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Nutrient regimes and their effect on distribution of

phytoplankton in the Bay of Bengal

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Abstract:
The seasonal dynamics of nutrient ratios and abundance of phytoplankton cells from the central (CB) and western (WB) Bay of Bengal were studied during the Fall Intermonsoon (FIM; Sept-Oct 2002) and Spring Intermonsoon (SpIM; April-May 2003). The nutrient molar ratios of macronutrients such as nitrate to phosphate (N:P), nitrate to silicate (N:Si) and silicate to phosphate (Si:P) in the top 120 m were calculated for both FIM and SpIM. During both the seasons, the N:P ratios along the CB and WB were lower than 16, indicating nitrate deficiency. Whereas, along both transects the N:Si ratio was <1 and Si:P >3 in the top 20 and 40 m during FIM and SpIM respectively indicating Si enrichment. Relatively greater nutrient concentrations along the WB than the CB appear to contribute to higher phytoplankton abundance.
The preponderance of diatoms in the Bay could be attributed to rapid utilization of available nutrients in particular during FIM thus resulting in low N:Si ratios in the water column. Among diatoms, pennales were predominantly controlled by nutrients and their ratios. While, apart from nutrients, physical stratification, light and eddies also seem to influence the distribution and abundance of centrales.

Key words: Bay of Bengal; Phytoplankton; Diatoms; Community composition; Nutrients; N: P: Si ratio.

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1. Introduction

Stretching over a distance of ~2500 km between 22°N and the Equator (Berner et al., 2003) enclosing the Andaman Sea surrounding the Andaman and Nicobar Islands, the Bay of Bengal (BOB) comprises the north east part of the Indian Ocean. It experiences seasonal changes in the circulation due to semi annual reversing monsoon winds (Shetye et al., 1991). The large amounts of fresh water (ca.1.6 x 10^{12} m^3 yr^{-1}, Subramanian, 1993) discharged into the Bay give it an estuarine characteristic with low surface salinities over a large area. Thus, excess precipitation and river runoff over evaporation lead to very low salinities and highly stratified upper layers (George et al., 1994; Prasanna Kumar et al., 2002). This hampers exchange processes between the atmosphere, surface and deeper water layers that consequently affect the biological and biogeochemical processes (Ittekkot et al., 2003). A wide range of variations in the nutrient concentrations has been observed and, although many rivers drain in to BOB, the nitrate-depleted surface waters in the northern BOB suggest that there is no significant riverine input of nitrate and thus, nitrate is considered to be limiting the primary production (De Sousa et al., 1981) in the BOB. Additionally, the runoff may also affect the distribution and composition of the phytoplankton by influencing the circulation and mixing processes and in turn redistribution of nutrients.

Phytoplankton succession and community composition reflect the environmental conditions of the ecosystem, among which the availability of nutrients play a significant role (Dugdale, 1967; Rhyther and Dunstan, 1971; Smayda, 1980). If the supply of nutrients is less than the uptake by phytoplankton, nutrient concentrations decrease and limit additional growth of phytoplankton (Tilman et al., 1982). The limiting nutrient concentrations vary with season, location and phytoplankton
community structure (Fisher et al., 1992). Generally, nitrogen (N) limitation prevails in most of the marine systems (Fisher et al., 1992; Howarth, 1988). Principally, half-saturation constant, \( K_s \), for a limiting nutrient is greater than its ambient concentration and therefore regulates the growth of phytoplankton community. Changes in nutrient supply are often reflected in their ratios (Yin et al., 2001). Thus, elemental ratios (nitrate, phosphate and silicate) from water samples can sometimes be used as indicators of the status of nutrient loading or to predict productivity (De-Pauw and Naessens, 1991). When the nutrient levels are sufficient for a healthy growth of diatoms, the atomic nitrate to silicate to phosphate (N:Si:P) ratios within the cells is about 16:16:1 (Redfield et al., 1963; Brzezinski, 1985). Deviations from these ratios either in the nutrient availability or uptake indicate a potential for nutrient limited phytoplankton growth (Hecky and Kilham, 1988; Dortch and Whitledge, 1992). However, studies in the past (Parsons et al., 1961; Healy and Hendzel, 1979; Brzenzinski, 1985; Levasseur and Therriault, 1987) suggest that when the ambient ratios of dissolved N:P <10 and N:Si ratio <1 it is indicative of a potential N limitation whereas N:Si >1 and Si:P ratio <3 are indicative of Si limitation (Harrison et al., 1977).

