

Author version: *Environ. Monit. Assess.*, vol.182; 2011; 15–30

## **Dinoflagellate community structure from the stratified environment of the Bay of Bengal, with special emphasis on Harmful Algal Bloom species**

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**ABSTRACT** Harmful Algal Blooms have been documented along the coasts of India and the ill effects felt by society at large. Most of these reports are from the Arabian Sea, west coast of India whereas its counterpart, the Bay of Bengal (BOB) has remained unexplored in this context. The unique characteristic features of the BOB, such as large amount of riverine fresh water discharges, monsoonal clouds, rainfall and weak surface winds make the area strongly stratified. In this study, 19 potentially harmful species which accounted for approximately 14% of the total identified species (134) of dinoflagellates were encountered in surface waters of the BOB during November 2003 - September 2006. The variations in species abundance could be attributed to the seasonal variations in the stratification observed in the BOB. The presence of frequently occurring HAB species in low abundance ( $\leq 40$  cell  $L^{-1}$ ) in stratified waters of the BOB may not be a growth issue. However, they may play a significant role in the development of pelagic seed banks, which can serve as inocula for blooms if coupled with local physical processes like eddies and cyclones. The predominance of *Ceratium furca* and *Noctiluca scintillans*, frequently occurring HAB species during cyclone-prone seasons, point out their candidature for HABs.

**Keywords** *Ceratium furca* • *Noctiluca scintillans* • Bay of Bengal • Stratification • Cyclones • Eddies

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## Introduction

Harmful Algal Blooms (HABs) are natural phenomena; historical records indicate their occurrence long before the advent of human activities in coastal ecosystems. Recent surveys have demonstrated a dramatic increase and geographic spread in HAB events in the last few decades (Anderson 1989; Smayda 1990; Hallegraeff 1993). Thus, knowledge of the present geographic distribution and seasonal fluctuations in HAB species is important to understand globally spreading HAB events (GEOHAB 2001). In fact, Hallegraeff (2010) has reported that unpreparedness for such significant range expansions or spreading of HAB problems in poorly monitored areas will be one of the greatest problems for human society in the future.

Among the total marine phytoplankton species, approximately 7% are capable of forming algal blooms (red tides) (Sournia 1995); dinoflagellates are the most important group producing toxic and harmful algal blooms (Steidinger 1983, 1993; Anderson 1989; Hallegraeff 1993) accounting for 75% of the total HAB species (Smayda 1997).

Blooms result from a coupling mechanism involving physical, chemical and biological factors. Though dynamics of blooms is complex, the role or mechanism of chemical and biological factors are now reasonably understood (Fistarol et al. 2004; Solé et al. 2006; GEOHAB 2006; Adolf et al. 2007; Waggett et al. 2008). However comparable understanding about physical factors is lacking except for few examples (Maclean 1989; Karl et al. 1997; Belgrano, 1999; Yin et al. 1999). Impacts of these factors in combination with local inter-annual meteorological conditions will vary from one geographical location to the other and will thus influence bloom dynamics differentially.

HAB studies in Indian waters indicate reasonable reports on HABs and their impacts along the west coast of India. Direct impacts of HABs on human health have also been reported from Mangalore (Karunasagar et al. 1984); they related the death of a boy to an outbreak of Paralytic Shellfish Poisoning (PSP) following consumption of clams. Dinoflagellate toxins have also been recorded in shellfish from surrounding estuaries near Mangalore in 1985 and 1986 (Segar et al. 1989). Planktonic and cyst forms of *Gymnodinium catenatum*, a PSP-producing dinoflagellate from this region were detected later on (Godhe et al. 1996) and the importance of close monitoring of coastal waters, sediment and shellfish was highlighted.

Compared to the above regions, the Bay of Bengal (BOB), the eastern arm of the Indian Ocean, remains relatively unexplored in the context of HAB studies. The BOB is known for its unique characteristic features: large volume of freshwater input from river discharge and rainfall, warmer sea surface temperatures, monsoonal clouds and reversal of currents. The riverine input into this area injects loads of nutrients and suspended sediment

in the BOB (Gordon et al. 2002; Mukhopadhyay et al. 2006). These features point to the suitability of the BOB as a zone prone for algal blooms including HAB events. However, the strongly stratified surface layer of the BOB restricts the transport of nutrients from deeper layers to the surface (Prasanna Kumar et al. 2002). Thus, it is very interesting to understand the seasonal variations in dinoflagellate community structure in this inimitable geographic region.

Since taking oceanic cruises on regular intervals is not cost-effective, the ‘ships of opportunity’ programme, supported by the Indian Expendable Bathythermograph (XBT) project, was used. Therefore, the present study on the spatial and temporal distribution of dinoflagellates in the BOB, with emphasis on HAB species, is the first of its kind from the region. The following objectives were addressed. (1) Dinoflagellate distribution in the surface waters of the BOB and (2) Detailing of the HAB species present and their seasonal occurrence.

## **Materials and Methods**

### **Study area and sampling**

This study was conducted with the support of the XBT programme. Surface water samples were collected using steel buckets from the moving ship. This method was selected in order to minimize the physical damage to cells compared to the method of collecting samples using a pump. The samples were collected on 2 transects [Chennai to Port Blair (CP, 12 stations) and Port Blair to Kolkata (PK, 10 stations)] (Fig. 1), from passenger ships plying along these transects. Samples were collected at one degree intervals along both transect, from November 2003 to September 2006 covering different seasons. Among the sampling stations from CP (central BOB) and PK (northern BOB) transects, the majority were oceanic whereas, few stations are near the coast (Table 1). Samples (1L) were fixed with Lugol’s iodine solution for the laboratory enumeration and identification of dinoflagellates to the lowest possible taxonomic level.

### **Microscopic analysis**

The 1L sample was kept for settling for 48 hours. After that, the volume was brought down to 100ml and then to 10 ml final concentration after another 48 hours settling period (method modified from Hasle 1978). From this 10 ml final concentration, 3 ml concentrated sample was taken in a petri dish (3.8 cm diameter) and examined under an Olympus inverted microscope at 100X to 400X magnification. Identification of the dinoflagellate taxa was carried out using the keys provided by Subramanyan (1968), Taylor (1976), Tomas (1997), Horner (2002) and Hallegraeff (2003).

