

An ecological study of a marine plankton community based on the field data collected from Bay of Bengal

R.R. Sarkar^a, S.V. Petrovskii^{b,*}, M. Biswas^c, A. Gupta^d, J. Chattopadhyay^e

^a *Mathematical Modelling and Computational Biology Group,*

Centre for Cellular and Molecular Biology, Uppal Road, Hyderabad 500007, India

^b *Shirshov Institute of Oceanology, Russian Academy of Science, 36 Nakhimovsky Prospekt, Moscow 117218, Russian Federation*

^c *Department of Biostatistics and Epidemiology, Case Western Reserve University, Metro Health Centre, Cleveland, OH, USA*

^d *382 Parnasree, Kolkata 700060, India*

^e *Agricultural Science Unit, Indian Statistical Institute, 203 B.T. Road, Kolkata 700108, India*

Abstract

Effect of environmental factors and existence of harmful species in a community play an important role in generating hypothesis about the nature of interactions between species in an assemblage. The present paper attempts to establish the role of different hydrological parameters in the formation of plankton blooms and to look for a suitable form of functional response to describe the reduction of zooplankton population due to toxin producing phytoplankton (TPP). We consider the analysis of variance technique in regression model. In the analysis, first we try to check whether each of the zooplankton species has significant association with any of the physical parameters and TPP as a whole. Secondly, we consider the fact whether each of the zooplankton species has any association with the physical parameters and the TPP individually. Moreover, we propose a modified variance measure for detecting species association, taking into consideration some of the environmental variables and suggested a suitable functional form to describe the toxin production process by TPP population. We then incorporate our findings into a mathematical model and show that a sufficiently large increase in the toxin production rate can destabilize the plankton system's functioning and result in algae bloom.

Keywords: Plankton blooms; Toxin producing plankton; Zooplankton; Environmental factors; Species association

1. Introduction

In community studies, the species abundance patterns can be used to test or generate hypothesis about the nature of interactions between species in an assemblage. Indeed, such patterns have often been used to

infer the interactions directly. For instance, information on correlation/anticorrelation between different species can be used in order to distinguish between mutualistic and agonistic interactions. Better knowledge of the nature of interspecific relations leads to better understanding of the community dynamics and eventually to a possibility of biological control. Thus, the description and statistical analysis of species abundance pattern are of considerable interest.

The question whether individuals of a given species occur more frequently when a second species is also present or abundant was addressed by several researchers (e.g., Lloyd, 1967; Pielou and Pielou, 1968; Buzas, 1970; Taylor, 1979; Simberloff and Connor, 1981; Wiens and Rotenberry, 1981, etc.). A number of methods have been developed for testing whether such an association, or correlation, between two species exists in a given community. Pielou and Pielou (1968) were among the first to discuss a test for species association. Pielou (1972) proposed a variance measure for detecting species association that uses the presence or absence of data for k different species in N sampling units. He showed that the difference of the observed variance of the number of species per sampling unit and its expectation under the null hypothesis that all k species are independent could be used as a measure of the overall association among the species. Pielou (1972) was the first to compare the observed variance with the expected variance but similar methods have been suggested independently at least three times since then (Diamond and May, 1977; Järvinen, 1979; Schluter, 1982). Robson (1972) derived a statistic for testing the observed variance against the null model. The limitation to Pielou's measure is that it is confined only to presence and absence of data and as a result there is loss of information regarding species association. Schluter (1984) modified the test originally suggested by Pielou and showed that the ratio of the above-mentioned variances serves as an index of species association in samples and is more powerful than even Pearson's χ^2 test for comparing observed and expected frequency distribution of species in samples. Further, he has shown that the test may be generalised to handle population density data also. In Schluter's measure, however, the estimate of the expected variance used in the denominator may be zero and in such a case the measure is undefined and it becomes difficult to handle such a situation. McCulloch (1985) established

connections between those association tests and standard statistical tests and used them as a guide to proper interpretation of the association tests. He proposed that the association measure W used in the association tests is a multiple of Cochran's Q (Cochran, 1950; see also, Conover, 1980) for presence/absence data and a simple function of an F -statistics from a two-way (species by samples) analysis of variance for density data. In addition, he showed that the association measure could be viewed as an average of the pairwise correlation between species. He further suggested that association tests are sensitive to sample-to-sample differences and in some cases will not reflect species interactions at all. However, in the cases where the association tests are appropriate, the connections do provide information on the choice of accurate critical values.

The role of competition in species associations is still a subject of intense controversy. There has been extensive effort to determine the role of interspecific competition in structuring natural communities (see reviews by Schoener, 1983; Connell, 1983 and in Strong et al., 1984). Hastings (1987) determined the equilibrium structure of a competition model with an arbitrary number of species. These species were assumed to live on a large number of identical patches and all species were assumed to have similar characteristics. In his model, competition was introduced by letting the per species extinction rate on patches increase with the number of species. He showed that, with reasonable sample sizes and strong competition, it is not possible to show statistically that the resulting species distribution differ from random assortment. In a more realistic situation, when both species and islands differ, competition would be much more difficult to detect, so using species co-occurrence data to look for competition is unlikely to reveal even strong competition. Effect of environmental factors and existence of harmful plankton species in a marine community is very much important in this context. None of the above studies have considered the environmental effects on the species abundance and also ignored the existence of harmful species.

The dynamics of rapid and/or massive increase or decrease of plankton populations is an important subject in marine plankton ecology. Generally, nutrient levels and environmental conditions are the key factors affecting algae growth. The water must contain high level of inorganic nutrients (nitrogen and phosphorus)

for the algae to feed on and also water temperature and salinity levels must be within a certain range to enhance plankton growth. A frequent outcome of plankton blooms is massive cell lysis and rapid disintegration of large algae populations. This is closely followed by an equally rapid increase in the concentration of bacteria and by a fast de-oxygenation of water, which could be detrimental to aquatic plants and animals. Thus, such blooms hamper the growth of aquatic vegetation. In recent years, there has been considerable scientific attention towards harmful algal blooms (HABs) (e.g., see Anderson, 1989; Smayda, 1990; Hallegraeff, 1993; Blaxter and Southward, 1997; Stoermer and Smol, 1999; Morozov and Petrovskii, 2000; Chattopadhyay et al., 2002a,b). The adverse effects of HABs on human health, fishery, tourism and coastal recreation are well known. Nevertheless, despite the apparent importance of this issue, the effect of different hydrological parameters on the abundance of plankton species and on the frequency of plankton blooms is not yet well established and requires special attention. Hence, the experimental as well as mathematical and statistical studies are necessary.

