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Hydrodynamic control of microphytoplankton bloom in a coastal sea

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The influence of hydrodynamics on phytoplankton bloom occurrence/formation has not been adequately reported. Here, we document diurnal observations in the tropical Bay of Bengal's mid-western shelf region which reveal microphytoplankton cell density maxima in association with neap tide many times more than what could be accounted for by solar insolation and nutrient levels. When in summer, phytoplankton cells were abundant and the cell density of *Guinardia delicatula* reached critical value by tide caused zonation, aggregation happened to an intense bloom. Mucilaginous exudates from the alga due to heat and silicate stress likely promoted and stable water column and weak winds left undisturbed, the transient bloom. The phytoplankton aggregates have implication as food resource in the benthic region implying higher fishery potential, in carbon dioxide sequestration (carbon burial) and in efforts towards improving remote sensing algorithms for chlorophyll in the coastal region.

Keywords. Tidal influence; *Guinardia delicatula*; *Trichodesmium erythraeum*; *Guinardia striata*; remote sensing; bio-volume; chlorophyll; Bay of Bengal.

1. Introduction

Phytoplankton blooms attract worldwide attention because they are often harmful and affect the fishery resource of the sea, either positively or negatively. Close monitoring of phytoplankton blooms is expected to provide means to check and protect the oceanic/coastal ecosystem as well as to possibly link their occurrence to climate change (NOAA 2014). The influence of hydroptical, hydrochemical, hydrobiological and hydrogeological factors on phytoplankton abundance is known (Reynolds 2006). However, the interactive role of biological and physical factors in bloom formation is not clearly known (Prairie *et al.* 2012).

The Bay of Bengal in the tropical belt is a mesotrophic, less studied area, with high variability in phytoplankton distribution (Madhu *et al.* 2006; Prasanna Kumar *et al.* 2006). The Bay receives enormous fresh water flux from large and medium rivers of south Asia and through rainfall and this rainfall is affected by the Indian monsoon system consisting of seasonally reversing south-westerly (summer, May–September) and north-easterly (winter, October–January) winds (Gadgil 2003). In both the summer and winter monsoons,

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surface nutrient enrichment can happen, but by contrasting mechanisms. The summer winds cause upwelling away from river mouths. Close to river mouths surface freshening prevents upwelling due to the presence of a stagnant layer of less saline water leading to nutrient exhaustion at surface (McCreary *et al.* 2009), because of which phytoplankton production is restricted (Naik *et al.* 2011; D'Silva *et al.* 2012; Latha *et al.* 2014). The winter winds cool the surface and promote convection of surface water to depths in regions where there is no barrier layer at the surface, which also leads to surface nutrient enrichment (Vinayachandran and Mathew 2003).

There are reports of phytoplankton blooms in the western coastal Bay of Bengal, although not as much as in the case of the eastern Arabian Sea. The reported blooms include those of diatoms (e.g., *Asterionella japonica*), blue green algae e.g., *Trichodesmium* and dinoflagellates e.g., *Noctiluca* (D'Silva *et al.* 2012 and references therein). Nutrient availability (and light) alone does not give place to blooms in the western Bay of Bengal. Turbidity-river sourced in the coastal and also by tidal action in the estuarine regions, and cloud cover can severely restrict phytoplankton production by restricting the light field (Prasanna Kumar *et al.* 2002). The meso-scale eddies which are common in the western Bay of Bengal may or may not favour phytoplankton production depending on whether they cause upwelling (cold-core eddy) or sinking (warm-core eddy) (Prasanna Kumar *et al.* 2006). A less explored but important mechanism influencing phytoplankton abundance in the coastal region is the tidal oscillations (Blauw *et al.* 2012).

From a practical point of view, phytoplankton blooms have chlorophyll $a > 3\,\mu\mathrm{g\,L}^{-1}$, or when the (micro) phytoplankton abundance >1000 cells ml^{-1} even when chlorophyll does not exceed the threshold (Smayda 1997). Remote sensing which is routinely used to detect and monitor phytoplankton blooms is likely to miss bloom, if the bloom is transient due to hydrodynamic conditions and does not synchronize with the satellite pass. The complexities in chlorophyll retrieval based on satellite sensor data, e.g., the SeaWiFS in the Bay of Bengal (Tilstone *et al.* 2011) and on the regional to global scales (Siegel *et al.* 2013) indicate that high-resolution monitoring programs are essential in order to capture the natural variability of phytoplankton in coastal waters (Blauw *et al.* 2012). The objective of this paper is to make new high frequency observations in the mid-western shelf waters of the Bay of Bengal that would potentially reveal short-lived blooms.

2. Materials and methods

2.1 *Study area*

The western Bay of Bengal which borders the Indian east coast, Bangladesh and Sri Lanka receives large input of freshwater through rivers at regular intervals along the coast, e.g., the Ganga–Brahmaputra (G–B) river system, Mahanadi, Godavari, Krishna and Cauvery and several small rivers in between. In a coastal transect off Visakhapatnam on the east coast of India whose waters are not significantly affected by these point sources, three fixed stations where the water column is 20, 30 and 50 m deep were sampled during eight months (June 2013–February 2014). The stations are 2, 6 and 15 km away from the coast respectively (figure 1).

2.2 *Collection of samples and analyses*

The water samples were collected on board *CRV 'Sagar Paschimi'* of Ministry of Earth Sciences, India on a majority of cruises (6 of 8), and the hired '*MFV Srinivasa'* at other times, with the help of a Niskin bottle (5 L) from surface (–1 m), and 10, 20, 30 and 50 m depths. The sampling was at 2 hr intervals during the day time (08:00, 10:00, 12:00, 14:00, 16:00 hrs) at the 50 m bathymetric station (17°44.46′N, 83°29.6′E). At the other stations (20 and 30 m bathymetries), the sampling was done once while transiting to/from the time series station. A Seabird Electronics CTD measured the salinity and temperature. Standard methods were used carefully avoiding introduction of artifacts and using duplicates wherever necessary for the chemical analyses (dissolved oxygen and nutrients), measurement of pH and turbidity, and chlorophyll *a* estimation and (lugol's iodine fixed) phytoplankton enumeration adopting standard microscopic methods (UNESCO 1978; Chari *et al.* 2013a). Pearson correlation analysis was done for the phytoplankton abundance and bio-volume data, chlorophyll and nutrient concentrations in excel worksheets.

