Inter- and intra-annual variations in the population of *Tripos* from the Bay of Bengal

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***Tripos*, a species-rich ubiquitous thecate dinoflagellate, serves as an excellent biological indicator of the water mass in the oceans. The inter- and intra-annual variations in the surface-water distribution of *Tripos* along the shipping routes of Chennai (C)–Port Blair (P)–Kolkata (K) in the Bay of Bengal was evaluated from October 2006 to September 2011. The highest numbers were recorded during fall intermonsoon (October 2007) in the C–P transect, and southwest monsoon (July 2010) in the P–K transect. In the C–P transect high numbers of *T. furca* can be attributed to mesoscale eddies, whereas in the P–K transect, it can be attributed to riverine discharge. The results point that, *Tripos* persists throughout the year in the Bay of Bengal and tend to increase with the elevation of nutrients.**

Keywords: Bay of Bengal, currents, dinoflagellates, eddies, monsoon, micro-phytoplankton, *Tripos*.

DINOFLAGELLATES constitute one of the important groups of marine protists in all aquatic ecosystems and form the second most dominant group of the total of phytoplankton community[1,2]. It comprises a wide range of genera with 117 genus and 1555 species[3]. Amongst them, *Tripos* is one of the important ubiquitous marine thecate genera, whose distribution ranges from polar to tropical environments[4]. The *Tripos* species are slow-growing, found round the year[4–8], and are known to be a model species within the dinoflagellates for biogeographic and global change studies[9]. In relation to temperature some of its forms are referred as excellent water mass indicators, North Atlantic[4,10], Mediterranean Sea[11,12], Pacific[13,14], Arctic[15] and Indian Ocean[16]. Phytogeographical studies also showed close relationship of individual species with temperature, while some are fairly tolerant towards wide temperature range[8]. Recently, the taxonomy of this genus has been revised based on the numbers and arrangement of cingular plates. The freshwater species are referred to as *Ceratium* and the marine species renamed as *Neoceratium*[17]. Recently, Gómez[18] has elaborated on nomenclature priority of this species and reinstated genus *Neoceratium* to *Tripos*. The genus is strong-armoured, large-sized cells (100–300 μm) that is readily identified and distinctly characterized when preserved in any of the common fixatives[17].

In the waters around the subcontinent of India, *Tripos* species have been documented from the east and west coasts of India[19–24]. Taxonomic studies on dinoflagellates from the Indian Ocean date back to 1968 (ref. 16), although there is information available on dinoflagellates from several international expeditions as well as those that have passed through waters along the Indian subcontinent. Most of the authors studied *Tripos* qualitatively by reporting the presence of species in the form of description and illustration[25]. Taylor[25] pointed out that in the description of dinoflagellates, Matzenauer[26] had also omitted genus *Tripos*. However, from the above literature, we can say that information on the abundance and diversity at the spatio-temporal scale is lacking. The only tropical ocean being bounded by a continent to the north, the Indian Ocean comprising of the Arabian Sea and Bay of Bengal, hereafter referred to as BoB[27], is home for the semi-annually reversing monsoon wind system[28]. Changes in the environmental conditions (salinity, temperature, nutrients) driven by major riverine discharges and monsoon reversals (precipitation and wind) make the bay a unique system in the northern Indian Ocean. Given the understanding that the *Tripos* has been used as an indicator of water mass as stated above, a study was undertaken to map the distribution of *Tripos* in BoB for five years (October 2006–September 2011).

Materials and methods

Study area and sampling strategy

Surface water samples were collected from BoB, along the shipping route, viz. from Chennai to Port Blair (C–P, 81°00′E/13°00′N to 92°00′E/11°23′N) and Port Blair to Kolkata (P–K, 12°00′N/93°14′E–21°00′N/88°23′E) (Figure 1). Sampling was done at monthly intervals from 22 stations (separated by 1° intervals), 12 and 10 stations along C–P and P–K transect respectively, from October 2006 to September 2011 (Table 1). To depict the influence of monsoon and wind stress, monthly datasets are categorized into seasons as fall intermonsoon (FIM;

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October), northeast monsoon (NEM; November to February), spring intermonsoon (SIM; March to May) and southwest monsoon (SWM; June to September). March–May and October both experience moderate winds; hence these months are termed as intermonsoon (IM), spring intermonsoon and fall intermonsoon respectively. In order to see regional variability in the *Tripos* population along with its associated environmental variables, the C–P transect is also referred to as CPOS (stations 1 to 12) and the P–K transect that includes Andaman Region (AR; stations 13 to 15), P–K oceanic stations (PKOS; stations 16 to 21) and Riverine Mouth (RM; stations 22). When all the three regions are considered, it is referred to as P–K transect.

Environmental parameters

The vertical temperature profile of the water column was recorded by launching XBT-MK21-T7 Probes (Sippican Inc.) at 1° intervals. The conductivity of surface sea water was measured using Autosal and later converted into salinity; salinity accuracy of the instrument <0.002 and detection range 2–42.

For nutrient, 10 ml of sea-water samples was collected into 10 ml cryo-vials, immediately frozen in liquid nitrogen and then analysed for dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphate (DIP). The samples collected from October 2006 to October 2009 were analysed using Technicon Auto Analyzer. The precision of nitrate, nitrite and phosphate was ±0.02, 0.02 and 0.01 μmol l^{-1} respectively. The samples collected from November 2009 to September 2011 were analysed by auto analyser (Skylar, San ++) continuous flow analyser. For both the analyses, standard spectrophotometric procedures were followed using Grasshoff *et al.*[29].