## Data analyses

To evaluate seasonal differences, the observational period was classified into three seasons: Pre-Monsoon (PrM – February-March 04), South west monsoon (SWM - June 04, July 04, August 04, September 06) and Post monsoon (PoM - November 03, October 04).

Univariate measures [Shannon-Wiener diversity index ( $H'$ ), Margalef's species richness ( $d$ ) and Pielou's evenness ( $J'$ )] were analyzed using PRIMER (version 5, developed by PRIMER-E Limited, UK) and the variations in these were determined by two-way ANOVA. Two-way ANOVA was also performed on the dinoflagellate abundance data to evaluate spatial and temporal variation (Sokal and Rohlf 1981). Spatial variation in the dinoflagellate community and the abundance profiles of the five most dominant taxa during each sampling period in both transects are presented as SURFER plots using the SURFER 8 program (developed by Golden software Inc., USA). The percentage contribution of autotrophic, mixotrophic and heterotrophic forms of dinoflagellates in each sampling period was also calculated.

## Results

Taxonomic identification revealed 134 species of dinoflagellates in surface waters of the BOB during the observation period (Table 2). Further grouping of these identified species based on their nutritional mode, revealed 40 autotrophic, 50 mixotrophic and 44 heterotrophic species, indicated the dominance of mixotrophic forms (Table 2). Comparison of this report with earlier reported species from the same area (Taylor 1976; Jyothibabu et al. 2003; Paul et al. 2007) indicated 10 new dinoflagellate species (Table 2 species marked with †). Approximately 14% of the identified species were potential HAB species (Table 2 species marked with \*).

### Spatial and temporal distribution of dinoflagellate assemblages

The abundance of dinoflagellates ranged from 0-94 cell  $L^{-1}$  throughout the observation period at both CP and PK transects (Fig. 2). Though seasonal variation in dinoflagellate abundance was observed in both transects, the variation was statistically significant at only the CP transect (Table 3). The highest average abundance of dinoflagellates was observed during September 06 (48 cell  $L^{-1}$  at PK) followed by October 04 (40 cell  $L^{-1}$  at CP) whereas low abundance was recorded during June (21 cell  $L^{-1}$  at CP), and August 04 (22 cell  $L^{-1}$  at PK) (Fig. 2). The spatial variation in dinoflagellate abundance was not statistically significant in both transects (Table 3). Species richness and diversity varied significantly in the PK transect; species richness only across stations and diversity across both stations and seasons (Table 3). Mixotrophic dinoflagellates dominated across both transects, with the exception of October 04 at CP and September 06 at PK transects, that were dominated by heterotrophic

forms (Fig. 3). *Ceratium* was the dominant genus among the mixotrophic forms whereas *Protooperidinium* was the dominant heterotrophic form. *Ceratium fusus*, *C. teres*, *Gotoius abei*, *Oxytoxum scolopax*, *Protooperidinium ovatum* and *Scrippsiella trochoidea* were among the abundant forms in both the transects. *Amphisolenia bidentata*, *Ceratium pentagonum*, *C. symmetricum*, *Oxytoxum globosum* and *Prorocentrum belizianum* were abundant only in CP transect (Fig. 4a) whereas *Ceratium extensum*, *C. furca*, *Dinophysis miles* and *Noctiluca scintillans* were abundant only in the PK transect (Fig. 4b).

#### Seasonal variation in HAB species

Overall, 19 potentially HAB species were encountered in this area (Table 2). Some HAB species were present during all the seasons throughout the study period. These frequently occurring species were *Ceratium furca*, *C. fusus*, *Dinophysis* sp., *Gonyaulax polygramma*, *Gonyaulax* sp., *Noctiluca scintillans*, *Prorocentrum* sp., *Scrippsiella trochoidea*, *Scrippsiella* sp. (Table 2). Season-specific trends were also observed. *Alexandrium minutum*, *Prorocentrum lima* and *Protooperidinium crassipes* occurred only during PrM whereas *Dinophysis caudata*, *D. miles*, *Prorocentrum micans*, *P. mexicanum*, *P. minimus*, *Gymnodinium* sp. and *Gambierdiscus* sp. were found during SWM and PoM periods. *Gonyaulax polyedra* and *G. spinifera* occurred in PrM and PoM but not during SWM. In contrast to this, *Prorocentrum belizianum* and *P. sigmoides* occurred only during the SWM.

#### Discussion

The BOB is a semi-enclosed tropical basin, distinguished by a strongly stratified surface layer and a seasonally reversing circulation (Shetye et al 1996). It is also influenced by monsoonal winds and enormous freshwater influx. The surface stratified water column of the BOB restricts the vertical transport of nutrients from the bottom layers to the surface, and therefore phytoplankton productivity as well (Prasanna Kumar et al. 2002). The stratification is especially intense during the SWM period (Prasanna Kumar et al. 2004) due to the influx of freshwater through precipitation and riverine discharges. The average annual riverine discharge varies from the northern to southern bay with maximum discharge at north ( $10^{12}$  m<sup>3</sup> from Ganges and Brahmaputra), medium at central ( $8.5 \times 10^{10}$  m<sup>3</sup> from Krishna and Godavari) and minimum at southern bay (UNESCO, 1988) resulting in variation in surface water salinity. Our study revealed that dinoflagellate abundance in surface waters was generally in the range of 0-94 cell L<sup>-1</sup> and did not vary significantly across stations (Table 3). This could be related to the environmental conditions of the study area. Stratified water columns, with their characteristic oligotrophic conditions, tend to promote stasis of the resident population, rather than promoting growth or blooms (Smayda 2002). In fact, many studies (McGill 1973; Paul et al. 2008) have reported that the surface waters of the BOB are nitrate-deficient. Low surface PO<sub>4</sub><sup>3-</sup>-P values of 0.1 µg-at L<sup>-1</sup> have also been recorded in the Bay of Bengal and Andaman Sea (Kabanova 1964, Rozanov 1964). Though the stratified BOB environment supported a

rather homogeneous dinoflagellate community in surface waters, significant seasonal variations in abundance and species diversity of the dinoflagellate community were observed (Table 3). Minimum values were observed during SWM, correlating to the intensification of the stratified layer, and maximum during the withdrawal of the SWM and PoM (Fig. 2).