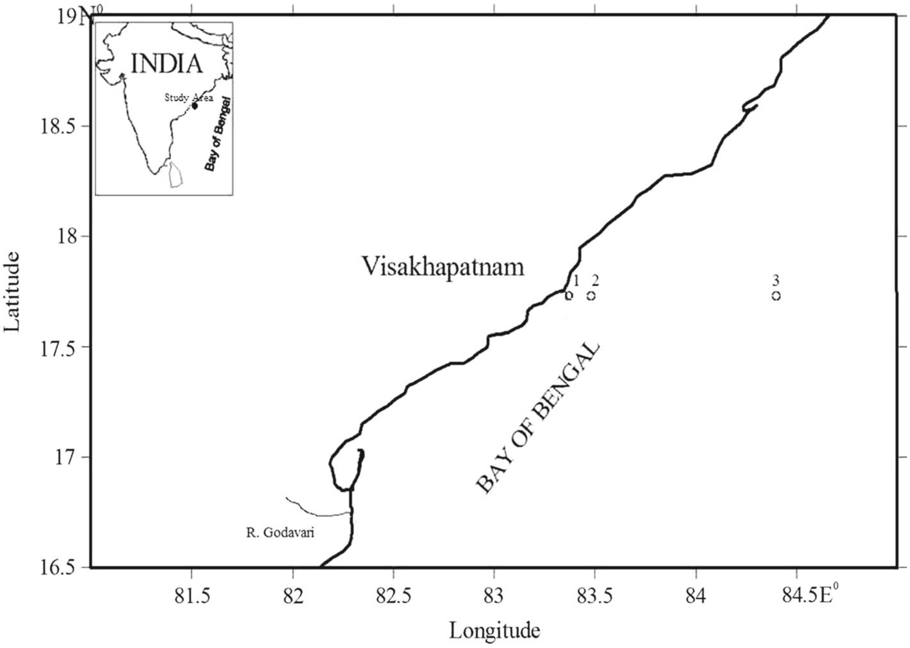

Figure 1. Study area showing stations at different water depths namely, 20 m (1), 30 m (2) and 50 m (3). (At stations 1 and 2, only surface samples were collected once. At station 3, sampling was done at all depths, i.e., surface, 10, 20, 30 and 50 m during each campaign five times in a day, i.e., 8:00, 10:00, 12:00, 14:00 and 16:00 hrs).

3. Results

3.1 *Hydrography*

The region is microtidal (tidal range <1.5 m during the study period), the tides being semidiurnal. During mid-day (12:00–14:00 hrs) when the solar insolation (and biological production) is at peak, neap tide occurred in June, July, September, and December campaigns, springtide occurred in August, and a transitional tide occurred in October, January and February campaigns (figure 2). Salinity was lowest in October ($\sim 22 \times 10^{-3}$) and highest in August (35.35, figure S1). Although the tidal range was only 0.5 m in August, salinity was in tune with the tide and the tidal excursion (salinity difference between the spring and neap tides, Δ_{Salinity}) was greatest (2.73), at the surface. Spring tide, however, caused salinity minima at depths. During October also, spring tide produced salinity minima at 10–30 m ($\Delta_{\text{Salinity}} = 1.6$) and had no effect at surface. In December, the Δ_{Salinity} was the least (∼1.2), and a tidal oscillation confined to the upper 10 m water occurred. During other campaigns, salinity had no relation to tide.

The water column was moderately cooler than at surface and the temperature difference between surface and bottom water (Δ_{T}) was <2°C (figure S1). In December, a 2.13°C temperature inversion was seen at 20 m with respect to surface, which is attributed to the surface cooling during winter (December). The effect of intense solar heating is seen in July with 4.5–6.8°C heating of the water column as the day progressed. During July, dissolved oxygen was more enriched in surface water (average, 256 μM) as compared to the rest of the campaigns (226). But in the same month (July), dissolved oxygen concentration was among the lowest cf., ∼110 μM at 50 m depth, which synchronized with the lowest pH observed (7.7) in the study (figure S1). There was a steep oxycline, attributed to stability of the water column in July. The concentration of nutrients was low and complex (figure S1). However, with the limited data of nitrate that we had (June, July and August, 2013; range: 0.8–20.4 μM), phosphate correlated excellently and yielded the relationship: Phosphate = 0.0566 × Nitrate with $R^2 = 0.57$ ($n = 75$, $p < 0.0001$). Chlorophyll *a* (figure 3a) was also low (range: 0.69–3.41 μg L^{-1}), and was not related to nutrients.

3.2 *Phytoplankton abundance and distribution*

Phytoplankton belonged to 133 species, mostly of diatoms (Centrics 73; Pennales 22) and less of dinoflagellates (33), blue green (BG) algae (3) and silicoflagellates (2) (table S1). The cell densities were highest for *Guinardia delicatula*, *G. striata* and *Trichodesmium erythraeum* (figure 4) in some

