



# Do phytoplankton communities evolve through a self-regulatory abundance–diversity relationship?

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## ABSTRACT

A small group of phytoplankton species that produce toxic or allelopathic chemicals has a significant effect on plankton dynamics in marine ecosystems. The species of non-toxic phytoplankton, which are large in number, are affected by the toxin-allelopathy of those species. By analysis of the abundance data of marine phytoplankton collected from the North-West coast of the Bay of Bengal, an empirical relationship between the abundance of the potential toxin-producing species and the species diversity of the non-toxic phytoplankton is formulated. A change-point analysis demonstrates that the diversity of non-toxic phytoplankton increases with the increase of toxic species up to a certain level. However, for a massive increase of the toxin-producing species the diversity of phytoplankton at species level reduces gradually. Following the results, a deterministic relationship between the abundance of toxic phytoplankton and the diversity of non-toxic phytoplankton is developed. The abundance–diversity relationship develops a unimodal pathway through which the abundance of toxic species regulates the diversity of phytoplankton. These results contribute to the current understanding of the coexistence and biodiversity of phytoplankton, the top-down vs. bottom-up debate, and to that of abundance–diversity relationship in marine ecosystems.

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## 1. Introduction

Understanding the relationship between ecosystem function and community diversity is a central theme in terrestrial and aquatic ecology. However, unlike plants and herbivores in the terrestrial world, our knowledge of biodiversity patterns for plankton community is limited (Irigoién et al., 2004). Due to the fundamental unpredictability of plankton dynamics, an extreme diversity of phytoplankton species is observed in aquatic ecosystems. Driven by an array of different mechanisms, a non-equilibrium condition prevails in plankton community, which leads to the coexistence of taxonomically diverse species under a limited variety of resources (Hutchinson, 1961; Richerson et al., 1970; review by Roy and Chattopadhyay, 2007a). Apart from the external factors, pressures related to community dynamics itself play key role in regulating the diversity of phytoplankton. Example are: the resource competition among the species that generates oscillation and chaos (Huisman and Weissing, 1999) and the adaptive divergence in pigment concentration of different species (Stomp et al., 2004). In some cases, the biomass–diversity relationship for aquatic ecosystems shows similarity with that for terrestrial ecosystems (Irigoién et al., 2004).

However, in other cases this relationship is dissimilar from that in terrestrial and some benthic ecosystems (Duarte et al., 2006). Moreover, the cause–effect relationship between community structure (for which species diversity is a measure) and community function (for which production is a measure) is still debated (Duarte et al., 2006). In view of these studies, the question remains unanswered as to how a universally accepted relationship between the biomass and the diversity pattern at species level can be established.

Phytoplankton species have the ability to liberate some “toxic” or “allelopathic” agents (e.g., Arzul et al., 1999; review, Cembella, 2003). In general the number of toxic-phytoplankton species is remarkably smaller than the number of other phytoplankton that are non-toxic (NTP) (review, Cembella, 2003); so far, only 30–50 species of phytoplankton have been identified as toxic. Laboratory experiments and field studies have claimed that, irrespective of their taxonomic variety, the presence of toxic species has a significant impact on the overall plankton dynamics (Ives, 1961; Nielsen et al., 1990; Kozłowski-Suzuki et al., 2003; Roy et al., 2006). It is well known that toxic substances released by toxin-producing phytoplankton (TPP) have a significant inhibitory effects on the grazer zooplankton (e.g., Kirk and Gilbert, 1992).

A number of recent experimental as well as field studies have established that the toxic chemicals released by TPP potentially act as allelopathic agents among the plankton species (Arzul et al., 1999; Rengefors and Legrand, 2001; Granéli and Johansson,

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2003; Fistarol et al., 2004). Due to this allelopathic effect, the presence of toxic phytoplankton reduces the competitive disadvantage among phytoplankton species (Hulot and Huisman, 2004; Sole et al., 2005). Further, Roy and Chattopadhyay (2007b) have reported that 'toxin-allelopathy' due to TPP can prevent competitive exclusion among the phytoplankton species. When toxin-allelopathy of a third species mediates the interaction between two non-toxic phytoplankton, the weak competitor that would otherwise be excluded, coexists stably with the strong competitor (Roy and Chattopadhyay, 2007b). Thus, the complex allelopathic effect of TPP has a potential role in modulating the community structuring of phytoplankton species. These studies have opened the scope for investigating a potential cause–effect relationship between abundance of toxin-producing species and the community structure at species level of the other phytoplankton species.

