

The response of microzooplankton (20 – 200µm) to coastal upwelling and summer stratification in the southeastern Arabian Sea

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Abstract

During the late summer monsoon (LSM), coastal upwelling and river runoff have increased the nutrient concentration in the inshore region of the southeastern Arabian Sea. This has resulted in elevated chlorophyll *a* (av. $40 \pm 18 \text{ mg m}^{-2}$), phytoplankton abundance (av. $474 \pm 116 \times 10^6 \text{ ind. m}^{-2}$) and primary production (av. $917 \pm 616 \text{ mgC m}^{-2} \text{ d}^{-1}$). Diatoms were the major component of the phytoplankton community (av. $60 \pm 8 \%$ of the total abundance) during this period, followed by dinoflagellates ($18 \pm 12\%$). However, the inshore locations of 10 and 13°N transects behaved differently, with an exceptional abundance of phytoflagellates ($>10^{10} \text{ ind.m}^{-2}$). The microzooplankton (MZP) community was comprised of heterotrophic dinoflagellates (av. 60%), ciliates (av. 30%) and copepod nauplii (av.5%); these showed marked variation in abundance between stations. The highest abundance (av. $283 \times 10^4 \text{ ind.m}^{-2}$) was at the inshore location of 10°N transect, where phytoflagellates were abundant. Contrasting to the LSM, intense surface layer stratification and depletion of nitrate (with a nitracline at 60m depth), observed in the southeastern Arabian Sea during the spring intermonsoon (SIM) period, caused low phytoplankton abundance (av. $141 \pm 86 \times 10^6 \text{ ind. m}^{-2}$), chlorophyll *a* (av. $19 \pm 11 \text{ mg m}^{-2}$) and primary production (av. $146 \pm 68 \text{ mg C m}^{-2} \text{ d}^{-1}$). High temperature ($>29^\circ\text{C}$) and nitrate-depleted surface waters favoured the proliferation of *Trichodesmium erythraeum* at most of the locations. Total abundance of MZP during the SIM was markedly low (av. $20 \times 10^4 \pm 13 \times 10^4 \text{ ind. m}^{-2}$), as was the species richness and diversity (0.36 ± 0.02 and 0.57 ± 0.15 , respectively) compared to the LSM (1.17 ± 0.31 and 2.72 ± 0.34 respectively). During the SIM, the MZP community that occurs in the southeastern Arabian Sea is important, since smaller individuals are widespread and form the majority of phytoplankton community. The present study points also to the fact that the MZP could play an important role, even in nutrient-enriched environment where smaller phytoplankton are abundant.

Key words: tintinnids, heterotrophic dinoflagellates, summer monsoon, upwelling, stratification, species diversity, eastern Arabian Sea

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1. Introduction

Microzooplankton (MZP), the heterotrophic form of microplankton (20 - 200 μ m), plays a significant role in pelagic ecosystems, as they transfer autotrophic carbon to higher trophic levels (Porter et al., 1985; Pierce and Turner 1992). Measurements on grazing activity in the marine environment show that MZP is an important consumer of phytoplankton (Burkill et al 1993a; Burkill et al., 1993b; Verity et al., 1993; and Miller, 1993), heterotrophic flagellates and bacteria (Azam et al., 1983). Earlier literature indicates that MZP is ecologically significant in stratified waters, as they transfers majority of primary carbon to higher trophic levels; where as in nutrient enriched environments, most of the autotrophic carbon (contributed mostly by diatoms) is transferred directly to higher trophic levels (Cushing, 1989). However, this understanding has been refined considerably during the last decade and it is now reasonably well accepted that MZP plays an important role in controlling the phytoplankton production in nutrient enriched environments, such as the Southern Ocean and estuaries (Smetacek et al., 2004., Froneman and Bernard., 2004, Jyothibabu et al., 2006).

The southeastern Arabian Sea, in the northwestern Indian Ocean, has pronounced seasonality in its biological characteristics, mainly with respect to the monsoon system. During the summer monsoon period (May - September), coastal upwelling and river runoff enhance the biological production along the southwestern coast of India (Madhupratap et al., 1990; Nair et al., 1992). Utilising the high level of nutrients available in the surface waters, diatoms proliferate and occur in high abundance, forming the major component of phytoplankton standing stock (Madhupratap and Haridas, 1990; Nair et al., 1992; and Sawant and Madhupratap, 1996). However, some recent observations from the southwest coast of India have shown that, when the upwelling process weakens (September - October), the green flagellates and dinoflagellates form a major component of the phytoplankton community (Ramaiah et al., 2005; Sahayak et al., 2005; and Roy et al., 2006). On the other hand, during the spring intermonsoon period (March - May), the southeastern Arabian Sea is exposed to primary heating (summer); this is characterized by weak winds and intense solar radiation, making the surface layer of the ocean highly stratified (Prasannakumar and Prasad, 1996). Such strong stratification results in a scarcity of nutrients in the upper euphotic column (upper 60m has near zero concentration of nitrate), which eventually leads to low phytoplankton biomass and production (Bhattathiri et al., 1996). The phytoplankton community during this period consists mainly of smaller diatoms and cyanobacteria (Nair et al., 1992; Sawant and Madhupratap, 1996; and Anoop et al., 2007).

The mesozooplankton community of the southeastern Arabian Sea and its seasonal response are reasonably well known (Panikkar, 1968; Haridas et al., 1980; Madhupratap, et al., 1990; Madhupratap and Haridas, 1990; and Nair et al., 1992). There is a pronounced enhancement in the mesozooplankton biomass along the southwestern coast of India, during the summer monsoon period (Panikkar, 1968; Haridas et al., 1980; and Madhupratap and Haridas, 1990). However, the MZP community of this region has not been studied in detail (Gauns et al., 1996). If green flagellates occur abundantly along the southwestern coast of India during the late summer monsoon period (LSM) as reported by Ramaiah et al., 2005 and Roy et al., 2006, then the possible trophic role of MZP in the region would be significant in transferring the primary organic carbon, to higher trophic levels (Cushing, 1989). Such an assumption is supported by several recent studies in the upwelling regions of the northwestern Arabian Sea, where smaller phytoplankton forms a major component of the primary producers, during the LSM period (Brown et al., 1999, 2002; Shalapyonok et al., 2001). Likewise, MZP graze a significant portion (~50%) of the daily primary production, thereby resulting in modest carbon export fluxes (Landry et al., 1998; Buesseler, 1998). Against this background, we have studied the southeastern Arabian Sea during late summer monsoon (September 2003) and spring intermonsoon (April 2004) periods, with the following objectives : (a) to generate baseline information on the composition, abundance and ecology of MZP; and (b) to understand the response of MZP on the phytoplankton community, resulting from coastal upwelling and summer stratification.

2. Materials and methods

2.1. Study area

The area of investigation was 8 to 13°N and 69 to 77°E (the southeastern Arabian Sea), which is bordered by the Indian subcontinent on its eastern side (Figure 1). During the summer monsoon period, upwelling and large amount of land and river runoff occurs along the eastern boundary of this region (Shetye et al., 1985., Muraleedharan and Prasannakumar, 1996) (Figure 1). Three major estuarine systems, such as the Ashtamudi (between 8° 53'N and 09° 02'N), Cochin backwaters (between 9° 30'N and 10° 10'N) and the Netravati - Gurupur (12° 48'N and 12° 53'N), empty in to the study area (Figure 1). As a result, during the summer monsoon period, surface salinity and water temperature remain low; nutrients and detritus load increase and light penetration decrease in the shelf region (Nair et al., 1992). The appreciable concentration of nutrients that persists in the surface waters of the inshore region, due to these processes, result in marked enhancement in phytoplankton standing stock and production (Banse, 1968; Madhupratap, et al., 1990; and Bhattathiri et al., 1996). Since the present study was undertaken

out during the late summer monsoon (LSM) throughout the southeastern Arabian Sea, the intensity of upwelling and land runoff is expected to be low (Madhupratap et al., 1990, Qasim, 2003) in comparison to the northern region (Madhupratap et al., 1990, Nair et al., 1992).

During the SIM period, in response to high solar radiation and weak winds, heat accumulates in the upper layers of the eastern Arabian Sea; this in turn, leads to the formation of shallow mixed layer depths (Prasanna Kumar and Prasad, 1996). In addition, the low saline, oligotrophic Bay of Bengal waters, which occupies the surface layers of the southeastern Arabian Sea during the period (Figure 2), intensifies stratification (Sanilkumar et al., 2003). Further, the lesser amount of rainfall during the period on the Indian subcontinent reduces considerably the volume of nutrient-rich river influx nearer to the coast (Qasim, 2003). Thus, stratified, low-nutrient Bay of Bengal waters and the reduction in nutrient concentration nearer to the coast cause an overall scarcity of nutrients in the upper euphotic column (the upper 60m of the water column has near-zero concentration of nitrate). This process leads eventually to low primary production and phytoplankton abundance, during the SIM (Bhattathiri et al., 1996). The phytoplankton community during this period consists mainly of smaller diatoms and cyanobacteria (Nair et al., 1992; Sawant and Madhupratap, 1996). Blooms of *Trichodesmium erythraeum* (a colonial cyanobacterium) are also an annual occurrence in the southeastern Arabian, Sea during the SIM period (Anoop et al., 2007).

The various sampling locations in the southeastern Arabian Sea are shown in Figure 1. The sampling was carried out onboard FORV *Sagar Sampada*, from 15 - 28 September 2003 (LSM) and from 12 - 18 April 2004 (SIM). Nineteen stations were sampled along 3 transects at 8, 10 and 13°N for physicochemical parameters, namely temperature, dissolved oxygen and macronutrients (nitrate, phosphate and silicate). Along each transect, water samples for the measurement of biological parameters, such as phytoplankton composition, chlorophyll *a*, primary production and MZP, were collected from two locations: one near to the coast (inshore) and one in the oceanic region (offshore). The inshore locations were selected in regions appropriate for the operation of *in-situ* primary productivity mooring system (which needs ~200m water depth).

2.2 Physical parameters

The vertical profiles of temperature and salinity for all of the study locations were recorded using a Conductivity Temperature Depth profiler (CTD - Seabird Electronics Sea sat, SBE 911 Plus, USA). Winds were monitored by the automated weather station onboard the ship and the Integrated Data Acquisition Software. The Mixed Layer Depth was taken as the depth (below the surface) at which a 1°C reduction in Sea Surface Temperature (SST) was observed.

2.3 Chemical parameters

The Go-flow bottles, mounted on a CTD rosette, were used to collect water samples from (8) discrete standard depths (0.5, 10, 20, 30, 50, 75, 100 and 120m), for measuring dissolved oxygen and macronutrients (nitrate, phosphate and silicate). Dissolved oxygen was estimated using Winkler's titration method. The concentration of nitrate and silicate were obtained using an autoanalyser (SKALAR, Model 51001-1), following the principles of Grasshoff (1983). Phosphate concentration in the study area was measured spectrophotometrically, following the methods of Grasshoff (1983).