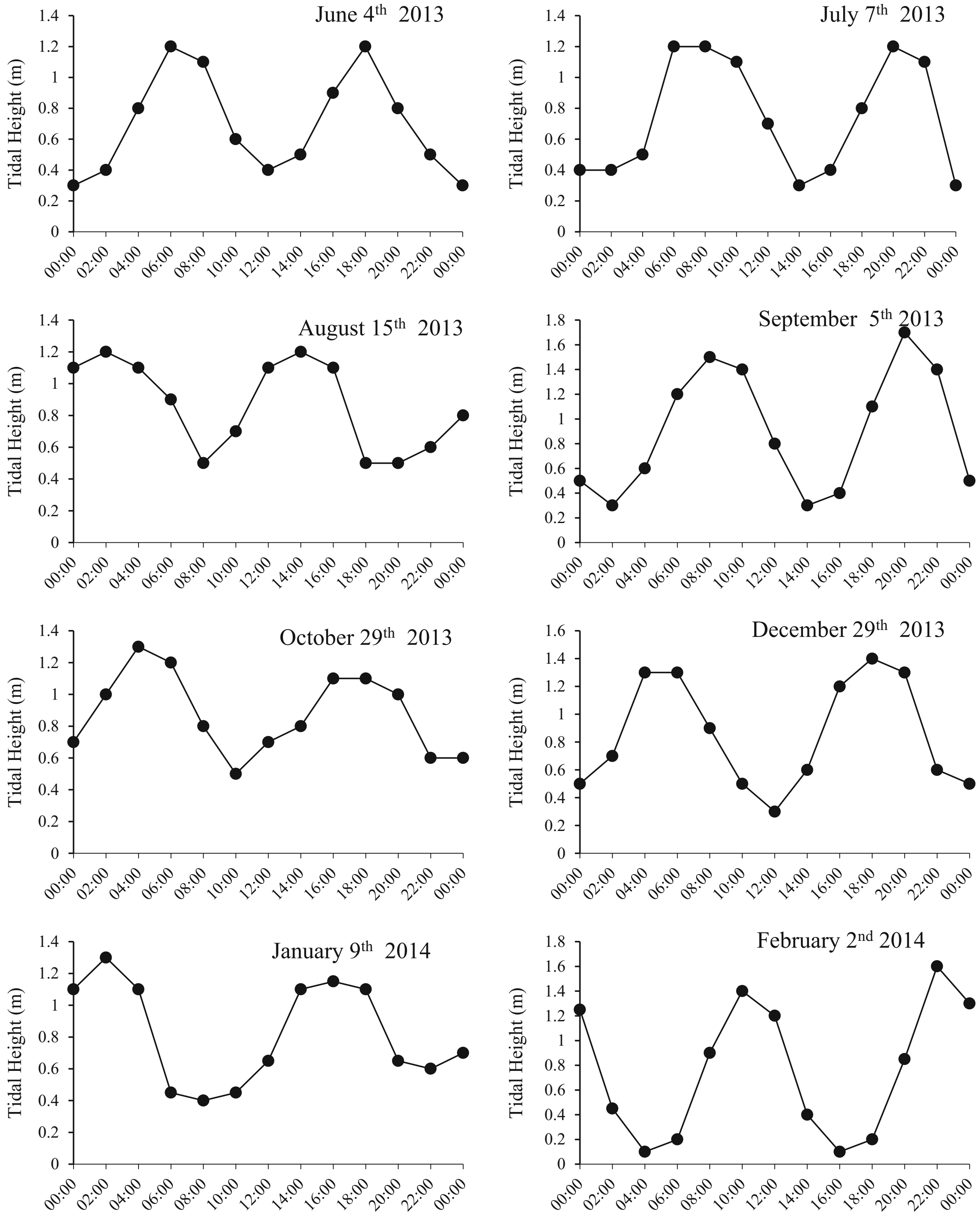

Figure 2. Tidal heights during 24-hr period of the sampling dates (June 2013–February 2014), i.e., from 8 hrs before the beginning of sampling to 8 hrs after the end of each field sampling. (X-axis: (1) 8:00; (2) 10:00; (3) 12:00; (4) 14:00; (5) 16:00 hrs).

samples. The total cell density of dinoflagellates ranged from 0 to 33 ml^{-1} with an average of 4, and most of the dinoflagellates were not represented in majority of the samples. They were relatively more enriched at surface and the more common species were *Ceratium trichoceros, C. furca* and *Prorocentrum micans.*

3.3 *Tidal rhythm of phytoplankton*

Peaks of phytoplankton abundance occurred in July at 10 m depth (cell count, 2547 ml^{-1}) and during September and December, at surface (817 and 577, respectively), all at 14:00 hrs. Phytoplankton density (figure 5), and in particular the abundance

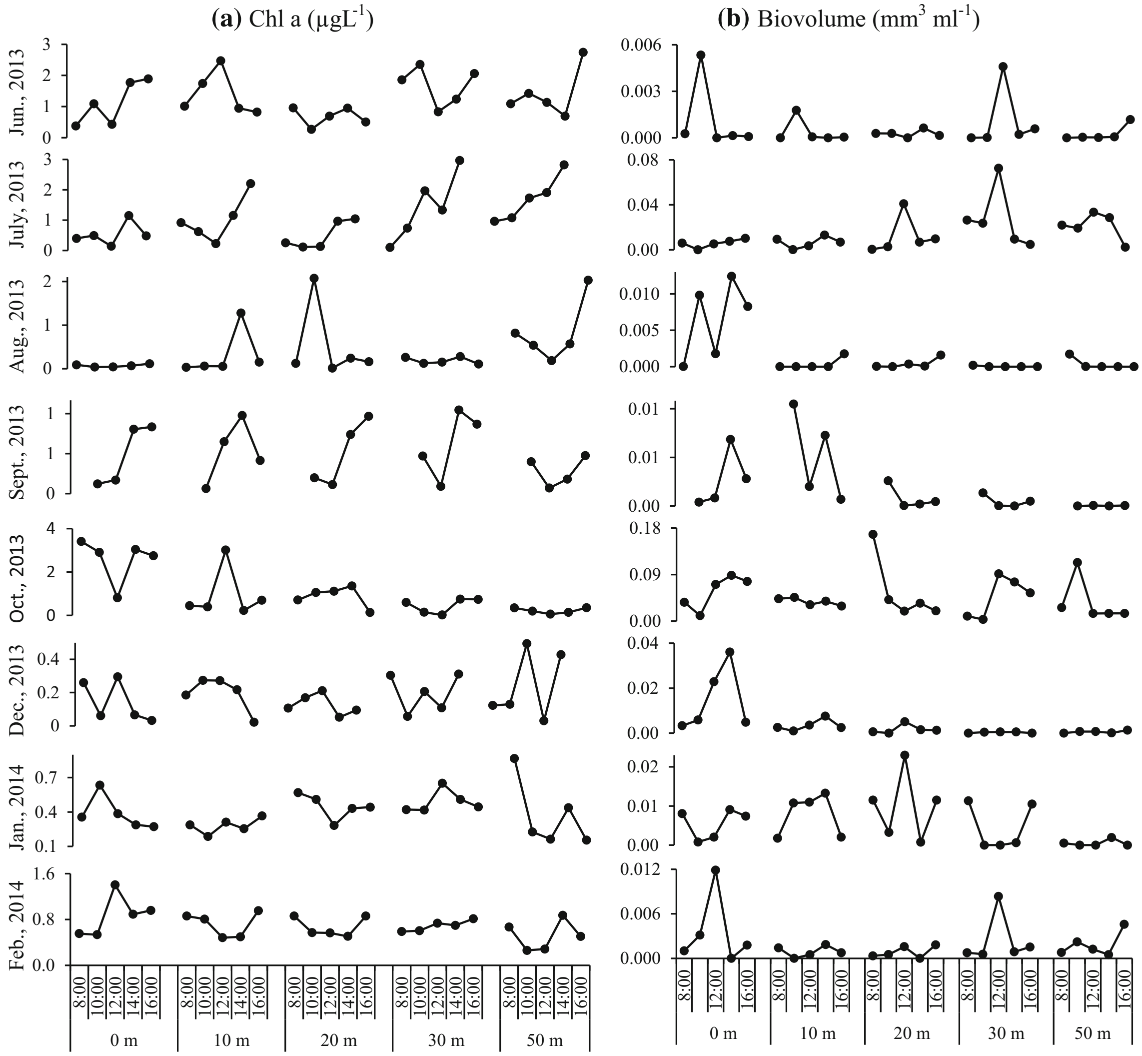

Figure 3. Time series concentrations of (**a**) chlorophyll *a* and (**b**) total phytoplankton biovolume in the water column during the 8 field campaigns at different depths of the water column (note: there were no observations at 8:00 hrs in September).