The goal of this article is to find based on analysis of a set of primary field data, a possible deterministic empirical relationship between the abundance of the potential toxin-producing phytoplankton and the community diversity at species level of those plankton that are large in number but not toxin producing (termed as non-toxic phytoplankton, NTP). We develop this relationship to discuss its implications in the context of understanding the regulation of phytoplankton diversity. The results contribute to the current understanding in relation to the community structure and community functioning of phytoplankton.

## 2. Method

### 2.1. Data collection

The data used here was collected in during a regular monitoring and identification of marine plankton population in the North-West coast of the Bay of Bengal. Frequency of the sampling in this area was every 2 weeks except the months of September and October. The details of the study area and sampling procedure have been reported elsewhere (e.g., Chattopadhyay et al., 2002; Roy et al., 2006).

### 2.2. Samples identified

A total of 115 species of phytoplankton has been identified in the water samples collected from the study area. These phytoplankton include 65 species of diatoms, 19 of green algae, 9 of cyanobacteria and 22 of dinoflagellates. The abundance of phytoplankton species was expressed in number of cells per liter (nos./l). A significant number of species of phytoplankton that have the ability to produce toxic or inhibitory compounds has been identified. This includes 13–15 species of phytoplankton known as either harmful or toxin producers (Chattopadhyay et al., 2002). The total list of those species (which has already been reported in Chattopadhyay et al., 2002; Roy et al., 2007) is the following: *Phaeocystis* sp., *Nitzschia* sp., *Favella* sp., *Cerataulina* sp., *Chaetoceros* sp., *Skeletonema costatum*, *Thalassiosira* sp., *Skujella thiebautii*, and the dinoflagellate group including *Noctiluca scintillans*, *Dinophysis* sp., *Peridinium* sp. and *Prorocentrum* sp. Further to mention that our sampling procedure did not include the identification of toxins from these species. Thus, instead of categorizing the species strictly based on their toxin liberation rate, we combined under the TPP group those species that are potentially toxin producers (either toxic or harmful). For the present study, we consider the sample data of plankton species for the period 2002–2004. The time series of TPP and NTP (based on the categorization mentioned above) for this particular time period has already been analyzed using a vector auto-regression model (Roy et al., 2007). The present study is based on the data set considered in Roy et al. (2007), and in categorizing the TPP and NTP groups we remain entirely consistent with that study.

### 2.3. Statistical analysis

Abundance data of phytoplankton species identified were taken here for statistical analysis. Correlations and other calculations were done using the software MATLAB. The species diversity of a community consisting of  $N$  species was measured according to Shannon's diversity index (see for details, Rosenzweig, 1995) given by the following equation:

$$X = -\sum_{i=1}^N p_i \log(p_i) \quad (1)$$

where  $p_i = (n_i / (\sum_{i=1}^N n_i))$  represents the fraction of the abundance ( $n_i$ ) of species  $i$  with respect to the total abundance ( $\sum_{i=1}^N n_i$ ). However, the result of the overall analysis would be similar if any other measure of species diversity were used.