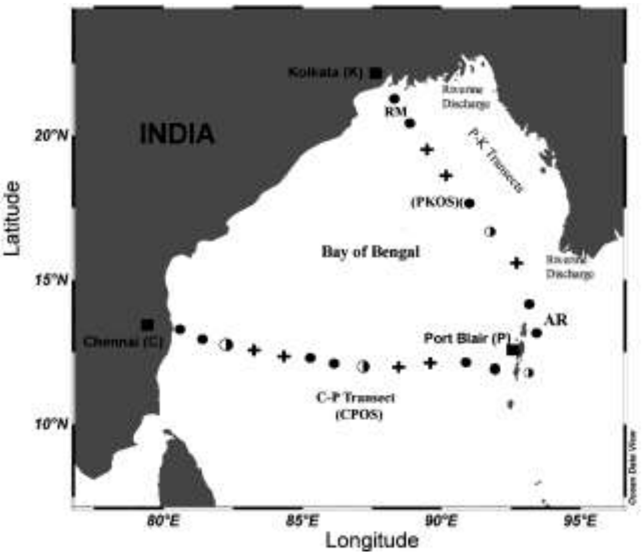

Figure 1. Map of sampling area showing 12 stations along Chennai–Port Blair (C–P) and 10 stations along Port Blair–Kolkata (P–K) transects. Symbol denotes sampling time. ●, Night hours (absence of sunlight); ◐, Late evening and early morning (faint sunlight); +, Day hours (presence of sunlight).

The wind speed data were obtained from APDRC (Asia Pacific Data Research Centre) data access (http://apdrc.soest.hawaii.edu) for the grid area of 7°38′N–21°38′N and 74°38′E–95°38′E. Rainfall data were obtained from NOAA (NOAA Earth System Research Laboratory), data access (http://www.esrl.noaa.gov/psd/data/gridded/data.unified.daily.conus.html) for the gridded area of 7°28′N–25°88′N and 7°88′E–97°28′E. The values of PAR were extracted from level-3 MODIS, 9 km resolution at each 1° interval from 10°95′E to 21°95′N and 80°04′E to 95°04′E data access (http://oceandata.sci.gsfc.nasa.gov).

For detection of eddies, SSHA images obtained from the 7-day snapshots of merged sea-level anomalies from live access server having a spatial resolution of 1/3 of a degree (http://las.aviso.oceanobs.com) during the period 2006–2008 coinciding with high microphytoplankton abundance.

Analysis of micro-phytoplankton

Plankton analysis was carried out with surface water samples collected from the moving ship at any given time. Two litres of water was collected from each station, and each one litre was fixed using acetic Lugol's (2%) iodine and buffered formaldehyde (0.6%). Samples were brought back to the laboratory, kept undisturbed for 48 h, concentrated to a final volume of 10 ml and stored in vials. The samples were analysed using an inverted microscope by placing 4 ml of preserved subsample each separately (2 ml of acetic Lugol's iodine and 2 ml of buffered formaldehyde) from the oceanic stations (stations 1–21), and 0.2–0.5 ml from RM in a petri dish of 3.8 cm diameter, with phase contrast attachment at 100× and 200× magnification. Micro-phytoplankton cells were identified based on identification keys provided by Subrahmanyan[16], Taylor[25], Tomas[30] and Horner[31]. Their abundance is expressed in terms of cells per litre. To study the *Tripos* species composition and distribution, samples preserved with acetic Lugol's iodine were used. We draw information of *Tripos* from the micro-phytoplankton population, since the sampling was carried out using the ships of opportunity. The *Tripos* abundance was further compared with other geographical regions.

The abundance of ciliates (*Rhabdonellopsis*, *Albatrossiella*, *Eutintinnus*, *Ormosella*, *Salpingella*, *Steenstrupiella*, *Xystonella*, *Dictyocysta* and *Salpingacantha*) to genus level was also enumerated from 1 litre of water sample preserved separately with buffered formaldehyde (0.6%).

Data analyses

The *Tripos* species that contributed to more than 0.5% of the total *Tripos* population were subjected to ordination

Table 1. Details of sampling dates (DD/MM/YYYY) with their respective codes sampled for 48 months along the Chennai to Port Blair route and for 38 months along the Port Blair to Kolkata route from October 2006 to September 2011

Chennai to Port Blair	Code
25/10/2006 to 28/10/2006	O6
11/11/2006 to 16/11/2006	N6
07/12/2006 to 09/12/2006	D6
02/01/2007 to 04/01/2007	JN7A
27/01/2017 to 30/01/2017	JN7B
26/02/2007 to 01/03/2007	F7
04/04/2007 to 06/04/2007	A7A
25/04/2007 to 27/04/2007	A7B
28/05/2007 to 30/05/2007	MY7
26/06/2007 to 29/06/2007	J7
21/07/2007 to 23/07/2007	JU7
31/08/2007 to 03/09/2007	S7
05/10/2007 to 08/10/2007	O7
09/11/2007 to 12/11/2007	N7
14/12/2007 to 17/12/2007	D7
12/01/2008 to 14/01/2008	J8
24/02/2008 to 26/02/2008	F8
24/03/2008 to 26/03/2008	M8
14/04/2008 to 16/04/2008	A8
08/05/2008 to 09/05/2008	MY8
18/07/2008 to 21/07/2008	JU8
21/08/2008 to 23/08/2008	AU8
18/09/2008 to 20/09/2008	S8
27/10/2008 to 30/10/2008	O8
10/11/2008 to 13/11/2008	N8
25/12/2008 to 27/12/2008	D8
13/01/2009 to 16/01/2009	JN9
18/02/2009 to 21/02/2009	F9
18/03/2009 to 21/03/2009	M9
16/04/2009 to 19/04/2009	A9
06/06/2009 to 09/06/2009	J9
10/07/2009 to 12/07/2009	JU9
13/08/2009 to 16/08/2009	AU9
12/09/2009 to 13/09/2009	S9
14/10/2009 to 17/10/2009	O9
09/11/2009 to 12/11/2009	N9
26/12/2009 to 28/12/2009	D9
22/01/2010 to 25/01/2010	JN10
17/02/2010 to 20/02/2010	F10
20/03/2010 to 23/03/2010	M10
21/04/2010 to 23/04/2010	A10
24/05/2010 to 27/05/2010	MY10
21/07/2010 to 24/07/2010	JU10
22/09/2010 to 26/09/2010	S10
26/11/2010 to 29/11/2010	N10
16/02/2011 to 19/02/2011	F11
09/05/2011 to 12/05 2011	MY11
20/09/2011 to 23/09/2011	S11