Nutrient limitation in natural phytoplankton communities is primarily identified from bioassays in which response of the phytoplankton community to N or P is measured by additions of one or both nutrients in micro/mesocosms or, inferred from elemental ratios (Havens, 2000). These ratios are therefore useful for predicting the phytoplankton abundance and assemblages. The ability to identify limiting nutrients thus becomes of considerable importance for our understanding of the ecology of phytoplankton. Moreover, measurements of elemental ratios in the water body and their effect on the phytoplankton community can provide evidences for possible
growth limitations. One of the main objectives of this study was to identify the effects of ambient nutrients and their ratios on the phytoplankton composition and distribution. In addition, effects of seasonal differences in the nutrient concentrations and their ratios on the phytoplankton abundance were also examined during this study. With this aim data on nutrients and phytoplankton from BOB collected under a multidisciplinary programme (Bay of Bengal Process Studies, BOBPS) during the Fall Inter Monsoon (FIM) and Spring Inter Monsoon (SpIM) have been analyzed in this study.

2. Materials and Methods

Sampling was carried out during FIM (September to October, 2002) and SpIM (April to May 2003) on onboard ORV Sagar Kanya. As illustrated in Fig. 1, a total of nine stations on two transects, one in the Central Bay (CB, along 88°E), and another along the Western Bay (WB, 81°-85°E) were sampled during both the cruises. Five stations were covered in the CB (CB1- CB5) and four along the WB (WB1-WB4).

Water samples were collected at all stations using a CTD (Sea Bird Electronics) rosette from eight discrete depths (near surface, 10 m, 20 m and thereafter at 20 m interval till 120 m). Sub sampling was done for estimation of nutrients which was immediately analyzed onboard using SKALAR autoanalyser. For analyzing phytoplankton cell counts (PCC) and phytoplankton composition, aliquots of water samples from each of the above depths were fixed in acid Lugol’s iodine (1 % w/v) and 3 % formaldehyde and stored in dark until taken up for analyses. A settling and siphoning procedure was followed to concentrate samples from 250 ml to 10 ml (Utermohl, 1958). For counting phytoplankton cells (size ≥ 5 μm) and identification of genera and species, two one-ml replicates of concentrated samples were transferred
into a Sedgewick-Rafter plankton counting chamber. All the 1000 squares in the Sedgewick-Rafter were examined microscopically using 20X – 40X objectives for the phytoplankton cells. Oil immersion 100X objective on a Zeiss (Axioskop, 2plus, Germany) microscope was also made use of for confirming the genera or species. Generic and species identification was done according to various keys (Lebour, 1978; Desikachary and Ranjithadevi, 1986; Desikachary and Prema, 1987; Desikachary et al., 1987; Constance et al., 1985; Tomas, 1996).

3. Results

3.1. Hydrology

A detailed description of the sea surface temperature (SST) and sea surface salinity (SSS) for FIM (also referred as postmonsoon) and SpIM (or, premonsoon) are provided in Kumar et al., (2004) and Prasanna Kumar et al., (2007). Briefly, the mean sea surface temperature (SST) during the FIM in the CB and WB was 28.70 ± 0.28°C and 29.98 ±0.54°C, respectively. A shallow 28°C isothermal layer of 20 m thickness was observed to be warmer by a degree in the northernmost location. On the other hand, the isothermal layer along the WB was generally of ~10 m thickness and warmer (>30°C). The sea surface salinity (SSS) in the CB was around 34 in the south, which decreased to 29 in the northern locations. Along the WB too the salinity decreased from 33 in the south to 25 in the north.

During SpIM, the SST generally did not vary much along both the CB and WB averaging 29 ±0.50°C. Along the CB, a shallow 10 m thick isothermal layer of 30°C was observed south of 15°N 88°E which became thicker (~30 m) and a degree colder in the north. A 30 m thick isohaline layer having a salinity of 33 was observed along
the CB with a few pockets of low salinity. A halocline was observed between 30 and 100 m below which there were minimal variations in the salinity, as was also seen during FIM.