The dominance of mixotrophic dinoflagellates in the study area could be a consequence of the prevalent low light and/or nutrient scarcity, conditions that are known to promote mixotrophy (Legrand et al. 1998; Stoecker et al. 2006). *Ceratium* and *Protoperdinium* were the most abundant representatives of the mixotrophic and heterotrophic forms in the BOB respectively (Fig 4); their unique characteristics of vertical migration, and heterotrophy are reasonably well understood (Baek et al. 2006, 2007; Baek et al. 2008 a,b,c; Latz and Jeong 1996; and references therein), and probably confer on them a competitive advantage in both coastal and oceanic environments.

In the context of the frequently occurring HAB species (hereafter FOS) recorded in the region; *Ceratium furca* and *C. fusus* showed a characteristic transect-specific distribution. *C. furca* was abundant only in the PK transect. *C. fusus* which was predominant in the PK transect (Fig. 3b) was abundant only during October 04 in the CP transect (Fig. 4a).

*C. furca* and *C. fusus* are characteristically found in stable stratified water columns (Baek et al. 2006, 2007). However, both species differ in several characteristics. In recent observations in Sagami Bay, Japan, Baek et al. (2009) reported that *C. furca* had a competitive edge over *C. fusus*, because of its efficient diel vertical migration capability (a 'biological' factor). *C. fusus* was stimulated by low salinity and showed dependence on external environmental conditions such as enhanced nutrient concentrations following fresh water discharge by heavy rainfall (combination of 'physical' and 'chemical' factors). In light of this, our observations point out that the water mass of the PK transect (which is in the northern BOB) is influenced by riverine discharge to a much greater extent compared to the CP transect (in the central BOB). Additionally, the differential capabilities of *Ceratium* species to acclimatize to such niches can be an important factor in determining their diversity and spatio-temporal distribution.

*S. trochoidea*, another FOS in the region, was abundant during September/February-March (Fig. 4). September is known as the period of withdrawal of SWM, during which cloud cover reduces, whereas March is known for clear sky and with no rainfall. Studies on the factors triggering the growth/bloom formation of *S. trochoidea*, point to different regulating factors. For e.g., in Hong Kong waters, the initiation, maintenance and disappearance of a *S. trochoidea* red tide was not directly driven by changes in nutrients (Yin et al. 2008). Subsequently, Zhuo-Ping et al. (2009) observed that the cell density of *S. trochoidea* was positively influenced by

high irradiance and further enhanced by iron concentration. These conditions of high irradiance could possibly be responsible for the predominance of *S. trochoidea* in March.

Blooms of *N. scintillans*, yet another FOS in the region, have been reported from Indian waters (Raghu Prasad 1953, 1956; Santha Joseph 1975; Naqvi et al. 1998; Eashwar et al. 2001; Mohanty et al. 2007; Gomes et al. 2008). Most of these blooms occurred during the SWM. Sriwoon et al. (2008) observed that *N. scintillans* blooms in the Gulf of Thailand were mainly influenced by the SWM. Since the SWM is a major meteorological event influencing the BOB, it is absolutely necessary to investigate in detail the factors sustaining the population of *N. scintillans* in the BOB and their bloom dynamics.

*Dinophysis* sp., another FOS in the region, was abundant during March at PK transect (Fig. 4b). *Dinophysis* are known to increase in cell density immediately after a storm-induced mixing event (Nishitani et al. 2005). They can also migrate through strong gradients and survive under unfavorable conditions (Setala et al. 2005). In a recent observation in Portuguese waters, Escalera et al. (2010) found that the increased numbers of *Dinophysis* was a result of physically-driven accumulation due to long-shore transport. They also found the bloom to be associated with much warmer temperatures. In our observation, its predominance during March indicates its preference for high temperature since this period is considered a warmer season in the BOB (Narvekar and Prasanna Kumar 2006).

Given that the FOS observed in our study ranged from 0-40 cell L<sup>-1</sup>, their presence may not be a population growth issue, as suggested by Smayda (2002). However, they may play a significant role in the development of pelagic seed banks of vegetative cells (Smayda 2002), which can serve as inocula for bloom events elsewhere, on the onset of favorable conditions. An earlier study (Avaria 1979) suggested that the Chilean frontal zone located 100km offshore supported a *Prorocentrum micans* bloom. Transport of offshore-seeded *Prorocentrum* and *Ceratium* blooms to inshore waters (Pitcher and Boyd 1996) also supports the above assumption.

Another intriguing aspect to be considered is the enhancement of phytoplankton biomass to bloom levels by physical processes occurring in the BOB like eddies (Gomes et al. 2000; Prasanna Kumar et al. 2004) and cyclones (Madhu et al. 2002; Vinaychandran and Mathew 2003; Rao et al. 2006). In both eddies and cyclones, bloom formation takes place due to transport of nutrients from bottom layers to the surface. During cyclones, due to strong wind speed, the stratified layer breaks and deepens the mixed layer, leading to introduction of nutrients into the surface layers whereas during eddies, Ekman pumping plays an important role in transporting nutrients to surface waters. Eddies are most likely to occur during the SWM (Prasanna Kumar et al. 2004) whereas cyclones are common during November (Madhu et al. 2002; Vinaychandran and Mathew, 2003; Rao et al. 2006). The combination of such physical effects including turbulence and advection, with the diverse behavioral

characteristics of dinoflagellates (e.g., migration, physiological adaptation) holds the key to understanding HAB dynamics in stratified oceanic areas. Even though some of these physical processes may play a crucial role in the formation of HABs, these processes are not well defined and thus knowledge in this context remains weak (GEOHAB 2003). For e.g., the above studies were based on remote sensing (chlorophyll *a*) and primary productivity values and none of the reported blooms/enhancement of phytoplankton biomass was taxonomically characterized. In this context, the present investigation pointing out the presence of *N. scintillans* and *C. furca* during November (Table 1) further strengthens their probable candidature for bloom formation in the region.

However, it should be noted that the present findings are based on the surface water distribution of dinoflagellates from the BOB, but taking in to account the fact that phytoplankton tend to gather more in sub-surface rather than surface waters, future studies on the depth-wise distribution of dinoflagellates and notably, HAB species, will be a step forward.