2.4 Chlorophyll-*a*, primary production & phytoplankton

Two liter water samples were collected from (7) standard depths (0.5, 10, 20, 50, 75, 100 and 120 m), using Go-flow bottles. These samples were then passed through GF/F filter papers, whilst the chlorophyll-*a* was extracted in 90% acetone, then analyzed spectrophotometrically (Strickland and Parsons, 1972). Water samples for primary productivity measurements (2 litre) were collected from the standard depths, before dawn (~ at 0500 hours); these were transferred to five clean Nalgene polycarbonate bottles, for the *in-situ* ¹⁴C experiment (UNESCO, 1994). Column values of chlorophyll-*a* and primary production were calculated, by integrating the discrete depth values (up to 120m). A 500 ml volume of water sample was collected from each standard depth and preserved in Lugol's iodine, to measure the abundance and composition of phytoplankton community. The samples were concentrated, following the settling and siphoning out the supernatant. 1ml of the concentrated samples were taken in to a Sedgwick rafter counting chamber and analyzed under an inverted microscope at 100 – 400x magnifications in accordance with the available published literature (Subrahmanyam, 1959; Thomas, 1997).

2.5 MZP

2.5.1 Composition and abundance

Water samples (5 – 8 liter) were collected from (7) discrete depths (0.5m, 10m, 20m, 50m, 75m, 100m ad 120m) for MZP. Organisms with a body size of between 20 – 200µm were accounted for only during this study. The water samples were prefiltered through a 200 µm bolting silk, to avoid the mesozooplankton: the filtrate was collected carefully into black polythene bottles. Although the screening of samples, through a 200µm sieve, may disturb the large and fragile MZP. This process is used widely in MZP sampling, for discarding the mesozooplankton (Froneman and McQuaid 1997; Putland, 2000; and Stelfox - Widdicombe et al., 2004). Subsequently, 3 – 8% of Acid Lugol's Iodine was added to the screened samples. These samples were concentrated then by a gravity settling and siphoning procedure. Thus, the samples were concentrated to a 100 ml volume and preserved in 1 - 3% acid Lugol's solution. Prior to the microscopic analysis, the initial sample concentrates of MZP were allowed to settle for 2 days. The settled samples in the Sedgwick rafter counting chamber, were observed then under an inverted microscope, with phase contrast optics at 100 – 400x magnifications. Although there some conflict exists regarding the suitable fixative for MZP, the Lugol's iodine is regarded as the most useful and that used most widely. Such an approach can cause minimal damage to different groups of the MZP community (Gifford & Caron., 2000). The organisms present in the samples were identified and categorized into four groups viz., heterotrophic dinoflagellates (HDS), ciliates (CTS), sarcordines (SDS) and crustacean nauplii (CNP). The CTS and HDS were identified down to species level wherever possible, whilst the SRS and CNP were identified down to group level, on the basis of the available literature (Kofoid and Campbell, 1939; Jorgenson, 1924; Marshall, 1969; Steidinger, 1970; Subrahmanyam, 1971; Taylor, 1976 a & b, 1987; Corliss, 1979; Maeda & Carey, 1985; Maeda, 1986; and Lynn et al., 1988). The abundance of MZP at different discrete depths (up to 120m depth) was integrated, to generate the water column values.

2.5.2 Analysis of Variance

Three-way analysis of variance (ANOVA) was used to study the significance of variability of MZP between locations, between species and between depths. Such an analysis assists also in understanding analysis also helps to see the station – species, station – depth and species - depth specificity/interaction, of CTS and HDS (Snedecor and Cochran, 1967).

2.5.3 Diversity

Diversity is a concise expression of how individuals of a community are distributed within the subsets of groups. To analyse mathematically and compare changes in aquatic communities, in response to environmental influence, diversity indices can be used as one of the tools.

2.5.4 Species richness (Margalef, 1968)

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

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

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

2.5.5 Species evenness (Heips, 1974)

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

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

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

2.5.6 Species diversity (Shannon and Weaver, 1963)

The advantage of this Index is that it takes into account the number of species and the evenness in distribution 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. Physico - chemical features

3.1.1. Late summer monsoon (LSM)

The wind direction and magnitude, during the study periods, are shown in Figure 3. The wind speed was clearly high during the LSM period (av. 5m s^{-1}). The wind was south-westerly in the open waters of the northern regions; however, closer to the coast and the open waters of the southern region, it was northerly/north-westerly (Figure 3A). The prevalence of upwelling was

evident in the vertical structures of temperature, dissolved oxygen, nitrate and silicate; the up-sloping of isolines were evident towards the coast (Figure 4). This pattern was more pronounced along 13°N, compared to 10 and 8°N; this is indicative of more intense upwelling occurring along the former transect. The low river runoff in the inshore region (along 8°N) was evident in the vertical structure of salinity. In the inshore location of the 10 and 13 °N transects, low salinity plumes were evident; these were more pronounced in the former location. The MLD was evidently high (> 45m) during the LSM period, except in the coastal locations where upwelling was prevalent (Figure 5A).

The dissolved oxygen concentration at all the inshore locations was markedly lower than their respective offshore locations (Figure 4). The lowest oxygen concentration in the surface waters was at the inshore station, along 10°N; here the 190µM contour was very close to the surface (~5m depth). In contrast, higher concentrations of nutrients were present in the surface waters of all the inshore locations, than the respective offshore locations. The 1µM concentration of nitrate was found at a 5m depth at the inshore stations of 10 and 13°N; however, was at a 20m depth at the inshore location of 8°N transect (Figure 4). Similarly, >3µM of silicate was present in the surface waters of all the inshore stations, with the highest concentration (~ 6µM) occurring along 10°N (Figure 4). The concentration of phosphate was higher also at the inshore locations, compared to the offshore region (Figure 4).

3.1.2. Spring intermonsoon (SIM)

The wind was uneven and, therefore, any specific pattern in the wind direction was not prominent during the period, *i.e.* was weak (avg. 3m s⁻¹) (Figure 3B). A warm surface layer (>29°C) was noticeable in the vertical structures of temperature. The prevalence of the Bay of Bengal low saline waters was also evident in the vertical salinity structures. The thickness of the low saline layer has reduced progressively towards the northern transects (Figure 6). The MLD was low (avg. 30m) over the study area (Figure 5B).

Dissolved oxygen concentration was high (>190µM) in the surface waters. The vertical distribution of nutrients and dissolved oxygen, at different depths showed more or less comparable concentrations in the inshore and offshore stations. The nitracline (1µM of nitrate) was found below a 60m depth at all of the locations studied. This pattern was similar to that of

the case with phosphate and silicate, where the surface waters were associated much lesser concentrations, compared to those of the summer monsoon (Figure 6).

3.2. Chlorophyll-*a*, primary production & phytoplankton

3.2.1. LSM

The chlorophyll-*a* concentration varied clearly between locations (av. $35 \pm 15 \text{ mg m}^{-2}$), with high values at inshore locations (av. $40 \pm 18 \text{ mg m}^{-2}$) compared to those offshore (av. $30 \pm 13 \text{ mg m}^{-2}$). The highest chlorophyll-*a* value (61 mg m^{-2}) was found at the inshore location, along 10°N (Table 1). The chlorophyll *a* maximum was found above 50m depth, at most of the stations (Figure 5 C). The primary production showed a similar trend to that of chlorophyll-*a*, with marked variability between locations (av. $657 \pm 494 \text{ mgC m}^{-2} \text{ d}^{-1}$). The primary production was higher within the inshore region (av. $918 \pm 616 \text{ mgC m}^{-2} \text{ d}^{-1}$), compared to that offshore (av. $397 \pm 166 \text{ mg m}^{-2}$); the highest were ($1630 \text{ mgC m}^{-2} \text{ d}^{-1}$) at the inshore station of the 10°N transect.

The abundance of phytoplankton cells at the inshore locations (av. $474 \pm 116 \times 10^6 \text{ ind. m}^{-2}$) was higher, compared to the offshore region (av. $259 \pm 69 \times 10^6 \text{ ind. m}^{-2}$). The highest abundance of phytoplankton was at the inshore locations of 10°N ($552 \times 10^6 \text{ ind. m}^{-2}$) (Figure 7A). Overall, diatoms formed the numerically-dominant component of the phytoplankton community (av. $60 \pm 8\%$) followed by dinoflagellates ($18 \pm 12\%$). The general trend in the numerical abundance of the common diatoms was in the order of: *Rhizosolenia* > *Nitzschia* > *Coscinodiscus* > *Chaetoceros* > *Thalassiosira* > *Skeletonema*. Similarly, the numerical abundance of common photosynthetic dinoflagellates followed the order of: *Ceratium* > *Prorocentrum* > *Dinophysis* > *Amphisolenia*. However, the abundance and composition of the phytoplankton at the inshore station, along 10 and 13°N , were different compared with other stations. At these locations, phytoflagellates (size av. $2 \pm 2 \mu\text{m}$) occurred in large quantities ($>10^{10} \text{ ind. m}^{-3}$). The most dominant diatom at these locations was *Nitzschia*; its abundance was markedly higher ($>30 \times 10^6 \text{ ind. m}^{-2}$), compared to that at other locations ($<50 \times 10^5 \text{ ind. m}^{-2}$).

3.2.2. SIM

The concentration of chlorophyll-*a* was markedly low during this period (av. $19 \pm 11 \text{ mg m}^{-2}$), with marginally higher values at the offshore locations (av. $23 \pm 11 \text{ mg m}^{-2}$), compared to those inshore (av. $15 \pm 8 \text{ mg m}^{-2}$). The highest chlorophyll-*a* value (39 mg m^{-2}) was recorded at the

offshore location, along the 13°N transect (Table 1). The chlorophyll-*a* maxima lay below 50m depth, for most of the stations (Figure 5D). The primary production was also low within the study area, with low variation between stations (av. $146 \pm 68 \text{mgC m}^{-2} \text{d}^{-1}$). Marginally higher values were found in the inshore region (av. $164 \pm 91 \text{mgC m}^{-2} \text{d}^{-1}$), compared to those offshore (av. $128 \pm 38 \text{mgC m}^{-2}$). The highest primary production ($170 \text{mgC m}^{-2} \text{d}^{-1}$) was at the inshore station of the 13°N transect.

The abundance of phytoplankton cells at the offshore locations (av. $151 \pm 119 \times 10^6 \text{ ind. m}^{-2}$) was higher compared to the inshore locations (av. $139 \pm 71 \times 10^6 \text{ ind. m}^{-2}$). The highest abundance of phytoplankton was at the inshore location, along 10°N ($218 \times 10^6 \text{ ind. m}^{-2}$) (Figure 7 B). Diatoms formed the dominant component of the phytoplankton community (av. $30 \pm 8\%$); these were followed by cyanobacteria ($25 \pm 12\%$). The general trend, in terms of numerical abundance, of the common phytoplankton was in the order of: *Trichodesmium* > *Rhizosolenia* > *Nitzschia* > *Coscinodiscus* > *Chaetoceros* > *Thalassiosira* > *Skeletonema*. Similarly, the numerical abundance of common photosynthetic dinoflagellates followed the order of *Prorocentrum* > *Amphisolenia* > *Ceratium*. The abundance of *Trichodesmium* at locations along the 13°N transect was unusual ($408 \times 10^4 \text{ cells m}^{-3}$ offshore and $144 \times 10^4 \text{ cells m}^{-3}$ inshore, respectively).