Several researchers have tried to explain the dynamics of plankton blooms by focusing on different factors such as nutrient upwelling (Edwards and Brindley, 1996), spatial patchiness (Mathews and Brindley, 1996) and species diversity (Pitchford and Brindley, 1998). Steele and Henderson (1993) and Edwards and Brindley (1996) observed that the choice of the func-

tional form for zooplankton mortality has a major influence on the blooms' dynamics. Probably, one of the main factors behind plankton bloom and species succession is the toxin produced by the harmful phytoplankton. During a HAB, the cumulative effect of all released toxins may affect other aquatic organisms causing their massive mortality. Reduction of grazing pressure of zooplankton due to toxin producing phytoplankton (TPP) can be one of the key parameter in this context (e.g., see Kirk and Gilbert, 1992). There is also good evidence that herbivore grazing plays a crucial role in the initial stages of a red tide outbreak (Uye, 1986). It is shown in both field studies (Nielsen et al., 1990) and laboratory studies (Ives, 1987; Nejtgaard and Solberg, 1996) that toxicity may be a strong mediator of zooplankton feeding rate. These observations indicate that TPP has a great impact on phytoplankton–zooplankton interactions. In particular, Chattopadhyay et al. (2002a) considered the effect of toxic chemicals on zooplankton in order to explain the mechanism for the occurrence of plankton blooms and its possible control.

Another interesting problem is the dynamics of externally forced systems. Massive phytoplankton blooms due to artificial eutrophication were observed in Seto Inland Sea, Japan (Prakash, 1987) and in Hong Kong Harbour (Lam and Ho, 1989). Plankton populations often fluctuate unpredictably due to the influences of fluctuating environment and the impact of environmental noise can change the dynamics of

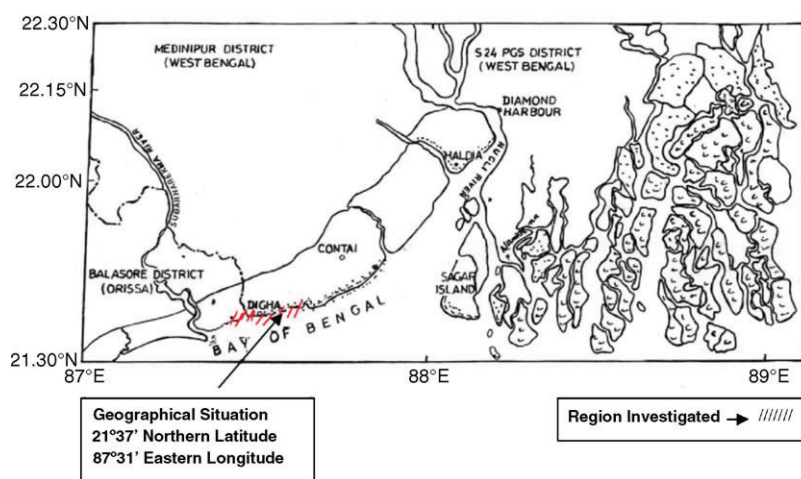


Fig. 1. A map of coastal region of West Bengal and part of Orissa, India. Dashed domain shows the area where the samples were collected.

given aquatic community significantly (Malchow et al., 2002, 2004). Sarkar and Chattopadhyay (2003) attempted to search a possible mechanism for controlling planktonic blooms by introducing environmental stochasticity in the phytoplankton–zooplankton system. Their field observations and mathematical analysis established the fact, that, both TPP and the level of artificial eutrophication may act as a controlling agent for planktonic blooms. These observations indicate that the toxic phytoplankton and environmental fluctuations play important role on the growth of the zooplankton population and have a great impact on phytoplankton–zooplankton interactions.

In this paper, we use field data on plankton abundance and species composition in order to reveal association between several zooplankton species and several toxic and non-toxic phytoplankton species as well as between species abundance and hydrological parameters. For that purpose, a modified variance measure is proposed to take into account some environmental variables. We then use the results of statistical analysis to look for a suitable functional form to parameterise the zooplankton population response to toxin producing phytoplankton. That parameterization is then incorporated into a mathematical model to study the system's stability and to demonstrate a toxin-driven mechanism of harmful algae bloom.

2. Field observations and results of statistical analysis

In order to reach the goals of this paper, we have used our field-collected samples for the period January 1999–December 2001. The study area extends from Talsari (Orissa, India) to Digha Mohana (West Bengal, India). Geographically, the area is situated between 21°37' Northern Latitude and 87°25' Eastern Longitude to 21°42' Northern Latitude and 87°31' Eastern Longitude. The geographical location of the study area is given in Fig. 1. Samplings were done aboard 10-m fishing vessel hired each time from Talsari fish landing center and over seven stations (three in near shore region, three in off shore region and one in river) nearly 2 km apart. Frequency of sampling was in every fortnight except the months of September and October. During that time sampling program had to be suspended because of high roughness of the sea. Plankton

Table 1a
Physical parameters

Oxygen dissolved in water
Temperature
Water pH
Salinity

samples were collected both from the surface and sub-surface water (1–2 m depth) by a horizontal plankton tow with a 20 μ m mesh net and 0.3 m in diameter. The collected samples were preserved in 3% formaldehyde in seawater. Counting of phytoplankton was made under microscope using Sedgewick–Rafter counting cell and are expressed in numbers/liter. Identification of plankton community was done following the method of Tomas (1997).

Analysis of the collected samples revealed the presence of, in total, 115 phytoplankton species of which 65 are diatoms, 19 are green algae (Chlorophyceae), 9 are blue greens (Cyanophyceae) and 22 are Dinoflagellates. Among the observed species, six diatoms are known to be harmful algae, i.e., *Chaetoceros* spp., *Skeletonema costatum*, *Cerataulina* spp., *Leptocylindricus* spp., *Nitzschia* spp. and *Phaeocystis* spp. (cf. Sournia, 1995). Although Sournia (1995) showed that, in general, Dinoflagellates contribute significantly into toxin production, in our study out of total 22 species of Dinoflagellates only three species were identified as harmful, i.e., *Dinophysis acuta*, *Noctiluca scintillans* and *Prorocentrum* sp. (cf. Richardson, 1997).

As we are mainly interested here to report the effect of TPP on zooplankton and the role of hydrological parameters, we choose 4 species of toxin producing phytoplanktons, 10 zooplankton species and 4 physical parameters for the study which are listed in the Tables 1a, 1b and 1c. In particular, among the TPP that we have chosen, species *Noctiluca scintillans* belonging to the group Dinoflagellates of the Division Dinophyta is a very common heterotrophic dinoflagellate and is known to feed on bacteria, diatoms, other flagellates and ciliate protozoans.

