Chapter 8

Discussion

Bay of Bengal (BOB), the northeastern part of the Indian Ocean is completely separated from the northwestern part, the Arabian Sea (AS) by the Indian peninsula. Between these two basins, Arabian Sea is one of the most productive regions of the world ocean (Ryther et al., 1966) and the physical and chemical forcings, which drive Arabian Sea production, is now fairly understood. The main attributes, which enhance the productivity of the area, are the coastal and open ocean upwelling during summer monsoon and the surface cooling in the northern Arabian Sea during winter (Madhupratap et al., 1996; Bhattathiri et al., 1996; Nair et al., 1999). These bring in higher amount of nutrients in to the upper ocean, which enhance the phytoplankton biomass and productivity of the Arabian Sea. Interestingly during spring intermonsoon mesozooplankton biomass remains unchanged although the phytoplankton biomass and primary production remains low in the AS. This peculiar phenomenon (Arabian Sea Paradox) was explained by understanding the microbial food web (microbial loop) that enhances the productivity during intermonsoon (Madhupratap et al., 1996; Ramaiah et al., 1996; Mangesh et al., 1996).

In contrast to the AS, most of the earlier studies in the Bay of Bengal depict it as a low productive system all through the year. The possible reasons suggested by the earlier researchers for the low phytoplankton biomass and PP in the BOB were the unavailability of nutrients in the upper layers due to stratification, heavier cloud coverage and turbidity arising from sediment fluxes that limit effective penetration of solar radiation in the upper euphotic column (Radhakrishna et al., 1978 a&b; Qasim, 1977; Gomes et al., 2000; Prasanna Kumar et al., 2002; Madhupratap et al., 2003). The field observations where further supported by the chlorophyll $a$ distribution in the BOB derived from observations by satellites (Sea WiFS), which showed very low chlorophyll $a$ values (Gomes et al., 2000 and Prasanna Kumar et al., 2002). The most recent study, during summer monsoon
(recall that during this season column primary production in the southwest coast increases up to 2000 mgC m\(^{-2}\) due to upwelling) in the BOB by the JGOFS - India group observed PP values between 328 - 520 mgC m\(^{-2}\) d\(^{-1}\), which was comparable with the primary productivity of the AS during spring intermonsoon which is relatively oligotrophic period (Madhupratap et al., 2003). Compared to AS, literature available on different biological aspects of the BOB are less and a comprehensive approach to explain the oligotrophy of BOB in particular is scanty. The preceding findings that discussed the general understanding on the hydrography and productivity of the twin Seas (AS and BOB), which are supportive to infer the results obtained during the present study from the Bay of Bengal during different seasons.

7.1. Physicochemical environment

7.1.1. Winter monsoon

During winter monsoon, distribution of sea surface temperature (SST) showed marked latitudinal variations with maximum (29.2\(^{o}\)C) in the southernmost transect and minimum in the northernmost transect (20.5\(^{o}\)N). This was apparently due to the increasing intensity of winter towards north. Atmospheric cooling during winter is a common phenomenon in the northern Indian Ocean and its intensity increases towards north (Hastenrath and Lamb, 1970). Sea surface salinity showed clear coastal – offshore variations where low saline waters (<30 psu) prevailed along the entire coast. This was mainly due to the high freshwater discharge from various rivers in to the bay from Indian peninsula. Minimum values of SSS was observed at the coastal stations along latitudes 15, 19 and 20.5\(^{o}\)N. These areas are considerably influenced by the Krishna (near 15\(^{o}\)N) and Ganges - Mahanadi (19 and 20.5\(^{o}\)N) river discharges. Emptying of the major rivers of India in to the Bay of Bengal and its consequences on the physical characteristics of coastal waters of the Bay of Bengal were well reported. The stratification due to freshwater influx could be noticed even at a depth of 100m over most of the shelf areas of the Bay of Bengal (Suryanarayana, 1988). During the present study, fluctuations of mixed layer depth were mostly corresponding to the intensity of salinity stratification.
Generally higher MLD was observed in the oceanic regions where relatively high saline surface waters were present. On the other hand northern regions (19°N and 20.5°N) apparently had low MLD due to strong salinity gradients in the surface layers along these transects. The vertical salinity structure in the upper layers showed clear frontal structures (2-5 psu gradients in the upper layers) towards the coast especially along the transects which were near to the river mouths and was a clear evidence of the river discharge into the Bay. Higher attenuation coefficient (low transparency) during the season along the coastal transect was due to the high suspended and particulate materials derived from the heavy river discharge. The transparency of the water column along the east coast of India varies greatly from season to season depending on the land runoff and associated suspended load and the Bay of Bengal receives about $16 \times 10^8$ tonnes of silt annually through river discharges, which considerably increase the turbidity of the water column (Suryanarayana, 1988).

During the winter monsoon season, the cold dry air (humidity <45%) from the continents blown over northwestern BOB and thus the atmospheric conditions were favorable for cooling of surface waters and the resultant winter convection. But the heat loss in the surface waters by the atmospheric cooling does not trigger convective overturning in the Bay. The low saline surface layers attains low temperature due to atmospheric cooling but fails to impart it to the deeper waters due to the lack of sinking. This ultimately results in strong thermal inversion and stratification. The low saline waters compensate the static stability loss by the atmospheric cooling, which ultimately result in the absence of winter convection. In the northwestern BOB, thermal inversions of varying magnitude is a known feature and studied by many oceanographers (Sankaranarayana & Reddy, 1968; Rao & Sastry, 1981; Suryanarayana et al., 1993 and Pankajakshan et al., 2002).

