

Seasonal variation of microzooplankton (20 – 200µm) and its possible implications on the vertical carbon flux in the western Bay of Bengal

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Abstract

Stratification (throughout the year) and low solar radiation (during monsoon periods) have caused low chlorophyll *a* and primary production (seasonal av. 13 – 18 mg m⁻² and 220 – 280 mg C m⁻² d⁻¹ respectively) in the western Bay of Bengal (BoB). The microzooplankton (MZP) community of BoB was numerically dominated by heterotrophic dinoflagellates (HDS) followed by ciliates (CTS). The highest MZP abundance (av. 665 ± 226 × 10⁴ m⁻²), biomass (av. 260 ± 145 mg C m⁻²) and species diversity (Shannon weaver index 2.8 ± 0.42 for CTS and 2.6 ± 0.35 for HDS) have occurred during the spring intermonsoon (SIM). This might be due to high abundance of smaller phytoplankton in the western BoB during SIM as a consequence of intense stratification and nitrate limitation (nitracline at 60m depth). The strong stratification during SIM was biologically evidenced by intense blooms of *Trichodesmium erythraeum* and frequent *Synechococcus* – HDS associations. The high abundance of smaller phytoplankton favors microbial food webs where photosynthetic carbon is channeled to higher trophic levels through MZP. This causes less efficient transfer of primary organic carbon to higher trophic levels than through the traditional food web. The microbial food web dominant in the western BoB during SIM might be responsible for the lowest mesozooplankton biomass observed (av. 223 mg C m⁻²). The long residence time of the organic carbon in the surface waters due to the active herbivorous pathways of the microbial food web could be a causative factor for the low vertical flux of biogenic carbon during SIM.

Key words: microzooplankton, food web, chlorophyll *a*, primary production, stratification, species diversity, synechococcus, Bay of Bengal, Indian Ocean

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1. Introduction

Microzooplankton (20 – 200 μm) play a significant role in energy transfer through marine pelagic food web and hence their ecology and dynamics receive attention worldwide (Beers & Stewart, 1971; Godhantaraman & Uye, 2001; Quevedo et al., 2003). Due to small body size, microzooplankton (MZP) have higher weight specific physiological rates such as feeding, respiration, excretion and growth than large zooplankton (Verity, 1985; Fenchel, 1987). They efficiently feed on pico and nanoplankton that are generally unutilized by large zooplankton (Marshall, 1973; Nival & Nival, 1976) and act as a significant food source for a variety of invertebrate and vertebrate predators (Robertson, 1983; Stoecker & Capuzzo, 1990; Fukami et al., 1999).

The Bay of Bengal (BoB), the eastern part of the northern Indian Ocean, is landlocked in the north by the Asian continent. All the major rivers of India (Krishna, Kavery, Godavari, Mahanadi, Brahmaputra, Ganges) flow into the BoB. During monsoon periods (June to September – Summer monsoon, November to February – Winter monsoon), large volume of freshwater and suspended sediments reaches in to the BoB through these rivers ($1.6 \times 10^{12} \text{ m}^3$ of fresh water influx reaches BoB per year: Subramanian, 1993). The resulting low salinity plays a major role in various exchange processes between the atmosphere, surface and deep waters that eventually affect the biological and biochemical processes (Ittekkot et al., 1991; Prasannakumar et al., 2002).

The BoB is conventionally referred as an oligotrophic system where nitrate depletion in the surface waters (intense during spring intermonsoon period) and shortage of solar radiation (during monsoon periods) restrict the phytoplankton growth (Gomes et al., 2000; Prasannakumar et al., 2002; Madhupratap et al., 2003; Madhu et al., 2006). Due to the lack of solar radiation during monsoon periods, the phytoplankton community does not efficiently utilize the high amount of nutrients present in the inshore regions. This unutilized river - borne nutrients would eventually be lost into the ocean depths along with settling particles (Sengupta et al., 1977; Madhupratap et al., 2003). Another important factor causing oligotrophy in the western BoB is the low saline surface layer that inhibits the advection of nutrients from the subsurface (Prasannakumar et al., 2002). Although BoB is known to be oligotrophic, the vertical fluxes of biogenic carbon are comparable in magnitude with the highly productive Arabian Sea (northwestern part of the Indian Ocean). This is possibly due to the aggregation of biogenic carbon with mineral particles of the river runoff which increase the speed of settling (Ittekkot et al., 1991). Another possible mechanism suggested for the high vertical organic flux in the BoB is the

occurrence of mesoscale eddies capable of enhancing biological production (Prasannakumar et al., 2004).

Information on the plankton community of the BoB is very limited (Achuthankutty et al., 1980; Nair et al., 1981; Rakesh et al., 2006). The MZP community of the open waters of BoB has not received an earlier study. Therefore, information available on MZP from the east coast of India is confined to the tintinnids inhabiting in the near shore and estuarine waters (Krishnamurthy & Naidu, 1977; Godhantaraman & Krishnamurthy, 1997; Mishra & Panigrahy, 1999; Godhantaraman, 2001; Gauns et al., 2005). Although the plankton food webs in stratified and mixed marine waters and its consequences on the biogeochemistry of ecosystems have been recognized (Azam et al., 1983; Cushing, 1989), there is a scarcity of such information from the western BoB. The surface layer stratification and oligotrophy of BoB give a general impression that MZP stock in the system could play an important role in transferring primary organic carbon to higher trophic levels. Therefore, the present study was planned (a) to generate baseline information on the abundance, biomass of microzooplankton in the BoB (b) to understand the influence of the seasonally varying environment on MZP in the BoB and (c) to infer the possible role of MZP in the seasonally varying vertical biogenic flux in the BoB.

2. Methods

The various sampling locations in the western BOB are shown in Figure 1. Samplings were carried out onboard FORV *Sagar Sampada* during March 2001 (spring intermonsoon - SIM), December 2001 (winter monsoon - WM) and July 2002 (summer monsoon - SM). Altogether, 28 stations were sampled in 6 transects (along 11, 13, 15, 17, 19 and 20.5°N) for physical parameters such as salinity and temperature. Out of the 28 stations, 17 ($A_1 - A_{17}$) were sampled for chemical (nitrate and dissolved oxygen) and biological parameters (chlorophyll *a*, primary production, MZP and mesozooplankton). The stations at each transect were categorized into inshore (station near to the coast), offshore (station at the center) and oceanic (station farthest from the coast). To maintain the same depth of sampling and to address the same extent of the upper water column in all the stations, the inshore stations were fixed in ~200m depth zones.

2.1. Temperature, salinity and transparency

A bucket thermometer was used to measure the Sea Surface Temperature (SST). Sea Surface Salinity (SSS) was measured by an autosal (Guidline 8400A) calibrated with the standard

seawater (IAPO, Charlottenlund slot, Denmark). The vertical profile of temperature and salinity of each station was collected from the respective sensors of the Conductivity Temperature Depth Profiler (Seabird Electronics Sea sat, SBE 911 Plus, USA) and the data were used for understanding the general hydrography of the region. Due to the high fresh water influx in the study area, the Mixed Layer Depth (MLD) was taken as the depth at which the sigma – t values is greater than the surface value by 0.2 (Prasannakumar et al., 2004). Secchi disc was operated in the inshore and oceanic stations for measuring the transparency and thereby to assess the variability of the euphotic column. Three times of the secchi depth was considered as the approximate lower limit of the euphotic column (Prickard & Emery, 1982).

2.2. Dissolved oxygen and nitrate

The Go Flow bottles mounted on a CTD rosette were used to collect water samples from 9 discrete depths (0.5m, 10m, 20m, 30m, 50m, 75m, 100m, 120 and 150m) for measuring dissolved oxygen and nitrate. Water samples for dissolved oxygen were carefully collected into glass bottles and analyzed subsequently following Winkler's titration method. The concentration of nitrate in the water samples was analyzed by an autoanalyser (SKALAR, Model 51001-1) following the principle of Grasshoff (1983).

2.3. MZP

The heterotrophic organisms with a body size between 20 – 200µm were only considered for the study. Water samples (5 – 7 liter) were collected from 8 discrete depths (0.5m, 10m, 20m, 50m, 75m, 100m, 120m and 150m) for MZP were gently prefiltered through a 200 µm bolting silk to remove the mesozooplankton. Although the screening of samples through 200µm sieve may disturb large and fragile MZP, this process is widely used in MZP sampling for discarding the mesozooplankton (Froneman and McQuaid 1997; Putland, 2000; Stelfox - Widdicombe et al., 2004). Subsequently, 3 – 8% of Acid Lugol's Iodine was added in to these samples. These samples were then concentrated by gravity settling and siphoning procedure. Thus the samples were concentrated to 100 ml volume and preserved in 1 - 3% acid Lugol's solution. Prior to the microscopic analysis, the initial sample concentrates of MZP (1litre) were allowed to settle for 2 days. Subsamples of the settled samples were taken in Sedgwick rafter counting chamber and observed under an inverted microscope with phase contrast optics at 100 – 400x magnifications. Although there are some conflict existing regarding the suitable fixative for MZP, the Lugol's iodine is regarded as the most useful one and widely used that can make minimum damage to

different groups of MZP community (Gifford & Caron., 2000). The organisms present in the samples were identified and categorized in to four groups viz., heterotrophic dinoflagellates (HDS), ciliates (CTS), sarcordines (SDS) and crustacean nauplii (CNP) based on literature. The CTS and HDS were identified down to the species level wherever possible and the SRS and CNP were identified down to the group level following available literature (Kofoid and Campbell, 1939; Jorgenson, 1924; Marshall, 1969; Steidinger, 1970; Subrahmanyam, 1971; Taylor, 1976 a & b, 1987; Gopinathan & Pillai, 1975; Corliss, 1979; Maeda & Carey, 1985; Maeda, 1986; Lynn et al., 1988). Appropriate body dimensions of the organisms were measured using a micrometer and the cell volume was determined based on the geometric shapes. Available numerical factors were used to calculate the organic carbon content of CTS ($0.19 \text{ pgC } \mu\text{m}^{-3}$ - Putt & Stoecker, 1989), HDS ($0.14 \text{ pgC } \mu\text{m}^{-3}$ - Lessard, 1991), SRS ($0.0026 \text{ pgC } \mu\text{m}^{-3}$ for acantherians and $0.018 - 0.18 \text{ pgC } \mu\text{m}^{-3}$ for foraminifers- Michaels et al., 1995) and CNP (16 ngC per individual -Uye, 1982). The abundance and biomass of MZP at different discrete depths were mathematically formulated to address the surface layer (upper 10m water column - values at the 0.5m and 10m were integrated) and the entire water column (values from 0.5m to 150m were integrated).

2.4. Chlorophyll *a* & primary production

Two litre of water samples were collected from 7 standard depths (0.5, 10, 20, 50, 75, 100 and 120 m) using Go Flo bottles. These samples were then passed through GF/F filters and the chlorophyll *a* was extracted in 10 ml 90% acetone (Qualigens AR, Mumbai). The measurement of chlorophyll *a* was carried out using a spectrophotometer following the procedure of Strickland & Parsons (1972). Water samples for estimating primary productivity (2 litre) were obtained from seven standard depths before dawn (~ at 0500 hours) and transferred to five clean Nalgene polycarbonate bottles for the insitu ^{14}C experiment (UNESCO, 1994). Column values of chlorophyll *a* and primary production were calculated by integrating the discrete depth values up to 120m.