To detect the significant changes in the diversity value, when considered against the abundance of toxic species, a change-point analysis was performed following the approach of Taylor (2000). Suppose  $X_i$ ,  $i = 1, 2, \dots, T$  represent the values of diversities corresponding to TPP abundances (sorted in ascending order) observed in  $T$  sampling times. From these data, the cumulative sums (CUSUM)  $S_i$ ,  $i = 0, 1, \dots, T$  were calculated using the formula  $S_i = S_{i-1} + (X_i - \bar{X})$ ,  $i = 1, 2, \dots, T$ , where  $\bar{X} = (1/T) \sum_{i=1}^T X_i$  is the average of  $X_i$ . A change was first detected using an estimator with the magnitude of the change given by  $S_{\text{diff}} = S_{\text{max}} - S_{\text{min}}$ , where  $S_{\text{max}} = \max_{i=0, \dots, T} \{S_i\}$  and  $S_{\text{min}} = \min_{i=0, \dots, T} \{S_i\}$ . A confidence interval of the change is determined for apparent change by performing a bootstrap analysis and using the formula: confidence level = [(number of bootstrap for which  $S_{\text{diff}}^0 < S_{\text{diff}}^0 / \text{number of bootstrap sample performed}] \times 100\%$ . The whole analysis was carried out using the software package Change-Point Analyzer (Taylor, 2000).

Non-linear regression analysis of the proposed model with the field data was performed using the MATLAB software.

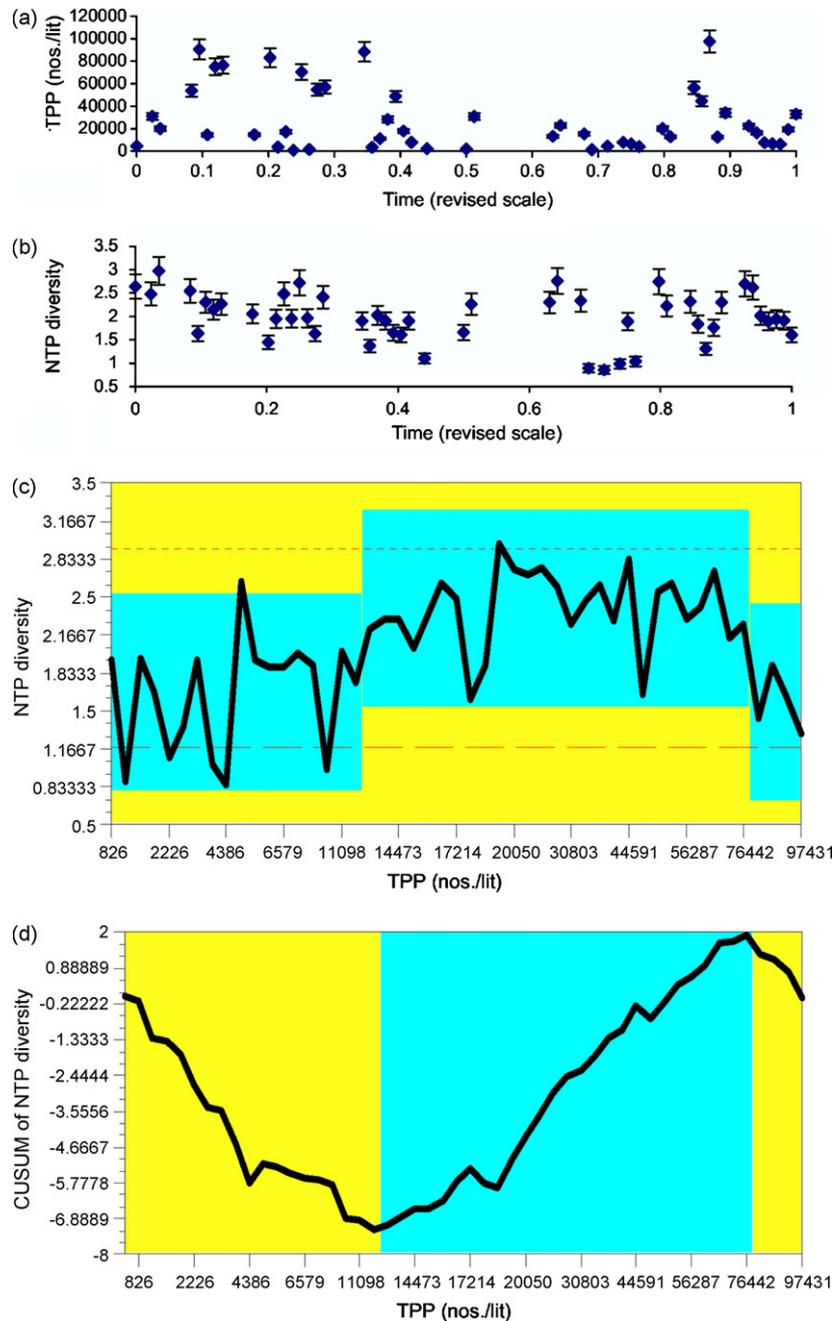
## 3. Phytoplankton diversity pattern and the abundance of potential TPP group