## **Conclusions**

The present study is the first of its kind detailing the HAB species from the stratified surface waters of the BOB and their seasonal occurrence. The frequently occurring HAB species indicate their ability to survive even under such conditions; their low abundance in the region may not be a growth issue but they may serve as inocula for blooms if coupled with population triggering physical process like eddies and cyclones in the region. In this scenario, the characteristic ability of FOS like *C. furca* and *N. scintillans* and their predominance during cyclone-prone months, make their candidature stronger for future blooms in the region.

## **Acknowledgements**

We are grateful to Dr. S.R. Shetye, Director of the National Institute of Oceanography (NIO), for his support and encouragement. We are thankful to our colleagues of the department and cruise participants for their help at various stages of the work. We acknowledge the funding support received from the Ministry of Earth Sciences (MOES) under the Indian XBT programme and the Ballast water management programme, funded by the Directorate General of Shipping, India. RKN is grateful to CSIR for awarding the senior research fellowship (SRF) and also to POGO-SCOR for providing a fellowship to avail phytoplankton taxonomy training in SZN, Italy. This is an NIO contribution (No. #####).



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## Legends to figures

**Fig. 1** Study area map showing station locations along the Chennai–Port Blair (CP) and Port Blair-Kolkata (PK) transects in the Bay of Bengal

**Fig. 2** Spatio-temporal variation in total dinoflagellate abundance ( $\text{cell L}^{-1}$ ) along the Chennai–Port Blair (CP) and Port Blair–Kolkata (PK) transects in (a) Nov 03, (b) Feb-Mar 04, (c) Jun 04, (d) Jul-Aug 04, (e) Oct 04 and (f) Sep 06.

**Fig. 3** The percentage contribution of autotrophic, mixotrophic and heterotrophic dinoflagellates along the (a-e) Chennai–Port Blair (CP) and (f-j) Port Blair–Kolkata (PK) transects. (a) Feb 04, (b) Jun 04, (c) Jul 04, (d) Oct 04, (e) Sep 06, (f) Nov 03, (g) Mar 04, (h) Aug 04, (i) Oct 04 and (j) Sep 06.

**Fig. 4** The five most abundant species during each sampling period at the (a) Chennai–Port Blair and (b) Port Blair-Kolkata transects. The maximum diameter of circle corresponds to average  $9 \text{ cell L}^{-1}$ .