The isothermal layer along the WB was thicker (~40 m) and warmer (> 30°C) south of 16°N and became colder by a degree and thinner (~10 m) towards the north. With a salinity of 33.5, the surface waters north of 15°N were fresher by 0.5. In general, isohalines shoaled from south to north in the upper 100 m. The SSS averaged 33 ±0.30 along both transects.

3.2. Nutrient Ratios

Fig. 2A and Fig. 3A illustrating the average nitrate to phosphate ratios (N:P ratio) for the two seasons indicate a concurrent increase with depth up to 120 m. In general, the N:P ratio was lower than the classical Redfield ratio of 16:1 throughout the sampling depth. In FIM, the N:P ratios showed a significant negative relation (r = -0.48, p ≤ 0.01; n = 30) with PCC only along the WB. In SpIM, high N:P ratio was observed in the surface at CB2 and CB3 while at other stations it was lower than 3, while along the WB the N:P ratio in the surface was only slightly below Redfield ratio (Fig. 3A) at WB1. During SpIM, the N:P ratios did not show a significant relation with the PCC along both transects (CB: N:P = r = 0.12, p ≥ 0.49; n= 37; WB: r = -0.11, p ≥ 0.56; n= 32).

The N:Si ratio in the top 30 m in both transects was in general < 1 with no spatial variation during both seasons (Fig. 2B; Fig. 3B) suggesting higher silicate concentration relative to nitrate. During FIM, higher N:Si ratios (>1.70) at the intermediate depths (60 to 80 m) were observed (Fig. 2B). The N:Si ratios showed a
significant positive relationship with the PCC only along CB \((r = 0.38, p \leq 0.02; n = 39)\). During SpIM, the N:Si ratio values increased rapidly with depth upto 80 m along CB and 40 m along WB where they reached >1.11 (Fig. 3B), coinciding with high PCC. The N:Si ratio had a positive relation with PCC along both transects though not statistically significant (CB: \(r= 0.11; p \leq 0.5; n= 37\), WB: \(r = 0.35; p \leq 0.05; n = 32\)).

The ratio of silicate to phosphate (Si:P) showed a progressive decrease with depth as illustrated in Fig. 2C and Fig. 3C. The surface waters showed a higher than 16:1 ratio in both seasons except in CB during FIM indicating a strong deficiency of P relative to Si. The highest Si:P ratio which was close to 72, was observed in surface waters in the SpIM along the CB transect. This was due to high surface silica (~2.13 \(\mu\)M; figure not shown) along this transect. There were large scale variations in the surface waters and, the Si:P ratio was >3 throughout the water column. In deeper waters below 40 m, the Si:P ratio was lower than 16:1 but >3 in both seasons and transects indicating low Si which was, in any case, not in limiting levels. The Si:P ratios showed a negative relation with the total phytoplankton cell counts (PCC) in both seasons and transects. But had a significant relation with PCC along the CB in FIM \((r = -0.41; p \leq 0.01; n = 39)\) and WB in SpIM \((r = -0.54; p \leq 0.00; n = 32)\).

### 3.3. Phytoplankton distribution

The abundance of phytoplankton (PCC; cells x 10^3 L^-1) during FIM and SpIM along CB and WB is illustrated in Fig. 4A and Fig. 4B, respectively. During FIM, the abundance was higher mostly in the top 60 m along both transects. The concentration of the phytoplankton was more towards the south in the CB with the highest surface abundance observed at CB1 (3.2 x 10^3 L^-1). While along the WB, the phytoplankton abundance was more in the northern locations viz. WB3 and WB4. The surface
concentration of phytoplankton was in the range of $0.48 - 22.76 \times 10^3\text{L}^{-1}$ increasing northwards with the highest abundance observed at WB4.