Table 1b
Toxin producing phytoplankton species

<i>Chaetoceros</i> spp.
<i>Nitzschia</i> spp.
<i>Noctiluca scintillans</i>
<i>Favella francisca</i>

Table 1c
Zooplankton species

<i>Sagitta</i> spp.
<i>Vogtia glabra</i>
<i>Eucalanus</i> sp.
<i>Paracalanus</i> sp.
<i>Tintinnopsis</i> spp.
<i>Oikopleura</i> sp.
<i>Nauplius</i>
<i>Sphaerocapsa cruciate</i>
<i>Helicostomella subulate</i>
<i>Eutiminius</i> sp.

This species has already been reported as harmful when appearing in plankton blooms and it exerts adverse ecological effects via toxins production to other pelagic organisms including fish. This species is taxonomically a phytoplankton but functionally it is a phagotroph or heterotroph. Among zooplankton species, we chose *Paracalanus* belonging to the group Copepoda, which dominates the zooplankton community in practically all oceans over the world, and they are the major herbivore, which determine the form of the phytoplankton–grazing curve.

In order to process the collected data, we use the analysis of variance technique (ANOVA) in regression model. We use the density dependent statistical analysis; that helps us to incorporate our findings more easily into the mathematical model (see the next section), which is also formulated in terms of population densities. The analysis has been done in two steps. Firstly, we have tried to check whether each of the zooplankton species has significant association (correlation) with any of the physical parameters and TPP as a whole. Thus, we have taken the eight covariates (physical parameters and TPP) and have considered the null hypothesis that there is no association between different variables. The corresponding statistics follows *F* distribution and if it is greater than the significant value then the null hypothesis has to be rejected and it can be concluded that there is a significant association between the physical and biological variables. Secondly, we have checked whether each of the zooplankton species has any association with the physical parameters and the TPP individually. In this case, we have considered the null hypothesis that there is no association between a zooplankton species and a single physical parameter/TPP. As well as in the previous case, if the *F*-value is greater than the significant value

then we reject the null hypothesis and conclude that there is a significant association.

2.1. The test for species association

We have already mentioned in the introduction that there are several limitations in Pielou’s measure and Schluter’s measure for testing species association. For that reason, to study the species association we have used the analysis of variance technique in regression model. We have analysed the data on 10 zooplankton species considering them as dependent variables while four physical parameters and four TPP species were considered as independent variables, each of them having 30 observations. Correspondingly, we have considered the following linear regression equation:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_5 + \beta_6 X_6 + \beta_7 X_7 + \beta_8 X_8 + \varepsilon$$

where **Y** is the *n*-vector of the zooplankton species densities, **X_i** the *n*-vector of the physical parameters and TPP densities (*i* = 1, . . . , 8), β_i the regression coefficients and ε is the error term.

Now we considered the null hypothesis **H₀**:

$$\beta_1 = \beta_2 = \beta_3 = \beta_4 = \beta_5 = \beta_6 = \beta_7 = \beta_8 = 0$$

i.e., “Is there any significant association between the dependent and independent variables?”

Our method follows the steps given below.

First we have estimated the parameters.

The above regression equation can be written as **Y = Xβ + ε**, where **X** is a *n* × 9 matrix with the first column as a unit vector 1:

$$\text{Then } \beta = (\mathbf{X}'\mathbf{X})^{-1}\mathbf{X}'\mathbf{Y}$$

Next, we have used the analysis of variance technique (Rao, 1965).

The unconditional sum of squares: $R_0^2 = (\mathbf{Y} - \mathbf{X}\beta)'(\mathbf{Y} - \mathbf{X}\beta)$ and has *n* − *p* − 1 = 21 d.f. (here, *n* = 30, *p* = 8).

Now, let us consider that the **H₀** is true. Then the regression equation becomes **Y = β₀ + ε**.

Then, the estimate of the parameter is $\beta_0 = (1/n) \sum Y_i$.

The conditional sum of squares is $R_1^2 = (\mathbf{Y} - \mathbf{X}\beta_0)'(\mathbf{Y} - \mathbf{X}\beta_0)$ and has *n* − 1 = 29 d.f.

Table 2
Analysis of regression equation

	d.f.	S.S.	M.S.	F
Regression	p	$SSR = R_1^2 - R_0^2$	$MSR = SSR/p$	$F = MSR/MSE \sim F_{p, n-p-1}$
Residual	$n-p-1$	$SSE = R_0^2$	$MSE = SSE/(n-p-1)$	

Table 3
F-values obtained for different zooplankton species from data analysis

Zooplankton species	F
<i>Sagitta</i> spp.	1.455309
<i>Vogtia glabra</i>	3.033706*
<i>Eucalanus</i> sp.	2.029067
<i>Nauplius</i>	3.139377*
<i>Paracalanus</i> sp.	3.677749*
<i>Sphaerocapsa cruciata</i>	0.5098742
<i>Eutimimus</i> sp.	2.368202
<i>Helicostomella subulata</i>	2.834533*
<i>Tintinnopsis</i> spp.	2.834533*
<i>Oikopleura</i> sp.	5.302536*

Note: The significant value of F statistic at 95% level of significance is $F_{8,21} = 2.425$.

* Values are significant.

Then the reduction in the residual sum of squares is $R_1^2 - R_0^2$ which is due to regression and has $p = 8$ d.f.

The analysis is then given in the Table 2 and the results (different F-values) obtained from our field observation and data analysis are given in Table 3. For values of $F > 2.425$ we can conclude that the null hypothesis H_0 is rejected and thus the zooplankton species have strong association with the physical parameters and/or TPP species.

Next, we have observed the case of individual association. For this purpose, we have considered the inde-

pendent parameters individually and determine the association with the zooplankton species. The regression equation then becomes $Y = \beta_0 + \beta_1 X_1 + \varepsilon$ and the null hypothesis H_0 becomes $\beta_1 = 0$.