3.3. MZP

3.3.1 Composition and abundance

LSM

Protozoans were the major component (av. of 90%, in abundance) of the MZP community; were composed of HDS, CTS, and SDS, in which the first two groups were predominant. The HDS outnumbered CTS at all of the locations, except at the inshore locations of 10 and 13°N transect, where it was *vice - versa* (Figure 8). A total of 28 species of HDS were recorded from the study area, where 86% of the species were restricted to the upper 75m of the water column (Table 2). The only two species of HDS that were found below 75m depths were *Podolampas palmipes* and *Ornithocercus magnificus*. The highest number of species of HDS belonged to *Protoperidinium* (15 species) followed by *Podolampas* (4 species) and *Ornithocercus* (3 species). Although CTS were numerically the second dominant group of the MZP community in the study area, their number of species was markedly higher (46 species, belonging to 35 genera) than HDS (29 species, belonging to 7 genera) (Table 3). The general order of numerical abundance of CTS was

Amphorella > *Codonellopsis* > *Salpingella* > *Eutintinnus* > *Strombidium*. However, at the inshore location of 10 and 13°N, the order was *Helicostomella* > *Dadayiella* > *Salpingella* > *Codonellopsis* > *Strombidium* > *Amphorella* > *Eutintinnus*, which was different from other locations. SDS was the third group of protozoans and their contribution varied from $7 \pm 2\%$ of the total abundance. CNP was the metazoan component of the MZP, with an av. $5 \pm 2\%$ of the total abundance.

The abundance of MZP in the study area during the period varied clearly between stations (av. $103 \times 10^4 \pm 89 \times 10^4$ ind. m^{-2}), with the highest (283×10^4 ind. m^{-2}) at the inshore location of the 10°N transect. The total abundance at the inshore locations of the 10 and 13°N transects was higher than the respective offshore locations (Figure 9). The inshore station of 10°N apparently had exceptionally high abundance, with respect to the offshore location. However, such prominent variation was not found along 8°N and 13°N (Figure 9). The abundance of MZP was high in the upper 20m of the water column, at all the locations. The highest abundance of MZP (283×10^4 ind. m^{-2}) was in the inshore location of 10°N. This was due to the exceptionally high abundance of tintinnids, dominated by *Dadayiella ganymedes* and *Helicostomella subulata* (Tintinnina – Ciliata). Micrometer measurements showed that *Dadayiella ganymedes* had a total body length of $90 \pm 20 \mu m$ and a lorica (oral) diameter of $30 \pm 10 \mu m$. *Helicostomella subulata* was smaller in size, compared to *Dadayiella ganymedes*, with a total length of $50 \pm 10 \mu m$ and an oral diameter of $20 \pm 5 \mu m$.

SIM

The general composition of the MZP was similar to that of the LSM period, with a major contribution made by protozoans (av. 83%, in abundance). The difference in abundance between heterotrophic dinoflagellates and ciliates was only marginal, at most of the locations (Figure 8). Moreover, the abundance of CTS and HDS has markedly decreased during SIM, compared to the LSM. A total of 20 species of heterotrophic dinoflagellates were recorded from the study area, in which >60% of the species were found at all of the depths studied (Table 2). The heterotrophic dinoflagellates of the genus *Ornithocercus* had the highest representation of species (3 species) followed by *Protoperidinium* (3 species) and *Podolampas* (3 species). Similar to the summer monsoon period, the ciliates were the second dominant group at most of the locations, during the period, with a representation of 17 species belonging to 7 genera (Table 3). The general order of numerical abundance of CTS was *Rhabdonella* > *Salpingella* > *Codonellopsis* > *Eutintinnus*. The total contribution of SDS was less (av. $6 \pm 2\%$), compared to the summer monsoon period. However,

the percentage contribution of copepod nauplii to the total MZP community has increased clearly during the SIM period ($av.8 \pm 2\%$). However, the abundance of copepod nauplii, during the SIM period, was more or less same as during the late summer monsoon (Figure 8). The total abundance of MZP in the study area during the SIM period was clearly lower ($av.20 \times 10^4 \pm 13 \times 10^4 \text{ ind.m}^{-2}$) compared to the LSM period (Figure 9). Unlike the summer period, the MZP abundance at all the inshore locations remained low (Figure 9): there was no exceptional increase in any of the MZP species, as observed during the LSM period. At most of the locations, the abundance of MZP was relatively high in the upper 50m of the water column.

3.3.2 Variability - 3way ANOVA

During the LSM, the abundance of MZP in the inshore regions has varied significantly, between locations and between depths. Here, variation of MZP abundance between locations was more significant than between depths, as evident in the F - Ratio (Table 4). Thus, the location - depth interaction effect was more significant in the inshore regions, compared with the location - species interaction effect. In the offshore region, variations in MZP between locations, between species and between depths were significant, with the highest F - value associated with the former (Table 4). The location - species interaction was also more prominent in the offshore region, compared to species - depth interaction.

During the SIM, variations in MZP between locations was not significant in the inshore region, but between species and between depths were significant. Therefore, species - depth interaction was significant only in the inshore region (Table 4). In the offshore region, variation of MZP between species was the only significant variable, leading to no significant interaction effect between location and species, species and depths and location and depth.

3.3.3 Diversity indices

During the LSM, the species diversity and richness of MZP was markedly higher in the 10 and 13°N, transects compared to 8°N (Figure 10). The highest diversity and richness of MZP was at the inshore location of 10°N, followed by the 13°N transect. The species evenness was more or less same at all of the locations, during this period. The species diversity and richness of CTS were found to be higher than that of HDS in the inshore stations of 10 and 13°N, whereas at all the other stations it was the reverse (Figure 11). The highest species richness and diversity of CTS

was at the inshore stations of 10°N, whilst the highest diversity and richness of HDS was in the offshore location of 10°N (Figure 11).

During the SIM period, species richness, evenness and diversity of MZP were much lower compared to the LSM (Figure 10). Locations along the 8°N transect had relatively high diversity indices, compared to the other locations. The low diversity indices during the period were also evident, when CTS and HDS were treated separately. Relatively high diversity indices of CTS were found at the locations along 10°N, compared to other locations. However, the HDS diversity indices in most of the stations were more or less same (Figure 10).

4. Discussion

The prevalence of coastal upwelling during the LSM was evident in the vertical structure of temperature, salinity and nutrients. The signatures of coastal upwelling (up-sloping of isolines, towards the coast) were found to be less pronounced along 8°N compared to 10 and 13°N. This pattern was related to the sampling being undertaken during September (LSM), when upwelling is reported to diminish in the southern part of the southwest coast of India (Shetye et al., 1985; Madhupratap et al., 1990). This characteristic was supported further by the low winds (av. 5m S⁻¹), which prevailed along the 8°N transect, compared to 10 and 13°N. The occurrence of low salinity plumes in the surface waters of the inshore locations, along the 10 and 13°N transects during the LSM period, could be the result of the flushing of neighbouring estuarine/river systems. The Cochin backwaters, the largest estuarine system along the west coast of India that receives the influx of six rivers, join the southeastern Arabian Sea through two bar mouths located between 10°N and 10.15°N. Similarly, the Netravati - Gurpur estuarine system and the River Mulki meets Arabian Sea between 12°50' and 13°00'N (Figure 1). During the summer monsoon period, these rivers bring large quantities of freshwater in to the Arabian Sea, altering the physicochemical properties of the water column (Banse, 1968; de Souza et al., 1996).

The chemical response of upwelling, such as the advection of nutrients into the upper euphotic column, was evident in the inshore regions during the LSM. Earlier studies have indicated that the input of freshwater from land and river runoff may suppress the surfacing of deepwater, through upwelling (Banse, 1968; de Souza et al., 1996). Since the inhibition of upwelling by freshwater may be significant closer to the coast, the present sampling resolution is somewhat inadequate to address this interesting process. The southward-flowing West Indian Coastal Current (WICC), during the summer monsoon, is supposed to bring high saline waters in

to the southeastern Arabian Sea during the summer monsoon period (Shankar et al., 2002). Therefore, the low saline - high nutrient waters, observed in the surface waters of the inshore regions during the LSM, appears to be of river origin. The neighbouring estuarine system, the Cochin backwaters, is associated with exceptionally high levels of nutrients during the summer monsoon period (nitrate av. $10\mu\text{M}$, silicate av. $80\mu\text{M}$ and phosphate av. $3\mu\text{M}$), which eventually forms a part of the coastal regions of the eastern Arabian Sea (Jyothibabu et al., 2006).

During the SIM period, the high amount of solar radiation, low winds and the presence of low salinity Bay of Bengal waters had apparently caused a shallow mixed layer in the study area. These three factors have been identified as the major causative factors for the formation of 'warm pool' in the southeastern Arabian Sea, during the SIM period (Sanilkumar et al., 2003). The intrusion of low saline Bay of Bengal waters into the Arabian Sea begins with the setting of winter monsoon current (WMC), during November; this persists until April (Masson et al., 2005), which increases the surface layer stratification and depletion of nitrate (de Souza, et al., 1996; Bhattathiri et al., 1996). In addition, the low river influx also causes the scarcity of nitrate in the surface layers of the inshore locations of the southeastern Arabian Sea during the SIM. Thus the entire study area has become nitrate limited during SIM period. In contrast to nitrate, during the SIM period, the surface waters of the study area had higher dissolved oxygen concentration (av. $200\mu\text{M L}^{-1}$) than LSM (av. $180\mu\text{M L}^{-1}$); this is possibly due to the low amount of biological decomposition, as pointed out by Jyothibabu et al., 2006. The mixing of the surface waters, due to active wind forcing, may also be a reason for the low oxygen concentration in the surface waters of the eastern Arabian Sea, during summer monsoon period (Sarma, 2004).

4.1. The response of phytoplankton

During the LSM period, the elevated concentration of nutrients in the surface waters of the inshore regions of the southeastern Arabian Sea results in high phytoplankton standing stock and production (Madhupratap, et al., 2001; Bhattathiri et al., 1996). This was found to be characteristic of the LSM period of the present study, also where there were high values of chlorophyll-*a* (av. $40 \pm 18 \text{ mg m}^{-2}$), phytoplankton abundance (av. $474 \pm 116 \times 10^6 \text{ ind. m}^{-2}$) and primary productivity (av. $817 \pm 721 \text{ mgC m}^{-2} \text{ d}^{-1}$) at the inshore locations. During the LSM, the highest concentrations of chlorophyll-*a* (61 mg m^{-2}) and primary productivity ($1630 \text{ mg C m}^{-2} \text{ d}^{-1}$) were at the inshore location of 10°N (Table 1); this is due to the high concentration of nutrients

prevailing in the surface layer, at this station (Figure 4). The magnitude of primary productivity at the different locations co - varied approximately with the chlorophyll-*a* distribution (Table 1). The phytoflagellates and *Nitzschia* dominated the phytoplankton community of the inshore locations along 10 and 13°N transects; were different from the remainder of the locations. The prevailing low salinity plume, containing high concentrations of silicate and nitrate, might have influenced the sustenance of these phytoplankton species. Along the west coast of India, marked variations in the dominant phytoplankton community, with respect to the prevailing nutrient concentration, have been reported (Sawant and Madhupratap, 1996; Roy et al., 2006). Similarly, the high abundance of *Nitzschia* in the nutrient enriched coastal waters and the estuarine systems (Cochin backwaters) have also been reported (Sawant and Mdhupratap, 1996; Menon et al., 2000; and Jyothibabu et al., 2006). The high occurrence of phytoflagellates and small diatoms appears to be a feature of the many upwelling systems (Cushing, 1989; Garrison et al., 1998; Brown et al., 1999); this is certainly an understudied aspect of the system.