of *Guinardia delicatula* (figure 5a) synchronized with tide, the maxima and minima occurring at the neap and spring tides respectively at all depths in the water column during July, and in the upper 10 m water column during September and December. In October, the cell count was reasonably high (average, 274 ml^{-1}), but chlorophyll *a* among the highest (2.6 $\mu\text{g L}^{-1}$) in the upper 10 m water (figure 3a). *Thalassionema nitzschioides*, *Thalassiothrix frauenfeldii* and *Pseudonitzschia seriata* contributed majorly (up to 71%, figure S1), and there was no tidal rhythm in their distribution. During June, despite neap tide occurrence at noon, and during other campaigns (months) in which the neap tide occurred at other times during the day (August, January and February), no such oscillations were shown.

Guinardia delicatula constituted a predominant fraction of total phytoplankton cell count at 10 m (92%) (table 1) followed by surface (82%) and 20 m (65%) during July at neap tide. Remarkably, *G. striata* representation in the cell count was also high and synchronized with neap tide, but its peak representation in phytoplankton was confined to the 20–30 m water layer (4%–10%). During September too, *G. delicatula* showed tidal rhythm and its representation (to phytoplankton) was highest at neap tide but at surface (64%) (table 1). *G. striata* represented less to phytoplankton at its peak at 10 m at neap tide (35%). In December, *T. erythraeum* represented dominantly the phytoplankton cells, close to neap tide, at surface (82%). The next major species was *Oscillatoria* sp. (11%), also a diazotroph. At 10 m, however, majority

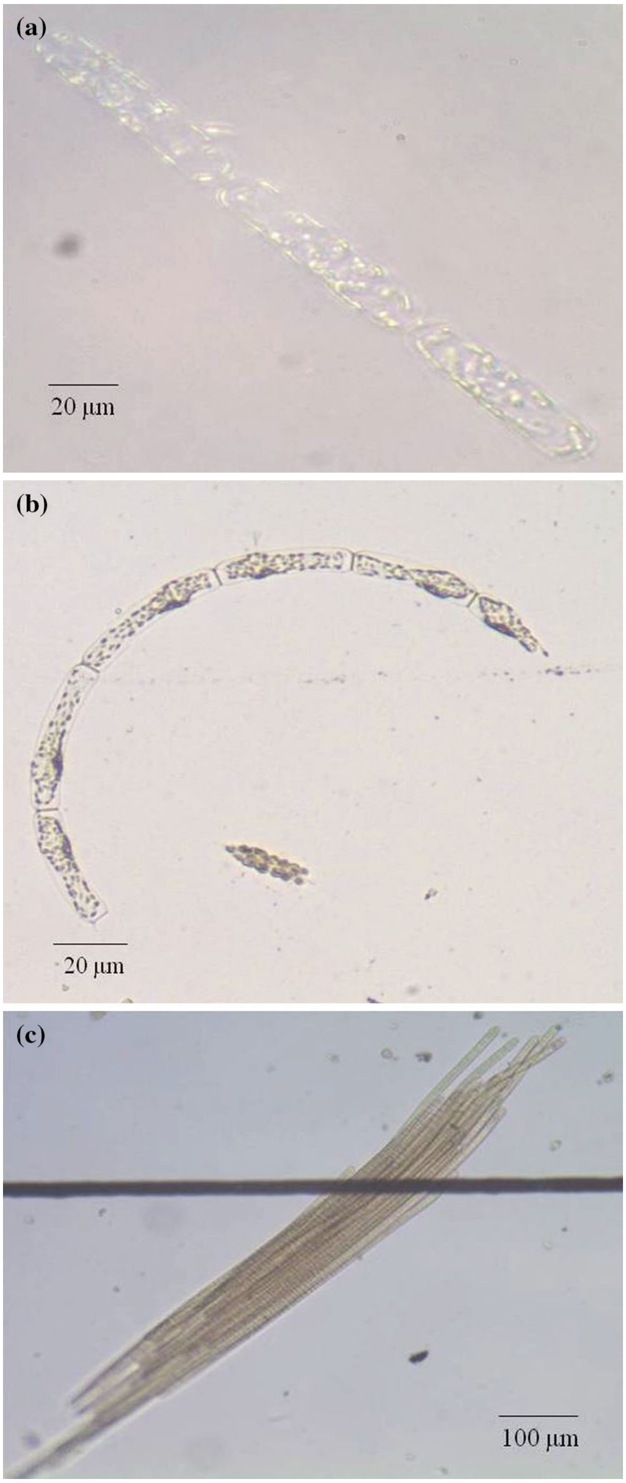

Figure 4. Typical microscopic images at ×10 magnification: (**a**) *Guinardia delicatula* (3 cells in chain), (**b**) *Guinardia striata* (6 cells) in July samples and (**c**) *Trichodesmium erythraeum* bundle in December samples.

were centric diatoms (24%), in which *G. delicatula* (19%) and *Bacteriastrum delicatulum* (17%) were the better represented (table S1).

3.4 *Phytoplankton bio-volume and its relationship to chlorophyll 'a'*

From the phytoplankton cell shapes and dimensions as viewed under the microscope, the average of 3–5 representative cells of each species of all campaigns, equivalent spherical diameter (ESD) and average cell bio-volume (BV) were computed, using standard methods (Hillebrand *et al.* 1999; Sun and Liu 2003) (figure 3b). The ESD and BV varied inter-species by factors of 24 and 14,000, respectively from the largest *Rhizosolenia robusta* (table 1) to the smallest *Thalassionema nitzschioides* (table 2). *G. delicatula* is smaller than *G. striata* and *T. erythraeum* (table 1).