Proceeding similarly as above we have $F \sim F_{1,28}$. Thus, we reject the null hypothesis H_0 if $F > 4.2$. The results obtained from our data analysis concerning the association of each zooplankton species with the hydrological parameters and the TPP species individually are shown and explained in Tables 4 and 5, respectively. We have observed in our field-collected samples that the variance in the species abundances is small. For example, in Table 5, we observed that, except for a few cases, all the F-values are below 95% level of significance. Since most of the species do not have strong influence on the dynamics due to very low abundances and not significant correlations, we have not considered their influences and we have discussed only those species, which have high abundances and strong correlations. Moreover, if we observe the species abundances over year-to-year then we found that the variances are small (we omit the details for the sake of brevity). Therefore, we have neglected the influence of variability on the statistical robustness and also have not considered the influence of seasonality for fortnightly collected data. Further, we have used the average of all the data collected over seven stations where we collected

Table 4
F-values obtained from our data analysis depicting the association between different zooplankton species with the hydrological parameters

Zooplankton species	Temperature	pH	Salinity	Dissolved oxygen
<i>Sagitta</i> spp.	0.6298618	1.080656	0.3034033	5.617222*
<i>Vogtia glabra</i>	0.3499245	0.8818994	0.4017733	4.54605*
<i>Eucalanus</i> sp.	0.329278	1.731545	1.244313	10.29324*
<i>Nauplius</i>	0.03766475	1.355344	1.36431	3.062378
<i>Paracalanus</i> sp.	0.2370121	2.149041	0.0365161	13.00259*
<i>Sphaerocapsa cruciata</i>	0.02599495	0.5987141	2.215722	1.337612
<i>Eutimimus</i> sp.	2.887205	0.7577197	2.567232	2.410258
<i>Helicostomella subulata</i>	4.192361*	0.0575023	1.727197	3.470369
<i>Tintinnopsis</i> spp.	5.102181*	0.1050237	1.385446	3.512541
<i>Oikopleura</i> sp.	0.4673887	0.4760498	1.071541	0.1650846

* Values are significant at 95% level of significance.

Table 5

F-values obtained from our data analysis depicting the association between different zooplankton species with the TPP species

Zooplankton species	<i>Chaetoceros</i> spp.	<i>Nitzschia</i> spp.	<i>Noctiluca scintillans</i>	<i>Favella franciscana</i>
<i>Sagitta</i> spp.	1.520099	0.01043841	1.064833	0.003221674
<i>Vogtia glabra</i>	1.912566	0.8051882	0.03151465	0.9159299
<i>Eucalanus</i> sp.	4.657467*	0.1033835	0.6232938	0.06469811
<i>Nauplius</i>	9.24596*	2.180279	4.847778*	0.2153488
<i>Paracalanus</i> sp.	0.0104787	1.007272	0.06946201	0.9844788
<i>Sphaerocapsa cruciate</i>	0.0138113	0.0001501455	0.2459822	0.1311681
<i>Eutintinnus</i> sp.	11.88364*	5.104188*	0.05401933	0.0150741
<i>Helicostomella subulate</i>	17.66668*	4.109958	0.1716282	0.03902014
<i>Tintinnopsis</i> spp.	1.125753	54.54808*	0.4371176	4.502899*
<i>Oikopleura</i> sp.	0.5838282	1.482145	0.07489041	41.85221*

* Values are significant at 95% level of significance.

our samples (not the annual mean). This process also reduces the chance of spatial variability in the ANOVA. As in our observed data set we have not seen such remarkable changes (the chronological patterns for the species abundances are more or less same over the years), hence, we have neglected the variability due to chronological changes.

It is interesting to observe that the zooplanktonic species *Sagitta* spp., *Vogtia glabra*, *Eucalanus* sp. and *Paracalanus* sp. have strong correlation with the dissolved oxygen whereas *Helicostomella subulate* and *Tintinnopsis* spp. have strong correlation with the temperature. Further, we also observe that there exists an association between the following zooplankton–TPP pairs: *Eucalanus* sp.–*Chaetoceros* spp., *Nauplius*–*Chaetoceros* spp., *Nauplius*–*Noctiluca scintillans*, *Eutintinnus* sp.–*Chaetoceros* spp., *Eutintinnus* sp.–*Nitzschia* spp., *Helicostomella subulate*–*Chaetoceros* spp., *Tintinnopsis* spp.–*Nitzschia* spp., *Tintinnopsis* spp.–*Favella franciscana* and *Oikopleura* sp.–*Favella franciscana*. Among them, the association between *Helicostomella subulate*–*Chaetoceros* spp., *Tintinnopsis* spp.–*Nitzschia* spp. and *Oikopleura* sp.–*Favella franciscana* is especially strong.

3. A mathematical model of toxic plankton bloom

Harmful algae blooms are known to have an adverse and destructive impact on marine ecological communities, see the references in Section 1. Although this

issue has been under intensive study for more than two decades, the factors initiating HABs have not always been identified and often not well understood. In particular, the role of the toxins produced by the toxic phytoplankton species has not been properly addressed. Recently, Chattopadhyay et al. (2002a) showed that the toxic substances may enhance bloom termination, however, their role in the bloom initiation remains unclear. In this section, we are going to make an insight, by means of mathematical modelling, into possible mechanisms through which the toxins affect the dynamics of plankton systems and can possibly enhance or initiate harmful plankton blooms.

It should be mentioned that, during the last two decades, a lot of work has been done regarding mathematical modelling of aquatic ecosystems and plankton dynamics (e.g., see Suzuki et al., 2000; Omlin et al., 2001; Reynolds et al., 2001; Edwards et al., 2004; Ludovisi et al., 2005). However, the models taking into account the impact of TPP on the community dynamics (in particular, in order to identify the factors initiating or enhancing HABs) are still rare.

We assume that during the time preceding HAB as well as in its initial stage the environmental conditions such as water temperature and nutrients concentration remain constant so that the phytoplankton intrinsic growth rate can also be regarded as constant. Thus, the main factor controlling the growth of phytoplankton population dynamically is the grazing by zooplankton. In its turn, toxins produced by the harmful phytoplankton species affect the zooplankton species. Considering logistic growth for phytoplankton, we arrive at the following equations:

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K} \right) - \alpha f(P)Z \quad (1)$$

$$\frac{dZ}{dt} = \kappa \alpha f(P)Z - \mu Z - \theta g(P)Z \quad (2)$$

where P is the density of TPP, Z the density of zooplankton, r the phytoplankton per capita growth rate, α the predation rate, κ the food utilization coefficient, μ the zooplankton natural mortality (in the absence of toxins) and $f(P)$ is the predator response function. The additional zooplankton mortality due to the effect of the phytoplankton-produced toxins is taken into account by the last term in Eq. (2), where θ is the rate of toxin production and function $g(P)$ describes the dependence of toxin production on the phytoplankton density. Due to their biological meaning, all the parameters here are positive.

Apparently, the properties of Eqs. (1) and (2) depend on the form of $f(u)$ and $g(u)$. The predator response $f(u)$ is usually assumed to be either Holling II or III. Since many zooplankton species exhibit active foraging behaviour, Holling III type seems to be more appropriate:

$$f(P) = \frac{P^2}{\gamma^2 + P^2} \quad (3)$$

where γ is the half saturation phytoplankton density.