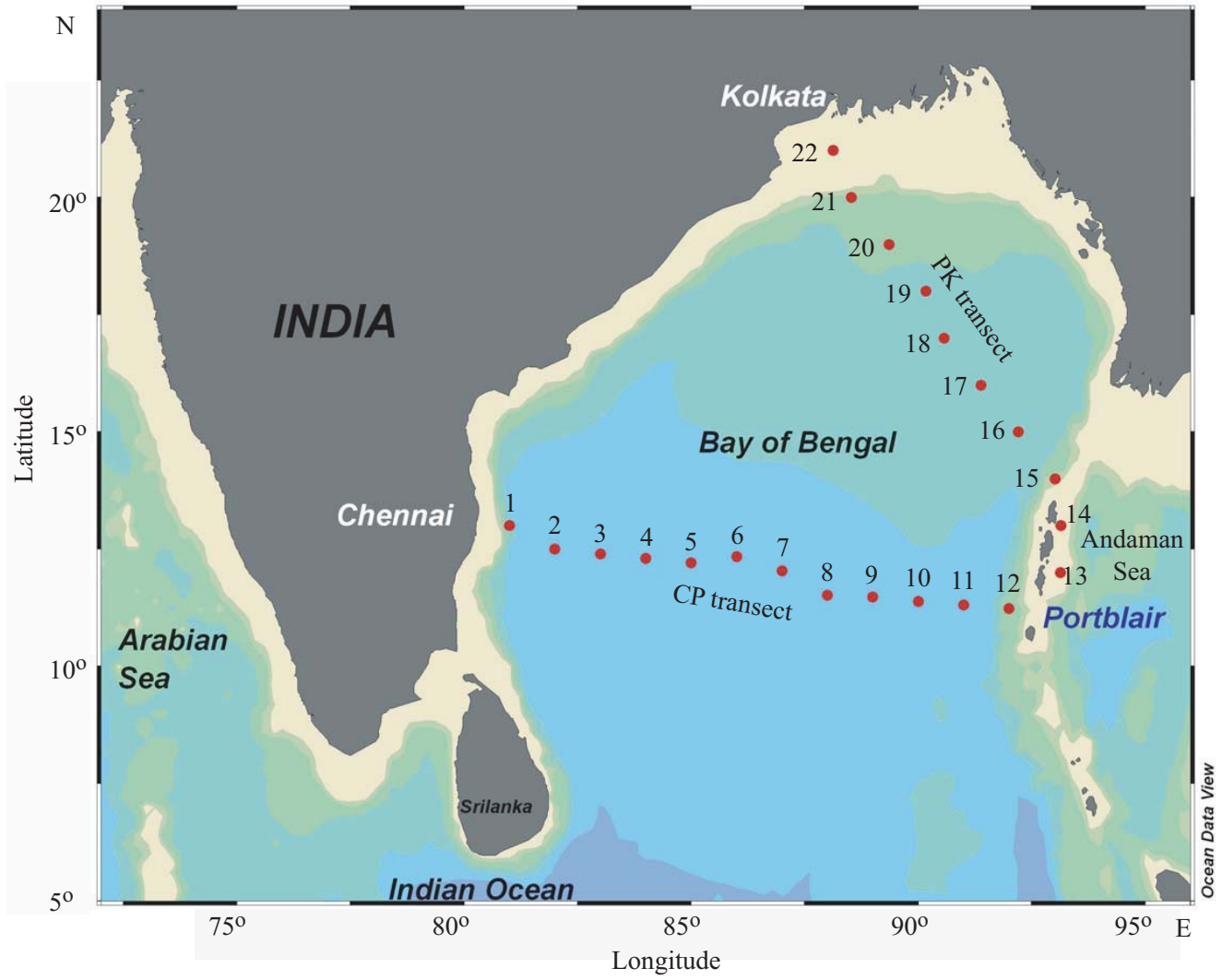


Fig. 1

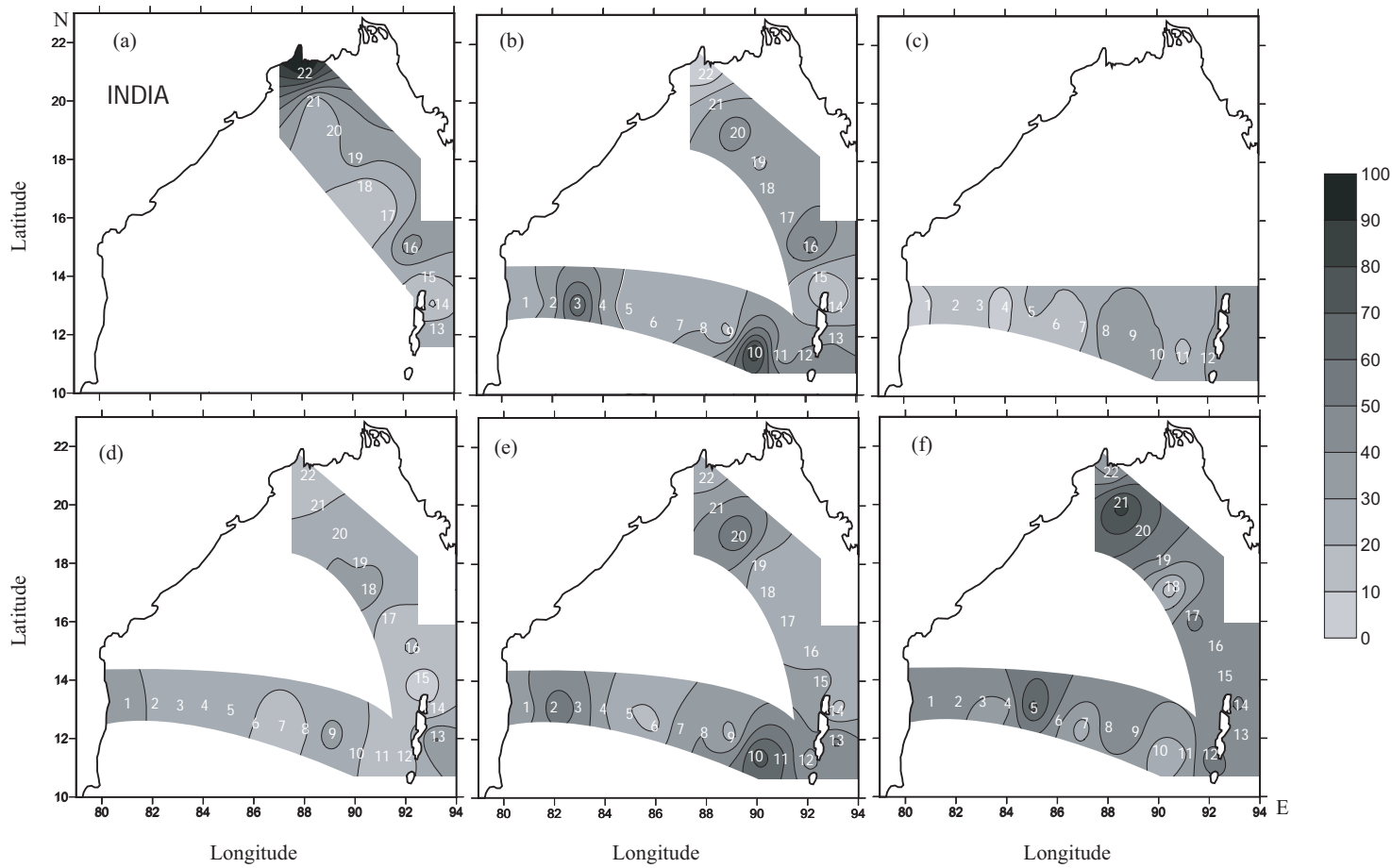
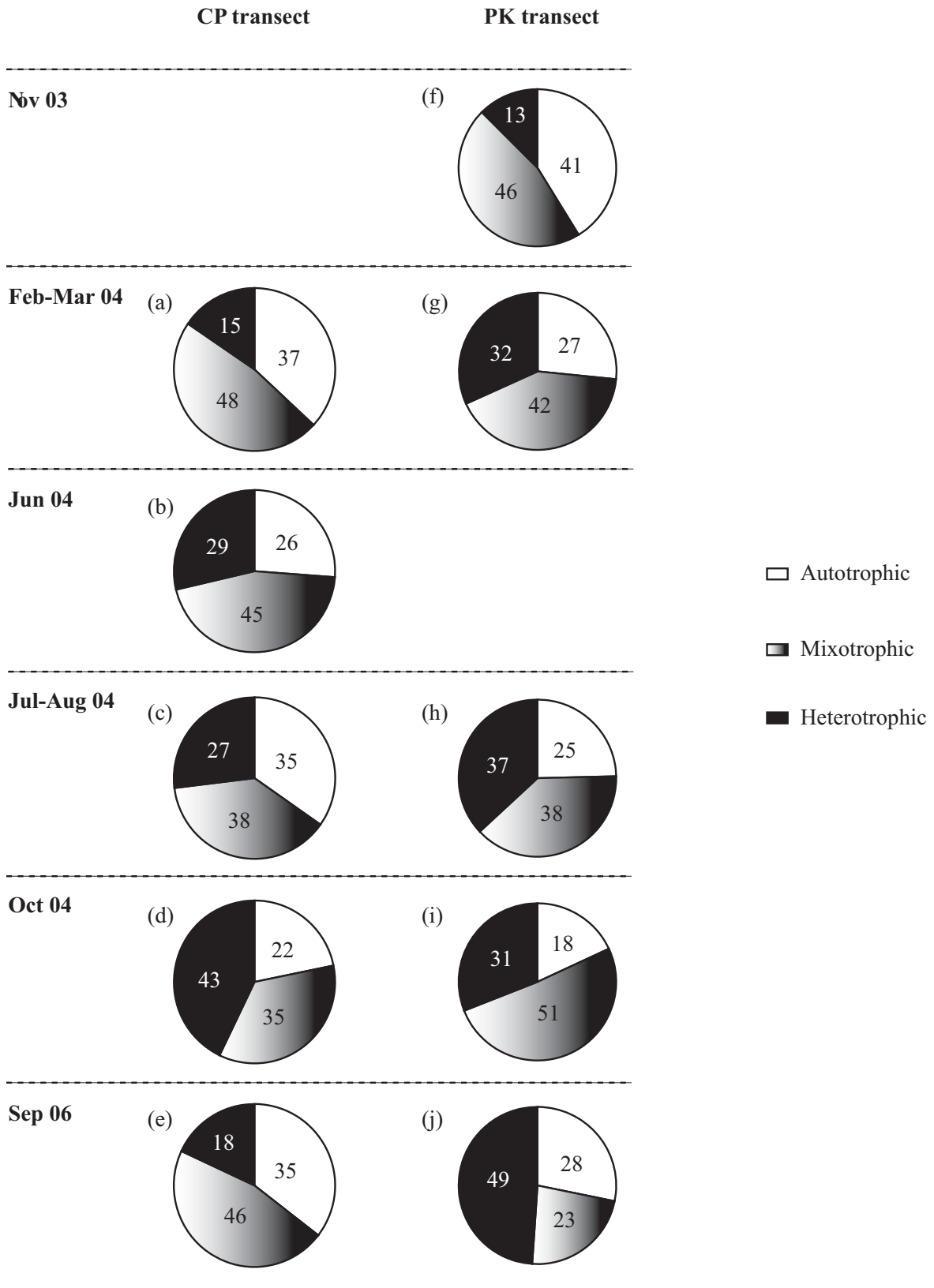
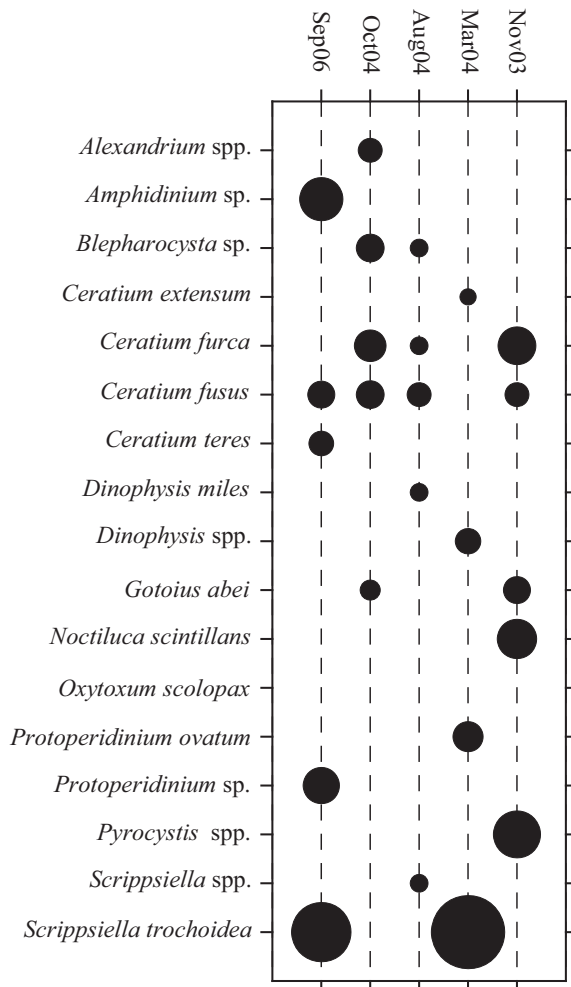