The total phytoplankton BV is highest in October and reached 0.171 $\mathrm{mm^3 ml^{-1}}$ at 20 m (08:00 hrs) when chlorophyll *a* was also high (figure 3b). This was despite the fact that the cell density was low at surface (average, ∼370 $\mathrm{ml^{-1}}$) (table S1). The phytoplankton distribution in this month consisted of mainly diatoms *Thalassiothrix fraunfeldii* (average, 31%), *Skeletonema costatum* (19%), *Ditylum sol* and *Thalassionema nitzschioides* (12% each), *Chaetoceros curvisetus* (11%), *Odontella sinensis* (9%) and *O. mobiliens* (6%) (table S1). To the BV, the larger cell sized species namely *D. sol*, *O. sinensis* and *O. mobiliens* contributed as much as 60–100% (average±SD, 85±11%, $n = 25$). In July, when the phytoplankton (*G. delicatula*) density was the highest, *G. delicatula* constituted as much as 92% of cell density but its contribution to BV was only 21.1% at 10 m depth (table 1). Considering the Rhizosoleniaceae family of species, the cell density increased marginally to 95.3% (table 1), but their BV contribution shot up to 76.8% (data not shown) due to the large cell sized species such as *Rhizosolenia robusta.*

The BG algae contribution to total phytoplankton BV was high in December, January and February. In December, when the tidally rhythmic *T. erythraeum* cells dominated at surface, the contribution was 82% (table 1).

The graph of cell density or BV against chlorophyll *a* was highly scattered. On the other hand, the cell density related to BV when they were less than ∼800 cells $\mathrm{ml^{-1}}$ (i.e., excepting in July) and 0.07 $\mathrm{mm^3 ml^{-1}}$ (excepting in October) respectively (figure 6a). The coefficient of determination (R^2) was moderately high (0.38) but it is highly significant ($p < 0.0001$) in view of the large sample

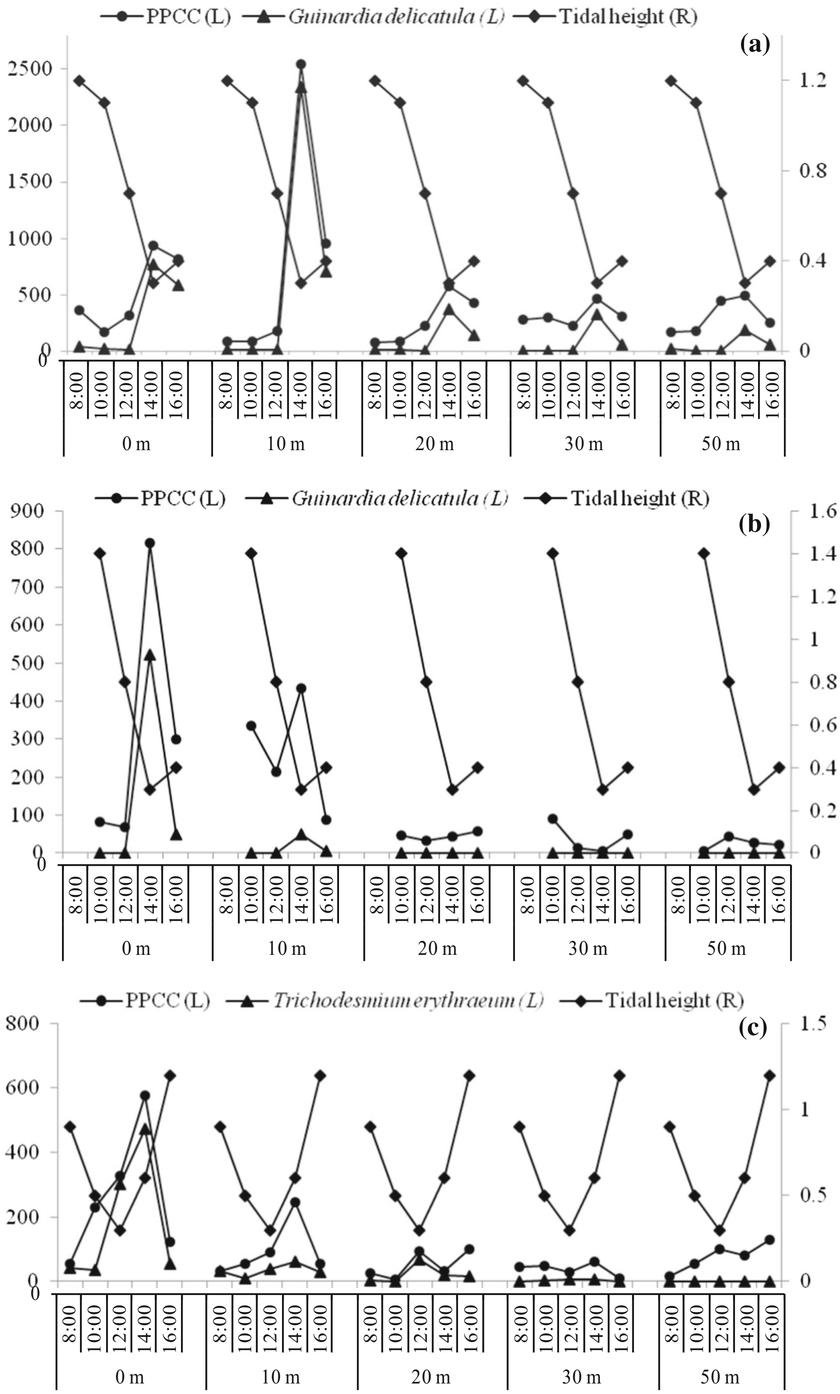

Figure 5. Diurnal variation in the water column of phytoplankton cell count (PPCC, left, L), and of *G. delicatula* abundance (L) in July (**a**) and September (**b**), and of *Trichodesmium erythraem* abundance (L) in December (**c**), overlaid on tidal height (right, R) (X axis, 1: 08:00 hr, 2: 10:00 hr, 3:12:00 hr, 4: 14:00 hr and 5: 16:00 hr). Units: Left axis (L): cells ml^{-1}, Right axis (R): meters.

size ($n = 238$). In this group of samples, there is a slightly weaker (negative) correlation of BV with salinity ($R^2 = 0.32$, $n = 238$) and this relation also is highly significant ($p < 0.0001$). The BV of phytoplankton rich samples (PPCC >800 cells ml^{-1}) is aligned with the regression line as shown (figure 6b).