The concentration of chlorophyll-*a* was very low (av. $19 \pm 11 \text{ mg m}^{-2}$) during the SIM period, as was the primary productivity (av. $146 \pm 68 \text{ mgC m}^{-2} \text{ d}^{-1}$), but with relatively high values in the inshore region (av. $164 \pm 91 \text{ mgC m}^{-2} \text{ d}^{-1}$). This pattern is likely to be related to the lack of nutrients in the surface waters. Bhattathiri et al., (1996) observed similar conditions over most of the eastern Arabian Sea, during the SIM period. Due to stratification (shallow mixed layer depth) a nitracline was present, as deep as 60m; this is typical of the Arabian Sea during the SIM. This is the reason for the high abundance of cyanobacteria in the Arabian Sea, during the SIM period, compared to the LSM (Burkill et al., 1993b). During the present study, *Trichodesmium erythraeum* was the most dominant phytoplankton species during the SIM and its abundance was exceptionally high ($40 - 144 \times 10^5 \text{ cells m}^{-3}$) in the surface waters at some locations, indicating nitrogen limitation. The nitrate limitation and high transparency also cause deep chlorophyll-*a* maxima, during the SIM (Bhattathiri et al., 1996).

4.2. The response of microzooplankton

The HDS form the most common component of the MZP community, in marine waters of the tropical and subtropical regions (Lessard, 1991; Quevedo et al., 2003). Although the quantitative significance of HDS in the eastern Arabian Sea had been identified in earlier studies (Gauns et al., 1996), very little has been known about the qualitative aspects. Therefore, the present study is the first of its kind from the eastern Arabian Sea, which provide qualitative

information on HDS of the MZP community (Table 2). During the LSM period, HDS was the most abundant group in all the offshore and inshore locations, along the 8°N transect. Here, diatoms dominated the phytoplankton community. At these locations, the richness and diversity of HDS were higher than those of the ciliates. This may be due to the ability of HDS to graze a wider range of prey, from small cyanobacteria to large diatoms; their diverse feeding mechanisms enable them to survive in a variety of environments (see reviews by Gains and Elbrachter, 1987; Hansen, 1991; Lessard, 1991; and Stoecker, 1999). The high evenness of HDS, found at all of the locations during the LSM, is indicative also of their adaptability to environments with contrasting prey quality and availability.

During the SIM, the abundance of CTS and HDS reduced considerably, but the difference in their relative abundance was marginal (Figure 8). In marine systems, the ciliates and phytoplankton biomass have been shown to be correlated positively (Lynn & Montagnes, 1991; Leaky *et al.*, 1996). Although some smaller ciliates may graze picoplankton-sized cells (Rassoulzadegan *et al.*, 1988; Sherr and Sherr, 1988), they are not able to meet their entire food requirements based on bacteria; hence, they are not considered to be the major bacterivores in oceanic waters (Pierce and Turner, 1992). Therefore, the positive correlation between ciliates and bacteria found in some studies likely to reflect their common utilization of phytoplankton-derived food and substrate, or the indirect predator prey relationship between them, via grazing on bacterivores nanoflagellates (Verity, 1993a). Similarly, several studies have shown that the HDS are active grazers on nano - microplankton sized phytoplankton cells (Gains and Elbrachter, 1987). Hence, the marked decrease in larger phytoplankton cells could be one of the reasons for the low abundance of HDS, during the SIM. On the other hand, the abundance of copepod nauplii remained more or less similar during the SIM and LSM. The ability of copepod nauplii to survive in tropical oligotrophic waters, by meeting their food requirements solely from a diet of bacteria and picoplankton (Roff *et al.*, 1995), could be the reason for this pattern.

During the LSM period, CTS was the most dominant group of the MZP community at the inshore locations of the 8 and 10°N transects, where phytoflagellates and small diatoms were abundant. The richness and diversity of CTS were also higher at these locations, compared to all of the other stations. The highest abundance of ciliates was in the inshore station of 10°N, where tintinnids such as *Dadayiella ganymedes* and *Helicostomella subulata* occurred in high abundance. Abundance of tintinnids in marine systems is related to the availability of small diatoms and phytoflagellates (Godhantaraman and Krishnamuthy, 1997; Heinboeckel *et al.*, 1979). The largest

particle size that could be ingested by tintinnids averages around 50% of their oral aperture (Splitter 1973; Rassoulzadegan et al., 1981, 1988). The size for *Dadayiella ganymedes* and *Helicostomella subulata* is <10µm indicating the suitability of phytoflagellates as their primary food source. This assumption was confirmed by microscopic observations, where the phytoflagellate was visible inside the body of the tintinnids (Figure 12). The culture experiments of Paranjape (1980) further support the observation that the *Helicostomella subulata* are efficient grazers of phytoflagellates. Similarly, the preferences of *Dadayiella ganymedes* to graze on nanoplankton cells are also well documented (Bernard and Rassoulzadegan., 1990; 1993).

The high abundance of MZP in the inshore locations of the 10 and 13°N transects, during the present study, seems to be a persistent feature of the region during summer monsoon period. Gauns et al., (1996) recorded a 4 – 20 times increase in total MZP abundance almost for the same geographical region, during the peak summer monsoon (July – August) of 1994. Elsewhere a marked enhancement of the tintinnids population was noted along the New Zealand coast, during an upwelling period (Chang, 1990). The subsequent grazing experiments undertaken by James et al., (1996) showed that tintinnids existed over the area, mostly to utilise the nanoplankton as the primary food source. Therefore, the high MZP community found in some inshore regions of southeastern Arabian Sea, during the LSM period, may have significant impact on the phytoplankton community; thereby, increasing the efficiency of the grazing food web. Conversely, this may also reduce the vertical carbon flux, as observed by Landry et al., (1998) in the western Arabian Sea.

The information available shows a pronounced enhancement in the mesozooplankton biomass along the southwestern coast of India, during the summer monsoon period (Panikkar, 1968; Haridas et al., 1980; Madhupratap and Haridas, 1990). Such enhancement could be related primarily to the enhancement in phytoplankton standing stock, as a result of nutrient enrichment through coastal upwelling and land runoff. However, the simulation model developed by Parsons and Kessler (1986) showed clearly that the presence of MZP, during the introduction of freshwater plumes, can enhance zooplankton production by some order of magnitude. Similarly Madhupratap and Parulekar, (1993) have reported high zooplankton density in the Arabian Sea, when ciliate abundance was high. This observation suggests that the higher abundance of MZP in the inshore region of the southeastern Arabian Sea (as observed during the LSM period) could be one of the reasons for the occurrence of high mesozooplankton biomass, during the summer monsoon period.

It is accepted generally that the phytoplankton cells occurring in stratified marine environments are generally smaller compared to those living in relatively less stratified conditions (Plat, 1983; Cushing, 1989; and Yentsch & Phinney, 1995). In the eastern Arabian Sea, intense surface layer stratification occurs during the SIM period; this is evidenced by the deep nitracline, at 60m. The high abundance of *Trichodesmium erythraeum* observed during the period supports also the severe nitrate depletion in the surface layers. The species which are adapted to survive in nitrate-depleted conditions are smaller diatoms, flagellates and cyanobacteria (Johnson and Sieburth, 1979; Burkill et al., 1993; and Yentsch and Phinney, 1995). MZP are efficient in consuming nanoplankton (Bernard and Rassoulzadegan, 1993; Johnson and Sieburth, 1979), whilst copepods and other larger zooplankton are unable to efficiently crop the smaller sized phytoplankton (Marshall, 1973). Therefore, during the SIM period, MZP may possibly be playing a vital role in transferring the primary organic carbon, from the smaller phytoplankton, to mesozooplankton.

The significant variability in the MZP, between species and between water depths, was common during both LSM and SIM period, indicating the spatial heterogeneity (Quevedo et al., 2003). Further, the variability of the MZP between locations was also significant during the LSM. This was related mainly to the high species richness and diversity of tintinnids, at some of the locations. Conversely, variation in the MZP between locations was not significant during the SIM, since there was no pronounced increase in MZP abundance at any of the stations. Tintinnid diversity in marine systems is related closely to prey size diversity, rather than competitive interactions or predation (Dolan et al., 2002). As expected the numerical abundance of phytoflagellates differed markedly between the locations, during the LSM. The high abundance of phytoflagellates within certain water depth zones (in the upper 20m water column), along the 10 and 13°N transects, and during the LSM could be the reason for the high location - depth specificity of MZP, at the inshore locations. In contrast, location - depth interaction was not prominent in the offshore region, during the LSM. The case was similar for all locations during the SIM period; this could be related to the absence of any pronounced availability of preferred organic food of MZP, within any specific depth zones. Similarly, species - depth interaction was also prominent in the offshore locations, during the summer monsoon; likewise, at all the locations during the SIM period. The marked variability of phytoplankton quality, at different depth strata of more stable environments (Burkill et al., 1993b), could provide the explanation.

It is notable that the aloricate ciliates were confined to only a few species, restricted to a few locations, during both periods of study. The relatively high abundance of aloricate CTS associated with high phytoflagellates during the LSM period is indicative of a prey - predator relationship (Chang, 1990). An earlier study undertaken in the central and western Arabian Sea showed that aloricate ciliates are numerically more significant than tintinnids (Leaky et al., 1996). However, the abundance of aloricate CTS was found to be low during both periods of the present study. One plausible reason for this could be the sampling methodology, where organisms below 20 μ M were not considered (due to the inability of the microscope used to resolve the taxonomic details of organisms <30 μ M). Therefore, there could be some underestimation of the aloricate ciliates during the present study. Nonetheless, the importance of the present data set is that it constitutes the first information available on the MZP community of upwelling systems along the Indian Coast.

In recent times, the conventional understanding of the trophic role of MZP, in nutrient-enriched marine environments, has undergone rapid revision. This was mainly due to the extensive use of modern techniques, such as phytoplankton pigment characterization (using HPLC) and flow cytometry, complemented by fluorescence microscopy and grazing experiments (Yentsch and Phinney, 1995; Garrison et al., 1998; and Brown et al., 1999). Nowadays, it has become reasonable to accept the significant contribution of pico /nanoplankton as primary producers in the nutrient - enriched systems. Given the fact that small phytoplankton are ubiquitous in marine environments (Yentsch and Phinney, 1995), the abundant MZP community in any environment may function as an important link between the smaller phytoplankton and large zooplankton. The present observation is in support of the above process being active in the nutrient - enriched inshore waters of the southwest coast of India, where the MZP appears to play an important functional role in mediating phytoflagellates biomass, to higher trophic levels. Although MZP grazing was not measured during the present study, their high occurrence (corresponding to that of phytoflagellates) indicates their functional relationship with the smaller phytoplankton cells. The short generation times of MZP enable them to respond rapidly to changes in food availability; thereby, exert an impact on phytoflagellates, through grazing. The tintinnids play exactly the same role in temperate waters during episodic blooms of *Phaeocystis*, where they vigorously graze on the motile cells (Admiraal and Venekamp., 1986; Stelfox - Widdicombe et al., 2004).

Information is limited on the abundance of phototropic pico/nanoplankton occurring in the upwelling areas of the Indian coast, basically in relation to: (a) the focus of the earlier works were on the large size classes of phytoplankton (diatoms and dinoflagellates) using light microscopy (Subrahmanian, 1959; Sawant et al., 1996); and (b) overlooking the small fractions, due to the practical difficulty in characterising pico/nanoplankton using light microscopy. Measurements using flow cytometry and phytoplankton pigment characterisation, supplemented by fluorescence microscopy, are some of the efficient methods to overcome these problems. A very recent study undertaken by Roy et al (2006), based upon HPLC measurement showed clearly the dominance of picoplankton and prymnesiophytes along the southern part of the west coast, during the late summer monsoon (Roy et al., 2006). Additionally, recent data available from the northwestern Arabian Sea suggest also that the upwelling areas sustain an abundant community of the smaller phytoplankton, during the late summer monsoon (Garrison et al., 1998; Brown et al., 1999, 2002). Therefore, further studies are necessary to understand the quantitative significance of pico and nanoplankton more clearly and, as such the possible role of MZP as an important grazer. Estimation of the size-fractionated phytoplankton community is another possibility, to improve our understanding on the quantitative distribution of smaller phytoplankton along the west coast of India.