Using the abundance data of the NTP group containing seventy eight species, the well-known Shannon diversity index is calculated as a measure of NTP diversity at species level. The abundance of TPP shows fluctuations over time (Fig. 1(a)), and the diversity of NTP group also exhibits fluctuating pattern (Fig. 1(b)). However, the pattern of variation of NTP diversity against TPP abundance is non-monotonic, and the variation depicts certain changes in the trend of correlation with TPP abundance (Fig. 1(c)).

To detect significant changes in the diversity pattern of NTP species with TPP abundance, we perform a change-point analysis (Taylor, 2000). The ranges of TPP abundance under which the significant changes both in the value of NTP diversity and the corresponding cumulative sum (see, Section 2) occur are obtained as different shades of the output (Fig. 1(c) and (d)). The analysis detects two significant changes in the diversity of NTP species (Fig. 1(c) and Table 1). The first point where a change occurs is at TPP abundance 12,844 (nos./l) with 99% level of confidence interval (11,098 and 14,473 nos./l) (Table 1). A second significant change is detected at TPP abundance 76,442 nos./l (with 98% level of confidence interval (70,290 and 83,043)). For the first change point the diversity increases from 1.6559 to 2.3971, whereas the diversity decreases from 2.3971 to 1.5718 for the second one (Table 1).

Based on the change-point analysis, the TPP values may be categorized in to three ranges (Table 1). In the sampling the abundance of TPP is very likely (probability 0.92) to remain below a very high value (biomass up to 80,000 nos./l, see Table 1). Further, their abundance may reach very high values ( $> 80,000$  nos./l) with a low probability (probability 0.08) – a situation beyond the second change point detected (Fig. 1(c)). Very high values of toxic species may lead to harmful algal blooms (HAB) (Hallegraeff, 1993). If the abundance of TPP lies either below the first change point or below the second change point, the correlation between TPP abundance and NTP diversity is significantly positive ( $r = 0.395$ ,  $P < 0.05$  and  $r = 0.495$ ,  $P < 0.0005$ , respectively, Table 2). However, the correlation pattern changes from positive to negative ( $r = -1.945$ ,  $P = 0.07$ , Table 2) if the abundance of TPP always lies above the second change point (in our data, if more than 80,000 nos./l).

Because harmful algal blooms hamper significantly most phytoplankton species leaving only one or a few of the blooming species to persist at a very high biomass (Hallegraeff, 1993), the negative trend of NTP diversity at a very high level of TPP biomass may be expected. However, the change of the diversity pattern (Table 1) and the corresponding correlation analysis (Table 2) suggest that, if the abundance of the toxic species does not go beyond a very high value, the diversity of non-toxic species is favoured significantly by



**Fig. 1.** (a) TPP abundance over the observed time point re-scaled to (0–1). (b) NTP diversity over the revised time scale. (c) and (d) Detection of significant changes of NTP diversity with TPP abundance by change-point analysis. The figures are the output of the software Change-point Analyzer. Change of shades indicate the the point where a significant change has occurred. (c) Significant changes in NTP diversity, (d) significant changes in the corresponding cumulative sum calculated using the diversity values (details in Section 2). Two significant change in NTP biomass is detected, the first one at TPP biomass 12844 nos./l where NTP diversity changes from 1.6559 to 2.3971, and the second one at TPP biomass 76442 nos./l where NTP diversity changes from 2.3971 to 1.5718. The details of these changes is given in Table 1.