Port Blair to Kolkata	Code
03/11/2006 to 05/11/2006	N6A
23/11/2006 to 25/11/2006	N6B
16/01/2007 to 19/01/2007	JN7
13/02/2007 to 15/02/2007	F7
02/03/2007 to 04/03/2007	M7
12/04/2007 to 14/04/2007	A7
02/05/2007 to 04/05/2007	MY7
05/06/2007 to 08/06/2007	J7
06/07/2007 to 10/07/2007	JU7A
24/07/2007 to 26/07/2007	JU7B
07/09/2007 to 09/09/2007	S7
20/10/2007 to 23/10/2007	O7
18/11/2007 to 21/11/2007	N7
19/12/2007 to 21/12/2007	D7
18/01/2008 to 21/01/2008	JN8
08/03/2008 to 11/03/2008	F8
18/04/2008 to 24/04/2008	A8
13/05/2008 to 16/05/2008	MY8
28/08/2008 to 30/08/2008	AU8
25/09/2008 to 28/09/2008	S8
05/11/2008 to 07/11/2008	N8
06/01/2009 to 08/01/2009	JN9A
26/01/2009 to 28/01/2009	JN9B
24/03/2009 to 27/03/2009	M9
20/04/2009 to 23/04/2009	A9
12/06/2009 to 14/06/2009	J9
17/07/2009 to 20/07/2009	JU9
20/08/2009 to 22/08/2009	AU9
21/09/2009 to 24/09/2009	S9
21/10/2009 to 24/10/2009	O9
19/11/2009 to 21/11/2009	N9
28/01/2010 to 31/01/2010	JN10
25/03/2010 to 27/03/2010	M10
31/05/2010 to 03/06/2010	J10
25/07/2010 to 27/07/2010	JU10
04/10/2010 to 07/10/2010	O10
28/02/2011 to 02/03/2011	M11
29/09/2011 to 01/10/2011	S11

analysis. The relationship among *Tripos*, ciliates and environmental parameters (sea-surface temperature (SST), sea-surface salinity (SSS), DIN, DIP, wind speed, rainfall and PAR) was evaluated separately for CPOS, and P–K transect by performing canonical correspondence analysis (CCA), CANOCO version 4.5 (ref. 32). An automatic selection, on seven environmental variables was performed, and using a Monte Carlo permutation test and statistical significance of each variable was tested under the reduced model with 999 permutations. Only those stations were considered for which physicochemical data was available.

Results

Hydrography

Along CPOS, low SST (26.1–29.9°C) was observed during monsoon (NEM and SWM) and relatively higher during SIM and FIM (28.2–31.0°C). Along the P–K transect (PKOS, AR and RM), low SST was observed during NEM (24.3–30.0°C) and relatively higher values during FIM, SIM and SWM (27.9–30.9°C). The SST was lowest during NEM (irrespective of the region), and this trend was observed in all the five years. The CPOS comprises of stations that are away from riverine influence, whereas AR and RM are closer to the Irrawaddy and Ganges–Brahmaputra river basins. The SSS was relatively high in CPOS (29.2–34.4) when compared to P–K transect (25.7–34.4). Low SSS was observed during SWM, especially in RM and was relatively high during SIM and FIM (Tables S1–S3, see Supplementary Material online).

Nutrient concentrations in the surface waters of the BoB were below detectable range for most part of the year, especially during SIM. In CPOS, maximum concentration of DIN and DIP was observed on some occasion during the monsoons, and was up to 3.02 and 2.88 μmol l^{-1}. In PKOS, it was in par with CPOS. However, in AR and RM it was noticed that the concentration was up to 4.23 μmol l^{-1} for DIN and 3.08 μmol l^{-1} for DIP (Table S1–S3, see Supplementary Material online).

The variations in wind speed and PAR in all the four regions are presented in Tables S1–S3 (see Supplementary Material online). In all the regions, high wind speed was recorded during the SWM, followed by NEM, whereas low wind speed was recorded during IM. PAR was also high during IM, and low during SWM and NEM.

Rainfall showed a different pattern. High precipitation was noticed during SWM and NEM in the entire CPOS, whereas during SWM it was observed in the P–K transect (Tables S1–S3, see Supplementary Material online). However, we could also see the intra-annual variation, where rainfall was also recorded during SIM in the stations of AR.

Based on the SSHA mesoscale eddy was identifiable on 4 occasions. The first eddy had a centre at 13°00′N lat. and 83°00′E long. The second eddy had a centre at 18°50′N and 87°00′E. The third and fourth had a centre at 16°00′N and 85°00′E and13°00′N and 83°00′E (Table S4, Figure S1 *a–d*, see Supplementary Material online).