The present study supports the recent observations in the upwelling regions of the Arabian Sea, that smaller phytoplankton also contribute significantly to primary production in the nutrient-enriched systems (Brown et al., 1999, 2002; Shalapyonok et al., 2001; and Roy et al., 2006). Therefore, the abundant MZP community may function as an import link between smaller phytoplankton and larger zooplankton, in any environment. Further, the active grazing activity of MZP, even during the period of upwelling, would be contributing significantly to the net plankton heterotrophy in the eastern Arabian Sea (as suggested by Sarma 2004). The active grazing by MZP on phytoplankton cells may possibly reduce the vertical fluxes of biogenic carbon, as observed in the western Arabian Sea (Landry et al., 1998; Buesseler, 1998). Since many of these recent understandings differs from our traditional scientific understanding, further research on these aspects are imperative, to verify the views described in this paper.

Conclusions

During the LSM period, river runoff and upwelling have caused high nutrient concentrations in the surface waters of the southwestern coast of India, supporting high phytoplankton abundance.

The phytoplankton community of the inshore locations, along the 10 and 13°N transects, was largely contributed to by green flagellates ($>10^{10}$ ind. m^{-2}) and, to a lesser extent, by small diatoms ($> 40^6$ ind. m^{-2}). This high abundance of phytoflagellates supported the exceptionally high abundance of two species of tintinnid ciliates (*Dadayiella ganymedes* and *Helicostomella subulata*). During the SIM, nutrients were scarce in the surface waters of the entire southeastern Arabian Sea with a nitracline, at 60m depth), as a consequence of strong stratification. The intense surface layer stratification during the period has caused low phytoplankton abundance, standing stock and productivity. This feature has favoured also the proliferation of *Trichodesmium erythraeum*, throughout a major part of the study area. Since the larger zooplankton are inefficient in cropping the smaller phytoplankton species (Marshall, 1973; Johnson & Sieburth, 1982), which are numerically dominant during the SIM period, the prevailing MZP community could play a vital role in transferring the primary organic carbon, from smaller phytoplankton to mesozooplankton. Further, this study also points towards the fact that MZP could function as an important grazer of phytoplankton, even in nutrient-enriched environments, if smaller phytoplankton are abundant.

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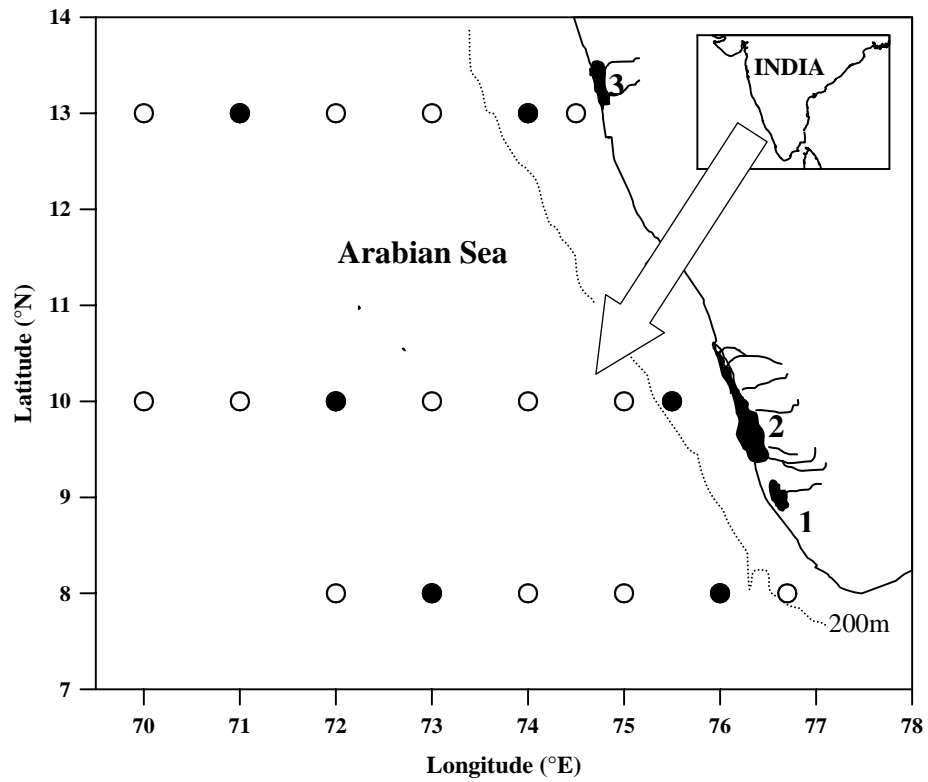


Figure1. Station locations. Filled circles indicate locations where physicochemical and biological measurements were undertaken. Open circle indicate locations where physicochemical data alone were collected. Locations 1, Ashtamudi estuary; 2, Cochin backwaters; and 3, Netravati – Gurpur estuary

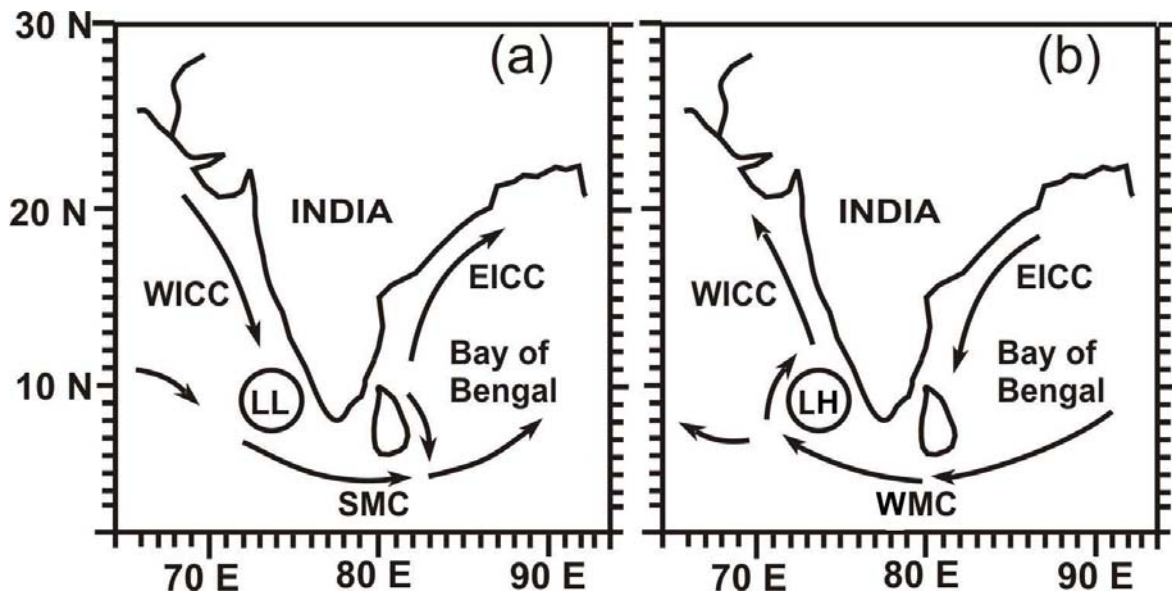


Figure 2. Schematic picture of the coastal current pattern in the Arabian Sea and Bay of Bengal, during: (a) summer monsoon; and (b) spring intermonsoon period (based on Sanilkumar et al., 2000 and Masson et al., 2005). Key: WICC –West Indian Coastal Current; LL – Lakshadweep Low; LH – Lakshadweep high; SMC – Summer Monsoon Current; EICC – East Indian Coastal Current; and WMC – Winter Monsoon Current

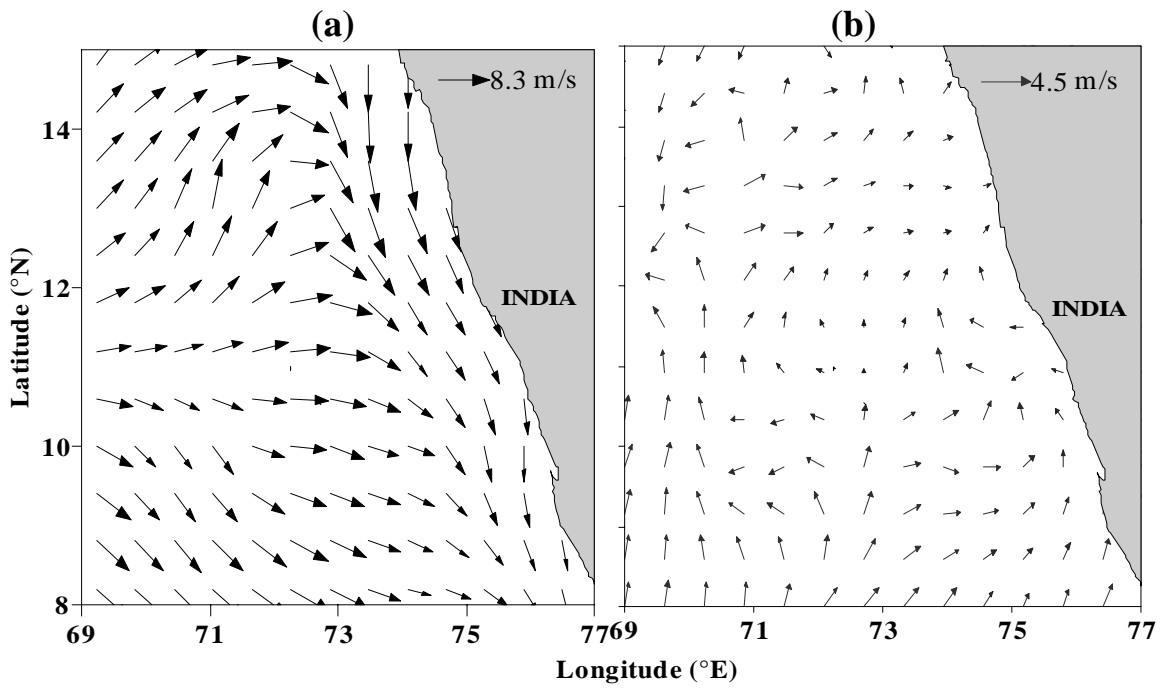


Figure 3. Wind pattern during; (a) late summer monsoon; and (b) spring intermonsoon periods