Fig. 2

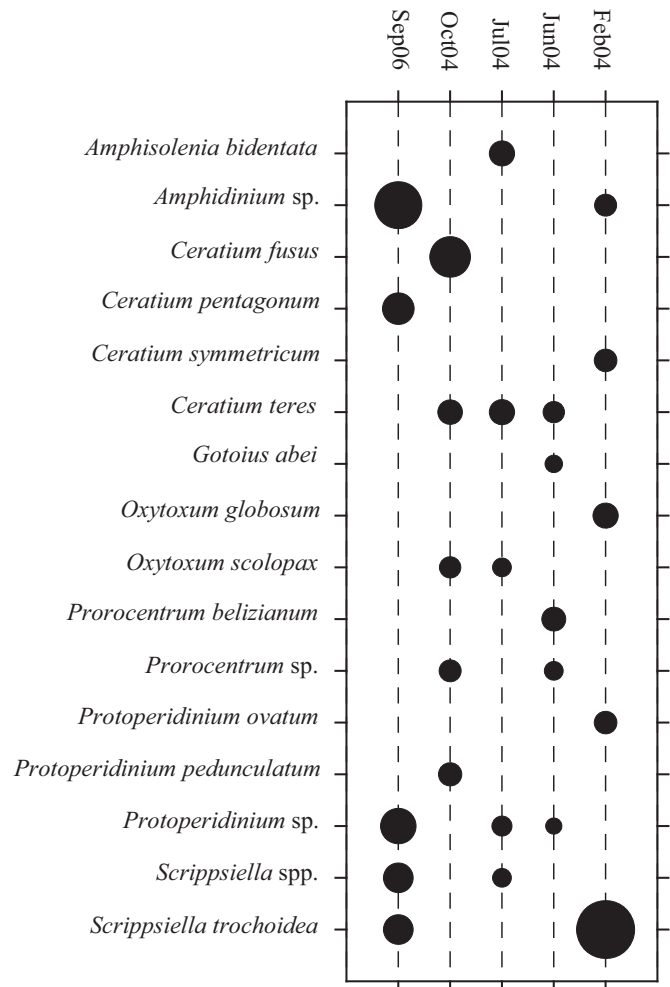




**Fig. 3**



b)



a)

Fig. 4

**Table 1** Station details of Chennai-Port Blair (CP) and Port Blair-Kolkata transects. \*near coastal stations

<b>Stations</b>	<b>Lat (N)</b>	<b>Long (E)</b>
CP transect		
1	13.04	81.07
2	13.09	82.03
3	13.09	83
4	13.04	84.05
5	13.05	85.05
6	12.49	86
7	12.38	87
8	12.23	88.03
9	12.1	89
10	11.52	90.05
11	11.41	91.04
12*	11.28	92.07
PK transect		
13*	12.03	93.14
14*	13.01	93.14
15	14	92.56
16	15.01	92.24
17	16.08	91.29
18	17.09	90.43
19	18	90.12
20	19	89.3
21	20	88.5
22*	21.05	88.14