Micro-phytoplankton community and abundance

Total micro-phytoplankton abundance varied from 25 to 6.3 $\times 10^4$ cells l^{-1} along the CPOS transect and 30 to 2.7 $\times 10^5$ cells l^{-1} along the P–K transect. The highest abundance was observed during SWM followed by NEM. However, at AR and RM the abundance was also high during SIM and FIM (Figure 2 *a* and *d*). The trend was opposite in the case of dinoflagellates, except at RM and AR (Figure 2 *b* and *e*). Diatoms were the dominant group with respect to their numbers, whereas dinoflagellates was the highest with respect to its taxonomic composition (data not shown). Apart from diatoms and dinoflagellates, high numbers of ciliates were also encountered in the AR and RP. Their abundance varied from 5 to 200 cells l^{-1} along CPOS and up to 1000 cells l^{-1} along RM (Figure 2 *c* and *f*).

Tripos species composition and community structure

Tripos abundance varied from 5 to 125 cells l^{-1} along the CPOS and up to 280 cells l^{-1} along the P–K transect (Figure 3 *a* and *b*). Altogether 40 species of *Tripos* were recorded, of which 29 were common to the two transect (Table 2). It was also noticed that 10 species were exclusively found along the C–P and 1 species along the P–K transect (Figures S2 and S3, Tables S5–S8, see Supplementary Material online). Along the CPOS, maximum abundance of *Tripos* was noticed at station 5 during FIM and SIM, and at station 7 during NEM, whereas along the P–K transect the highest abundance was observed in the RM during SWM–IV then followed by SIM. In addition, *T. furca*, *T. fusus*, *T. muelleri* and *T. lineatus* having the potential to form blooms were also encountered.

Tripos distribution in the C–P and P–K transects

Tripos abundance along the CPOS showed inter- and intra-annual variations as illustrated in Figure 3 *a* and *b*. The highest abundance (125 cells l^{-1}) was observed during FIM (October 2007 and October 2008), and the abundance was low during October 2006 and October 2009 (40 cells l^{-1}). During November, which is a northeast monsoon month, *Tripos* was widely distributed.

During the later stage of SIM, abundance was high and reached up to 60 cells l^{-1}, and these high numbers continued in the initial stages of SWM and decreased at the end of SWM. On an inter-annual scale, September 2010 was an exception yielding high numbers.

Along the P–K transect, irrespective of the seasons, maximum abundance was recorded at RM, followed by AR, and ranged from 100 to 280 cells l^{-1}. In PKOS, the cell abundance was on par with CPOS (Figure 3 *b*).

Comparison of Tripos with different biogeographical regions

A comparison of the *Tripos* abundance in different regions of the oceans is provided in Table 3. In the open ocean the abundance is generally low. Higher abundance of *Tripos* population have been reported from the Sagami Bay, Buyukcekmece Bay and Chesapeake Bay and have been related to nutrient regeneration (decay of *Noctiluca scintillans*), higher DIN concentration (up to 10.79 μmol l^{-1}) and availability of feed *Strobilidium* spp. in the Chesapeake Bay.

Influence of environmental characteristics on the distribution of Tripos

The CCA was used to link the distribution of *Tripos* species to environmental variables. The orientation and arrow lengths shown in Figure 4 *a* and *b* (environmental