Concerning $g(P)$, recently Chattopadhyay et al. (2002a) assumed that it belongs to the one of the following types:

$$\begin{aligned} \text{(a) } g(P) &= P, & \text{(b) } g(P) &= \frac{P}{\omega + P}, \\ \text{(c) } g(P) &= \frac{P^2}{\omega^2 + P^2} \end{aligned} \quad (4)$$

where ω is the half saturation phytoplankton density. However, subsequent analysis of theoretical stability did not make it possible to give a preference to any one of these parameterizations. Thus, the question about a more appropriate functional form of $g(u)$ remained open. Intuitively, since function $g(P)$ gives additional zooplankton mortality due to the impact of toxins, and the toxin concentration is likely to increase with the concentration P of toxin producing species, function $g(P)$ should be unboundedly increasing for large P rather than exhibiting saturation. The present study aims to establish this fact basing on the analysis of

available field data. To achieve this goal, we have used the data of 10 zooplankton species and 4 toxin producing phytoplankton species, namely *Chaetoceros* spp., *Nitzschia* spp., *Noctiluca scintillans* and *Favella franciscana*, see Tables 1b and 1c.

In our method, we again consider the regression equation:

$$\mathbf{Y} = \mathbf{X}\beta + \varepsilon$$

where \mathbf{Y} denotes the zooplankton species, \mathbf{X} denotes TPP species for different functional forms of $g(P)$, β the coefficient and ε is the error.

Using the same procedure as above, we estimate β and calculate the error sum of squares as $R_0^2 = (\mathbf{Y} - \mathbf{X}\beta)'(\mathbf{Y} - \mathbf{X}\beta)$ denoting them as R_1^2 , R_2^2 and R_3^2 , respectively, for the three forms of $g(P)$. The functional form, which is most suitable to explain the variation in the data should correspond to the smallest error. The values of R_1^2 , R_2^2 and R_3^2 were calculated for those zooplanktons and the TPP species that have been earlier found to be significantly correlated. Since the concentration of the corresponding plankton species is very large, we have scale these values to mean variance for given species. The results are shown in Table 6; they correspond to a hypothetical value $\omega = 0.06$ which was chosen from several other values by “trial-and-error” method in order to reach a better agreement with the field data. (Note that this value is also in a good agreement with the range 0.02–0.1 obtained for the half saturation value by Edwards and Brindley (1999).) Thus, we observe that for the two cases where the inter-species coupling is really strong (i.e., *Tintinnopsis–Nitzschia* and *Oikopleura–Favella*), $g(P) = P$ gives much better result than the other two options.

Now, we are going to consider how toxins can affect the stability of the plankton system. In order to attain certain generality, we choose the following parameterization for the density dependence rather than the simple linear growth given by Eq. (4a):

$$g(P) = \frac{P^{(1+n)}}{(\delta + P)} \quad (5)$$

where n and δ are non-negative parameters. Apparently, the linear case considered above corresponds to $n = 1$, $\delta = 0$.

Table 6
The error sum of squares for significantly correlated zooplankton and TPP species

Functional forms	Zooplankton species	
TPP species: <i>Chaetoceros</i> spp.		
	<i>Eucalanus</i> sp.	<i>Nauplius</i>
Type I	0.390440892	0.331066486
Type II	0.304379498	0.334107123
Type III	0.30517961	0.334826391
TPP species: <i>Nitzschia</i> spp.		
	<i>Eutimninus</i> sp.	<i>Tintinnopsis</i> spp.
Type I	0.346189537	0.151247668
Type II	0.326796696	0.424301318
Type III	0.327013768	0.424451014
TPP species: <i>Noctiluca scintillans</i>		
	<i>Nauplius</i>	
Type I	0.345089917	
Type II	0.329366325	
Type III	0.325543758	
TPP species: <i>Favella franciscona</i>		
	<i>Tintinnopsis</i> spp.	<i>Oikopleura</i> sp.
Type I	0.325795908	0.212643342
Type II	0.337045115	0.393621172
Type III	0.337158977	0.393735486

From (1)–(3), (5) we arrive at the following system describing toxic phytoplankton–zooplankton functioning:

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K} \right) - \alpha \left[\frac{P^2}{\gamma^2 + P^2} \right] Z \tag{6}$$

$$\frac{dZ}{dt} = \kappa\alpha \left[\frac{P^2}{\gamma^2 + P^2} \right] Z - \mu Z - \theta \left[\frac{P^{(1+n)}}{\delta + P} \right] Z \tag{7}$$

The idea of our analysis is as follows. The functioning of phytoplankton–zooplankton community with a relatively low phytoplankton density during the periods preceding harmful algae blooms can be interpreted, in terms of the models (6) and (7), as existence of a stable steady state. Then, the beginning of a bloom can be regarded either as the loss of stability or disappearance of this steady state followed by a significant increase in the TPP density.

The steady states arise, as usual, as the intersection points of the zero-isoclines of the system. From Eq. (6), we immediately obtain:

$$Z = \left(\frac{r}{\alpha} \right) \left(1 - \frac{P}{K} \right) \left[\frac{\gamma^2 + P^2}{P} \right] \tag{8}$$

Since Eq. (7) is linear with respect to Z , corresponding isocline is given by vertical lines situated at $P = P^*$ where P^* is the solutions of the following equation:

$$\kappa\alpha \left[\frac{P^2}{\gamma^2 + P^2} \right] - \left[\mu + \theta \left\{ \frac{P^{(1+n)}}{\delta + P} \right\} \right] = 0 \tag{9}$$

Remarkably, the number of solutions of Eq. (9) depends on parameter values. Fig. 2a shows, for tentative parameter values, the first and second terms of Eq. (9), which, describe zooplankton growth and mortality, respectively. The larger is the value of the toxin production rate θ , the faster is the increase in zooplankton mortality, cf. curves 1–3. It is readily seen that for sufficiently small θ (cf. curve 1 in Fig. 2a) Eq. (9) has two solutions, P_1 and P_2 , which correspond to two steady states in the phase plane of the systems (6) and (7), see Fig. 3 below. However, with the increase in θ the values of P_1 and P_2 gradually approach each other so that the two corresponding steady state finally merge and disappear, cf. Fig. 2b. Moreover, numerical simulations of the systems (6) and (7) show that, while the higher steady state is always unstable (a saddle-point), the lower steady state is stable for sufficiently small toxin production rate but it loses its stability at a certain critical value of θ (marked by point A in Fig. 2b). Since there is no other steady states in this part of the phase plane (it is straightforward to see that the trivial steady state (0,0) is always unstable unless $r < \mu$ which is biologically unrealistic), both the loss of stability and the disappearance of the lower steady state lead to a fast and significant growth of phytoplankton density which tends asymptotically to the upper value $P = K$. This scenario seems to be in a very good agreement with the intuitive expectations on the role of toxins in plankton dynamics and toxic algae blooms.