**Table 1**  
Significant changes in NTP diversity obtained from change-point analysis. Confidence level for inclusion in Table was 90% and the confidence interval was 95%. Bootstraps = 1000, and sampling without replacement. Categories are based on the ranges of TPP values between two consecutive change points.

Change at TPP abundance (nos./l)	Confidence interval (nos./l)	Confidence level	Diversity from	Diversity to
12,844	(11,098, 14,473)	99%	1.6559	2.3971
76,442	(70,290, 83,043)	98%	2.3971	1.5718
Category	TPP abundance ( $x$ ) (nos./l)	Probability of TPP occurrence	Cumulative probability	NTP diversity Mean $\pm$ S.D.
1	<13,000	0.39	0.39	1.6857 $\pm$ 0.5013
2	13,000–80,000	0.53	0.92	2.4039 $\pm$ 0.3388
3	>80,000	0.08	1.0	1.5718 $\pm$ 0.2579

**Table 2**

Results of regression analysis. S.D. – standard deviation; d.f. – degrees of freedom. The parameters of the proposed model were estimated through non-linear regression using Matlab.

Linear regression		
Range of TPP abundance (x) nos./l	r	P
<13,000	0.395	<0.045
< 80,000	0.495	< 0.0005
> 80,000	-1.945	0.07
All	0.151	0.149
Non-linear regression		
Proposed model	$y = y_m \left( 1 - \exp\left(\frac{-Ax}{y_m}\right) \right) \exp\left(\frac{-Bx}{y_m}\right)$	
Total species	78	
$y_m$	4.357	
$A$	$0.32884 \times 10^{-3}$	S.D. $\pm 0.32 \times 10^{-5}$ , $P < 0.001$
$B$	$0.49707 \times 10^{-4}$	S.D. $\pm 0.51 \times 10^{-5}$ , $P < 0.001$
d.f	47	
$R$	0.646	
$F$	76.57	
		$P < 0.001$
		$P < 0.001$

the toxic species (also reported in Roy et al., 2007). Thus, the effects of TPP abundance is to increase the diversity of the NTP species up to a certain level, and to decrease it beyond that.

#### 4. A deterministic relationship to predict variation of NTP diversity with TPP

The pattern of diversity change of NTP species and the corresponding correlation analysis suggests that a deterministic relationship between the abundance of the TPP species and the diversity of NTP species is derivable under the following two assumptions: (i) under normal conditions (i.e., non-blooming condition), an increment in the biomass of TPP species increases the diversity of NTP species to a maximum saturation level and (ii) diversity of NTP suffers from a gradual inhibition when the TPP species exerts a massive dominance in the system. And given a value of TPP biomass, the diversity of NTP could be determined by a resultant of those two effects.

Suppose that the maximum diversity that a combination of  $N$  species may achieve is given by  $y_m$ . From the first assumption, given a level of TPP abundance (say  $x$ , an independent variable) the diversity of NTP species (say  $y$ , dependent on  $x$ ) may be written as follows:

$$y = y_m \left( 1 - \exp\left(\frac{-Ax}{y_m}\right) \right). \quad (2)$$

The parameter  $A$  may be defined as a measure of the increment in diversity of NTP species due to an increase in unit abundance of TPP. It follows from the above equation that under normal conditions, i.e., non-blooming conditions, the diversity of NTP species will gradually increase with TPP abundance to a saturation level  $y_m$ .

To include the inhibition effect of the toxic species that may be effective significantly at a very high abundance (i.e., at blooming conditions), we introduce in Eq. (2) a gradually decreasing term:  $\exp(-Bx/y_m)$ . The parameter  $B$  may be defined as a measure of the allelopathic inhibition of TPP on the diversity of NTP species. The combined effect of TPP abundance on the diversity of NTP can be expressed as follows:

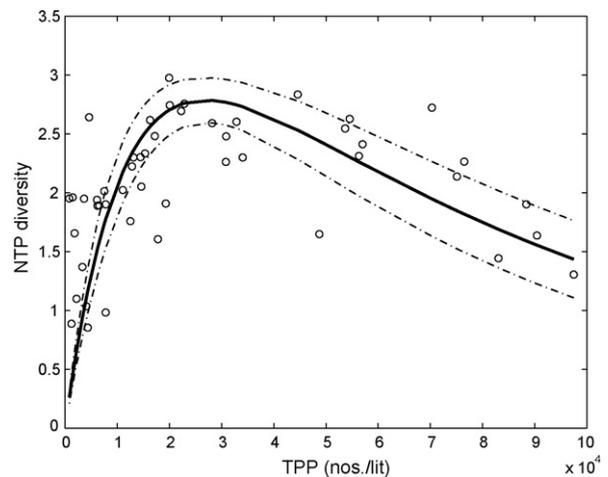
$$y = y_m \left( 1 - \exp\left(\frac{-Ax}{y_m}\right) \right) \exp\left(\frac{-Bx}{y_m}\right). \quad (3)$$

It is clear from Eq. (3) that, if the abundance of TPP ( $x$ ) is low, the effect of allelopathic inhibition is negligible, and the corresponding abundance–diversity relation leads to Eq. (2). However, for high values of TPP abundance ( $x$ ) the diversity value ( $y$ ) decreases exponentially.

The TPP abundance and NTP diversity relationship (3) is analogous to the well-known light intensity and photosynthesis relationship with photo-inhibition effect (Platt et al., 1980). The analogy of the structure of functional form (3) with that of the Platt equation might be suggestive to convey that the resultant effect of toxin-allelopathy due to TPP in determining the diversity pattern of NTP species is similar to that of the light intensity in regulating the primary production.

##### 4.1. Estimation of parameters of abundance (TPP)–diversity (NTP) relationship

The parameters of the abundance–diversity relationship (3) can be estimated from the abundance data of the species using the non-linear regression method (Marquardt, 1963). The Shannon diversity index (see, Section 2) has a maximum value if ( $n_1 = n_2 = \dots = n_N = 1/N$ ), and  $y_m = \log(N)$ , where  $N$  = number of NTP species. Using the field data we estimate the parameters of the proposed deterministic relationship (Table 2). The non-linear regression analysis gives a statistically significant fit of the model with the field data (Fig. 2 and Table 2). The results of the non-linear analysis provide support for the relationship proposed between the TPP abundance



**Fig. 2.** Non-linear regression with the abundance of TPP- and diversity of NTP-relationship predicted as in model (2). The Shannon diversity of NTP species is fitted to the abundance (nos./l) of TPP. The solid line represents the fitted model with the data presented in open circles. The dashed lines depict the predicted model at 95% confidence level. The estimates of the model parameters with the respective confidence interval are given in Table 2.

with the NTP diversity. The values of the parameters  $A$  and  $B$  estimated are of order  $10^{-4}$  and  $10^{-5}$ , respectively (Table 2). In a different context, Sole et al. (2005) reported that the best fit of the allelopathy parameter that provided a good agreement between their theoretical interaction model and an experimental data was in the range ( $10^{-5}$  to  $10^{-6}$ ). Thus, numerical order of the best-fit estimate of the allelopathic-inhibition parameter ( $B$ ) in our proposed TPP-abundance – NTP-diversity relationship (3) is in good agreement with that of the allelopathic parameter of the theoretical interaction model analyzed by Sole et al. (2005).

## 5. Discussion

Given a relationship between the species biomass and the community diversity, either for a terrestrial or for an aquatic ecosystem, a question likely to follow immediately is, “which is the cause and which is the effect?” (Duarte et al., 2006). In connection to the phytoplankton community, our recent studies (Roy et al., 2006; Roy and Chattopadhyay, 2007a, b; Roy et al., 2007) claim that the group of TPP species are potential candidate for maintaining the community diversity. However, how the diversity of the phytoplankton species are actually related with the abundance level of the potential TPP species was unknown so far. Relying on a set of field data for phytoplankton community, we develop a deterministic cause–effect relationship between the abundance of TPP and the species diversity of NTP. The abundance–diversity relationship developed includes the abundance of TPP as a ‘cause’ and the diversity of NTP species as an ‘effect’. That the change of species diversity in this case is indeed due to the TPP abundance is further inferred from Roy et al. (2007) – one of our associated studies in this context with the same data set. As we have mentioned before, the samplings were done as a time series, and not that the ones with high cell content sampled in a row. Using a vector auto-regression model Roy et al. (2007) analyzed the time series of TPP and NTP (for the same sampling period) and inferred that the abundance of TPP essentially is a significant ‘cause’ for modulating competitive interaction among NTP group.