2.5. Mesozooplankton

A Multiple Plankton Net (Hydro - Bios, mouth area 0.25 m^2 , mesh width $200 \mu\text{m}$) with an electronic depth sensor was operated vertically to collect mesozooplankton samples. Samples were collected from the bottom of thermocline to the surface to get a fair representation of the euphotic column. The zooplankton collections were carried out around the noon to avoid the possible error on biomass due to vertical migration. Mesozooplankton biomass was measured as

displacement volume and then converted to organic carbon using numerical factors proposed by Madhupratap & Haridas, 1990 (1ml displacement volume = 0.075g dry weight; 32.5% of the dry weight represent the organic carbon content – Gauns et al., 2005).

2.6. Statistical analyses

Three-way Analysis of Variance (ANOVA) was used to study the significance of variability of MZP between stations, between species and between depths. This analysis also helps to see the station – species, station – depth and species - depth specificity/interaction of CTS and HDS (Snedecor & Cochran, 1967). In representative stations Multi Dimensional Scaling (MDS) analysis was carried out to see the species clustering/specificity at different discrete depths using Plymouth Routine in Marine Environmental Research) (PRIMER - Clarke & Gorley, 2001). The primary goal of the MDS is to detect meaningful underlying dimensions that allow the researcher to explain observed similarities or dissimilarities (distances) between the investigated objects. MDS attempts to arrange "objects" (in the present case MZP species abundance at different depths) in a space so as to reproduce the observed similarities. As a result, we can explain the distances in terms of dissimilarity between species occurring in different depths. In more technical terms, it uses a function minimization algorithm that evaluates different configurations with the goal of maximizing the goodness-of-fit (or minimizing "lack of fit"). Stress (measures of goodness of fit), the most common measure that is used to evaluate how well (or poorly) a particular configuration reproduces the observed distance matrix (please see <http://www.statsoft.com/textbook/stmulasca.html> for further details).

Diversity is a concise expression of how individuals of a community are distributed in subsets of groups. To analyze changes in MZP community due to environmental influence, following diversity indices were also used.

2.6.1 Species richness (Margalef, 1968)

Species richness is the number of different species in a particular area

$$D = (S-1)/\log_e^N$$

S is the number of species and N is the total number of individuals of all the species in the sample.

2.6.2 Species evenness (Heips, 1974)

Species evenness is the relative abundance with which each species are represented in an area

$$E = e^{(H(S) - 1/S - 1)}$$

H (S) is the species diversity in bits of information per individual and S is the number of species

2.6.3 Species diversity (Shannon and Weaver, 1963)

The advantage of this index is that it takes into account the number of species and the evenness of the species. The index is increased either by having more unique species, or by having a greater species evenness.

$$H(S) = -\sum [p_i (\log_2 p_i)]$$

$P_i = n_i/n$ (proportion of the sample belonging to the i^{th} species).

3. Results

3.1. Physicochemical environment

During WM, marked latitudinal variation of SST was prevalent in the study area (26 – 29°C) with a decreasing trend towards north. The SST in the region was highest during SIM (33 – 34° C) followed by the SM (27 – 30°C) and its latitudinal variation was not prominent during these periods (Figure 2). SSS was markedly low in localized regions along the coast during WM and in the north during SM. SSS at station A7 (24) and A16 (25) were the lowest during WM and in all other stations its variability was not pronounced (32 – 34) (Figure 2). During WM, MLD was low (<15m) at station A7 and A16 compared to all other locations (18 – 50m) due to high river influx. Similarly, during SM, at stations A13 and A17, SSS was markedly low (29 and 28) compared to all other stations (32 – 33) due to the high river influx. A similar decrease (<10m) was found in the MLD in these stations compared to all other stations (20 – 55m). The variation in SSS between stations was minimum during SIM (32 –34). The MLD in the entire region was low during SIM that varied from 8 – 25m. Among different seasons studied, the MLD was deeper during SM (av. 40m) and WM (av. 35m) compared to SIM (av. 17m). During all the three periods, the euphotic depth was generally decreasing towards the north and inshore stations (Figure 3). Seasonally, the euphotic depth was highest during the SIM (av. 107m) followed by WM (75m) and SM (66m). In the vertical structures of the temperature, salinity and sigma – t, the signature of the cold core eddy (upheaval of isolines) was evident in the subsurface layers (below

30m) along 15°N transect during WM (Figure 4). The core of the eddy was situated in the offshore region between 13 and 15°N transect as evident in the satellite imagery of the sea level anomaly (Figure 4)

Dissolved oxygen concentration in the upper layers (upper 50m water column) was higher during SIM compared with WM and SM periods. The decrease of dissolved oxygen concentration during SM and WM compared to SIM was more evident in the inshore stations (Figure 5). During SM, dissolved oxygen concentration at any specific depth in the upper 50m-water column was lower by 15 – 20 μ M less compared to SIM (Figure 5). The concentration of nitrate was below 0.5 μ M in the surface waters during all the three seasons (Figure 6). Depletion of nitrate in the surface waters was severe during SIM where nitracline (1 μ M contour of nitrate) was at deeper depth (60m) compared to WM (35m) and SM (30m) (Figure 6). However, during WM, 1 μ M of nitrate was found at 20m of the station A15 where cold core eddy was centered.

3.2. Biological parameters

3.2.1. Chlorophyll *a* and primary production

Surface chlorophyll *a* concentration in the study area was highest during SM (av. 0.24 ± 0.17 mg m⁻³) followed by WM (av. 0.16 ± 0.23 mg m⁻³) and SIM (av. 0.09 ± 0.07 mg m⁻³) (Table 1). Column chlorophyll *a* also showed a similar trend with high values during SM (18 ± 11 mg m⁻²) compared with WM (av. 14 ± 3.5 mg m⁻²) and SIM (av. 13 ± 3.6 mg m⁻²). Elevated chlorophyll *a* (19 mg m⁻²) was found at station A8 during WM due to the cold core eddy. Similar to the surface chlorophyll *a*, surface primary production was also highest during SM (av. 11 ± 13 mgC m⁻³ d⁻¹) followed by WM (5.5 ± 3.1 mgC m⁻³ d⁻¹) and SIM (5 ± 4.4 mgC m⁻³ d⁻¹) (Table 1). However, seasonal variation in the column values of primary production was not substantial (av. 265 ± 130 mgC m⁻² d⁻¹ during SM, av. 245 ± 86 mgC m⁻² d⁻¹ during WM and av. 242 ± 96 mgC m⁻² d⁻¹ during SIM).

Vertical distribution of chlorophyll *a* showed clear seasonal trends (Figure 7). During SM and WM periods, the high concentration of chlorophyll *a* was mostly within the upper 20m-water column. In contrast, chlorophyll *a* concentration was high in the subsurface layers (50 – 75m) during SIM period (Figure 7). Three extensive blooms of *Trichodesmium erythraeum* (Cyanophyta) were observed at different locations of the study area during SIM (Figure 8). These

blooms showed an average geographical coverage of 10 Km² each. Two blooms were located off Karaikkal where one was in the coastal region (11°N, 80° 60'E) and the other one in the oceanic region (10° 58'N, 81° 50'E). The third bloom was located in the oceanic regions off south of Kolkota (19° 44' N, 89° 04'E).

3.2.2. MZP

3.2.2.1. Composition

Protozoans were the dominant component of the MZP community. They consist of heterotrophic dinoflagellates (HDS), ciliates (CTS), and sarcordines (SDS) in which the first two groups were predominant. HDS contributed substantially to the total abundance of MZP. They contributed to 68% of the total abundance during WM, 64% during SM and 51% during SIM (Figure 9). Altogether 57 species of HDS were recorded in the study where the dominant genera were *Protoperidinium*, *Phalacroma* and *Ornithocercus* (Table 2). CTS was the second abundant group and their percentage contribution to the MZP community was relatively high during SIM (33%) (Figure 9). Although CTS were numerically the second dominant group only, the generic and species diversity were more (75 species belonging to 35 genera) than that of the HDS (57 species belonging to 12 genera) (Table 2). The numerically dominant genera of CTS were *Amphorella*, *Codonellopsis*, *Eutintinnus*, *Salpingella* and *Strombidium* (Table 2). Seasonal variation was prominent in the species abundance of CTS where the highest number (78 species) was observed during SIM followed by SM (60 species). Conversely, the HDS species abundance showed only marginal variation seasonally (48 during SM, 47 during SIM and 50 during WM). Among the CTS, loricates dominated quantitatively and qualitatively throughout the study with 31 genera and 72 species over aloricates with 4 genera and 6 species. SDS was the third group of protozoans present in the MZP community and their contribution varied from 7 - 9% of the total abundance and CNP was the metazoan component with 6 - 11% of the total abundance (Figure 9).

3.2.2.2. Abundance and biomass

Abundance of MZP in the surface waters (represent discrete depth values integrated up to 10m depth) was highest during SM (av. $175 \pm 38 \times 10^4 \text{ m}^{-2}$) compared with the WM and SIM (av. $49 \pm 10 \times 10^4 \text{ m}^{-2}$ and av. $51 \pm 11 \times 10^4 \text{ m}^{-2}$ respectively). However, MZP column values (represent discrete depth values integrated up to the 150m depth) were highest during SIM (av. $665 \pm 226 \times 10^4 \text{ m}^{-2}$) followed by SM (av. $575 \pm 180 \times 10^4 \text{ m}^{-2}$) and WM (av. $350 \pm 109 \times 10^4 \text{ m}^{-2}$).

²) (Table 3). Biomass of MZP showed similar trends with highest surface biomass during SM period (av. $48 \pm 18 \text{ mg C m}^{-2}$) and highest column biomass during SIM (av. $260 \pm 145 \text{ mg C m}^{-2}$). The MZP was high at shallow depth zones during WM & SM (upper 20m water column) and at deep depth zones during SIM (50 – 75m) (Figure 10). During WM & SM, dinoflagellates were clearly high in the surface waters compared to CTS (Figure 11). During SIM, the abundance of dinoflagellates and CTS were high in subsurface layers, but the enhancement of the latter was more pronounced (Figure 11). Five species of CTS viz, *Salpingella acuminata*, *S. decurtata*, *S. gracilis*, *S. stenosoma* and *Salpingacantha ampla* occurred exclusively in the deeper waters, which never appeared above 20m in the water column. These species occurred in relatively deep zones (50 – 75m) during SIM compared to the monsoon seasons where they occurred in more shallow depth zones (20 – 50m).

Correlation between MZP biomass and phytoplankton standing stock was more during the SIM ($p < 0.01$, $r^2 = 0.38$, $n = 103$) compared to WM ($p < 0.01$, $r^2 = 0.15$, $n = 108$) and SM ($p < 0.01$, $r^2 = 0.13$, $n = 94$) possibly due to the seasonal variability in the qualitative composition of phytoplankton prey and optimum temperature. To understand this more clearly, correlation between phytoplankton biomass and the biomass of HDS and CTS were analyzed separately. HDS were significantly correlated with phytoplankton standing stock during WM ($p < 0.01$, $r^2 = 0.35$, $n = 103$), SIM ($p < 0.01$, $r^2 = 0.28$, $n = 103$) and SM ($p < 0.01$, $r^2 = 0.38$, $n = 103$) and the coefficient of determination was comparable in all the seasons. However, CTS were less correlated with the phytoplankton standing stock during SM ($p < 0.01$, $r^2 = 0.11$, $n = 103$) and WM ($p < 0.01$, $r^2 = 0.21$, $n = 103$) compared to SIM ($p < 0.01$, $r^2 = 0.44$, $n = 103$).