**Table 2** Taxonomic list of identified dinoflagellates during the study period along the CP and PK transects (\* potentially HAB species, † new reporting). The values outside bracket indicate the range of abundance during that month and values inside the bracket indicates the frequency of occurrence at CP (total 12 stations) and PK (total 10 stations) transects during the respective sampling months

Autotrophic dinoflagellates	CP transect					PK transect				
	Feb04	Jun04	Jul04	Oct04	Sep06	Nov03	Mar04	Aug04	Oct04	Sep06
<i>Alexandrium concavum</i>		0-2 (1)								
<i>Alexandrium</i> spp.			0-2 (2)		0-9 (1)			0-2 (1)	0-20 (1)	0-6 (1)
<i>Amphidinium</i> sp.*	0-7 (5)	0-2 (1)	0-2 (1)	0-5 (3)	0-12 (10)			0-8 (2)	0-5 (1)	0-9 (8)
<i>Amphisolenia bidentata</i>		0-2 (2)	0-8 (7)	0-3 (1)	0-3 (3)			0-2 (1)		0-9 (3)
<i>Amphisolenia globifera</i>										0-3 (2)
<i>Blepharocysta</i> sp.		0-4 (2)	0-4 (3)	0-8 (2)				0-4 (5)	0-8 (6)	0-3 (1)
<i>Ceratocorys armata</i>	0-2 (1)						0-2 (1)			
<i>Ceratocorys horrida</i>		0-4 (2)		0-3 (1)		0-2 (2)				
<i>Corythodinium constrictum</i>		0-2 (1)					0-4 (2)			
<i>Corythodinium elegans</i>			0-4 (1)	0-3 (1)	0-3 (1)					0-3 (1)
<i>Corythodinium michaelisarsii</i>				0-8 (2)						
<i>Corythodinium reticulatum</i>	0-2 (2)						0-2 (2)			
<i>Corythodinium tessellatum</i>		0-2 (2)	0-2 (1)	0-3 (2)	0-3 (3)	0-2 (2)				0-3 (2)
<i>Corythodinium</i> sp.			0-2 (1)		0-3 (1)					
<i>Ensiculifera</i> sp.									0-5 (1)	
<i>Gambierdiscus</i> sp* †								0-4 (1)		
<i>Goniodoma polyedricum</i>		0-2 (2)				0-6 (2)	0-2 (1)		0-5 (1)	
<i>Goniodoma sphaericum</i>	0-6 (3)				0-3 (1)		0-6 (1)	0-2 (2)	0-5 (1)	0-3 (2)
<i>Gonyaulax brevisulcata</i>										0-3 (1)
<i>Gonyaulax digitalis</i>				0-5 (1)						
<i>Gonyaulax grindleyi</i>	0-2 (1)									
<i>Gonyaulax monospina</i> †					0-3 (1)					0-3 (1)
<i>Gonyaulax polyedra</i> *	0-4 (4)			0-3 (1)			0-2 (1)			
<i>Gonyaulax polygramma</i> *	0-8 (1)	0-2 (1)	0-2 (1)	0-8 (4)	0-6 (1)	0-4 (2)	0-4 (1)	0-4 (2)	0-8 (3)	0-6 (2)
<i>Gonyaulax scrippsae</i>	0-4 (1)		0-2 (2)		0-3 (1)	0-6 (3)				
<i>Gonyaulax spinifera</i> *	0-4 (4)			0-3 (1)		0-4 (1)	0-2 (2)			
<i>Gonyaulax</i> sp.	0-2 (1)	0-2 (2)	0-2 (2)	0-3 (1)	0-6 (6)	0-2 (1)	0-4 (2)	0-6 (1)	0-3 (2)	0-3 (5)
<i>Gymnodinium</i> spp.*			0-2 (1)	0-5 (1)	0-6 (3)			0-6 (1)		0-6 (3)
<i>Oxytoxum globosum</i>	0-26 (1)									
<i>Oxytoxum laticeps</i>				0-3 (1)	0-6 (3)	0-2 (1)				0-6 (4)
<i>Oxytoxum scolopax</i>	0-3 (5)	0-2 (2)	0-4 (6)	0-8 (4)	0-3 (5)		0-6 (2)	0-2 (2)	0-5 (1)	0-3 (4)
<i>Oxytoxum sceptrum</i>		0-2 (1)	0-4 (5)	0-3 (4)				0-2 (3)		0-3 (1)
<i>Oxytoxum</i> sp.	0-6 (3)	0-2 (1)					0-2 (2)			0-3 (1)
<i>Podolampas bipes</i>		0-2 (3)		0-3 (1)	0-3 (2)	0-2 (1)			0-5 (1)	0-6 (2)
<i>Podolampas elegans</i>	0-4 (3)						0-2 (1)			
<i>Podolampas palmipes</i>	0-4 (4)	0-2 (2)	0-2 (3)	0-3 (3)	0-6 (1)		0-2 (1)	0-2 (1)	0-5 (1)	0-3 (1)
<i>Podolampas spinifera</i>		0-2 (1)	0-2 (2)	0-3 (1)					0-5 (1)	
<i>Pyrophacus steinii</i>	0-2 (1)			0-3 (1)		0-2 (3)	0-2 (1)			0-18 (1)
<i>Pyrophacus</i> spp.				0-5 (2)						
<i>Torodinium teredo</i> †					0-3 (2)					