The curves shown in Fig. 2 are obtained for $n = 1$; however, it is not difficult to see that the properties of the systems (6) and (7) remain similar to those described above for any positive δ and n although actual shape of the curves can be somewhat different.

In order to find out more details about and the system’s stability, Eqs. (6) and (7) are also studied by means of computer simulations. Fig. 3 shows the phase plane structure obtained for $\theta = 0.2$. In this case, there is a large domain (above the curve 4) corresponding to a stable functioning of the system: starting from any initial conditions chosen from above curve 4, the system

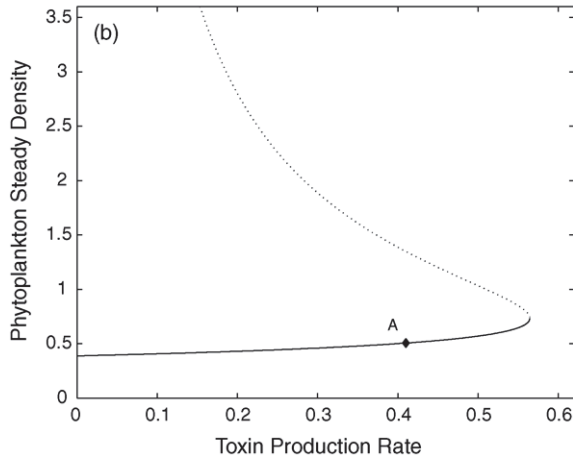
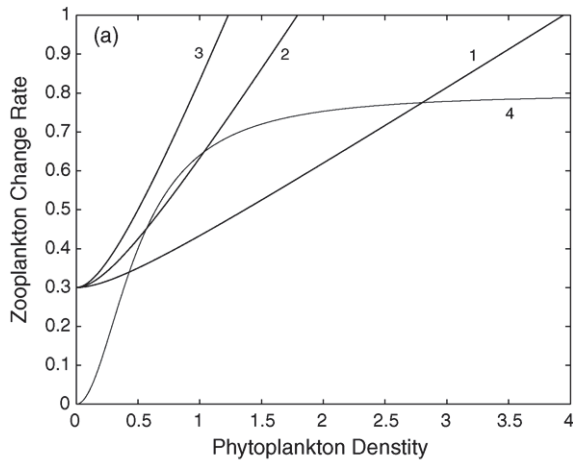


Fig. 2. Changes in the system's stability with an increase in the toxin production rate. (a) The rate of zooplankton mortality due to the impact of toxins (curves 1–3) for different values of θ , curve 1 for $\theta=0.2$, curve 2 for $\theta=0.5$, curve 3 for $\theta=0.8$ and the rate of zooplankton growth (curve 4) given by Holling type II functional response, cf. Eq. (3). Other parameters are: $n=1$, $\kappa=0.8$, $\alpha=1$, $\gamma=0.5$, $\mu=0.3$, $\delta=0.5$. Intersections of the curves correspond to the steady states of the system. (b) The steady state value of phytoplankton density vs. toxin production rate, on the right of point A the steady state is unstable. The dotted curve corresponds to the other steady state, which is always unstable (a saddle-point).

gradually approaches the stable equilibrium, a typical trajectory is shown by curve 5. Thus, in the case that the rate of toxin production is not very high, zooplankton is a controlling factor and a bloom can only begin if its density falls sufficiently low, i.e., below curve 4.

However, an increase in the toxin production rate changes the situation completely. Fig. 4 shows the

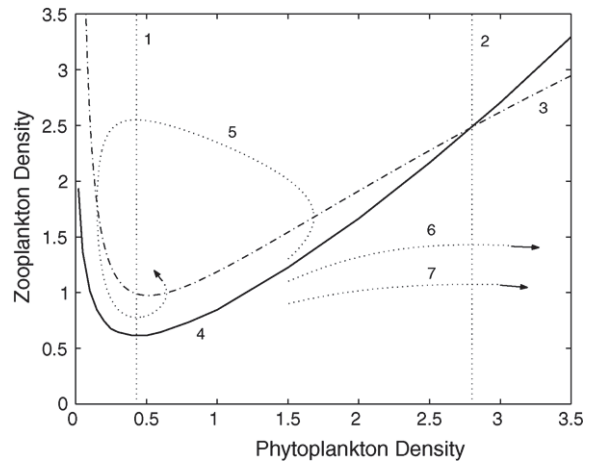


Fig. 3. The phase plane of systems (6) and (7) in the case that there exists a stable steady state. Parameters are: $\theta=0.2$, $n=1$, $K=20$, $r=1$, $\alpha=1$, $\kappa=0.8$, $\gamma=0.5$, $\mu=0.3$, $\delta=0.5$. Curves 1 and 2 show the zero-isoclines for zooplankton ($dZ/dt=0$), curve 3 shows the zero-isoclines for phytoplankton ($dP/dt=0$). The domain above curve 4 is the attraction basin of the stable steady state. Curve 5 gives a typical system trajectory corresponding the stable functioning (no plankton bloom), curves 6 and 7 correspond to the loss of stability (e.g., due to a decrease in the zooplankton abundance) and can be interpreted as the beginning of algae bloom.

phase plane for $\theta=0.5$ when the two steady state still exist but the lower state becomes unstable (the part of the solid curve on the right of point A in Fig. 2b). In this case, there is no domain corresponding to a stable system's functioning and any initial condition initiate algae bloom (a typical system's trajectory is shown by curve 4). Zooplankton is too much depressed by the toxin and cannot control phytoplankton growth any more. The situation stays qualitatively the same for larger values of θ when the steady states disappear, see Fig. 4b obtained for $\theta=0.8$.