3.2.2.3. Species variability, interaction and diversity

The abundance of CTS and HDS between stations, between species and between depths were significantly different ($p < 0.01$) during all the three periods of the study (Table 4). The specificity of HDS and CTS on stations were insignificant during all the three periods ($p > 0.05$). CTS and HDS showed highly significant species - depth interaction ($p < 0.01$) during all the three seasons except for the latter during SIM where the relation was not significant. Similarly, station - depth interactions of CTS and HDS were highly significant during SIM ($p < 0.01$) but found to be insignificant during WM and SM ($p > 0.05$) (Table 4). The preference of CTS and HDS towards particular depths was evident in the MDS analysis also (Figure 12). The ciliates present in the 20 – 75m-depth zone showed similarity during SIM, indicating less specificity for any particular

depth, but during WM and SM the preference towards specific depth was more as evident from the higher F ratio for CTS during WM (6.58) and SM (9.53) compared to SIM (4.23). Similarly, HDS showed more specificity for depths during WM (only 10 and 20m depths showed some similarity) and SM (only 0.5 and 10m only showed some similarity). The overall species diversity, richness and evenness of CTS were higher during the SIM period (av. 2.7 ± 0.2 , 3.1 ± 0.8 and 2.5 ± 0.3 , respectively) compared with SM (av. 2.3 ± 0.3 , 2.5 ± 0.3 and 2.2 ± 0.1 , respectively) (Table 5). Conversely, the species diversity, richness and evenness of dinoflagellates during the SIM (av. 2.6 ± 0.4 , 2.1 ± 0.6 and 2.3 ± 0.2 , respectively) were comparable in magnitude with SM (av. 2.5 ± 0.2 , 2.1 ± 0.3 and 2.3 ± 0.1 , respectively).

3.2.2.4. Association of cyanobacteria with HDS

The occurrence of cyanobacteria associated with several species of HDS was noticed during the study. Under the epifluorescence microscope, using the blue filter, the intense orange fluorescence of the phycoerythrin pigment of the cyanobacterial cells was distinctly visible. The general size ($\sim 2.5\mu\text{m}$ diameter), morphology and the presence of phycoerythrin pigment suggest that the cyanobacterial cells were *Synechococcus*. The association of HDS and *Synechococcus* in oligotrophic marine environments was documented in several earlier studies (Taylor 1976a; Gordon et al., 1994; Jyothibabu et al., 2006). The HDS species that showed cyanobacterial symbionts were *Ornithocercus magnificus*, *O. heteroporus*, *O. quadratus*, *O. steinii*, *O. thumii*, and *Histioneis hyaline* in which the first four species were predominant (Figure 13). These dinoflagellates were restricted to the upper 50 and 75m water column during monsoon and SIM period, respectively. The total occurrence of these dinoflagellates and the incidence of cyanobacterial association showed clear seasonal trends. During the SIM period, out of 1747 specimens of potential dinoflagellate species observed under the microscope, 1538 (96%) had cyanobacterial cells inside their body. During WM and SM, the frequency of incidence of cyanobacterial associations was low in magnitude. Out of 964 specimens of potential dinoflagellate species observed during the WM period, only 140 (15%) had cyanobacterial cells. Similarly, among 955 specimens observed during SM, only 131 (14%) specimens had cyanobacterial endosymbionts (see Jyothibabu et al., 2006 for more details).

3.2.3. Mesozooplankton biomass

The mesozooplankton biomass of the study area was high during WM (av. $777 \pm 433 \text{ mg C m}^{-2}$) and SM (av. $628 \pm 499 \text{ mg C m}^{-2}$) compared to SIM period (av. $223 \pm 236 \text{ mg C m}^{-2}$) (Table 6). During WM and SM zooplankton biomass distribution showed noticeable geographical

variations with high biomass in the southern region of the study area during the former period and vice versa during the latter period. However, during SIM such geographical variation was not evident in the distribution of zooplankton biomass (Table 6). Copepods were the predominant group in the community (seasonal av. 67 – 72%).

4. Discussion

4.1. Physicochemical environment

During WM, the intensity of atmospheric cooling in the BoB decreased towards the northern latitudes (Hastenrath & Lamb, 1979). The occurrence of low saline waters (<30) found localized along the coastal region during this period was due to the freshwater discharge (Suryanarayana & Murthy, 1988). The river runoff is found to play an important role in reducing the transparency and mixed layer depth (MLD) in the BoB (Vinayachandran et al., 2002). During the WM period, the MLD decreased with increased freshening (causes stratification) along the coastal and northern regions (north of 19°N). As a result, the nitracline was lowered to ~ 35m depth, where as in the cold core eddy region it was traceable at 20m depth. The high nutrient content brought by river seems to be restricted to the very coastal regions (Prasannakumar et al., 2002) and therefore is not reflected in the present measurements. However, the high amount of suspended materials brought by rivers has caused low euphotic column along the inshore regions (av.75m).

The increased solar radiation during SIM has caused a 2- 3°C increase in the SST and high SSS indicated low river runoff. The poleward flowing East Indian Coastal Current probably pushed the low saline surface waters to the offshore region resulting in low saline patches away from the coast (Sanil Kumar et al., 1997). Thus, the warm and low saline waters in the offshore region during SIM have amplified the stratification leading to nitrate limitation in the surface layers (av. MLD was 20m and nitracline was 60m). The intense solar radiation and low freshwater influx have increased the euphotic column depth (av. 108m) during SIM.

Similar to the SIM features, high SST (with minimum spatial variability) prevailed during SM (Varkey et al., 1996) but, the SSS decreased in the northern region due to the high amount of rainfall and river runoff (Subramanian, 1993). The high amount of suspended sediment flux from the river and the thick cloud cover during the SM period markedly reduced the euphotic column (av. euphotic depth was 60m). Due to the prevailing southwest monsoon winds during SM, the MLD was relatively high in most of the study area compared to SIM & WM.

4.2. Biological environment

4.2.1. Phytoplankton standing stock and productivity

The low seasonal average values of phytoplankton standing stock and production in the BoB (13 – 18 mgm⁻² and 220 – 280 mg C m⁻² d⁻¹ respectively) truly represented the oligotrophy of the system. Strong stratification prevents the upliftment of nutrients from the base of the thermocline to the upper euphotic column as the nitracline was found below 30m depth during all the three seasons studied. During SIM, due to intense surface layer stratification (lowest MLD), the nitracline was at 60 m depth thereby causing intense depletion of nitrate in the surface layers.

The decrease in the euphotic column during monsoon periods was suggestive of the low solar radiation during which, phytoplankton resides in the upper 50m water column (Gomes et al., 2000; Madhu et al., 2006) as evidenced in the shallow chlorophyll *a* maxima. Nitrate was sparsely available in the surface layer during this period compared to SIM and this might have supported the growth of phytoplankton community in the surface layer. On the other hand, even with high solar radiation available during SIM, high phytoplankton standing stock remained in the subsurface layers (30-75m) due to the extreme depletion of nitrate in the surface layers (Gomes et al., 2000).

The mesoscale eddies have been reported to promote primary production in the BoB (Gomes et al., 2000; Prasanna Kumar et al., 2002.). The cold core eddy centered along 15°N transect during the WM period sustained the highest chlorophyll *a* value of the season (16 mg m⁻²). Normally, a cold core eddy produces marked enhancement of biological production through pumping of nutrients into the upper euphotic column (McGillicuddy & Robinson, 1997). During the present WM observation, the eddy was prominent only in the subsurface waters which probably caused moderate biological production.

4.2.2. MZP

In the western BoB, HDS was the most abundant group contributing 51 – 70% of the MZP community in abundance during different seasons. This was in agreement with earlier observations that HDS forms the major component of MZP in the oligotrophic marine waters of tropical and subtropical regions (Lessard, 1991; Quevedo et al., 2003). The present study is the first of its kind from the western BoB that gives baseline information on the qualitative composition of the HDS community (Table 2). High quantitative occurrence of HDS (av.65%)

could be due to their diverse modes of feeding in diverse environmental conditions (reviews by Gains & Elbrachter, 1987; Hansen, 1991; Lessard, 1991). The specific growth rate of HDS is less than that of CTS, but they outnumber the latter in oligotrophic environments due to the ability to utilize a wider range of prey through diverse modes of feeding (Jeong, 1999).

The CTS formed the second numerically dominant MZP component with 14 – 33% of the community. This was comparable with the values obtained from the Arabian Sea (15 – 43%), off southern California (18 – 32%) and Northern Adriatic (12 - 52%) (Gauns et al., 1996; Beers & Stewart, 1971; Revelante & Gilmartine, 1983). However, a noticeable decrease in aloricate CTS as reported earlier (Gauns et al., 2005) remains unexplained. The oligotrophic marine waters are found to exhibit significant amount of aloricate ciliates compared to tintinnids (Quevedo et al., 2003). One plausible reason for the low abundance of aloricate ciliates could be the exclusion of organisms below 20 μ M due to limitations in the sampling methodology. Despite this fact, the importance of the present study is that this forms the first detailed information on the MZP community from the BoB.

The availability of preferential food and a warm condition are the key factors, which favor the CTS in marine ecosystems (Heinbokel, 1978; Taniguchi & Kawakami, 1983; Verity, 1986; Godhantaraman & Krishnamurthy, 1997). HDS increase with phytoplankton stock mostly contributed by larger diatoms (Hansen, 1991). Thus the larger phytoplankton stock in warm waters could be one of the reasons for the high abundance of MZP in the surface layers. During SIM, although the temperature in the surface layers was the highest, the phytoplankton standing stock was markedly low that might have caused low MZP abundance. During the WM, the surface waters were cooler by 2 – 4°C compared to the SIM and SM and this might have caused low ciliate abundance and a general decrease in the total abundance of MZP. The depth at which the MZP and phytoplankton standing stock reached the peaks varied seasonally. The depth of the highest MZP existed frequently above the depth of the highest phytoplankton biomass during SIM, but during SM & WM this difference in depth was not clear. This result agrees with the observation of Suzuki & Taniguchi (1998) that both layers (MZP maxima and chlorophyll *a* maxima) are identical where the chlorophyll maximum layer is shallow but the MZP maximum layer occur just above the chlorophyll maximum layer where the latter is deep.

The phytoplankton cells in strongly stratified marine environments are smaller compared to those in relatively less stratified conditions (Johnson & Sieburth, 1979; Platt, 1983; Cushing, 1989; Yentsch & Phinney, 1995). Even though stratification in the BoB persists throughout the year, it was more intense during SIM as evidenced by the deepest nitracline (60m) observed during SIM. The blooms of *Trichodesmium erythraeum* were evidence of the severe nitrate limitation in the surface layers. Interestingly, the total phytoplankton standing stock during SIM was comparable in magnitude with WM and SM. The quantitatively comparable phytoplankton standing stock during SIM even at extreme nitrate limitation indicates a change in the phytoplankton species composition.