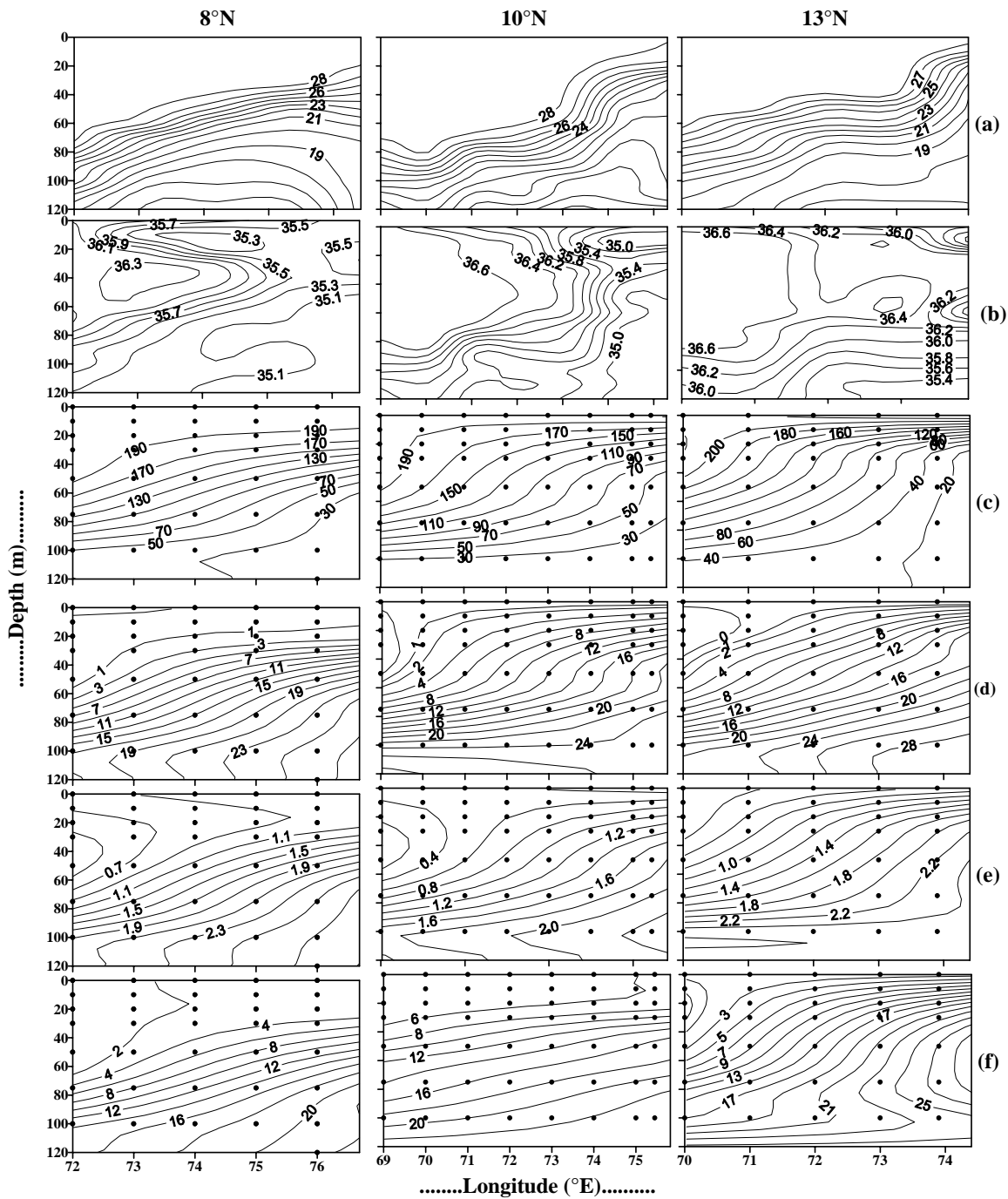


Figure 4. Vertical structure of (a) temperature ($^{\circ}\text{C}$) (b) salinity, (c) dissolved oxygen (μM) (d) Nitrate (μM) (e) Phosphate (μM) (f) Silicate (μM) along different transects during late summer monsoon. For transect locations, see Figure 1.

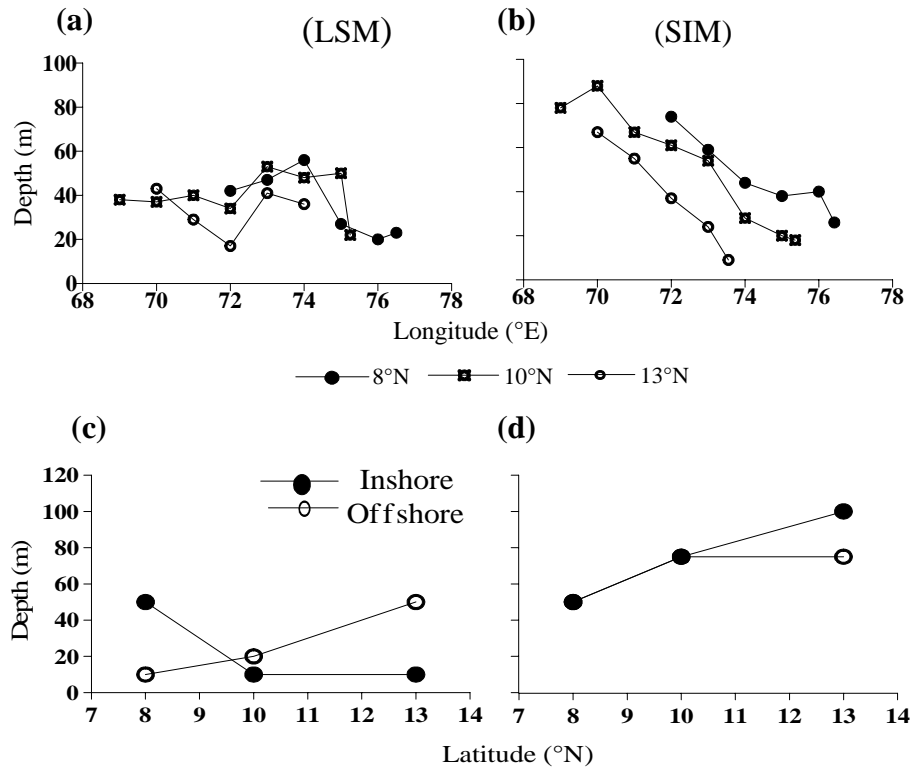


Figure 5. The variation of mixed layer depth (a & b) and the chlorophyll-*a* maxima (c & d)

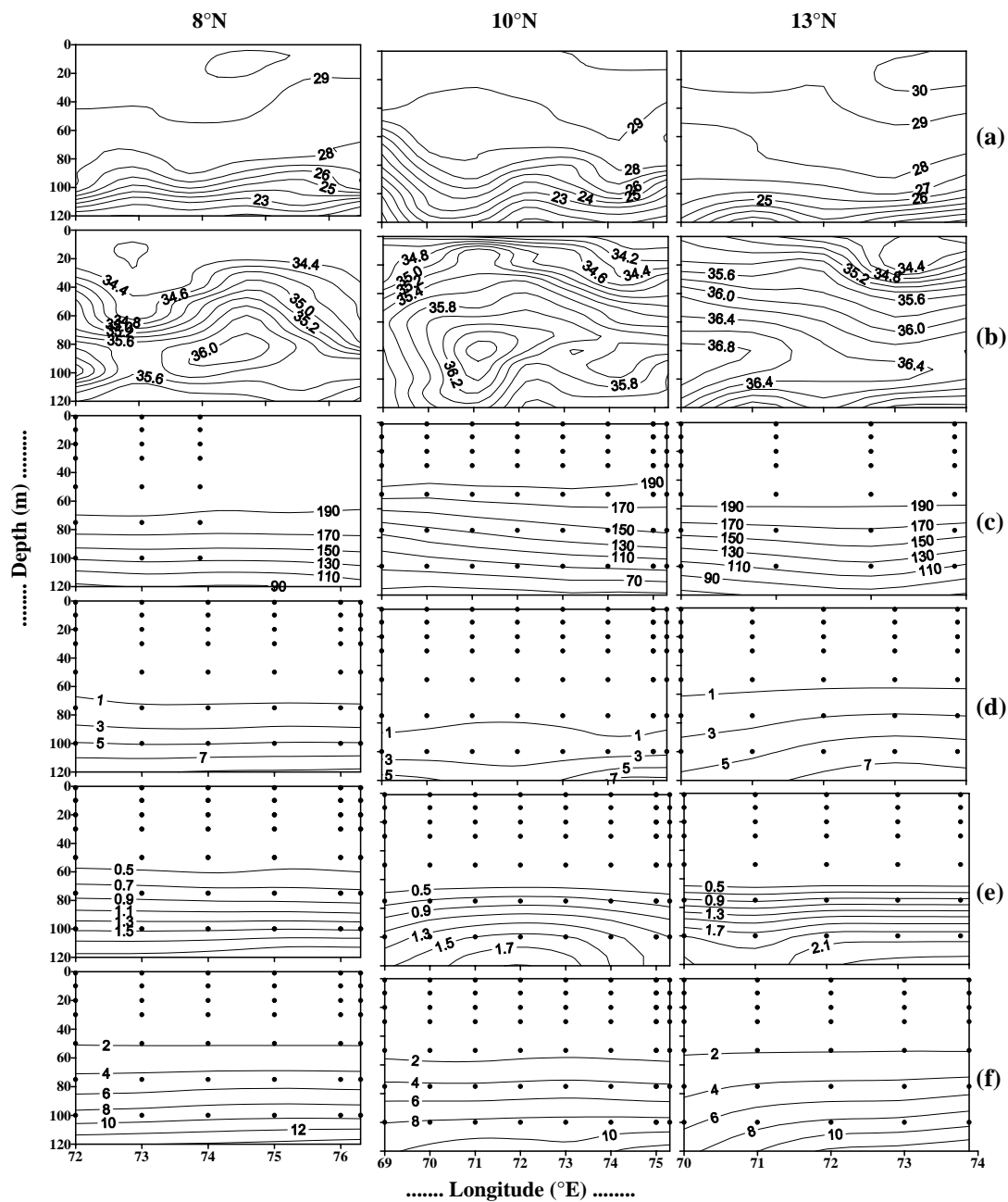


Figure 6. Vertical structure of (a) temperature ($^{\circ}\text{C}$) (b) salinity, (c) dissolved oxygen (μM) (d) Nitrate (μM) (e) Phosphate (μM) (f) Silicate (μM) along different transects during spring intermonsoon. For transect locations, see Figure 1.