During SpIM (Fig. 4B) the preponderance of phytoplankton was lower in the CB compared to the WB. Along the CB, the surface PCC ranged from $0.16$ to $0.64 \times 10^3$ cells L$^{-1}$ with the highest abundance at CB4. While, the surface PCC ranged from $0.04$ to $1.08 \times 10^3$ cells L$^{-1}$ along the WB. However, the highest PCC was observed at station WB3 at a depth of $40$ m ($19.48 \times 10^3$ cells L$^{-1}$).

3.4. Phytoplankton Composition

Distribution of mean PCC and mean abundance of centrales and pennales in the top 120 m along both transects during FIM and SpIM is shown in Fig. 5A and 5B. Similarly, Figs. 6 and 7 depict the distribution pattern of the predominant species. In general diatoms dominated during these seasons. Centrales were predominant in the top 40 m along both CB and WB during FIM. In the deeper column, pennales were dominant (Fig. 5A). During SpIM, pennales dominated at all depths along the CB. Along WB however, the centrales dominated in the top 80 m (Fig. 5B). Among the predominant phytoplankton (species that contributed $\geq 5\%$ of the total PCC) recorded during FIM (Fig. 6), *Thalassionema nitzschioides* and *Thalassiosira* spp were present in all the stations along the CB. While *Navicula* spp was observed at all the nine stations, *Rhizosolenia styliformis* was observed only at three stations (CB1, CB5 and WB4) which were eddy influenced regions (Prasanna Kumar et al., 2004, 2007). *Chaetoceros lorenzianus* and *Chaetoceros curvisetus* were in higher abundance in the top 20 m during FIM along the WB. During SpIM, *Trichodesmium* spp, *Coscinodiscus* spp, and *Pseudo-nitzschia* spp, were the predominant forms in the CB.
While *Chaetoceros didymus*, *Bacteriastrum comosum* and *B. furcatum* were in higher numbers along the WB at deeper depths at 40 – 80 m coinciding with the ideal N:Si (1:1) ratios. However during SpIM similar to FIM, *Navicula* spp was observed at all the stations and was also one of the predominant species along both transects.

(Approximate Location of Figure 5)


Along both transects *Rhizosolenia alata*, *R. styliformis*, *R. imbricata*, *Leptocylindrus danicus*, *L. mediterraneanus*, *Navicula* spp, *N. distans*, *N. messanensis*, *Nitzschia longissima*, *N. angularis*, *Pseudo-nitzschia* spp, *Thalassionema nitzchioides*, *Synedra* spp, *S. ulna*, *Biddulphia mobiliensis*, *Chaetoceros* sp, *C. curvisetus*, *Coscinodiscus* spp, *C. concinnus*, *Hemiaulaus hauckii*, *Fragilariopsis doliolus* and *Thalassiothrix fauenfeldii* dominated in waters below 40 m that was rich in nitrate and where the N:Si ratios >1 during FIM and SpIM.
4. Discussion

In the BOB, the winds are weak and variable during FIM and SpIM, representing the primary and secondary heating seasons (Narvekar and Prasanna Kumar, 2006). The riverine influx peaks during FIM and is least during SpIM. As a result of the high amounts of fresh water influx, the surface salinity is reduced to as low as 29 and 25 along the CB and WB during FIM inducing a strong halocline and stratification in the top 50 m. Due to the minimal riverine input into the BOB during SpIM, the surface salinity is higher along both transects with the halocline deepening to 100 m. Moreover, higher concentrations of surface nitrate (~0.5 – 1.5 µM) and silicate (~15 µM) observed during FIM along WB could be attributed to the riverine influx. A similar presence of the nutrients in the euphotic depth (60-80 m) during SpIM can be attributed to eddy pumping as suggested by Prasanna Kumar et al (2007). However, the N:P ratios in the top 60 m (where light levels are usually adequate for photosynthesis), along both transects in both seasons were <10 suggesting nitrate as limiting to the phytoplankton. The N:Si ratios were <1 suggesting Si enriched nutrient regime in the top 40 m. Lower Si:P ratio (< 16:1)- an indication of poor silica waters (Harrison et al., 1977), however apparently do not limit the phytoplankton since the Si:P ratio were always > 3 throughout the 0-120 m water column in the BOB both during FIM and SpIM. The high abundance of diatoms (>90%) vis-à-vis dinoflagellates could be attributed to the high Si:P or low N:Si ratios. Such realms are reported to support diatom dominated systems (Bethoux et al., 2002).