The species adapted to survive in nitrate-depleted conditions such as smaller diatoms, phytoflagellates and cyanobacteria (Johnson & Sieburth, 1979; Yentsch & Phinney, 1995) might have numerically dominated the phytoplankton community in the BoB during SIM. CTS are very efficient in consuming these phytoplankton cells (Rassoulzadegan & Goston, 1981; Bernard & Rassoulzadegan, 1993; Johnson & Sieburth, 1982). Therefore, the marked increase of smaller phytoplankton cells in the BoB during SIM could be the reason for the significant correlation between phytoplankton and ciliate biomass. Conversely, during monsoon periods, more nitrate was available in the surface layers (nitracline at 30- 40m depth) eventually favoring large phytoplankton cells. CTS are unable to consume large phytoplankton cells and this may lead to an insignificant correlation between MZP and chlorophyll *a* during monsoon periods. The advantage of HDS to consume different size classes of organisms such as small cyanobacterial cells and large diatoms is well documented (reviews by Gains & Elbrachter, 1987; Hansen, 1991; Lessard, 1991). Thus HDS could be an efficient consumer of phytoplankton through out the study and this may be the reason for it's the observed consistent correlation with phytoplankton standing stock. The highest percentage abundance of HDS (82%) inside the cold core eddy may also be due to the high abundance of their preferred prey (large phytoplankton) as reported by Vaillancourt et al., (2003).

The significant variability of MZP between species, between depth and between stations were indicative of spatiotemporal heterogeneity. Although the oligotrophic open ocean systems are more homogenous than less physically stable systems, populations become scattered over space in a heterogeneous, patchy distribution (Quevedo et al., 2003). The MZP species were widely distributed in the study area as evidenced by the low species station interaction. This may be due to the similarity in the major environmental factors in most of the stations. The most

important factor that influences the MZP distribution in tropical regions is salinity and due to the river runoff, marked reduction in salinity is expected in the coastal regions of western BoB. However, during WM & SM, the SSS was less variable (<2) between inshore, offshore and oceanic regions except in some localized regions (Figure 2). This may be due to the fact that the inshore stations were located in the continental slope regions (~200m depth) and therefore the pronounced impact of low salinity was not reflected in these stations. The phytoplankton standing stock regulating the MZP distribution was also comparable in magnitude between stations during different seasons (Table 1) and favoured low specificity of MZP on stations. On the other hand, the high specificity of CTS and HDS on specific depths may be due to the variability in the optimal conditions.

In the Multi Dimensional Scaling (MDS) analysis, CTS and HDS showed high depth specificity during WM & SM. However, the species in the high chlorophyll layer (upper 20m water column) were found to be more similar indicating the availability of their common food. During SIM, although the CTS showed depth specificity, identical species were found in the subsurface depths (20, 50 and 75m) in the MDS analysis, indicating many of their common trophic requirements. The species of HDS in the 20 – 75m water column were more similar during SIM thereby showing low species depth interaction. This may be due to the similar phytoplankton prey in these depths as a result of strong stratification.

The occurrence of *Synechococcus* – HDS associations was markedly higher during the SIM period compared with the SM and WM. During the SIM, strong stratification causes depleted nitrate concentration in the upper water column (upper 60 m water column had $<0.01 \mu\text{M}$), possibly favouring the proliferation of cyanobacteria cells. During this period, dissolved oxygen concentration in the surface waters (upper 50 m) of the western BoB was higher than other seasons. The higher oxygen concentration could retard the process of nitrogen fixation by inactivating the enzyme involved in nitrogen fixation (nitrogenase). The more frequent occurrence of cyanobacterial cells inside the body of heterotrophic dinoflagellates during the SIM may, therefore, be an advantage through exposure to reduced oxygen concentrations. Cyanobacterial cells inside the body of dinoflagellates may be more efficient in nitrogen fixation than their relatives in the surrounding water (Jyothibabu et al., 2006). Unfortunately, published work on the quantitative significance of *Synechococcus* population inhabiting in the BoB is absent. However, a very recent pigment measurement in the BoB using HPLC indicates high abundance of *Synechococcus* population in the BoB (Unpublished data – Rajdeep et al., National Institute of Oceanography, Goa, India). The *Synechococcus* population inhabiting in the neighboring Arabian

Sea was quantified by Burkill et al., 1993 showing their abundance as high as 10^7 cells l^{-1} in the upper 50m-water column. Several species of tintinnids viz *Salpingella acuminata*, *S. decurtata*, *S. gracilis*, *S. stenosoma* and *Salpingacantha ampla* that have showed high occurrence in the subsurface layers during SIM period have small oral size (<10 μ m) and solely/ preferably feed on *Synechococcus* cells (Bernad & Rassoulzadegan, 1993). Based on the environmental conditions described above, the high abundance, diversity and biomass of MZP found in the western BoB during the SIM period seem to be a consequence of intense stratification and nitrate limitation

Another possible mechanism that may support high MZP biomass in the marine environment is through the heterotrophic pathway of the microbial food web, the microbial loop, where the bacteria derive energy from dissolved organic carbon (DOC) and transfers it to mesozooplankton through several intermediates. The high availability of DOC is essential for the establishment of an active microbial loop. In the western BoB, the total living content of plankton is low throughout the year (Gauns et al., 2005, Madhu et al., 2006) and therefore the chances of a high DOC pool derived from plankton biomass is unreasonable. However, the enormous river influx, mostly during WM & SM, can bring large quantities of terrogenous DOC into the BoB. There is no previous systematic seasonal measurement on the heterotrophic bacterial abundance and DOC pool in the BoB. The available information show that the bacterial abundance during summer monsoon period is markedly higher than the intermonsoon fall (non - monsoonal period) indicating the relatively high DOC during the former period from the river influx. Therefore, it appears that the high MZP biomass observed during the SIM period is a result of the increased activity of the herbivorous pathways of the microbial food web and not through bacterial loop which may be significant in the BoB during monsoon periods.

4.2.3. Possible food web structure and vertical carbon flux

It is obvious from the present study that there was marked decrease in the zooplankton biomass in the BoB during SIM, even when the phytoplankton standing stock remained unchanged. A possible reason could be the predominance of the herbivorous pathways of the microbial food web during SIM (Yentsch & Phinney, 1995). The highest abundance, biomass and diversity of MZP during the SIM period support the above contention. In strongly stratified tropical waters, phytoplankton with smaller cell size form the major component (Yentsch & Phinney, 1995). Copepods and other zooplankton are unable to crop the small phytoplankton efficiently (Marshall, 1973; Johnson & Sieburth, 1982) and therefore in such conditions MZP

transfer the primary organic carbon to mesozooplankton (Pathway 2). However, the trophic transfer efficiency of microbial food web is less compared with the traditional food chain due to several intermediate steps involved (Cushing, 1989). Consequently, less amount of primary carbon reaches the higher trophic level through microbial food web and this could be the reason for the low mesozooplankton biomass during the SIM period. A major consequence of the microbial food web is the distribution of photosynthetic carbon at multitrophic levels (widely dispersed) thereby facilitating a long residence time in the upper layers of the ocean (Landry et al., 1998; Buesseler, 1998). On the contrary, due to more mixed surface layers during SM and WM, traditional food web could be more active in the BoB compared to SIM leading to more efficient transfer of phytoplankton carbon to the mesozooplankton level.

The seasonal variation in the degree of dominance of microbial vs traditional food web may have implications on the vertical fluxes of biogenic carbon in the BoB. The vertical flux of biogenic carbon in the BoB is clearly low during the SIM compared to the monsoon periods (Ittekkot et al., 1991). The low amount of primary production and less freshwater input during SIM are thought to be the reasons for this (Ittekkot et al., 1991). However, several recent studies show that the phytoplankton biomass and production in the BoB do not change appreciably during different seasons (Prasanna Kumar et al., 2004; Gauns et al., 2005; Madhu et al., 2006). Therefore, based on the present measurement, we propose the predominance of microbial food web as a mechanism responsible for the low vertical flux of biogenic carbon in the BoB during SIM. However, more work would be needed to substantiate this hypothesis.

5. Conclusion

The present study ascertains the oligotrophy of BoB with low annual phytoplankton biomass (av. $13 - 18 \text{ mg m}^{-3}$) and primary production (av. $220 - 280 \text{ mg C m}^{-2} \text{ d}^{-1}$). The thermohaline stratification (throughout the year) and the low solar radiation and turbidity (during monsoon periods) are the causative factors for this. The surface layer stratification was strongest during SIM (MLD 20m and deepest nitracline 60m) compared to monsoon periods (MLD 30 – 50m and nitracline 20 – 50m). The MZP abundance, biomass, and diversity were clearly high during SIM. Interestingly, the mesozooplankton biomass was markedly higher during WM & SM compared to SIM even when the phytoplankton biomass and production were constant during all the three periods. We propose that the seasonality in the relative dominance of the herbivorous microbial food web and traditional food web are responsible for this. During SIM, due to the intense nitrate limitation in the surface layer cyanobacteria and small phytoplankton cells

dominate in the environment favoring the herbivorous pathways of the microbial food web. Contrary to this, during monsoon periods, due to relatively more concentration of nitrate in the surface layers, population of large phytoplankton tend to increase, favoring a more active traditional food web. Due to the low trophic transfer efficiency of the microbial food web, less amount of primary carbon reaches the higher trophic level during SIM causing low mesozooplankton biomass. Therefore, during SIM, along with the low 'sinking effect' of river influx (Ittekkot et al., 1991), the predominance of microbial food web could be another mechanism responsible for the low vertical flux of biogenic carbon in the BoB (Landry et al., 1998). Size fractionated phytoplankton-standing stock and measurements of pico/nano phytoplankton using Flow Cytometry are two potential possibilities to test the seasonality in the relative dominance of microbial and traditional food web as proposed in this paper.