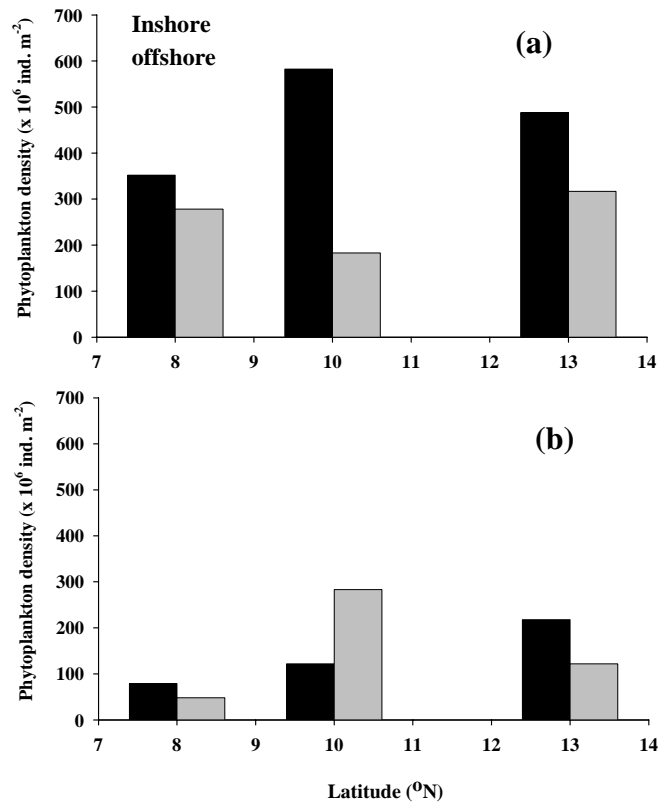


Figure 7. Phytoplankton abundance during (a) late summer monsoon (LSM) and (b) spring intermonsoon (SIM)

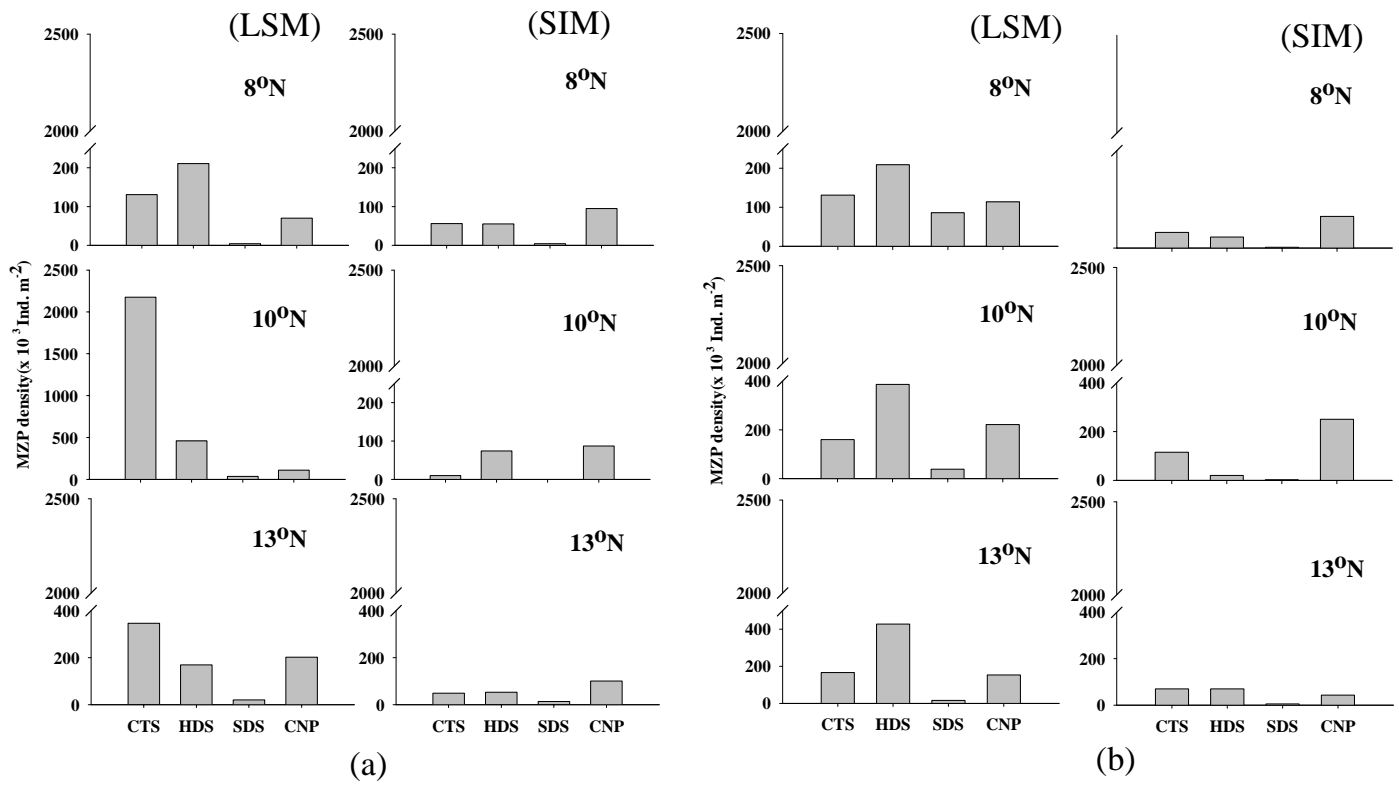


Figure 8. Abundance of major components of MZP during the late summer monsoon (LSM) and spring intermonsoon (SIM) periods, in the (a) inshore and (b) offshore regions

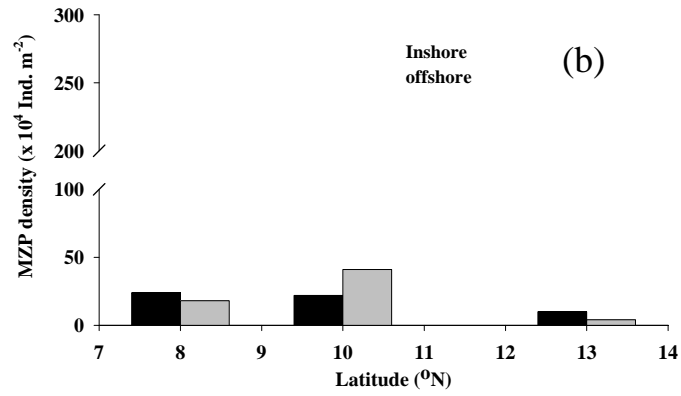
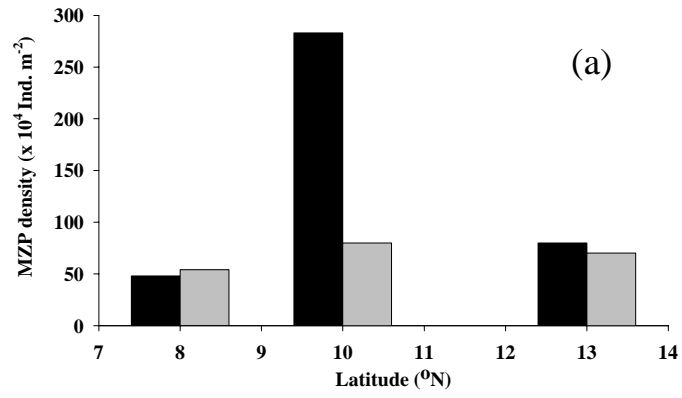


Figure 9. Abundance of MZP during (a) late summer monsoon and (b) spring intermonsoon periods

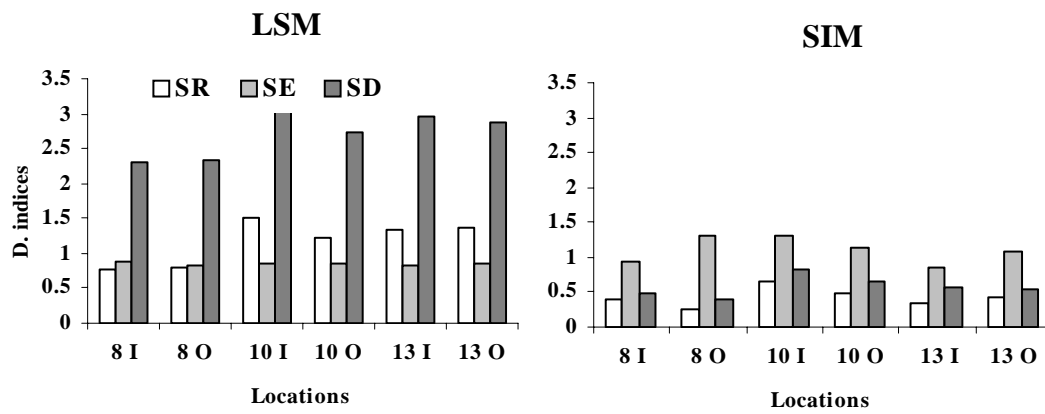


Figure 10 – Diversity indices of MZP during (LSM) late summer monsoon and (SIM) spring intermonsoon periods (SR – Species richness, SE – Species evenness, SD – Species diversity)

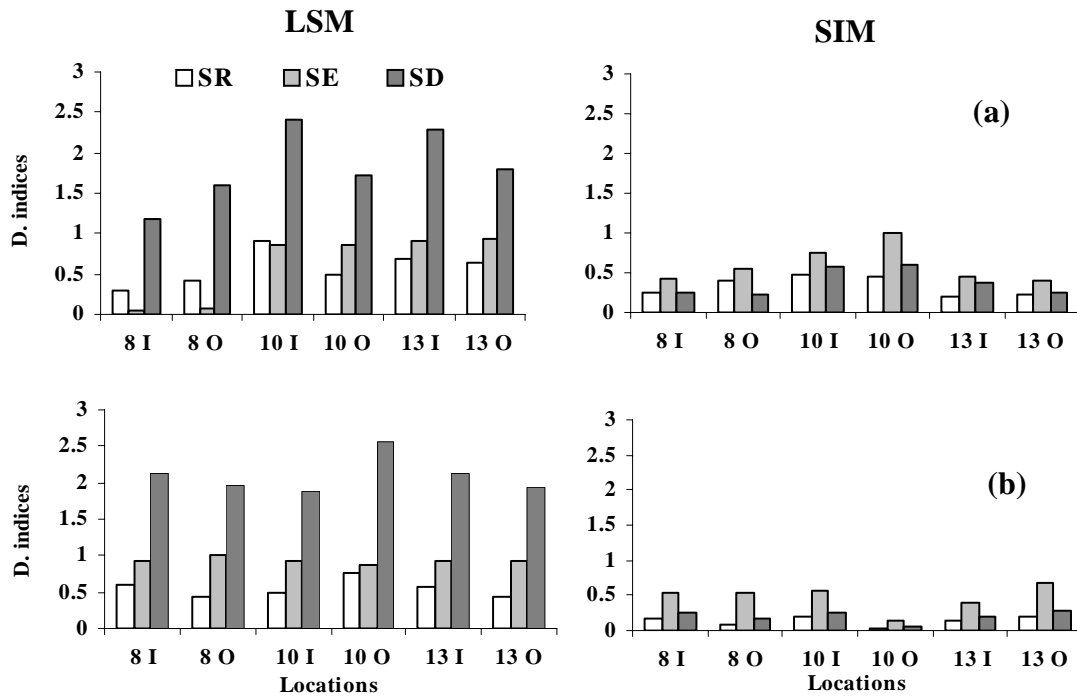


Figure 11. Diversity indices of (a) ciliates and (b) heterotrophic dinoflagellates (SR – Species richness, SE – Species evenness, SD – Species diversity). I – inshore; and O - offshore

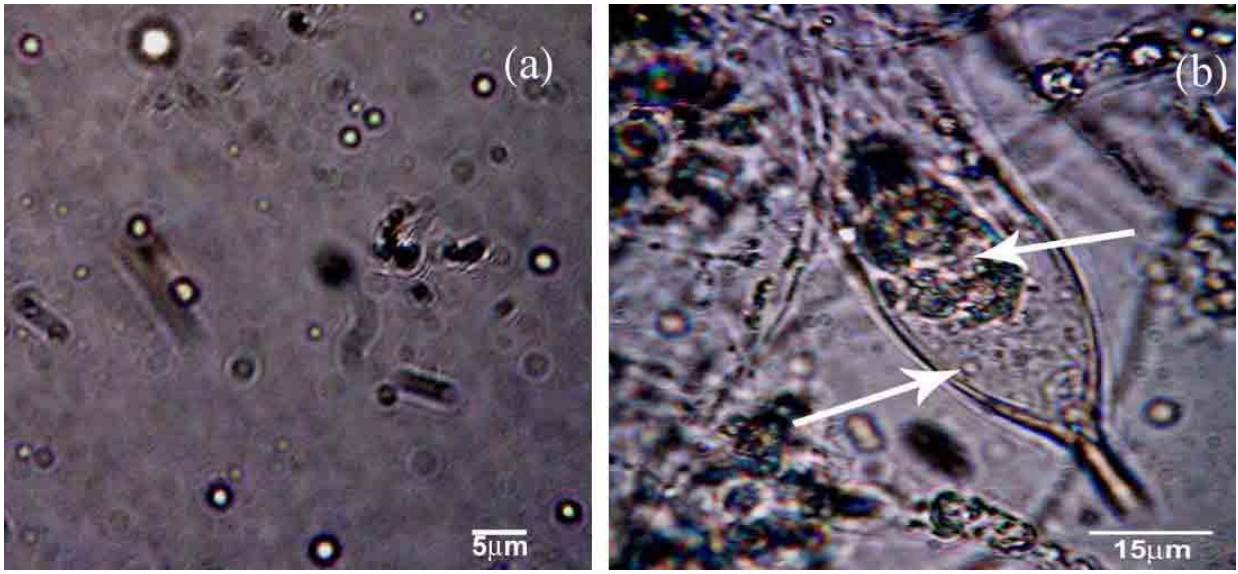


Figure 12 – Photomicrograph of the (a) phytoflagellates (b) phytoflagellate inside the body of the tintinnid