**Table 2 (Contd.)**

Mixotrophic dinoflagellates	CP transect				PK transect					
	Feb04	Jun04	Jul04	Oct04	Sep06	Nov03	Mar04	Aug04	Oct04	Sep06
<i>Alexandrium minutum</i> *	0-10 (1)									
<i>Ceratium arietinum</i>									0-3 (2)	
<i>Ceratium azoricum</i>					0-3 (1)	0-2 (1)				
<i>Ceratium candelabrum</i> f. <i>depressum</i>			0-2 (1)	0-3 (1)						0-3 (1)
<i>Ceratium contortum</i>	0-5 (3)						0-4 (1)			
<i>Ceratium declinatum</i>		0-2 (1)	0-2 (1)	0-5 (4)	0-9 (4)				0-5 (1)	0-9 (3)
<i>Ceratium deflexum</i>				0-3 (1)					0-8 (1)	
<i>Ceratium dens</i>					0-3 (1)					
<i>Ceratium extensum</i>							0-4 (4)	0-6 (1)		
<i>Ceratium furca</i> *	0-2 (1)		0-2 (2)	0-5 (4)	0-9 (5)	0-20 (5)		0-6 (4)	0-13 (4)	0-18 (4)
<i>Ceratium fusus</i> *	0-6 (4)	0-2 (4)	0-2 (3)	0-13 (9)	0-6 (4)	0-20 (1)	0-4 (1)	0-6 (5)	0-8 (7)	0-12 (3)
<i>Ceratium gibberum</i>	0-2 (1)									
<i>Ceratium horridum</i>			0-2 (2)		0-6 (2)			0-2 (1)		0-3 (1)
<i>Ceratium karstenii</i>	0-2 (4)						0-2 (1)			
<i>Ceratium kofoidii</i>		0-2 (1)	0-2 (1)			0-2 (1)				
<i>Ceratium lineatum</i>			0-2 (2)	0-3 (2)	0-3 (1)				0-5 (1)	0-3 (1)
<i>Ceratium lunula</i>							0-2 (1)			
<i>Ceratium macroceros</i>		0-2 (3)	0-2 (1)			0-2 (3)		0-2 (1)		
<i>Ceratium pentagonum</i>					0-9 (7)			0-2 (1)		0-3 (1)
<i>Ceratium schmidtii</i>			0-2 (2)	0-5 (3)	0-3 (1)				0-8 (2)	
<i>Ceratium symmetricum</i>	0-10 (4)			0-3 (1)			0-2 (2)			
<i>Ceratium teres</i>		0-8 (6)	0-8 (7)	0-8 (7)	0-9 (7)	0-4 (1)		0-2 (1)	0-3 (2)	0-12 (3)
<i>Ceratium trichoceros</i>	0-2 (2)						0-8 (1)			
<i>Ceratium tripos</i>		0-2 (1)	0-2 (1)			0-2 (1)				
<i>Ceratium vultur</i>	0-4 (1)									0-3 (1)
<i>Ceratium</i> spp.			0-2 (1)	0-3 (2)	0-3 (3)				0-5 (1)	
<i>Dinophysis caudata</i> *								0-2 (1)	0-5 (1)	
<i>Dinophysis miles</i> *								0-12 (1)		
<i>Dinophysis schuettii</i>				0-3 (1)						
<i>Dinophysis</i> spp.	0-4 (5)		0-2 (2)	0-5 (2)			0-6 (6)		0-5 (1)	0-3 (1)
<i>Dissodium asymmetricum</i>						0-2 (1)				
<i>Prorocentrum arcuatum</i> †	0-2 (1)						0-4 (1)			
<i>Prorocentrum belizeanum</i> * †		0-24 (1)								
<i>Prorocentrum compressum</i>		0-2 (1)		0-5 (1)				0-2 (1)		
<i>Prorocentrum gracile</i>				0-8 (4)						
<i>Prorocentrum lenticulatum</i>	0-4 (1)									
<i>Prorocentrum lima</i> *							0-2 (1)			
<i>Prorocentrum micans</i> *	0-20 (1)		0-2 (2)	0-3 (1)	0-3 (2)			0-10 (1)	0-10 (2)	0-9 (1)
<i>Prorocentrum minimus</i> *	0-2 (1)		0-2 (1)	0-3 (1)				0-2 (1)		
<i>Prorocentrum mexicanum</i> *	0-5 (6)									
<i>Prorocentrum obtusum</i>				0-8 (3)					0-3 (2)	0-3 (2)
<i>Prorocentrum scutellum</i> †								0-2 (1)		
<i>Prorocentrum sigmoides</i> *			0-2 (1)		0-3 (1)					0-9 (4)
<i>Prorocentrum</i> sp.	0-2 (2)	0-14 (2)	0-4 (3)	0-8 (5)	0-9 (7)	0-4 (4)	0-4 (1)	0-6 (2)	0-8 (3)	0-6 (5)
<i>Pyrocystis fusiformis</i>			0-2 (1)	0-3 (1)						
<i>Pyrocystis hamulus</i>	0-2 (1)		0-4 (2)			0-2 (1)				
<i>Pyrocystis lunula</i>	0-4 (1)									
<i>Pyrocystis</i> spp.		0-2 (1)	0-2 (1)	0-3 (1)	0-3 (2)	0-14 (5)	0-6 (1)		0-5 (2)	0-3 (1)
<i>Scrippsiella trochoidea</i> *	0-14 (9)		0-2 (1)	0-3 (1)	0-9 (7)		0-26 (6)	0-4 (1)	0-5 (2)	0-15 (7)
<i>Scrippsiella</i> spp.		0-2 (1)	0-6 (5)	0-10 (3)			0-2 (1)	0-6 (3)	0-8 (1)	



**Table 2** Two-way ANOVA to evaluate the variation in total dinoflagellate abundance, species richness, evenness and diversity along the CP and PK transects

	CP transect					PK transect				
	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F<sub>s</sub></i>	<i>P-value</i>	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F<sub>s</sub></i>	<i>P-value</i>
Abundance										
Stations	11	3319	302	1	0.2817	9	3092	344	1	0.4943
Seasons	4	5025	1256	5	<b>0.0016</b>	4	3493	873	2	0.0663
Within sub-group error	44	10576	240			36	12994	361		
Total	59	18920				49	19579			
Species evenness										
Stations	10	0	0	1	0.1922	9	0	0	1	0.2578
Seasons	4	0	0	1	0.3145	4	0	0	2	0.0710
Within sub-group error	40	0	0			36	1	0		
Total	54	0				49	1			
Species richness										
Stations	10	10	1	2	0.1661	9	10	1	3	<b>0.0180</b>
Seasons	4	0	0	0	0.9585	4	3	1	2	0.1614
Within sub-group error	40	27	1			36	14	0		
Total	54	37				49	27			
Species diversity										
Stations	10	3	0	2	0.1033	9	4	0	2	<b>0.0338</b>
Seasons	4	1	0	1	0.4078	4	2	0	3	<b>0.0483</b>
Within sub-group error	40	6	0			36	6	0		
Total	54	9				49	12			