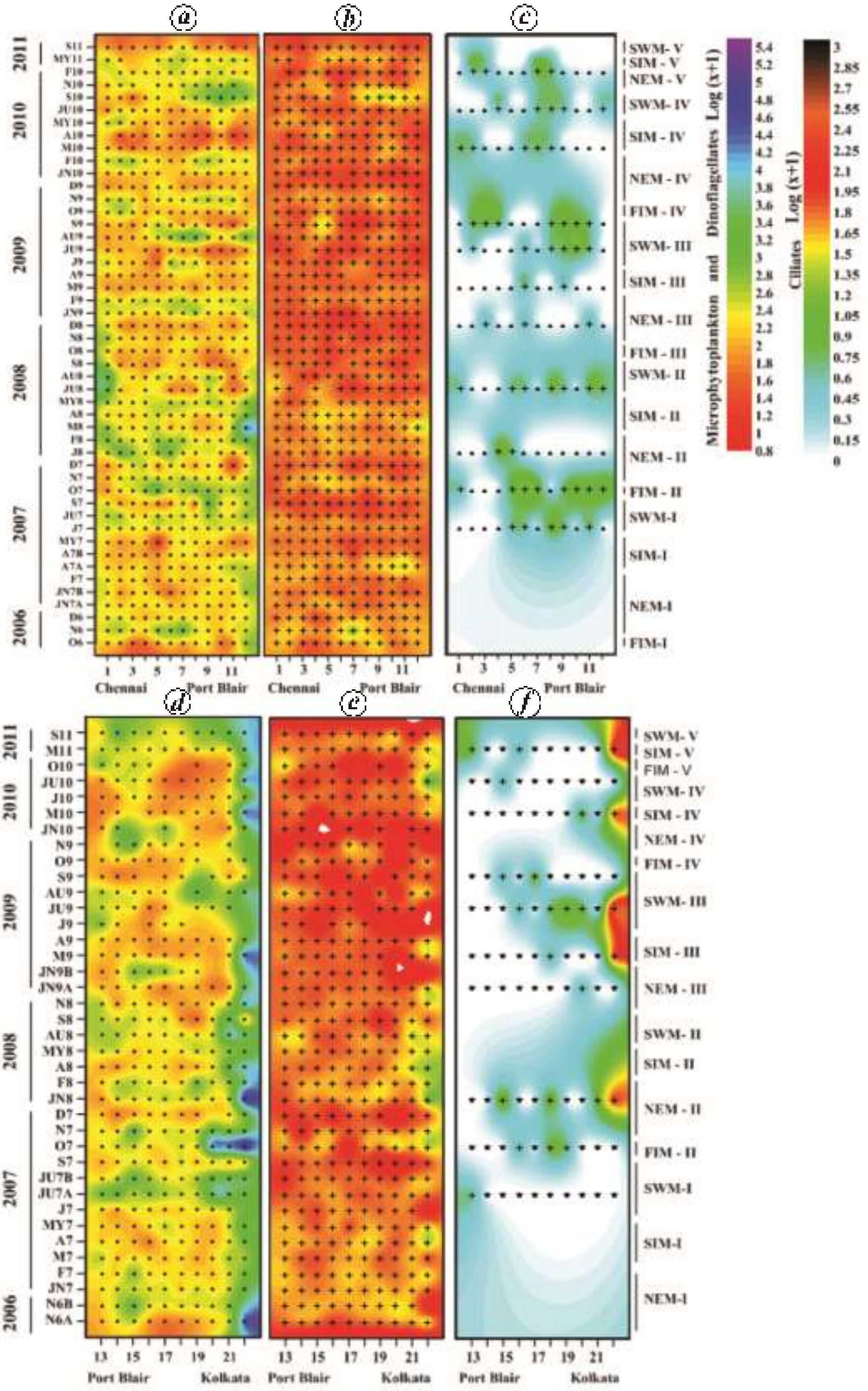

Figure 2 ***a–f*****.** Spatio-temporal variation of micro-phytoplankton (***a***, ***d***), dinoflagellate (***b***, ***e***) and ciliates (***c***, ***f***), abundance along the CPOS and P–K transect. The $\log(x + 1)$ transformed abundance values are used in the plot. + denotes presence of the taxa at sampled stations. * denotes the stations sampled where ciliates were not recorded. The sampling dates with their respective codes along the CPOS and P–K transect are provided in Table 1.

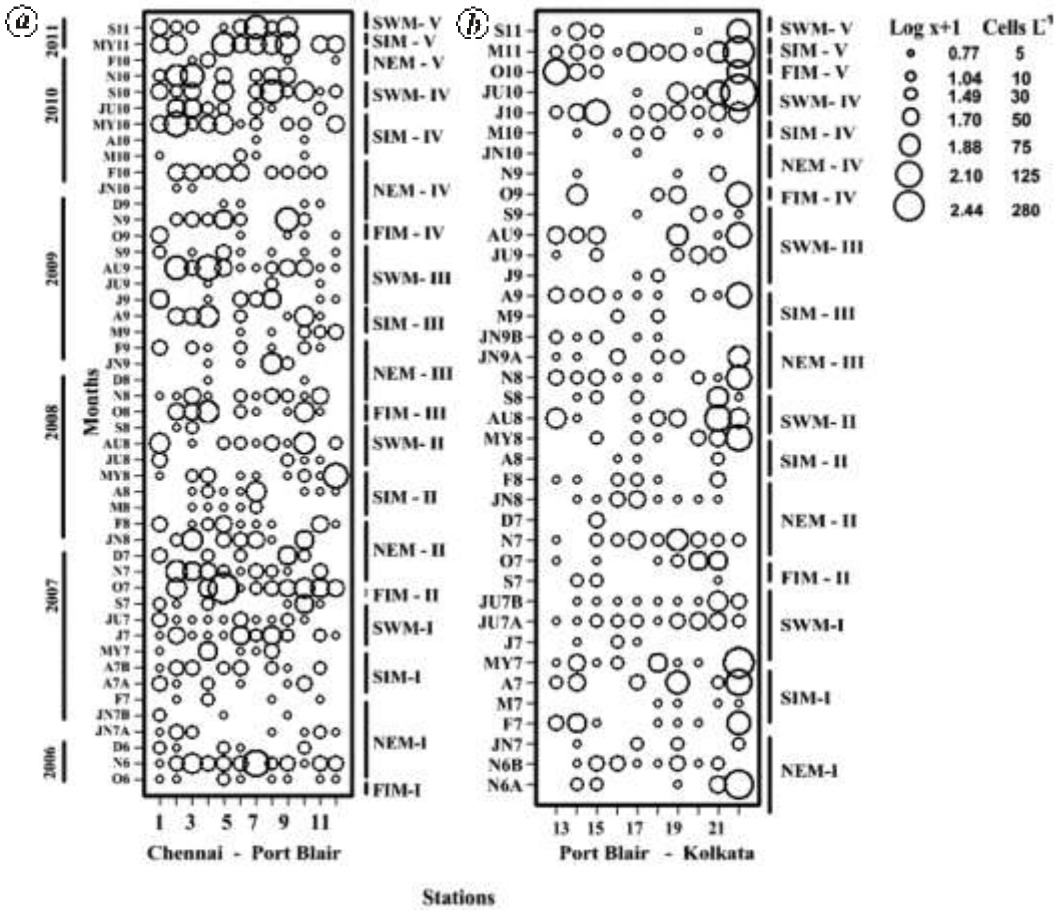

Figure 3 *a*, *b*. Spatio-temporal variation of *Tripos* along the CPOS (***a***) and P–K transect (***b***). The log(x + 1) transformed abundance values were used in the plot. The sampling dates with its respective codes along the CPOS and P–K transect are provided in Table 1.

variables) indicate their relative importance and approximate correlation to the axes. Arrows point in the direction of increase of the environmental gradient. Based on automatic selection and Monte Carlo permutation test of the total 7 environmental variables, SST and SSS was statistically significant in CPOS and P–K transect (Tables S9a and S10a, see Supplementary Material online).