4. Discussion

The biogeochemistry of the region agrees with previous reports (Chari *et al.* 2012, 2013b; Pandi *et al.* 2014). The significant relationship between nitrate and phosphate yields N:P ratio of 17.85:1 which is close to the Redfield ratio (16:1) and infers that

Table 1. *Species distribution during the phytoplankton cell count (CC) maxima and their average at neap tide (14:00 hrs) during July, September and December campaigns and their average equivalent spherical diameter (ESD, µm) (significant species only, cell count>2).*

	July (17)*		September (16)*		December (5)**		ESD#
Species name	CC	CC (%)	CC	CC (%)	CC	CC (%)	(µm)
Centric Diatoms							
Bacteriastrum furcatum	–	–	13	1.6	–	–	11.2
Chaetoceros curvicsetus	7	0.3	–	–	–	–	16.6
Chaetoceros coarctatus	–	–	–	–	30	5.2	26.1
Chaetoceros lorenzianus	–	–	3	0.4	–	–	49.4
Chaetoceros sp.	–	–	13	1.6	–	–	#
Corethron sp.	–	–	3	0.4	–	–	#
Guinardia delicatula	2343	92.5	523	64.1	–	–	19.7
Guinardia striata	33	1.3	107	13.1	–	–	46.2
Hemiaulus hauckii	–	–	10	1.2	–	–	#
Hemiaulus sinensis	–	–	3	0.4	–	–	27.3
Leptocylindrus sp.	–	–	13	1.6	–	–	#
Odontella aurita	10	0.4	–	–	–	–	50
Odontella mobiliensis	7	0.3	–	–	–	–	82.3
Rhizosolenia crassispina	–	–	3	0.4	–	–	84.9
Rhizosolenia imbricata	17	0.7	–	–	–	–	27.3
Rhizosolenia hyalina	–	–	3	0.4	–	–	#
Rhizosolenia pungens	23	0.9	3	0.4	–	–	51.2
Rhizosolenia robusta	7	0.3	–	–	–	–	183.1
Rhizosolenia setigera	3	0.1	–	–	–	–	36.7
Rhizosolenia styliformis	–	–	23	2.9	–	–	#
Pennate diatoms							
Asterionella japonica	–	–	33	4.1	–	–	21.1
Climacosphenia moniligera	3	0.1	–	–	–	–	136.8
Cylindrotheca closterium	–	–	–	–	3.33	0.6	19.5
Navicala sp.	7	0.3	–	–	–	–	55.9
Nitzschia sp.	13	0.5	–	–	–	–	19
Pleurosigma sp.	7	0.3	–	–	–	–	74.8
Pseudonitzschia pungens	40	1.6	–	–	–	–	11.9
Thalassiothrix longissima	7	0.3	53	6.5	–	–	20.8
Cyanobacteria							
Oscillatoria sp.	–	–	–	–	66.7	11.6	19
Trichodesmium erythraeum	–	–	–	–	473	82.0	52.6
Dinoflagellates							
Ceratium furca	3	0.1	–	–	–	–	#
Ceratium gibberum	–	–	–	–	3.33	0.6	#
Prorocentrum micans	3	0.1	–	–	–	–	#
Peridinium sp.	–	–	7	0.8	–	–	#
Total (all species)	2533	100	817	100	577	100	
Total (Rhizosoleniaceae)	2427	95.3	663	81.2	0	0	

Water depths: *10 m; **surface; #data not available.

the waters of June–August (for which the data were available) are mainly of oceanic origin (Chiranjeevulu *et al.* 2014), and there was no significant input of nutrients through terrestrial flux. The low salinity of October, however, is attributed to intense monsoon activity and dilution by the east India coastal current (Shankar *et al.* 2002).

4.1 *Cell number–total bio-volume–chlorophyll mismatch*

The calculated bio-volumes of different species agree broadly with those reported in other ecosystems, e.g., the Baltic (Olenina *et al.* 2006) and the northern Arabian Sea (Naz *et al.* 2013). In

Table 2. *Average cellular equivalent spherical diameter (ESD, μm) during non-PPCC maxima of significant (cell count>2) phytoplankton species (contd. from table 1).*

Species	ESD
Asteromphalus sp.	52.8
Bacteriastrum comosum	19.8
Bacteriastrum hyalinum	23.6
Chaetoceros affinis	23
Chaetoceros atlanticus	22.1
Chaetoceros borealis	17.9
Chaetoceros compressus	23
Chaetoceros constrictus	16.6
Coscinodiscus asteromphalus	90.1
Coscinodiscus excentricus	32.1
Coscinodiscus radiatus	33.1
Coscinodiscus sp.	48.1
Ditylum brightwelli	99.7
Ditylum sol	135.4
Leptocylindrus danicus	21.1
Melosira sp.	44.8
Melosira moniliformis	32.9
Odontella sinensis	181.7
Rhizosolenia alata	88.3
Skeletonema costatum	13.5
Thalassiosira sp.	17.1
Nitzschia longissima	23.1
Pseudo-nitzschia seriata	19.8
Thalassionema nitzschioides	7.9
Thalassiothrix frauenfeldii	9.4
Prorocentrum micans	44
Ceratium furca	82.5
Ceratium trichoceros	105.1
Oscillatoria sp.	19
Trichodesmium erythraeum	52.6

the study area, besides microplankton, nano and picoplankton constitute sizable fractions of the phytoplankton consortia (Pandi *et al.* 2014), and the fact that they have not been accounted, may explain partially the mismatch. The mismatch is also explained on the basis that a strict correspondence of chlorophyll *a* with bio-volume will happen only when the bio-volume-specific chlorophyll *a* is constant, i.e., in the case of monospecific species at a constant irradiance level (Hitchcock 1980) and physiological state (Sathyenranath *et al.* 2009).