Our present approach provides with a concrete functional relationship of the effects of TPP abundance on the NTP diversity. The unimodal structure of the relationship developed conveys that a moderate abundance of TPP species is desirable most for enhancing the diversity of phytoplankton at the species level. When the growth-limiting conditions (e.g., nutrient) increase rapidly, the TPP species are likely to gain an ‘extra’ advantage to form a bloom or bloom-like situation, and the phytoplankton diversity diminishes. On the other hand, for a very low nutrient condition the TPP species is likely to decrease, and the weak species of NTP would be excluded. Under this condition, the species diversity of phytoplankton decreases. Thus, the abundance–diversity relationship represents a self-regulatory pathway, where the abundance of TPP species always drives the species diversity of phytoplankton to a maximum.

Combined with the previous studies (e.g., Roy et al., 2007), the results here highlight that in general the dynamics and diversity of phytoplankton at species level is potentially regulated by the group of toxin-producing phytoplankton. Evolving as a part of the plankton community, the TPP species significantly controls the competitive interaction of other phytoplankton through toxin-allelopathy (Roy and Chattopadhyay, 2007b). And due to that effect the species diversity of the entire phytoplankton community is potentially maintained to a reasonable extent. In natural waters, several other factors – such as grazing and physical forcing – play crucial role in determining the species abundance of phytoplankton. However, while formulating this self-regulatory relationship,

we have used a set of direct field-data – a black-box output of numerous top-down and bottom-up effects of the natural water. Thus, the outcomes are independent of the structure and limitations embedded in most theoretical models.

Whether the top-down or the bottom-up effect is of greater importance for the regulation of a trophic level and species diversity is debated over the years (Hairston et al., 1960; Hunter et al., 1997). Concentrating on the field-collected samples, the current results propose a mechanism different from these two effects. It is noteworthy that the data set considered here is restricted only to the species-level interactions among the phytoplankton species belonging to a common trophic level. The results suggest that the coevolution of the phytoplankton species in natural waters under a limiting nutrient (bottom-up) is functionally modulated by toxin-allelopathy – an effect created and regulated in this case by the species of a common trophic level. This means that, beyond the top-down or bottom-up effects, it is a self-regulation through an appropriate species composition that acts as a powerful candidate for determining the community structuring and the species diversity of phytoplankton. In other words, toxin-allelopathy acts as a strong self-regulatory strategy of the phytoplankton community that functions effectively in maintaining the species diversity. Considering the wider implication of the result, the generality of this mechanism merits further experimental investigations.

Due to the complexity of dealing with natural phytoplankton communities, we had to make some simplified assumptions that need attention for further studies. While some toxic phytoplankton have been shown to have allelopathic effect on other phytoplankton, most phytoplankton (toxic or non-toxic) have not yet been tested for their allelopathic effects. Some laboratory experiments could give a clearer picture about the biochemical activities of individual species, thus on community diversity. Further, the results presented here are based on the sampling restricted to a specific zone, and the sampling points are limited. For example, the maximum cells/l in this area during the sampling period is about 100,000, and we did not observe during our sampling period too many occasions when the number of cells/l is higher than 80,000. These observations may not be sufficient to capture the essence of other locations, especially with regard to the exceptional high values of phytoplankton abundance. However, according to our study, when the abundance of TPP is far beyond the maximum value observed (in our sampling site), the diversity of NTP is likely to decrease. It would be interesting to validate the generality of this result for the other parts of the world ocean. Finally, since the species diversity tend to be different in temperate and cold waters, it would be worth testing the applicability of our results in these conditions. In short, the results presented here might open scope for a large scale sampling over the global ocean to address the issues concerned.

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