In the CPOS, CCA results showed that 10.74% of the total inertia (2.1%) in the species data could be explained by environmental variables (Figure 4 *a*). The CCA axes 1 and 2 (eigenvalues of 0.09 and 0.05 respectively) explained cumulative variance (49.5%) of the relation of species–environmental variables (Table S9, see Supplementary Material online). Based on the intersect correlation of environmental variables with the CCA axis, we could notice, *T. fusus*, *T. candelabrus* and *T. deflexus* preferred moderate to higher DIN concentration, whereas *T. trichoceros* preferred higher DIP. *T. karstenii* and *T. kofoidii* preferred higher rainfall, whereas *T. longirostrus*, *T. extensus* and *T. inflatus* preferred low SST. *T. furca* was not seen to be influenced by any of the environmental variables.

In the P–K transect, CCA results showed 3.9% of the total inertia (11.8%) in the *Tripos* was explained by environmental variables (Figure 4 *b*). The CCA axes 1 and 2 (eigenvalues of 0.27 and 0.09 respectively) explained 70.6% of the environmental variables (Table S10, see Supplementary Material online). Based on the intersect correlation of environmental variables with the CCA axis, we could notice that the cosmopolitan forms which are most dominant (*T. furca*, *T. fusus* and *T. horridus* preferred higher DIN, DIP, rainfall, photosynthetic active radiation and wind speed). The open ocean forms (*T. extensus*, *T. macroceros*, *T. schmidtii*, *T. inflatus* and *T. declinatus*) preferred higher SSS and SST.

Discussion

The BoB is characterized by unique features such as seasonally reversing monsoon winds that blow during May–September from the southwest and during November–February from the northeast, March–April and October (IM) being the months of transition phase with weak winds[28]. The bay is also known for its enormous fresh

Table 2. List of *Tripos* species recorded along the C–P and P–K transects from October 2006 to September 2011

Taxa	CCA codes	C–P	P–K
Tripos arietinus (Cleve 1900)	ar	5–10 (4)	5 (3)
Tripos azoricus (Cleve 1900)	az	5 (3)	5–10 (4)
Tripos belone (Cleve 1900)*	be	5 (1)	
Tripos boehmii (H. W. Grahm & Bronik 1944)	bh	5 (1)	10 (1)
Tripos brevis (Ostenf. & Johannes Schmidt 1901)	br	5–15 (24)	5–10 (5)
Tripos candelabrus (Ehrenb. 1859)	ca	5–20 (4)	10 (1)
Tripos concilians (Jorg. 1920)*	cc	5 (2)	
Tripos contortus (Gourret 1883)	co	5 (2)	5 (1)
Tripos declinatus (G. Karst. 1911)	de	5–20 (75)	5–10 (35)
Tripos deflexus (Kof. 1907)	df	5–10 (10)	5–20 (3)
Tripos dens (Ostenf. & Johannes Schmidt 1901)	dn	5–20 (3)	5–15 (7)
Tripos digitatus (F. Schutt 1895)*	di	5–10 (3)	
Tripos extensus (Gourret 1883)	ex	5–20 (14)	5–20 (5)
Tripos euarcuatus (Jorg 1920)*	eu	5 (1)	
Tripos furca (Ehrenb. 1834)	fr	5–40 (76)	5–240 (65)
Tripos fusus (Ehrenb. 1834)	fu	5–25 (69)	5–40 (47)
Tripos hexacanthus (Gourret 1883)*	hex	5 (3)	
Tripos horridus (Cleve 1897)	hr	5–30 (35)	5–60 (23)
Tripos incisus (G. Karst. 1906)*	inc	5 (1)	
Tripos inflatus (Kof. 1907)	inf	5–10 (17)	5–15 (14)
Tripos karstenii (Pavill. 1907)*	kar	5 (5)	
Tripos kofoidii (Jorg. 1911)	kof	5 (5)	20 (1)
Tripos lineatus (Ehrenb. 1854)	lin	5–20 (17)	5–10 (5)
Tripos limulus (C.H.G. Pouchet 1883)*	lim	5 (1)	
Tripos longirostrus (Gourret 1883)	lon	5–10 (9)	5 (3)
Tripos lunula (Schimper 1900 ex G. Karst. 1906)	lu	5 (1)	5 (1)
Tripos macroceros (Ehrenb. 1840)	mac	5–10 (13)	5–15 (5)
Tripos massiliensis (Gourret 1883)	mes	5–15 (5)	5 (2)
Tripos minutus (Jorg. 1920)*	min	5 (2)	
Tripos muelleri (Bory 1825)	tri	5–20 (21)	5–15 (5)
Tripos muelleri var. *atlanticus* (Ostenf. 1903)	tra	5 (5)	5–20 (4)
Tripos pentagonus (Gourret 1883)	pen	5–15 (26)	5–10 (11)
Tripos pulchellus (Schrod. 1911)	pul	5 (1)	5 (2)
Tripos ranipes (Cleve 1900)*	ran	5–25 (3)	
Tripos schmidtii (Jorg. 1911)	sc	5–20 (18)	5–15 (6)
Tripos setaceus (Jorg. 1911)**	se		5 (2)
Tripos symmetricus (Pavill 1905)	sy	5 (1)	5 (1)
Tripos teres (Kof. 1907)	te	5–15 (61)	5–20 (22)
Tripos trichoceros (Ehrenb. 1859)	trh	5–20 (25)	5–100 (18)
Tripos vulture (Cleve 1900)	vu	5–10 (6)	5–80 (10)

Values outside the brackets indicate variation in cell numbers (cells l^{-1}) and those inside the brackets indicate the number of occurrences. * and ** indicate species which were exclusively recorded in the C–P and P–K transects respectively. CCA codes for the species are also indicated,

water influx (riverine discharge and precipitation), vertical stratification, low light (due to cloud cover and silt), and low nutrients[33,34]. Under such environmental settings, only those organisms that have developed an alternate mechanism for switching mode of nutrition have the efficiency to cope up in an oligotrophic environment. Studies indicate that dinoflagellates thrive well in low nutrient condition through a wide range of nutritional modes[35,36]. The present study revealed that in the BoB, genus *Tripos* is known to be widespread in its distribution.

