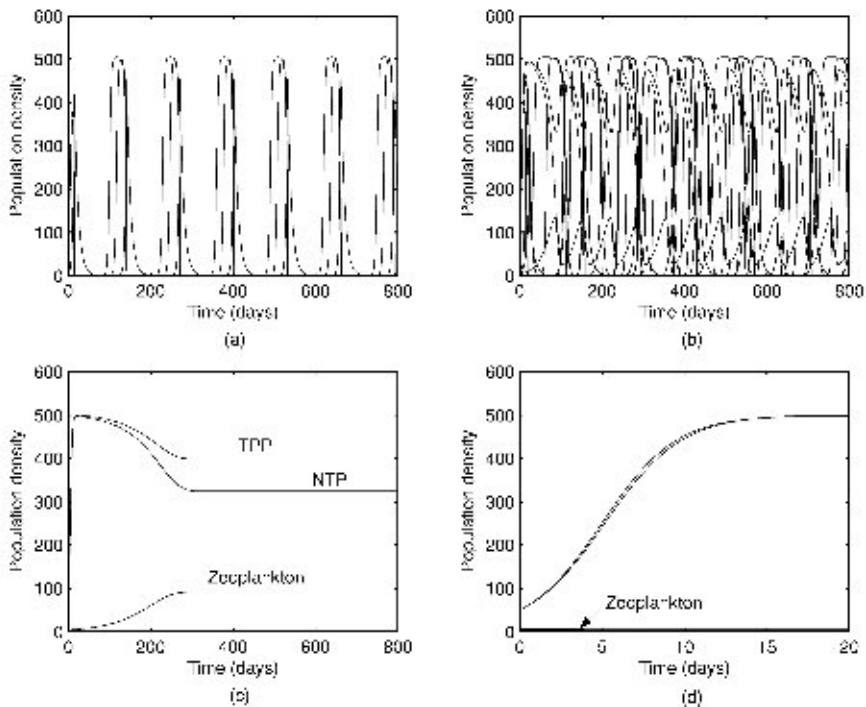


Fig. 8 Variation in toxin inhibition and plankton dynamics: (a) limit-cycle oscillation when $\xi_2 = 0$; (b) self-sustained oscillations for low values of ξ_2 ; (c) fragile-stable steady state of plankton dynamics, stability is obtained for ξ_2 in the range $0.354 < \xi_2 < 0.386$, illustrated the stability (stable focus) for $\xi_2 = 0.38$; (d) extinction of predator zooplankton for large value of toxin inhibition.

weather fluctuation, etc., or competition among plankton species, have been cited so far, for their non-equilibria (Scheffer et al., 2003). Structuring the overall plankton population as a combination of NTP, toxic phytoplankton, and zooplankton, here we demonstrate an internal mechanism within the plankton community that does not depend on the effect of external factors and competition, and that may be responsible for their paradoxical coexistence. The qualitative view and statistical analysis (also see, Roy et al., manuscript in preparation) of our data establish two distinct roles of TPP: the inhibitory role of toxic substances in reduction of zooplankton abundance by poisoning the grazer with toxic materials, and the role of toxin allelopathy in compensating the competitive disadvantage (also see, Hulot and Huisman, 2004) among the phytoplankton species. Recent studies show that the direct effect of toxic materials released by TPP on NTP (i.e., toxin allelopathy) weakens the interspecific competition (see, Solé et al., 2005) and stabilizes the dynamics of competitive phytoplankton species in the absence of zooplankton (see Roy and Chattopadhyay, 2006). In this paper, toxin inhibition on zooplankton is incorporated in a model of interacting NTP–TPP–zooplankton populations and the plankton dynamics are explored analytically and numerically using the field data. The study demonstrates that toxin inhibition on the grazer zooplankton

gives a significant feed-back to overall plankton dynamics, and the intensity of inhibition (ξ_2) regulates the overall dynamic behavior. The nonuniform fluctuation pattern of the abundance plankton species (see Fig. 2) suggest that overall all plankton dynamics change rapidly, and this change might be the result of switching of dynamics from one state to the other. We suggest that the so-called 'planktonic non-equilibria' can be viewed as a consequence of the switching of dynamics through self-sustained oscillations of different amplitudes and fragile-stable state. Results show that in the presence of TPP, the interspecific competition among phytoplankton species (which is weak because of toxin allelopathy) is not responsible for such switching of dynamics (Fig. 7). Sensitivity of dynamical state is found to be dependent (only) on the parameter of toxin inhibition on zooplankton. Variation in the intensity of toxin inhibition acts as a driving force for determining the dynamics of different-amplitude oscillations and switching of plankton dynamics through oscillation and stability. Undulating variation in the intensity of toxicity may be explained with the vacillation of abundance of TPP in the system (Fig. 2). The large fluctuations of the abundance of TPP in the field data (Fig. 2) indicate a large variation in the strength of toxicity in the system. Consequently, the dynamics of plankton are also likely to change from oscillations of different amplitude to stability and then again to oscillation, leading to the 'planktonic non-equilibria'. These results establish a prominent role of TPP in explaining dynamics of the overall plankton population as a combination of NTP, toxic phytoplankton, and zooplankton. The inherent switching of the plankton dynamics regulated by TPP, as described by our study, may be responsible for the waxing and waning of a large number of plankton species, leading to their coexistence and persistence of biodiversity.

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