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Figure 1

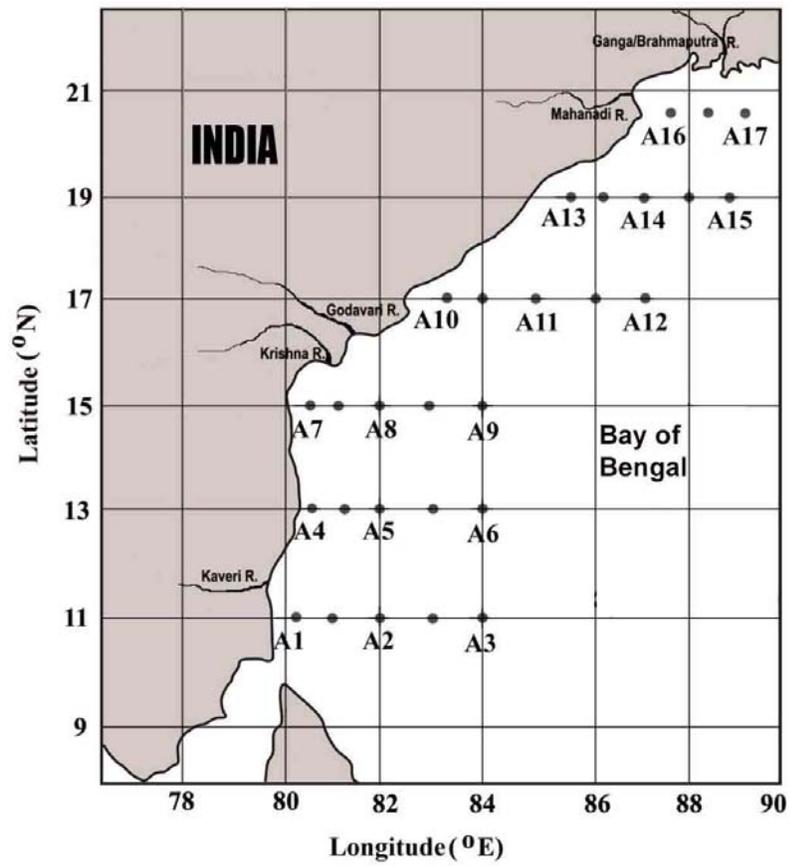


Figure 1 – Station locations

Figure 2

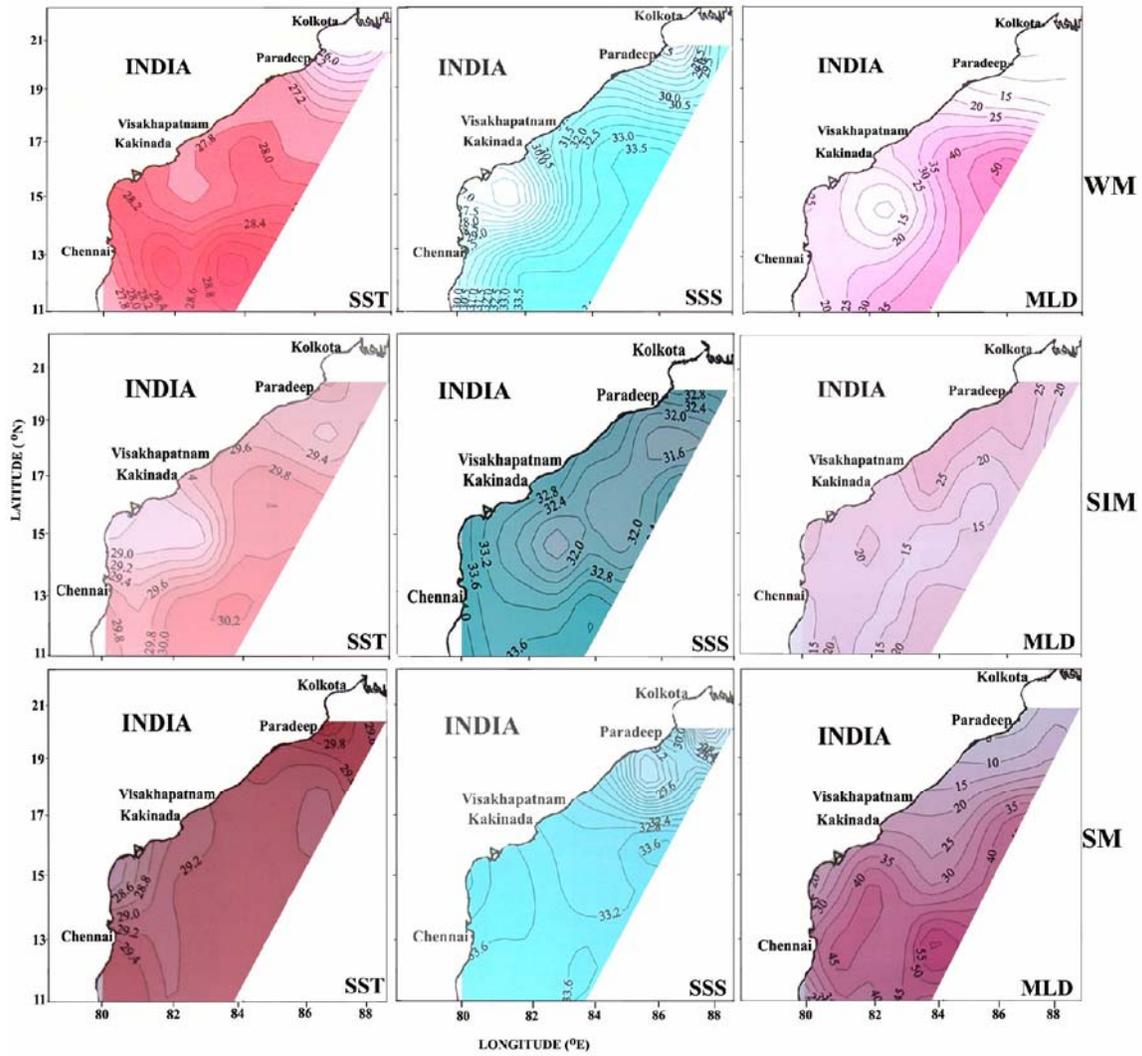


Figure 2 – Distribution of sea surface temperature (SST- °C), sea surface salinity (SSS - psu) and mixed layer depth (MLD - m) during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

Figure 3

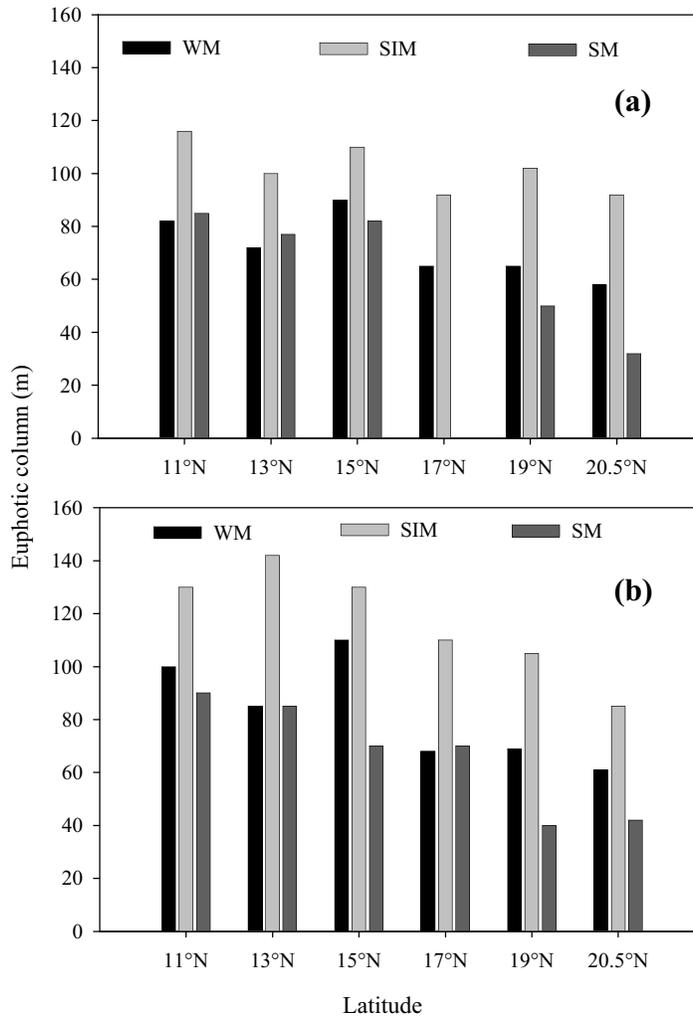


Figure 3 – Seasonal variability of euphotic column in the (a) inshore and (b) oceanic regions during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

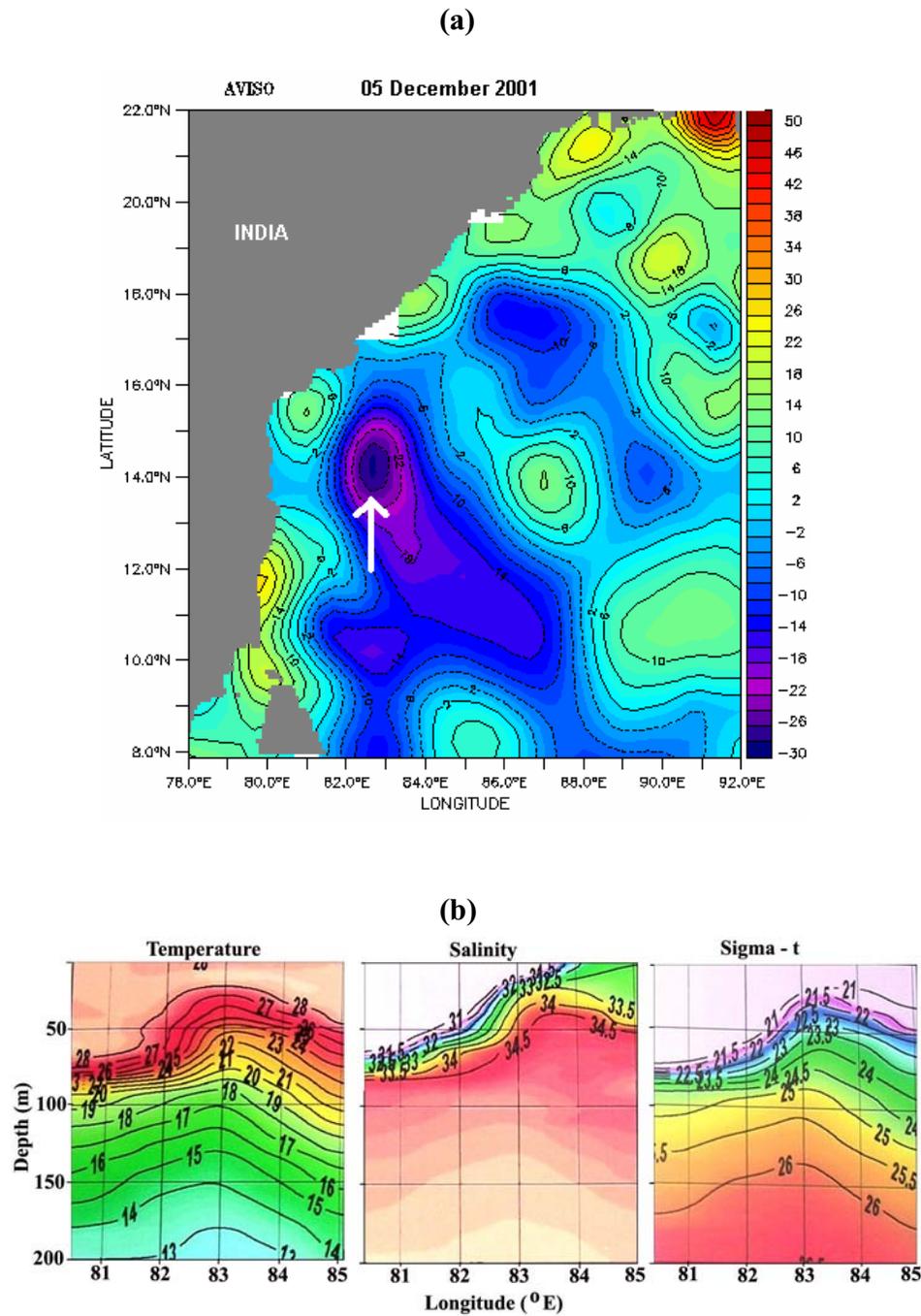


Figure 4 – Cold core eddy signatures (A) Sea level anomalies from Topex/Poseidon (core of the eddy is shown by the pointer) and (B) Vertical structure of temperature ($^{\circ}\text{C}$), salinity (psu), and sigma - t (Kg m^{-2}) along 15°N transect during winter monsoon