The phytoplankton abundance was in general higher along the WB during both seasons. However it was higher in the top 20 m during FIM and deeper during SpIM. This maybe attributed to higher concentrations of nitrate and silicate in the north...
(Prasanna Kumar et al., 2007) during FIM. Among the phytoplankton, centric diatoms such as, *Chaetoceros lorenzianus*, *C. curvisetus*, *C. didymus*, *Bacteriastrum furcatam* and *B. comosum* were concentrated along the WB irrespective of the season (Figs. 6; 7). With more cell volume it appears that centrales prefer relatively higher nutrient regions even within an oligotrophic Bay. Kobayashi and Takahashi (2002) also observed that this group prefers high nutrient regions *vis-à-vis* oligotrophic waters. Also, as suggested by Figueiras and Niell (1987), abundance of centric diatoms that was observed in the northern stations along the WB during FIM seems to be associated with greater physical stratification. The northern stations are also comparatively more turbulent and richer in nutrients than the southern stations. Increased occurrence of *Chaetoceros* spp has been indicative of higher nutrient concentrations in the western and central Pacific (Kobayashi and Takahashi, 2002). Among various species of diatoms, *C. lorenzianus* and *C. curvisetus* were more abundant at WB4 (Fig. 6) where higher nutrient concentrations were observed during FIM. Interestingly, although the cells of *Thalassiosira* spp were ubiquitously distributed along the CB, they were observed to be more abundant in the top 20 m at WB4 where Si was ~15 µM during FIM. The demand for Si by diatoms appears to differ with species (Mochizuki et al., 2002) and, such inter-species differences in silica requirements may be one reason for the observed differences in the distribution of *Thalassiosira* spp.

Higher amount of nutrients and a deeper euphotic depth (~80 m, Kumar et al., 2004) were observed to be conducive for the growth of *C. didymus*, *B. furcatum* and *B. comosum* during SpIM. Thus, in the BOB, in particular along the WB, ideal light conditions and high nutrient concentrations appear to be beneficial for the growth of these species at different depths.
Along the CB, the centric diatoms were either less than or just about the same in abundance as pennate diatoms. *Rhizosolenia stylyformis* is an exception among the centric diatoms having been previously reported from warm, oligotrophic waters (Venrick, 1969, 1971; Sournia, 1970; Villareal, 1991, 1994a, b; Guillard and Kilham, 1977) and eddy influenced regions (Vaillancourt et al., 2003). *Rhizosolenia* spp was one of the dominant species in the waters where the N:Si was <1 during FIM. Some of these species are known to contain endosymbiotic cyanobacteria (*Richelia intracellularis*), which can fix N\(_2\) gas (Venrick, 1974; Villareal and Carpenter, 1989). Moreover, *Rhizosolenia* spp are also known to undergo vertical migration in search of nitrate and then come to the surface for photosynthesis (Singler and Villareal, 2005). They are in a way thus independent of critical limits specifically nitrate and are more dependent on the light for photosynthesis. Hence, it can thrive even when the waters are nitrate depleted as observed in the CB. Due to the cosmopolitan nature and wide temperature tolerance of *Coscinodiscus* spp (Horner, 2002) this species was present at most of the stations along CB during SpIM and did not show any marked difference in its spatial distribution in the Bay.

Pennate diatoms have generally higher surface to volume ratio and thus are able to assimilate nutrients even when their concentrations are limited or, very low. Therefore they can thrive in the Bay better than the centric ones. A pennate such as *Thalassionema nitzschioides* representing >10 % of the population in the BOB is a known cosmopolitan species (Hasle and Syvertsen, 1996) and surviving in wide nutrient regimes (Abrantes, 1988). It was ubiquitously distributed at all the stations along CB during FIM. Usually, *T. nitzschioides* is reported from high productive regions (Schrader and Sorknes, 1990) and, also from low nutrient regimes (Kobayashi and Takahashi, 2002) similar to the observation in the present study where this
species was dominant in the CB rather than the nutrient elevated waters along the WB in FIM.