Latitude (⁰ N)	Chlorophyll- <i>a</i>				Primary production			
	Inshore		Offshore		Inshore		Offshore	
	LSM	SIM	LSM	SIM	LSM	SIM	LSM	SIM
8	31 (0.54)	5 (0.09)	30.8 (0.44)	10 (0.08)	568	74	376	169
10	61 (1.2)	10 (0.13)	41.5 (0.54)	15 (0.32)	1630	71	572	153
13	29 (1)	25 (0.32)	16.4 (0.22)	44 (0.50)	555	170	243	71

Table 1 – Chlorophyll-*a* (mg m^{-2}) and primary production ($\text{mgC m}^{-2} \text{d}^{-1}$), at the different stations. Chlorophyll-*a* maxima (mg m^{-3}) are shown in parentheses.

Species	8°N IS		8°N OS		10°N IS		10°N OS		13°N IS		13°N OS	
	LSM	SIM	LSM	SIM	LSM	SIM	LSM	SIM	LSM	SIM	LSM	SIM
<i>Dinophysis hastata</i>	+	+	-	-	-	+	+	-	+	-	-	-
<i>Gyrodinium sp.</i>	-	-	-	-	-	-	+	-	-	-	-	+
<i>Histioneis depressa</i>	-	-	-	+	-	-	+	-	-	-	-	-
<i>Ornithocercus magnificus</i>	+	+	+	+	+	+	+	+	-	+	+	+
<i>O. quadratus</i>	-	+	-	+	-	+	+	-	-	-	-	+
<i>O. steini</i>	-	+	-	+	-	+		+		+		+
<i>O. thumii</i>	+	+	-	-	-	-	-	-	-	+	-	+
<i>Phalacroma doryphorum</i>	-	-	-	-	+	-	+	-	-	+	+	-
<i>Phalacroma apicatum</i>	-	-	-	+	-	-	-	+	-	-	-	+
<i>Phalacroma rapa</i>	+	-	-	+	-	-	-	-	-	-	+	-
<i>Podolampus bipes</i>	+	-	-	-	-	-	-	-	+	+	-	-
<i>P. elegans</i>	-	+	-	-	+	+	+	-	-	-	-	-
<i>P. palmipes</i>	+	+	+	+	+	+	+	-	+	-	+	+
<i>P. reticulata</i>	+	-	+	-	+	-	+	-	-	-	-	+
<i>P. spinifera</i>	+	+	+	-	+	-	+	-	+	+	-	-
<i>Protoperidinium elegans</i>	-	-	-	-	-	-	+	+	-	-	+	-
<i>P. leonis</i>	-	-	-	-	-	-	-	-	+	-	+	-
<i>P. depressum</i>	-	-	-	-	+	-	-	-	+	-	-	-
<i>P. divergens</i>	+	+	-	+	+	+	-	-	+	+	+	+
<i>P. fatulipes</i>	+	-	-	-	-	-	-	+	-	-	+	-
<i>P. globulus</i>	+	-	+	-	+	-	-	-	-	-	-	-
<i>P. grande</i>	+	-	+	-	-	-	+	-	-	-	+	-
<i>P. nipponicum</i>	-	-	-	-	+	-	-	-	+	-	+	-
<i>P. oceanicum</i>	+	+	+	-	-	-	+	-	-	+	+	-
<i>P. ovum</i>	+	+	-	-	+	-	+	-	-	-	-	-
<i>P. pellucidum</i>	+	-	-	-	+	-	-	-	-	-	+	-
<i>P. pentagonum</i>	+	-	+	-	-	-	+	-	-	-	+	-
<i>P. tuba</i>	+	-	+	-	+	-	+	-	+	-	+	-
<i>P. claudicans</i>	+	-	+	-	-	-	-	-	+	-	+	-
<i>P. longipes</i>	+	-	+	-	-	-	+	-	+	-	-	-
<i>P. oblongum</i>	+	-	+	-	-	-	-	-	+	-	+	-

Table 2 – Distribution of HDS at different locations
(LSM – Late summer monsoon, SIM – Spring intermonsoon
+ indicate presence, - indicate absence, IS – inshore, OS – offshore)

Species	8°N IS		8°N OS		10°N IS		10°N OS		13°N IS		13°N OS	
	LSM	SIM	LSM	SIM	LSM	SIM	LSM	SIM	LSM	SIM	LSM	SIM
<i>Amphorella gracilis</i>	-	-	+	-	+	-	-	-	-	-	+	-
<i>A. quadrilineata</i>	-	+	+	-	-	+	-	-	+	-	+	-
<i>A. tetragona</i>	+	-	+	-	+	-	-	+	-	+	-	+
<i>Amphorides amphora</i>	-	-	-	-	+	-	-	-	+	-	+	-
<i>Ascambelliella obscura</i>	-	-	-	-	-	-	+	-	-	-	-	-
<i>Brandtiella pallida</i>	-	-	+	-	-	-	-	-	-	-	-	-
<i>Codonella acera</i>	-	-	-	-	-	-	+	+	-	+	+	-
<i>C. nationalis</i>	-	-	+	-	+	+	-	-	+	+	-	-
<i>Codonellopsis orthoceros</i>	-	-	-	-	+	-	-	-	-	-	+	-
<i>C. rotundata</i>	-	-	+	-	-	-	-	-	-	-	+	+
<i>C. tessellata</i>	-	-	-	-	-	-	+	+	-	-	+	+
<i>Cyttarocyclus vanhoeffini</i>	-	-	-	-	-	-	-	-	+	-	-	-
<i>Dadayiella ganymedes</i>	+	-	+	-	+	-	-	-	+	+	+	-
<i>Dictyocysta elegans</i>	+	-	+	+	+	-	+	+	+	-	+	-
<i>D. mitra</i>	+	-	-	-	+	-	-	-	-	-	-	-
<i>D. lepida</i>	-	-	-	-	+	-	-	-	-	-	-	-
<i>D. bulbosa</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Epipocyclus undella</i>	-	+	-	+	+	+	-	+	+	-	-	+
<i>E. reticulata</i>	+	+	-	-	+	-	+	+	-	+	-	+
<i>Eutintinnus elongatus</i>	+	+	-	+	+	+	-	-	-	-	+	+
<i>E. lusus undae</i>	-	-	+	-	-	+	-	-	-	+	+	+
<i>Favella brevis</i>	-	-	-	-	+	-	-	-	+	-	-	-
<i>Halteria sp.</i>	+	-	-	-	-	-	-	-	-	-	-	-
<i>Helicostomella subulata</i>	-	-	-	-	+	-	+	-	+	+	-	-
<i>Lohmaniella oviformes</i>	-	-	+	-	-	-	-	+	+	-	-	-
<i>L. spiralis</i>	+	-	-	-	+	-	-	-	+	+	-	-
<i>Parundella lohmani</i>	-	-	+	-	+	-	+	+	+	-	-	+
<i>P. messinensis</i>	-	-	+	-	-	-	-	-	-	-	-	-
<i>Petalotricha ampulla</i>	-	+	-	-	-	+	+	-	-	-	-	-
<i>Protorhabdonella simplex</i>	-	-	-	-	+	+	-	+	+	-	-	+
<i>Rhabdonella poculum</i>	-	-	-	+	+	-	-	-	-	-	-	-
<i>R. amor</i>	-	+	-	+	+	-	+	-	+	+	-	-
<i>R. spiralis</i>	+	+	+	+	+	+	-	-	-	+	+	+
<i>Salpingacantha ampla</i>	-	+	-	+	+	+	-	+	+	-	+	+
<i>S. undata</i>	-	-	+	-	-	-	-	-	-	-	+	+
<i>Salpingella acuminata</i>	+	+	+	-	+	+	+	-	+	-	+	-
<i>S. decurtata</i>	-	+	-	-	+	+	-	+	+	-	-	-
<i>S. gracilis</i>	-	-	-	-	+	-	-	-	-	-	+	-
<i>Steenostomella ventricosa</i>	+	-	-	-	-	-	-	-	-	-	-	-
<i>Steenstrupiella steenstrupii</i>	+	-	-	-	+	+	+	-	-	-	+	-
<i>Strombidium lagenula</i>	-	-	-	-	+	-	+	-	+	-	+	-
<i>Tintinnopsis mortensenii</i>	-	-	-	-	-	-	+	-	-	-	-	-
<i>T. radix</i>	+	-	-	-	+	-	-	-	-	-	-	-
<i>Undella globosa</i>	+	+	+	+	+	+	+	+	-	+	+	+
<i>U. hyalina</i>	-	-	-	-	+	-	-	-	+	-	+	-
<i>Xystonella treforti</i>	-	-	+	-	+	+	+	+	-	-	+	+

Table 3 – Occurrence of CTS species at different locations (IS – inshore, OS – offshore, LSM – summer monsoon, SIM – spring inter monsoon, + indicate presence, - indicate absence, IS – inshore, OS – offshore)

Samples	Source	Dof	MSS	F - Ratio
IS locations (LSM)	Locations (A)	2	7865370	9.33**
	Species (B)	78	2237530	2.65
	Depths (C)	6	4239820	5.03**
	AB interaction	156	1886060	2.24**
	BC interaction	468	864307	1.02
	AC interaction	12	3955890	4.69**
Error		936	843382	
OS locations (LSM)	Locations (A)	2	613795	4.21**
	Species (B)	78	415734	2.85**
	Depths (C)	6	115701	7.93**
	AB interaction	156	41089	2.82**
	BC interaction	468	36571	2.51**
	AC interaction	12	12900	0.88
Error		936	14589	
IS locations (SIM)	Locations (A)	2	5680	2.53
	Species (B)	51	10516	4.93**
	Depths (C)	6	9982	4.68**
	AB interaction	102	3069	1.44
	BC interaction	306	3471	1.63**
	AC interaction	12	3043	1.43
Error		612	2134	
OS locations (SIM)	Locations (A)	2	18466	2.02
	Species (B)	32	16050	3.34**
	Depths (C)	6	13438	4.79**
	AB interaction	64	5840	1.21
	BC interaction	192	9284	1.89**
	AC interaction	12	6392	1.33
Error		384	4807	

Table 4 - 3 way ANOVA for MZP abundance between stations, between species and between depths. Key: IS – Inshore; OS – Offshore; Dof – Degree of freedom; MSS – Mean sum of squares; and ** Significant at 1% level.