Figure 5

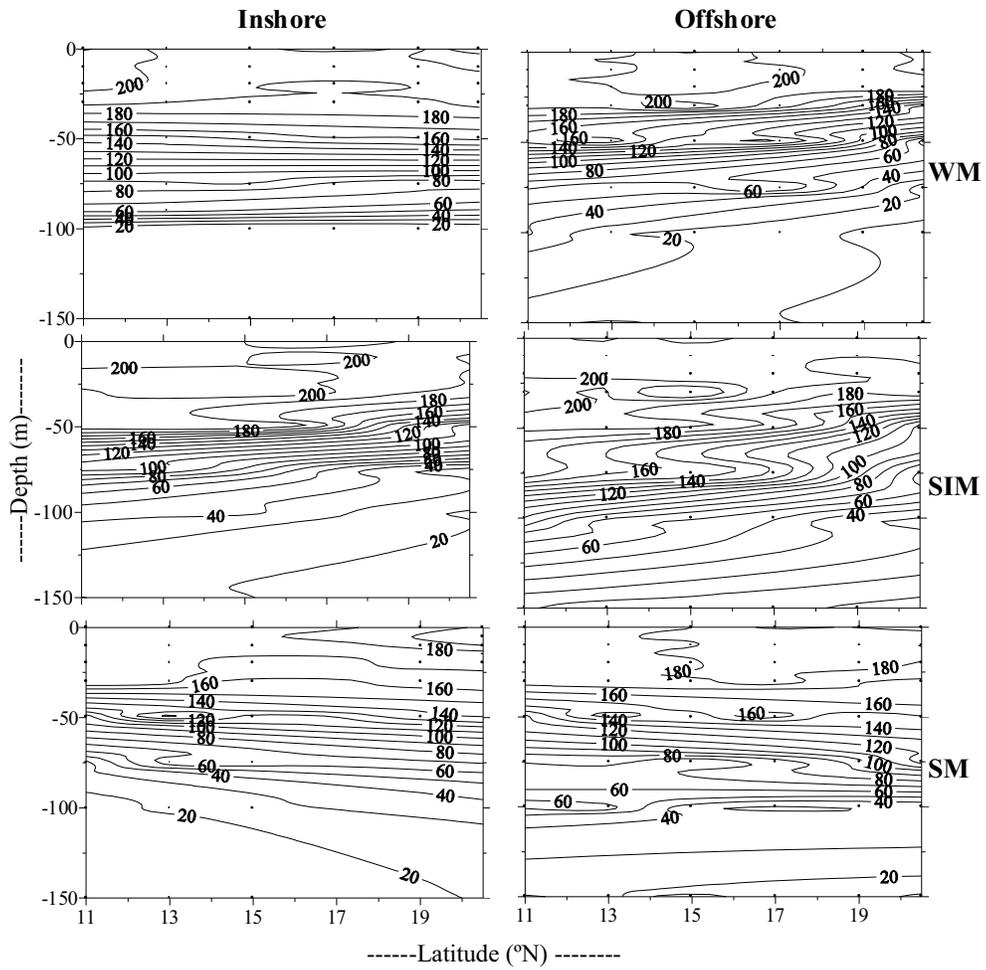


Figure 5 – Vertical distribution of dissolved oxygen during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

Figure 6

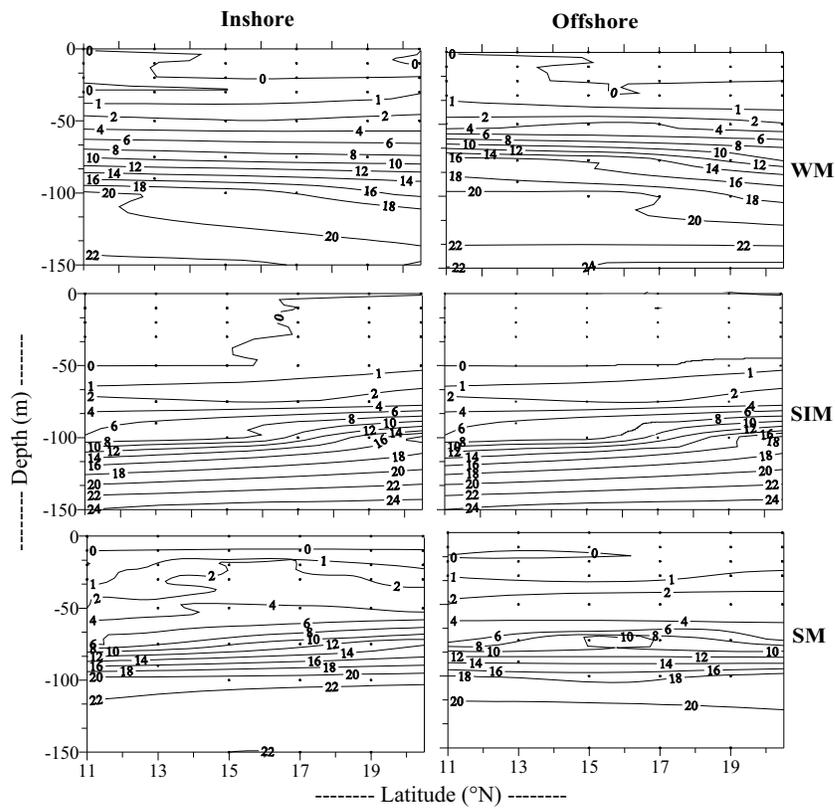


Figure 6 – Vertical distribution of nitrate during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

Figure 7

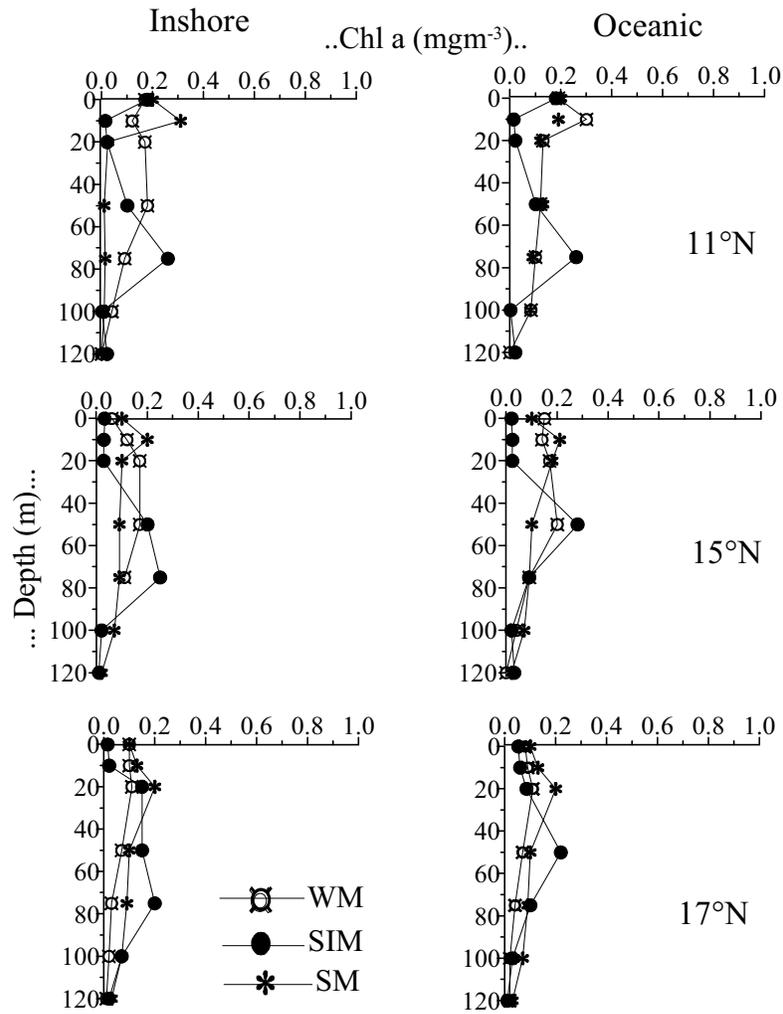


Figure 7 - Vertical distribution of chlorophyll *a* at representative locations during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

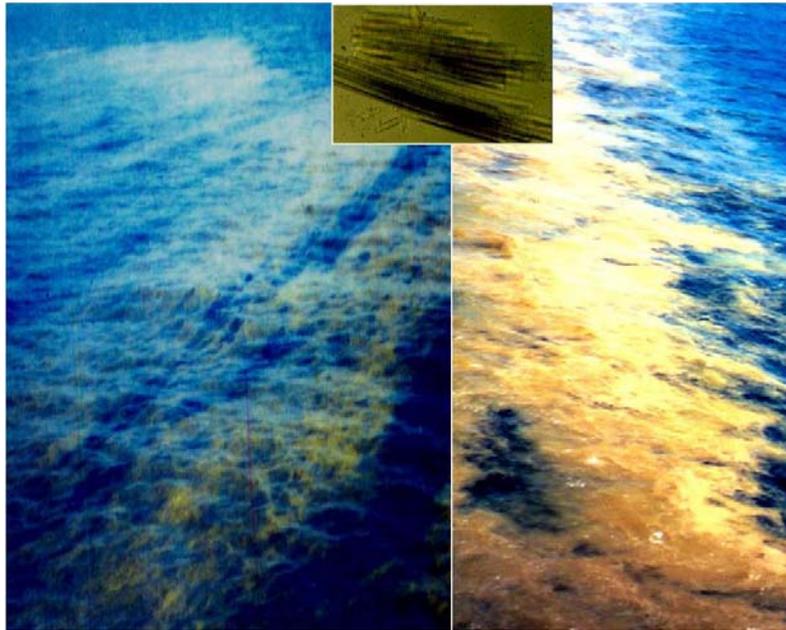


Figure 8 – *Trichodesmium erythraeum* bloom observed (trichomes magnified in the inset) during spring intermonsoon period.