In earlier studies (Pacific and NW Mediterranean)[8,12] large volume of water (~70 l) was utilized to enumerate *Tripos* and their abundance quantified was in the range of 0–24 cells l^{-1}. In this study we utilized only one litre of surface water sample. Inspite of this limited volume the numbers are comparatively higher (5–280 cells l^{-1}) than that observed in the Pacific and Mediterranean. In this study, we covered spatial (CPOS, PKOS, AR and RM) and seasonal (FIM, NEM, SIM and SWM) variations in the distribution of *Tripos* species. The stations of CPOS and PKOS are in the open ocean, and the AR and RM are more restricted to riverine discharge. Though all the four regions are influenced by seasonally reversing monsoons, the hydrographic settings (changes brought by variations in SSS) in these transects are different. In AR and RM, the main factors are precipitation and riverine discharge; Irrawady basin and Hooghly–Ganga estuarine complex are the major sources of freshwater influx[37]. In the CPOS

Table 3. Comparison of *Tripos* abundance and the two most dominant forms (*T. furca* and *T. fusus*) from different geographical regions

		Cell abundance			
Ocean/sea	Locality	*Tripos* spp. cells m^{-3}	*T. furca* cells m^{-3}	*T. fusus* cells m^{-3}	Reference
Indian	Bay of Bengal		0–2 × 10^4	0–2 × 10^4	23
Indian	Cochin backwaters	1.8–2 × 10^3			48
Indian	Jakartha Bay	5.1 × 10^5			49
Indian	Northwestern Red Sea		70–100,000		50
Pacific	Sagami Bay		7.5 × 10^7	1.1 × 10^7	40
Pacific	Sagami Bay		1.4 × 10^7	4.9 × 10^7	41
Pacific	North Pacific Central gyre	166–2399	0–38	0–5.5	7
Pacific	Eastern North Pacific	2000–22,000			8
Pacific	Tropical Central Pacific	48,000–108,000	12,000–24,000	40 × 10^3	51
Mediterranean	Büyükçekmece Bay, Sea of Marmara		5000 × 10^3		52
Mediterranean	East–west transects of the Mediterranean		1.4–1.6 × 10^5	17,000–230,000	53
Mediterranean	Mediterranean Gulf of Kalloni		2.84 × 10^6	2.1 × 10^6	54
Mediterranean	Ligurian sea	24,000			12
Mediterranean	Northwest Mediterranean	834–3734			55
Atlantic	Chesapeake Bay		7–480 × 10^6		56
Atlantic	East coast of USA		10,000	70,000	57
Atlantic	English Channel and North Sea	90 × 10^6			58
Arctic	Barent and Karas Sea	10–500 × 10^3			59
Atlantic	Brazil–Malvinas confluence region		0–20,000	0–20,000	60

and PKOS, precipitation is the main source of salinity variation. The prevailing mesoscale eddies in the CPOS are also known for high biological production[38]. Observations in this study indicate that the influence of eddies is restricted to upper 30 m of water column. Under such conditions, we observed distinct seasonality in the timing of occurrence of *Tripos*.

The number of species encountered was relatively higher along the CPOS than along the P–K transect. Most of the species recorded in the two transects (16 species; present during all four seasons) were widespread in the Bay, of which 15 species along C–P and four along P–K were noticed in all the four seasons. Among them, two species (*T. furca* and *T. fusus*) were dominant in both the transects (Tables S5–S8, Figures S2 and S3, see Supplementary Material online). Their dominance in these two contrasting environmental settings indicates that they can also tolerate a wide range of salinity (25–34). Investigations from the Sagami Bay, Japan, also showed similar results[39–41]. For example, *T. furca* was observed in salinities varying from 17 to 34 and *T. fusus* from 24 to 30. It was also observed that apart from low salinity, rainfall results in nutrient loading especially DIN into the coastal waters. In both field and laboratory studies densities and specific growth rates tend to increase with higher N : P ratios[41]. In our studies as indicated in CCA biplot, high number of *T. furca* was related to high DIN concentration (Figure 4 *b*).

The species that formed the second dominant group are *T. vultur*, *T. trichoceros*, *T. muelleri*, *T. teres*, *T. pentagonus*, *T. macroceros*, *T. longirostrus*, *T. lineatus*, *T. inflatus*, *T. horridus*, *T. extensus*, *T. deflexus* and *T. brevis*. Although these species were not found in relatively high numbers (except *T. tricoceros*) they were present during SWM, NEM, SIM and were absent during FIM (Figures S2 and S3, see Supplementary Material online). In both the transects especially open ocean (CPOS and PKOS), the following species *T. lunula*, *T. contortus* and *T. candelabrus* were exclusively observed during the monsoon (SWM and NEM). The ten exclusive species observed along the C–P transect were found in very low numbers and occurrence (Table 2). These results indicate that they are purely oceanic forms with unique water mass characteristics and prevail mostly in less stratified water with a salinity range 31–34. Dodge and Marshall[4] have observed tolerance of some of these species (*T. gracilis* var. *symmetricus*, *T. karstenii* and *T. ranipes*) to a maximum of 28°C. However, their occurrence in BoB indicates their tolerance to higher temperature (29–31°C).