The pennate diatoms are generally found in greater abundance in calmer and least upwelling zones (Pace et al., 1986). Thus, calmer waters with low wind speed and increased stability (Varkey et al., 1996) during SpIM in the BOB could be attributed to the high concentrations of pennates along the CB. High temperatures (> 30°C), calm waters and low nutrients, which are prevalent in the BOB during SpIM are ideal conditions also for the growth of *Trichodesmium* sp. In such nitrate depleted conditions which other diatoms and dinoflagellates circumvent, this cyanobacteria is able to fix atmospheric N\(_2\) (Dugdale et al., 1964; Goering et al., 1966; Qasim, 1970; Ramos et al., 2005) and form blooms. Interestingly, cell counts of *Pseudo-nitzschia* spp were found to be higher in deeper waters generally corresponding to higher nitrate levels. Our observations corroborated with the experimental results obtained by Carter et al (2005) highlighting that this species increased in abundance on additions of nitrate, suggesting it’s preference for nitrate replete conditions.

However, certain species which are observed in higher abundance in nitrate replete waters such as *Navicula* spp and *Thalassionema nitzschioides*, also showed sporadic appearances in the nitrate depleted waters suggesting the role of other factors such as light in the distribution of certain species. Light and nutrients (Mur et al., 1978; Sommer, 1983, 1985) play a major role apart from salinity (Rice and Ferguson, 1975) in the phytoplankton competition. Competition of species regulates species diversity, coexistence and dominance. The competition could be indirect which is caused by the production of inhibitory substances (Sharp et al., 1979) or direct that is caused by one or more factors (Taylor and Williams, 1975; Tilman et al., 1982)
including syntrophy. Forced by nutrient limitations, many species of phytoplankton get redistributed within the euphotic column and accumulate at depths having nutrient regimes that suit their specific growth demands, resulting in their predominance in these regimes. A similar scenario in the BOB where certain species appear to be seasonally dominant appears to prevail along both transects while some of them appear to be ubiquitous in the Bay.

5. Conclusions

The phytoplankton abundance, in particular in the CB appears to be controlled by the ambient nutrient concentrations. Within the community, the abundance of pennales though predominantly controlled by nutrient concentrations, show species specific response to varying nutrient ratios. In case of centrales, nutrient availability, physical stratification, light penetration and the occurrence of eddies apparently influence their distribution and abundance. Among the different ratios, the N:Si ratio in particular appears to effect the phytoplankton community structure. This study has provided for the first time details on phytoplankton species specific responses to different nutrient regimes and ratios from the Bay of Bengal which can be applied to other areas as well. However, further studies are needed to understand phytoplankton community responses to the changing nutrient ratios including those of the trace elements such as Fe, Mn, Co and their affect on the higher trophic levels in the Bay of Bengal.

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References


Figure captions:

Figure 1: Sampling locations in the Bay of Bengal along Central Bay (CB) and Western Bay (WB).

Figure 2: Vertical structure of the nutrient ratios: A) N:P, B) N:Si and C) Si:P along central Bay (CB1- CB5) and western Bay (WB1-WB4) during Fall Intermonsoon (FIM).

Figure 3: Vertical structure of the nutrient ratios: A) N:P, B) N:Si and C) Si:P along central Bay (CB1- CB5) and western Bay (WB1- WB4) during Spring Intermonsoon (SpIM).

Figure 4: Distribution of phytoplankton abundances (PCC, cells x 10^3 L^-1) during A) Fall Intermonsoon (FIM) and Spring Intermonsoon (SpIM) along Central Bay (CB) and Western Bay of Bengal (WB).

Figure 5: Seasonal distribution of mean Phytoplankton (PCC), Centrales (Cent) and Pennales (Penn) during A) Fall Intermonsoon (FIM) and B) Spring Intermonsoon (SpIM) along Central Bay (CB1- CB5) and western Bay of Bengal (WB1- WB4). Error bars denote standard deviation of the depth wise mean along each transect.

Figure 6: Distribution of predominant (>5%) phytoplankton in the BOB during FIM.

Figure 7: Distribution of predominant (>5%) phytoplankton in the BOB during SpIM.
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