4. Concluding remarks

The factors affecting plankton dynamics and the abundance of harmful phytoplankton species have been the subject of intensive research recently. In this paper, we made an attempt to clarify the role of different biological and environmental parameters during harmful plankton blooms and also tried to search a suitable functional form for describing the toxin liberation process. For this purpose, using the analysis of

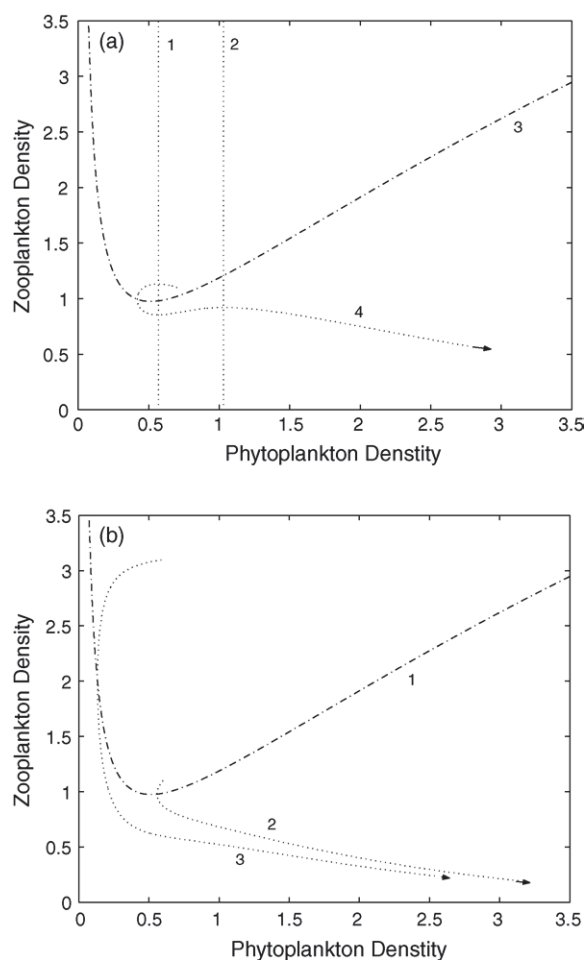


Fig. 4. Evolution of the phase plane with an increase in the toxin production rate θ . (a) The steady states exist but the lower state became unstable ($\theta=0.5$, other parameters are the same as in Fig. 2). (b) The steady states have disappeared ($\theta=0.8$, other parameters are the same as above). In both cases, the system's functioning is unstable which can be interpreted as the beginning of algae bloom.

variance technique in regression model, we checked whether each of the zooplankton species has significant association or correlation with either physical parameters or TPP species as a whole as well as individually. We obtained that there is a strong correlation between some zooplankton species and dissolved oxygen and/or water temperature. Motivated from the work of Chattopadhyay et al. (2002a), we proposed a modified variance measure in order to detect species correlation. We obtained that in some cases there exists a strong correlation between different zooplankton and

TPP species, in particular, for *Tintinnopsis–Nitzschia* and *Oikopleura–Favella*.

Based on the results of statistical analysis, we concluded that the function $g(P)$ which gives additional zooplankton mortality due to the impact of toxins should be unboundedly increasing for large P rather than exhibiting saturation and suggested an appropriate functional form to describe the toxin liberation process by toxin producing phytoplankton. We showed that the relevant choice of $g(P)$ contains a beautiful mechanism of algae bloom via loss of stability when the rate of toxin liberation θ exceeds a certain critical value. Although we are not going to discuss now in detail environmental factors that can possibly lead to an increase in toxin concentration, it seems that one such mechanism can be readily identified. It is well known that the beginning of harmful algae bloom is often preceded by a period of calm weather. Calm weather means low turbidity, which results in poor water ventilation and enhances toxin accumulation. Sufficiently high toxin concentration depresses zooplankton and, according to our findings, triggers algae bloom.

In this paper, we had to restrict our study to the currently available data collected during the last 3 years. From these data, it appears impossible to go into more detail of the plankton bloom mechanism, particularly, to give a reliable estimate of parameters n and δ in Eq. (5) for the toxin production density dependence or to distinguish between the impacts of toxins and low oxygen concentration. Continuing sampling is expected to provide this information as well as to shed light on many other related issues. A better understanding of the bloom phenomena will be helpful for marine ecologists and is hoped to eventually lead to biological control and better environmental management.

It should be mentioned that our present study leaves a few questions open. One of them concerns the impact of higher trophic levels, such as fish and/or carnivorous zooplankton, on the system's stability and system's response to an increase in the toxins concentration. Indeed, it has been shown in our recent work (Morozov et al., 2005) that predation of zooplankton by a higher predator can bring essential changes into the system functioning, although the effects of TPP have not been taken into account. A comprehensive study of the role of TPP in a "three-level" community, as well as in more complicated food webs, will become a focus of our future work.