Several physical factors such as wind, current, tidal flow and density gradient have been suggested to concentrate phytoplankton in specific areas and play an important role in its regulation[42]. Studies in the NE Atlantic Ocean have also shown distinct dinoflagellate community in two different current patterns[10]. The current along the east coast of India (EICC; East India coastal current) reverses seasonally during the monsoon. Its poleward phase is developed during March–April, and the equator phase begins as the SWM withdraws. The equatorward flow appears first in the north in September and by November it is present along the entire coast[43]. We could observe high wind speeds (11–15, 7–10 m/s) during June and November in CPOS and during July in PKOS, AR and RM. Since high density of *T. furca* is usually found in the coastal waters, its widespread occurrence in November in CPOS can be related to the influence of the above monsoon events.

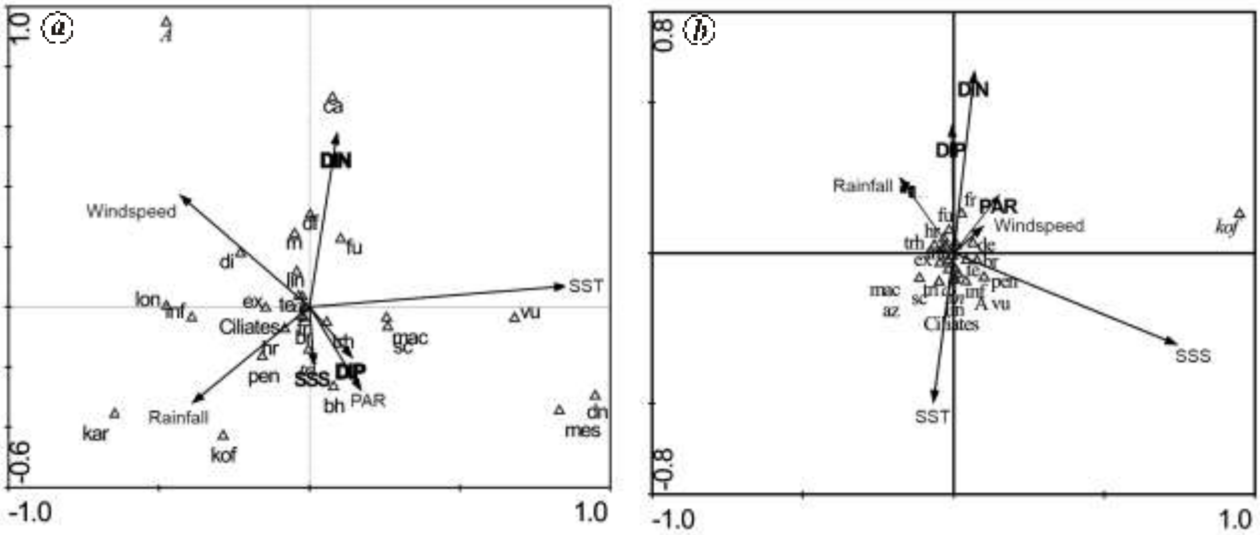

Figure 4. Ordination diagrams for CPOS (***a***), P–K transect (***b***), based on canonical correspondence analysis of *Tripos* and ciliates. The physico-chemical variables (temperature, salinity, dissolved inorganic nitrogen, dissolved inorganic phosphorus, rainfall and PAR) are indicated by arrows. Species abbreviations are listed in Table 2.

During IM the nutrient concentrations were below detectable levels, whereas during SWM and NEM, they were in the detectable range which can be attributed to rainfall. The distribution of field population of *T. furca* and *T. fusus* was positively related with DIN, DIP and increased wind speed[44]. We could also observe a similar trend with *T. furca* in BoB. However, the level of enrichment was considerably lower than that reported in the Sagami Bay. It is also evident from the CCA biplots (Figure 4 *a* and *b*), that one dominant form, i.e. *T. furca* persist under low DIN concentration, in the CPOS and the numbers tend to increase with elevated DIN in the stations of P–K transect.

The low numbers sustained in the oceanic stations can be attributed to species-specific nutrient adaptation using half-saturation constant (K_s) and have been evaluated by several authors[45–47]. K_s describes the ability of a species to take up low concentration of nutrients and thus determine the minimum nutrient concentration in which the species can grow. Dinoflagellates have low K_s compared with diatoms and raphidophytes. It has been reported that the half saturation constant for *T. furca* and *T. fusus* is low (0.15 μmol l^{-1}) for phosphate and high for nitrate (0.44 μmol l^{-1})[44]. Field and laboratory results also suggested that *T. furca* and *T. fusus* have a competitive advantage against other algal species under low nutrient conditions because of their low K_s values.

Conclusion

Observation of spatio-temporal variation in the dinoflagellate community of BoB revealed that *Tripos* is present round the year and is widespread in occurrence. Amongst the *Tripos* population, *T. furca* was the dominant form. The high numbers of *T. furca* recorded in AR, RM and in the C–P transect relate to the influence of monsoon, freshwater discharge and mesoscale eddies respectively. Dominance of *T. furca* was also observed with an increase in the ciliates population in AR and RM. Further studies on this association elucidating the depth-integrated information of *Tripos* community along with its environmental settings will be a step forward.

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