Figure 9

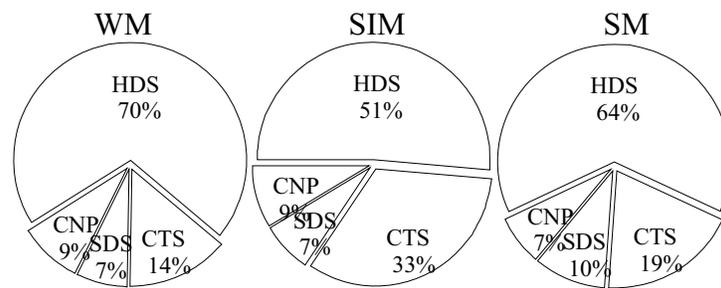


Figure 9 –Major components of MZP based on abundance during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

Figure 10

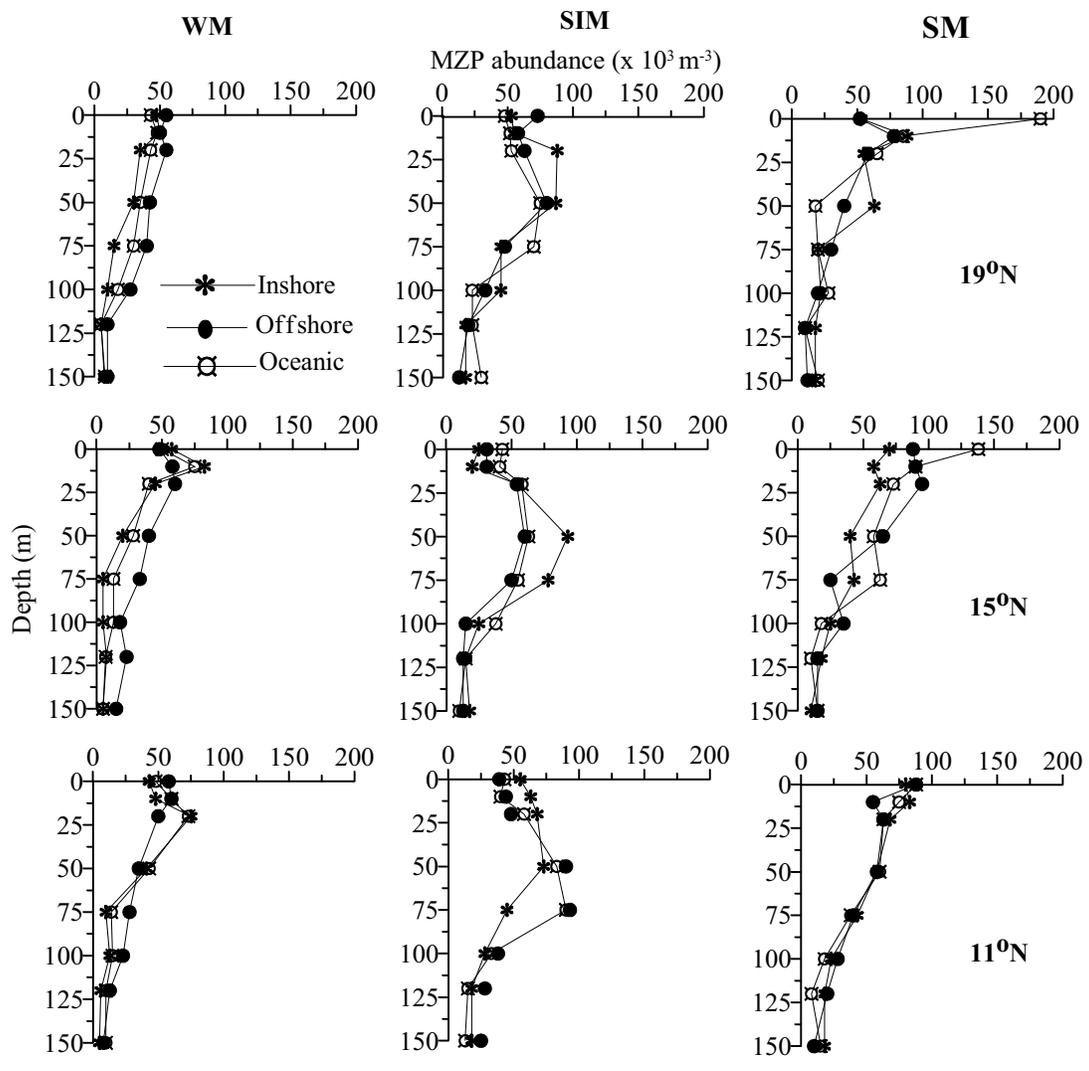


Figure 10 – Vertical distribution of MZP during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

Figure 11

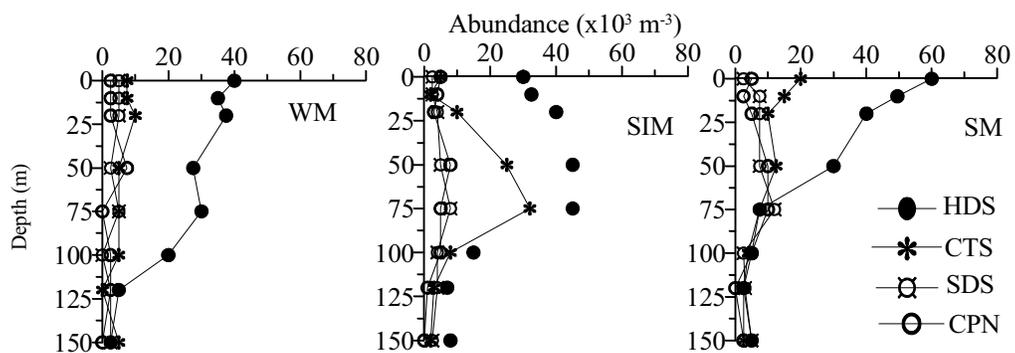


Figure 11 - Seasonal trend in the vertical distribution of heterotrophic dinoflagellates (HDS), ciliates (CTS), sarcodines (SDS) and CPN (copepod nauplii) during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

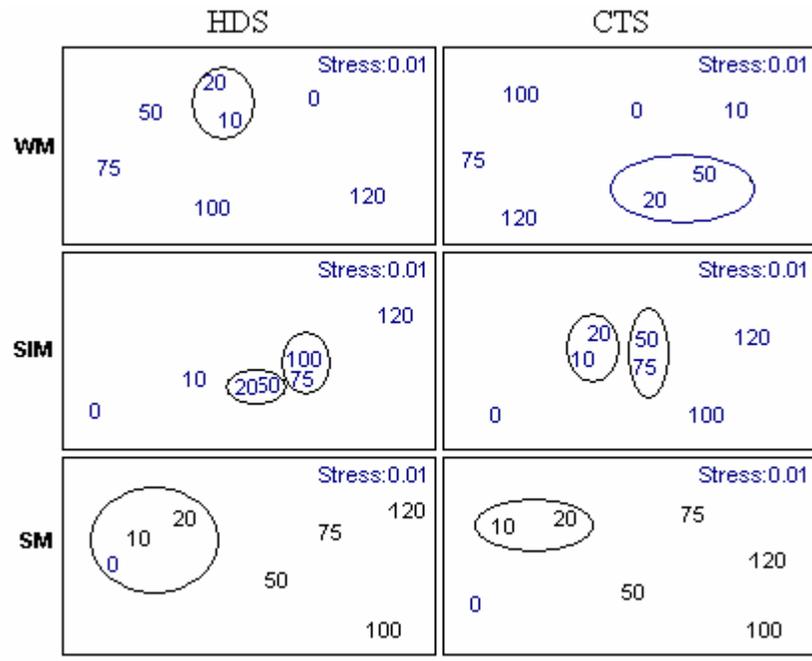


Figure 12 - General trend in the species depth specificity of MZP based on Multidimensional scaling (MDS) analysis for winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM). The numbers indicate the discrete depths of MZP samples. The depths at which high similarity in MZP species abundance were found are marked in circles

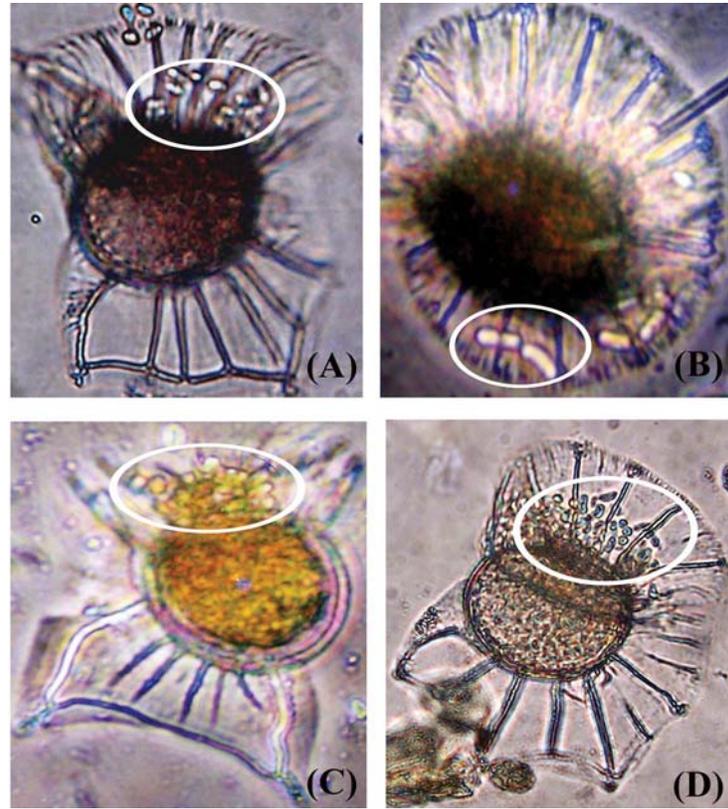


Figure 13 – Associations of *Synechococcus* with HDS (a) *Ornithocercus magnificus*, (b) *O. quadratus*, (c) *O. heteroporus* and (d) *O. thumii*

Figure 14

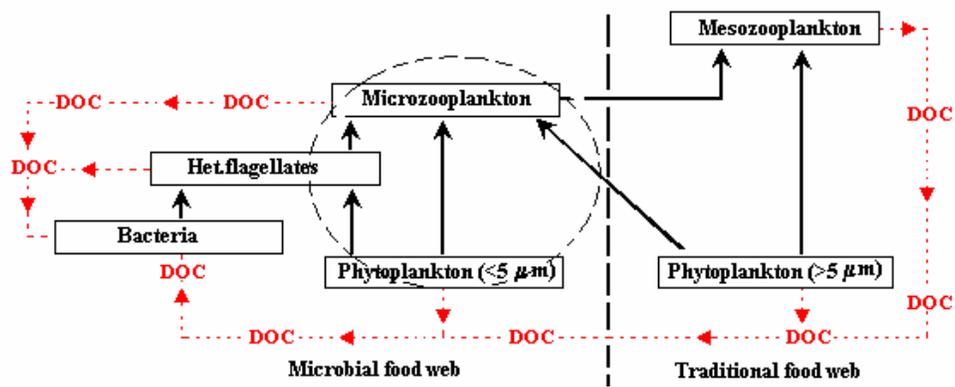


Figure 14 – Two possible pathways in the transfer of primary carbon to higher trophic levels in the BoB. The herbivorous pathways of microbial food web is shown by the circle

Seasons	S Chl. <i>a</i> (mg m ⁻³)	C Chl. <i>a</i> (mg m ⁻²)	S PP (mgC m ⁻³ d ⁻¹)	C PP (mgC m ⁻² d ⁻¹)
WM	0.16 ± 0.23	14 ± 3.5	5.5 ± 3.1	245 ± 86
SIM	0.09 ± 0.07	13 ± 3.6	5.0 ± 4.4	242 ± 96
SM	0.24 ± 0.17	18 ± 11	11 ± 13	265 ± 130

Table 1 – Seasonal variability of surface (S Chl. *a*), Column chlorophyll *a* (C Chl. *a*), surface primary production (S PP) and column primary production (C PP) during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