References

- Anderson, D.M., 1989. Toxic algae blooms and red tides: a global perspective. In: Okaichi, T., Anderson, D.M., Nemoto, T. (Eds.), *Red Tides: Biology, Environmental Science and Toxicology*. Elsevier, New York, pp. 11–21.
- Blaxter, J.H.S., Southward, A.J., 1997. *Advances in Marine Biology*. Academic Press, London, 386 pp.
- Buzas, M.A., 1970. Spatial homogeneity: statistical analyses of unispecies and multispecies populations of Foraminifera. *Ecology* 51, 874–879.
- Chattopadhyay, J., Sarkar, R.R., Mandal, S., 2002a. Toxin producing plankton may act as a biological control for planktonic blooms—field study and mathematical modelling. *J. Theor. Biol.* 215, 333–344.
- Chattopadhyay, J., Sarkar, R.R., Elabdllaoui, A., 2002b. A delay differential equation model on harmful algal blooms in the presence of toxic substances. *IMA J. Math. Appl. Med. Biol.* 19, 137–161.
- Cochran, W.G., 1950. The comparison of percentages in matched samples. *Biometrika* 37, 256–266.
- Connell, J., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 108, 207–228.
- Conover, W.J., 1980. *Practical Nonparametric Statistics*, second ed. Wiley, New York, 212 pp.
- Diamond, J.M., May, R.M., 1977. Species turnover rates on islands: dependence on census interval. *Science* 197, 266–270.
- Edwards, A.M., Brindley, J., 1996. Oscillatory behaviour in three component plankton population model. *Dyn. Stab. Syst.* 11, 347–370.
- Edwards, A.M., Brindley, J., 1999. Zooplankton mortality and the dynamical behaviour of plankton population models. *Bull. Math. Biol.* 61, 303–339.
- Edwards, A.M., Platt, T., Sathyendranath, S., 2004. The high-nutrient, low-chlorophyll regime of the ocean: limits on biomass and nitrate before and after iron enrichment. *Ecol. Model.* 171, 103–125.
- Hallegraeff, G.M., 1993. A review of harmful algae blooms and the apparent global increase. *Phycologia* 32, 79–99.
- Hastings, A., 1987. Can competition be detected using species co-occurrence data? *Ecology* 68, 117–123.
- Ives, J.D., 1987. Possible mechanism underlying copepod grazing responses to levels of toxicity in red tide Dinoflagellates. *J. Exp. Mar. Biol. Ecol.* 112, 131–145.
- Järvinen, O., 1979. Geographical gradients of stability in European land bird communities. *Oikos* 38, 51–69.
- Kirk, K., Gilbert, J., 1992. Variations in herbivore response to chemical defenses: zooplankton foraging on toxic cyanobacteria. *Ecology* 73, 2208.
- Lam, C.W.Y., Ho, K.C., 1989. Red tides in Tolo Harbor Hong Kong. In: Okaichi, T., Anderson, D.M., Nemoto, T. (Eds.), *Red Tides: Biology, Environmental Science and Toxicology*. Elsevier, New York, pp. 49–52.
- Ludovisi, A., Minozzo, M., Pandolfi, P., Illuminata Taticchi, M., 2005. Modelling the horizontal spatial structure of planktonic community in Lake Trasimeno (Umbria, Italy) using multivariate geostatistical methods. *Ecol. Model.* 181, 247–262.
- Lloyd, M., 1967. Mean crowding. *J. Anim. Ecol.* 36, 1–30.
- Malchow, H., Petrovskii, S.V., Medvinsky, A.B., 2002. Numerical study of plankton-fish dynamics in a spatially structured and noisy environment. *Ecol. Model.* 149, 247–255.
- Malchow, H., Medvinsky, A.B., Petrovskii, S.V., 2004. Patterns in models of plankton dynamics in a heterogeneous environment. In: Seuront, L., Strutton, P.G. (Eds.), *Handbook of Scaling Methods in Aquatic Ecology: Measurement, Analysis, Simulation*. CRS Press, Boca Raton, pp. 401–410.
- Mathews, L., Brindley, J., 1996. Patchiness in plankton populations. *Dyn. Stab. Syst.* 12, 39–59.
- McCulloch, C.E., 1985. Variance tests for species association. *Ecology* 66, 1676–1681.
- Morozov, A.Y., Petrovskii, S.V., 2000. Mathematical modeling of the initial stage of a “red tide” accounting for combined effect of various factors. *Oceanology* 40, 385–392.
- Morozov, A.Y., Nezlin, N.P., Petrovskii, S.V., 2005. Invasion of a top predator into epipelagic ecosystem can bring a paradoxical top-down trophic control. *Biol. Invasion* 7, 845–861.
- Nejstgaard, J.C., Solberg, P.T., 1996. Repression of copepod feeding and fecundity by the toxic haptophyte *Prymnesium patelliferum*. *Sarsia* 81, 339–344.
- Nielsen, T.G., Kiørboe, T., Bjørnsen, P.K., 1990. Effects of a *Chrysochromulina polylepis* sub surface bloom on the plankton community. *Mar. Ecol. Progr. Ser.* 62, 21–35.
- Omlin, M., Reichert, P., Forster, R., 2001. Biogeochemical model of Lake Zürich: model equations and results. *Ecol. Model.* 141, 77–103.
- Pielou, E.C., 1972. 2^k contingency tables in ecology. *J. Theor. Biol.* 34, 337–352.
- Pielou, D.P., Pielou, E.C., 1968. Association among species of infrequent occurrence: the insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. *J. Theor. Biol.* 21, 202–216.
- Richardson, K., 1997. Harmful or exceptional phytoplankton blooms in the marine ecosystem. In: Blaxter, J.H.S., Southward, A.J. (Eds.), *Advances in Marine Biology*, vol. 31. Academic Press, London, pp. 301–385.
- Pitchford, J.W., Brindley, J., 1998. Intraspecific predation in simple predator-prey models. *Bull. Math. Biol.* 60, 937–953.
- Prakash, A., 1987. Coastal organic pollution as a contributing factor to red tide development. *Rapports et Proces-verbaux des Reunions du Conseil Permanent International pour l'Exploration de la Mer* 187, 61–65.
- Rao, C.R., 1965. *Linear Statistical Inference and its Applications*. John Wiley, London, 324 pp.
- Reynolds, C.S., Irish, A.E., Elliott, J.A., 2001. The ecological basis for simulating phytoplankton responses to environmental change (PROTECH). *Ecol. Model.* 140, 271–291.
- Robson, D.S., 1972. Statistical tests of significance. *J. Theor. Biol.* 34, 350–352 (appendix to a paper by E.C. Pielou (1972)).
- Sarkar, R.R., Chattopadhyay, J., 2003. Occurrence of planktonic blooms under environmental fluctuations and its possible control mechanism—mathematical models and experimental observations. *J. Theor. Biol.* 224, 501–516.
- Schluter, D., 1982. Distribution of Galapagos ground finches along an altitudinal gradient: the importance of food supply. *Ecology* 63, 1504–1517.

- Schluter, D., 1984. A variance test for detecting species associations with some example applications. *Ecology* 65, 998–1005.
- Schoener, T., 1983. Field experiments on interspecific competition. *Am. Nat.* 122, 240–285.
- Simberloff, D.S., Connor, E.F., 1981. Missing species combinations. *Am. Nat.* 118, 215–239.
- Smayda, T., 1990. Novel and nuisance phytoplankton blooms in the sea: evidence for a global epidemic. In: Graneli, E., Sundström, B., Edler, L., Anderson, D.M. (Eds.), *Toxic Marine Phytoplankton*. Elsevier, New York, pp. 29–40.
- Sournia, A., 1995. Red tide and toxic marine phytoplankton of the world ocean: an enquiry into biodiversity. In: Lassus, P. (Ed.), *Harmful Marine Algal Blooms*. Lavoisier/Intercept, Paris, pp. 103–112.
- Steele, J.H., Henderson, E.W., 1993. The significance of interannual variability. In: Evans, G.T., Fasham, M.J.R. (Eds.), *Towards a Model of Ocean Biogeochemical Processes*. Springer-Verlag, Berlin, pp. 237–260.
- Stoermer, E.F., Smol, J.P., 1999. *The Diatoms*. Cambridge University Press, Cambridge UK, 246 pp.
- Strong, D.R., Simberloff, D., Abele, L.G., Thistle, A.B. (Eds.), 1984. *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton NJ.
- Suzuki, M., Sagehashi, M., Sakoda, A., 2000. Modelling the structural dynamics of a shallow and eutrophic water ecosystem based on mesocosm observations. *Ecol. Model.* 128, 221–243.
- Taylor, W.D., 1979. Sampling data on the bacterivorous ciliates of a small pond compared to neural models of community structure. *Ecology* 60, 876–883.
- Tomas, C.R., 1997. *Identifying Marine Diatoms and Dinoflagellates*. Academic Press, San Diego, 284 pp.
- Uye, S., 1986. Impact of copepod grazing on the red tide flagellate *Chattonella antiqua*. *Mar. Biol.* 92, 35.
- Wiens, J.A., Rotenberry, J.T., 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecol. Monogr.* 51, 21–41.