4.2 *G. delicatula tidal rhythm*

It is now recognized that tides can control phytoplankton distribution in estuaries (Cloern 1991; Lucas *et al.* 1999; Trigueros and Orive 2000) and in shallow coastal macrotidal regions of the coastal sea (Blauw *et al.* 2012; Houliez *et al.* 2013). Some species showed tidal flushing, some tidal enrichment and some were little affected in estuary (Cloern 1991). The dinoflagellate *Peridinium quinquecorne* showed movement to the near-surface layer during intense sunlight, but only during the incoming tide (Horstmann 1980). But tidal oscillations have not been reported in microtidal, shelf regions. Momentary bloom promotion in the coastal zone due to pycnocline outcropping at surface and vertical advection of nutrient-rich waters forced by energetic inertial current oscillations due to diurnal wind variability has been observed (Lucas *et al.* 2013). The photosynthetic potential ($P_{\max}$) is maximal at mid-day, and the available reports do not record greater than 10x enrichment of phytoplankton $P_{\max}$ with reference to the pre-dawn value (Prezelin *et al.* 1987).

In the present study, enrichment at neap tide during July (14:00 hrs) was by a factor of 29 for total phytoplankton and 234 for *G. delicatula* relative to the cell count at 8:00 hrs at 10 m depth. The corresponding enrichment factors at surface were 2.6 and 20.8, respectively. The enrichments should be expected to be even higher with respect to pre-dawn cell count, data of which are not available. Nutrient enrichment induced by diel changes in winds (Lucas *et al.* 2013) and deep water entrainment by internal waves (Prairie *et al.* 2012) is ruled out since winds were subdued and silicate decreased correspondingly from 2.59 to 1.03 μM and from 2.45 to 1.08 μM at surface and phosphate showed only marginal increase (from 0.26 to 0.38 μM at surface and from 0.26 to 0.28 at 10 m, respectively) at the time (figures S1 e, f). For the domination of *G. delicatula* in the phytoplankton assemblage, different types of fronts (Franks 1992) as possible causes are ruled out as the tidal range is small, sea floor is not steep sloping, there are no topographic barriers on the seafloor, and because of this, no distinct water masses could be recognized.

The negative linear relationship of phytoplankton biomass (bio-volume) with salinity (figure 5b) cannot be attributed to a possible nutrient dilution as nutrients were not related to salinity. It may, on the other hand, indicate a role for tides which cause oscillations in salinity and thereby redistribute the plankton biomass. This influence would not have been visible if only cell densities (and not bio-volume) were considered. In the case of *G. delicatula* (and *G. striata* to some extent) when they were present in large numbers, the neap tide was accompanying. Other species or even

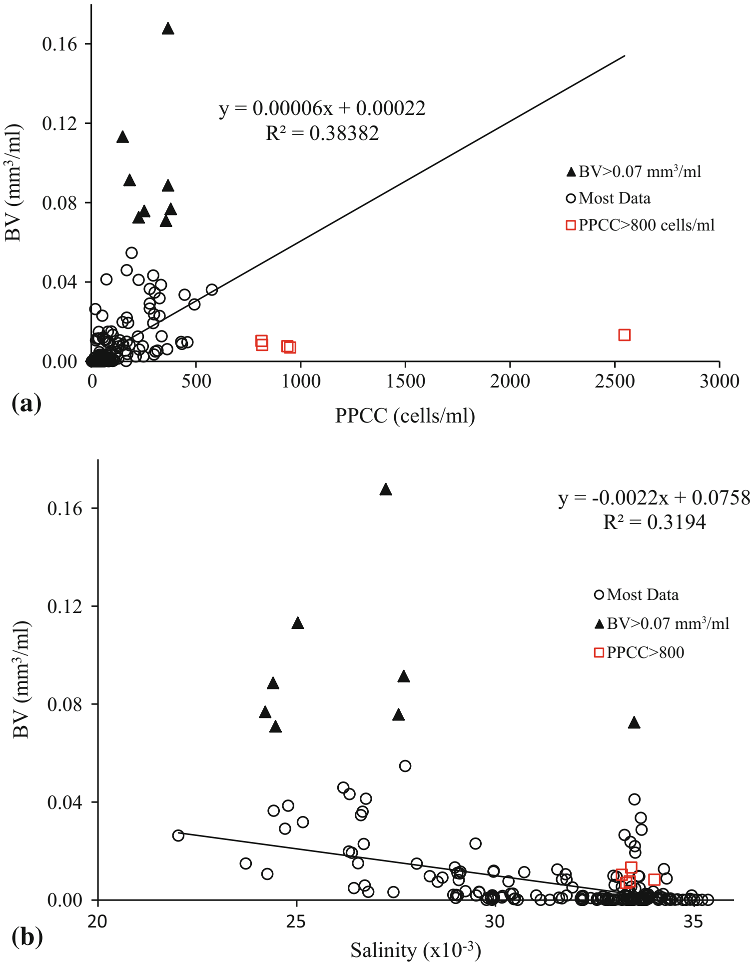

Figure 6. Plots of total phytoplankton bio-volume (BV) *vs.* (**a**) Total cell density (PPCC) and (**b**) salinity.

G. delicatula itself when it was present in lower abundance did not follow the tidal rhythm. Thus *G. delicatula* population is likely an aggregate-formed when the cell density exceeded a critical value. High-light–low-nutrient condition promotes aggregate formation via acceleration of transparent exopolymeric particles (TEP) release from algae (Mari and Kiorboe 1996), when the algal production has nearly exhausted the nutrients (Decho 1990) and solar insolation is at maximum. Silicate stress leads to loss of setae, thinning of the valves, increase of carbon cell quota, release of increased amounts of dissolved organic carbon (DOC) and increase in sinking rates (Flynn and Jézéquel 2000). As a proxy for DOC of *in situ* source, the intensity of tryptophan protein-like fluorescence (T) peak was measured as described in Chari *et al.* (2012). It was highest during July (8.91×10^{-3} Raman Units), among all sampling campaigns, in the upper 10 m water (our unpublished results). This was despite the fact that chlorophyll *a* (phytoplankton), considered the source of the T peak was not correspondingly high ($0.78\,\mu$g L^{-1}, figure 3a).

4.2.1 *Bloom mechanism*

When the tide was receding, phytoplankton of the coastal region drifts along the tidal current into the sea. As the tide was to return from the lowest level, the tidal amplitude being low (0.8 m), a gentle and steady physical forcing is established which causes zonation of the pre-existing phytoplankton (*G. delicatula*), aided by the solar insolation maxima. The zonation likely occurred closer to the time series station than the stations nearer the coast as the *G. delicatula* (phytoplankton) abundance decreased towards the shore at surface (St. 1 and St. 2, figure 1) during our return after the last time-series collection at 16:00 hrs (table S1).