CTS		
<i>Amphorella gracilis</i> ^(W, I, S)	<i>Protorhabdonella simplex</i> ^(I, S)	<i>O. skogsbergii</i> ^(S)
<i>A. intumescens</i> ^(W, I, S)	<i>Rhabdonella henseni</i> ^(W, I)	<i>O. steinii</i> ^(W, I, S)
<i>A. pachytoecus</i> ^(W, I, S)	<i>R. spiralis</i> ^(W, I, S)	<i>O. thumii</i> ^(W, I, S)
<i>A. quadrilineata</i> ^(W, I, S)	<i>R. amor</i> ^(W, I, S)	<i>Parahistioneis para</i> ^(W, I)
<i>A. tetragona</i> ^(I, S)	<i>R. elegans</i> ^(W, I, S)	<i>Phalacroma doryphorum</i> ^(W, I, S)
<i>Amphorellopsis acuta</i> ^(I, S)	<i>R. longicaulis</i> ^(I, S)	<i>P. purvula</i> ^(W, I, S)
<i>Amphorides minor</i> ^(I)	<i>R. poculum</i> ^(I)	<i>P. sp.</i> ^(S)
<i>Amplectella sp.</i> ^(W, I, S)	<i>Salpingacantha ampla</i> ^(W, I, S)	<i>P. cuneus</i> ^(W, I)
<i>Ascambelliella armila</i> ^(I)	<i>S. sp.</i> ^(W, I, S)	<i>P. favus</i> ^(W, I, S)
<i>A. retrusa</i> ^(W, I, S)	<i>Salpingella acuminata</i> ^(W, I, S)	<i>P. mitra</i> ^(I, S)
<i>Brandtiella palliada</i> ^(W, I, S)	<i>Salpingella attenuata</i> ^(W, I, S)	<i>P. rapa</i> ^(W, I, S)
<i>Canthariella pyramidata</i> ^(W, I, S)	<i>S. decurtata</i> ^(I, S)	<i>Podolampas bipes</i> ^(W, I, S)
<i>Codonella acera</i> ^(W, I, S)	<i>S. gracilis</i> ^(I, S)	<i>P. elegans</i> ^(W, I, S)
<i>C. amphorella</i> ^(W, I, S)	<i>S. stenostoma</i> ^(W, I, S)	<i>P. palmipes</i> ^(I, S)
<i>C. nationalis</i> ^(W, I, S)	<i>Steenstrupiella pozzi</i> ^(I, S)	<i>P. reticulata</i> ^(W, S)
<i>Codonellopsis ecaudata</i> ^(W, I)	<i>S. steenstrupii</i> ^(I, S)	<i>P. spinifera</i> ^(W, I, S)
<i>C. minor</i> ^(W, I, S)	<i>Stenosemella ventricosa</i> ^(I)	<i>Protoperidinium breve</i> ^(W, S)
<i>C. morchella</i> ^(I, S)	<i>Strombidium bilobum</i> ^(W, I, S)	<i>P. brevipes</i> ^(S)
<i>C. nipponica</i> ^(I, S)	<i>S. conicum</i> ^(I, S)	<i>P. conicum</i> ^(W, I)
<i>C. orthoceras</i> ^(I, S)	<i>Strobilidium minimum</i> ^(W, I, S)	<i>P. crassipes</i> ^(W, I, S)
<i>C. ostenfeldi</i> ^(W, I, S)	<i>Tintinnopsis beroidea</i> ^(I, S)	<i>P. curtipes</i> ^(W, I, S)
<i>C. tessellata</i> ^(I, S)	<i>T. butschli</i> ^(I)	<i>P. depressum</i> ^(W, S)
<i>Cyttarocylis acutiformes</i> ^(I, S)	<i>T. cylindrical</i> ^(W, I, S)	<i>P. divergens</i> ^(W, I, S)
<i>Dadayiella ganymedes</i> ^(I, S)	<i>T. directa</i> ^(W, I, S)	<i>P. elegans</i> ^(W, I, S)
<i>D. pachytoecus</i> ^(I)	<i>T. incertum</i> ^(I, S)	<i>P. fatulipes</i> ^(W, I, S)
<i>Dictyocysta duplex</i> ^(W, I, S)	<i>T. mortenseni</i> ^(I, S)	<i>P. globules</i> ^(W, I, S)
<i>D. elegans</i> ^(W, I, S)	<i>T. radix</i> ^(W, I, S)	<i>P. grandae</i> ^(W, I)
<i>D. lepida</i> ^(I, S)	<i>T. tocantinensis</i> ^(W, I, S)	<i>P. granii</i> ^(W, I)
<i>Epiplocycloids reticulata</i> ^(I)	<i>Undella dialata</i> ^(W, I, S)	<i>P. heteracanthum</i> ^(W, I, S)
<i>Epiplocylis undella</i> ^(W, I, S)	<i>U. globosa</i> ^(W, I, S)	<i>P. latistriatum</i> ^(W, S)
<i>Eutintinnus elongates</i> ^(W, I, S)	<i>U. hyaline</i> ^(W, I, S)	<i>P. leonis</i> ^(W, I, S)
<i>E. fraknoi</i> ^(W, I, S)	<i>Xystonella treforti</i> ^(W, I, S)	<i>P. longicollum</i> ^(S)
<i>E. lusus undae</i> ^(W, I, S)		<i>P. longipes</i> ^(W, I, S)
<i>E. tineus</i> ^(W, I, S)	HDS	<i>P. nipponicum</i> ^(I, S)
<i>Favella brevis</i> ^(I)	<i>Dinophysis acuta</i> ^(W, I, S)	<i>P. oblongum</i> ^(I)
<i>Halteria chlorelligera</i> ^(I)	<i>D. apicata</i> ^(W, I, S)	<i>P. oceanicum</i> ^(W, I, S)
<i>Helicostomella subulata</i> ^(I)	<i>D. hastate</i> ^(W, I, S)	<i>P. ovatum</i> ^(S)
<i>Leptotintinnus nordquisti</i> ^(W, I, S)	<i>Diplopsalis lenticula</i> ^(W, I, S)	<i>P. ovum</i> ^(I, S)
<i>Lohmaniella oviformis</i> ^(I, S)	<i>Gymnodinium abbreviatum</i> ^(W, I, S)	<i>P. pellucidum</i> ^(W, I, S)
<i>L. spiralis</i> ^(I)	<i>Gyrodinium sp.</i> ^(W, I, S)	<i>P. quarnerese</i> ^(W, I, S)
<i>Metacylis jorgenseni</i> ^(I)	<i>Heterodinium blackmanii</i> ^(W, I, S)	<i>P. steinii</i> ^(W, I, S)
<i>Parundella caudate</i> ^(I)	<i>Histioneis hyaline</i> ^(W, I, S)	<i>P. tuba</i> ^(W, I, S)
<i>P. lohmani</i> ^(W, I, S)	<i>H. striata</i> ^(W, I, S)	<i>P. pentagonum</i> ^(W, I, S)
<i>Petalotricha ampulla</i> ^(W, I, S)	<i>Noctiluca scintillans</i> ^(W, I, S)	<i>P. claudicans</i> ^(I, S)
<i>P. serrata</i> ^(I)	<i>Ornithocercus heteroporus</i> ^(W, I)	
<i>Proplectella claparedi</i> ^(I)	<i>O. magnificus</i> ^(W, I, S)	
	<i>O. quadratus</i> ^(W, I, S)	

Table 2 – Seasonal variability in the MZP species (W – WM, I – SIM, S – SM)

Table 3

Stations	WM		SIM		SM	
	A	B	A	B	A	B
A1	506 (53)	144 (15)	912 (42)	424 (17)	612 (143)	175 (44)
A2	310 (49)	91 (14)	728 (59)	265 (19)	649 (163)	210 (60)
A3	391 (46)	113 (13)	804 (42)	238 (12)	588 (168)	141 (47)
A4	451 (59)	128 (16)	702 (50)	240 (14)	622 (153)	150 (55)
A5	409 (46)	116 (17)	633 (40)	195 (10)	641 (183)	162 (59)
A6	457 (54)	159 (16)	652 (49)	201 (13)	588 (163)	141 (47)
A7	515 (53)	142 (14)	763 (23)	246 (10)	704 (179)	197 (40)
A8	306 (70)	86 (19)	664 (42)	207 (13)	552 (128)	131 (33)
A9	343 (63)	95 (17)	661 (73)	211 (19)	710 (228)	185 (61)
A10	367 (46)	111 (14)	714 (67)	199 (19)	-	-
A11	287 (39)	70 (10)	858 (72)	339 (23)	593 (170)	158 (37)
A12	247 (52)	69 (14)	872 (70)	234 (18)	477 (173)	113 (45)
A13	316 (42)	86 (11)	837 (54)	195 (13)	569 (141)	154 (32)
A14	316 (27)	88 (9)	797 (50)	223 (12)	528 (275)	122 (59)
A15	89 (48)	23 (58)	122 (65)	753 (15)	215 (130)	493 (27)
A16	205 (43)	56 (11)	367 (41)	139 (22)	323 (218)	112 (46)
A17	294 (46)	82 (12)	211 (34)	110 (12)	55 (188)	187 (79)
Average	350 (49)	103 (14)	665(51)	260 (15)	575 (175)	152 (48)

Table 3 – Seasonal variability of MZP (A) abundance ($\times 10^4 \text{ m}^{-2}$) and (B) biomass ($\times 10^3 \mu\text{gC m}^{-2}$). Surface layer values are given in parenthesis during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

Table 4

Source	WM	SIM	SM
Stations (A)	3.82 * (6.34*)	7.71* (2.36*)	2.45* (2.46*)
Species (B)	13.33* (28.97*)	9.64* (28.95*)	1.26* (18.75*)
Depth (C)	38.39* (84.85*)	47.01* (47.62*)	34.53* (79.31*)
AB interaction	1.356 (2.29)	0.978 (1.684)	1.81 (1.66)
BC interaction	6.58* (3.92*)	4.23* (1.66)	9.53* (3.82*)
AC interaction	1.08 (1.31)	2.62* (4.12*)	1.24 (1.86)

Table 4 – 3 way ANOVA for ciliates and heterotrophic dinoflagellates (in parenthesis) during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).
[* F ratio significant at 1% level]

Table 5

Season	R	I	H	E
WM	2.15 ± 0.33	0.73 ± 0.08	2.4 ± 0.3	2.2 ± 0.17
	(1.9 ± 0.17)	(0.48 ± 0.07)	(1.75 ± 0.12)	(1.95 ± 0.05)
SIM	3.06 ± 0.77	0.7 ± 0.09	2.7 ± 0.42	2.48 ± 0.37
	(2.11 ± 0.62)	(0.76 ± 0.08)	(2.6 ± 0.35)	2.28 ± 0.17
SM	2.46 ± 0.28	0.65 ± 0.08	2.3 ± 0.26	2.23 ± 0.12
	(2.1 ± 0.32)	(0.75 ± 0.05)	(2.5 ± 0.15)	(2.3 ± 0.08)

Table 5 - Community structure of CTS and HDS (in parenthesis) during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).

(R – Magalef’s index, I – Simpson’s index, H – Shannon weaver’s index, E – Heip’s index

Table 6

Lat. (°N)	WM	SIM	SM
11	650 ± 330	236 ± 37	572 ± 324
13	1145 ± 412	369 ± 82	392 ± 129
15	855 ± 601	267 ± 58	479 ± 341
17	854 ± 364	316 ± 134	866 ± 8
19	735 ± 436	477 ± 431	1248 ± 612
20.5	243 ± 18	325 ± 151	513 ± 290
Average	777 ± 433	223 ± 236	628 ± 499

Table 6 - Seasonal variation of mesozooplankton biomass (mgC m^{-2}) during winter monsoon (WM), spring intermonsoon (SIM) and summer monsoon (SM).