Ergoclines are sharp transition zones between high and null (or low) tidal energies of estuaries and estuary affected coastal regions in which regions of increased biological production are formed, as a result of the matching or resonance of physical scales with biological scales (Legendre *et al.* 1986; Ragueneau *et al.* 1996). The ergoclines so far investigated are of macrotidal regions. However, the present region is microtidal. Moreover, the cell densities of *G. delicatula* and *G. striata* reached maxima at 14:00 hrs during all summer samples irrespective of whether the neap tide was co-occurring or not (table S1). Ecological factors constitute the basic requirement, and the physical factors (tide) the trigger for the formation of the transient phytoplankton bloom.

We also performed, but on dates different from the present, time series measurements at 100 m bathymetric station, 60 km away from the coast, and 45 km offshore of station 3 (not shown in figure 1). The phytoplankton composition was completely different between that station and St. 3. In December 2013 and February 2014, phytoplankton cell densities were high (∼600 cells ml^{-1}), dominated by the pinnate diatom *Achnanthes brevipes* (84%) and *Trichodesmium erythraeum* (94%) respectively at the offshore station. *G. delicatula* was not represented, although *G. striata* did appear as a minor constituent (3–20 cells ml^{-1}; our unpublished results), thus ruling out offshore water as possible source of the coastal (St. 3, figure 1) phytoplankton (bloom) and *vice versa*.

The fraction of *G. delicatula* representing phytoplankton was lower at >10 m depth, and heavier celled taxa increased correspondingly. Down the water column, microbial exudates and binding material are increasingly decomposed by bacteria (Chow and Azam 1988) which results in weakening of adhesion in clusters of the aggregate. The occurrence of a deeper (20 m) maximum for *G. striata* (table S1) suggests that the mucilaginous TEP released by this species is likely less labile/preferred by bacteria than the TEP released by *G. delicatula*. The occurrence of *G. delicatula* bloom in a tropical sea, in the mid-summer, and at a lower level of abundance during the summer monsoon (September) raises questions regarding its adaptation. But more basically, the study points to the possibility that the earlier studies had missed the ambient concentrations due to dependence of *G. delicatula* abundance in the ecosystem on tide.

4.3 *Winter maximum of Trichodesmium erythraeum*

The alga is suspected to cause fish mortality by asphyxiation through gill damage by the algal filaments (Satpathy *et al.* 2007). *Trichodesmium* blooms are rarely reported, most of them during spring (Ramamurthy *et al.* 1972; Santhanam *et al.* 1994; Jyothibabu *et al.* 2003; Mohanty *et al.* 2010; Sahu *et al.* 2012), lasting for a day or two in the Bay of Bengal (Satpathy *et al.* 2007; Hegde *et al.* 2008; Shetye *et al.* 2013), and rarely in winter monsoon (Vinayachandran and Mathew 2003). Weak winds and water column stability, favourably disposed in the winter season are favourably factors for the *Trichodesmium* blooms (Madhu *et al.* 2006). The occurrence of *T. erythraeum* maximum at 14:00 hrs, instead of 12:00 hrs when the neap tide occurred (figure 5c) may indicate that a lag likely results from the larger size of bundles of the algal trichomes requiring a greater 'push' by the tide than in the case of *G. delicatula*.

The study terminated (after February 2014), before the onset of spring, but the distribution spread over the preceding 8 months does indicate that it is likely that the blooms at other times of the year were not captured because of the diurnal (i.e., tidal) component. We did not observe tidal rhythm during June, August, October, January and February campaigns, and attribute it to: (i) low phytoplankton abundance due to seasonal factors, (ii) phytoplankton was more constituted of nano- and pico-plankton that did not show the oscillation, (iii) turbulent water due to currents and wind, and (iv) the neap tide not occurring during mid-day.

4.4 *Concerns associated with G. delicatulatransient bloom*

G. delicatula blooms have not so far been reported from tropical regions. The maximum relative abundance reported in a tropical sea is <14% of the total phytoplankton, in the eastern Arabian Sea (Hegde *et al.* 2008). It is more commonly reported in the sub-tropical and sub-polar waters in which the blooms take place in late spring to early summer. Blooms of *G. delicatula* in the Indian coastal waters is of ecological concern as unialgal blooms of *G. delicatula* are believed to clog the gills of shell fish to the extent of inhibiting their growth (Lorrain *et al.* 2000) and because the alga is suspected to be a source of the toxic arsenic (III) and methylated arsenic (Howard *et al.* 1995).

The role exercised by hydrodynamics in facilitating the formation of a transient, short lived bloom offers both opportunities and challenges in remote estimation of chlorophyll *a* as blooms caused by tidal oscillations are likely missed by the satellites if their pass is not synchronizing. The phytoplankton aggregates since then have higher sinking rates, enrich the food resource in the benthic region (Nascimento *et al.* 2008), implying higher fishery potential. A faster export and burial of carbon on the seafloor will also result in increased carbon sequestration (Laurenceau-Cornec *et al.* 2015).

5. Conclusion

The study investigated the influence of hydrodynamic factors, in particular tides, in addition to the hydrochemical and hydrobiological factors on phytoplankton bloom development in the western Bay of Bengal. The study strongly indicates the influence of tides on species distribution and zonation in the microtidal coastal region. Blooms of *Guinardia delicatula*, a sub-tropical diatom are reported for the first time from a tropical sea. Its summer bloom at 10–20 m depth of the coastal region is attributed to a neap tide synchronizing with solar insolation maxima, weak winds and a stable water column. The station where the diel observations were made likely was occupied by the tidal front which could favour zonation of the pre-existing cells to a transient bloom. The bloom likely was as aggregate as its formation and was probably aided by transparent exopolymer particles released due to nutrient exhaustion and intense solar radiation. The bloom dissipated as quickly as it formed, and its high resolution dynamics could not be captured due to the limited number of diel observations.

The tidal rhythm, also shown by the taxonomically related *G. striata* (in summer, at depth) and the unrelated cyanophyte *Trichodesmium erythraeum* (in winter, at surface) supports the role of tides in zonation of these species. The bio-volume (and not cell density) captures, weakly though, the association between total phytoplankton and the stage of the tide (salinity). As the tidally driven zonation of phytoplankton is transient, it is most likely not captured by remote sensing satellites. The faster sinking rates associated with the aggregates of phytoplankton formed during bloom may mean a more efficient biological pump.

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