Another significant feature observed along the western Bay was the subsurface cold core eddy with high salinity, nutrient, and low dissolved oxygen waters, which was mostly intense below the surface layers. The eddy signatures were more prominent in the middle stations of the study area and along these
stations 1 μM contour of nutrients (nitrate and silicate) was found at relatively shallower depths (~40m) compared to coastal and oceanic stations. The mechanism, which generates the cyclonic eddy, is thought to be the circulation pattern. In November, by the onset of northeast monsoon the Bay of Bengal has a basin wide cyclonic circulation pattern (Eigenheer et al., 2000) with equator ward East Indian Coastal Current (EICC).

Introduction of fresh water in to the BOB reduces the mixed layer, led to the formation of halocline and a thick barrier layer (Rao et al., 1989). The formation of barrier layer in the BOB restricts the ocean – atmosphere interaction leading to the thin mixed layer and thus restricts the upward transport of nutrients. In the present study nutrients were found below 40m, which indicate the influence of stratification on vertical distribution of nutrients. The barrier formation was more pronounced in the northwestern BOB during summer and winter due to the increased fresh water influx during the periods (Rao et al., 1989).

7.1.2. Spring intermonsoon

Spatial variability of SST was minimum during the season and that could be directly linked to the maximum solar radiation available during the period. SST distribution during the period is indicative of the warming of the surface waters between winter and summer (Varkey et al., 1996). Contrasting to the other season SSS distribution showed peculiar pattern in the surface layers due to the influence of circulation. During the season relatively high saline waters were present in the coastal regions and pockets of low saline waters were found about 200 – 400km away from the coast. This was due to the strong East Indian Coastal Current (EICC), which flows poleward during the season and pushes the low saline waters away from the coast. Furthermore relatively less volume of freshwater reaches the southeast Bay during the season due to the lean discharge from the adjoining rivers. The anticyclonic circulation pattern with pole ward flowing EICC during spring intermonsoon is a well-known feature in the western Bay (Murty et al., 1968; Shetye et al, 1991; Sanil Kumar et al., 1997). Shetye et al., (1993) reported a warm water recirculation zone in the offshore region of the Western Boundary Current.
(WBC) and cool water eddy like structure in the coastward direction of this boundary current. These studies projected pole ward flowing western boundary current as the net effect of the local and remote forcing. Warm and low saline waters in the oceanic regions provide stratified surface layers and this was the reason for the shallow MLD observed along most of the oceanic regions. Strong stratification leads to the absence of nutrients in the surface layers and inhibit surfacing from deeper waters. During the present study nutrients (nitrate, phosphate, silicate) were found at relatively deeper depths (below 50m) due to stratification. The vertical thermal structure along 17°N exhibited warm surface isothermal layer, below which it exhibits gentle down curving of isotherms centred around 85°E (Fig. 3d). This feature is peculiar of a subsurface warm core eddy more conspicuous at 150m. Pockets of low silicate and phosphate at 75m depth along 15 – 17°N were confirmative of subsurface warm core eddy.

1.3. Summer monsoon

Warmer sea surface temperature was observed during the season and was comparable to the spring intermonsoon. Sea surface salinity showed marked north south variability. Relatively high saline waters (>33.5psu) was present in the south east coast, where as the north east coast had relatively low salinity and the lowest value of 25psu was observed near the coast along 20.5°N. Similar to SSS distribution MLD generally showed north – south gradients and along the south east coast it was relatively thicker (30 - 60m). The latitudinal difference in salinity during the season was due to the difference in the amount of monsoonal rain and the river water reaching in to the BOB. Northeast coast of India gets maximum rain fall during summer monsoon and the rivers in the region bring enormous quantity of fresh water and sediments that empty in to the Bay of Bengal (Ramage, 1984 and Suryanarayana et al, 1991) which reduces the surface salinity and transparency of the water column. The salinity stratification in the surface is the reason for the observed low MLD in the northern region.

Signatures of upwelling such as relatively colder waters at the surface layers, shallow mixed layer and nitracline (upsloping of isolines) near to the coast were
observed along 15°N. The prevailing southwesterly winds during the season give rise to southeastward Ekman transport at the surface and this could be the reason for the observed upwelling processes along 15°N. During the present observation upwelled waters remained as a narrow band, which strongly supports the earlier observation by Shetye et al., (1993). However along the southeast coast of India, the upwelled waters were confined below 75m (subsurface upwelling). In general the most important reason proposed for the lack of intense upwelling along the east coast such is the river discharge in the northwestern BOB that makes equator ward flow along the east coast and overwhelm the upwelling processes (Gopalakrishna & Sastry, 1985 and Shetye et al., 1991).

7.2 Biological environment

7.2.1. Winter monsoon

Vertical and horizontal distribution of chlorophyll a and PP in the BOB during different season showed similarity to the observations by many earlier researchers (Gomes et al., 2000 and Madhu et al., 2001). During winter monsoon, surface chlorophyll a varied from 0.01 – 0.2 mg m\(^{-3}\) and in most of the stations maximum phytoplankton biomass was in the upper 50m water column. Maximum column chlorophyll a (16 mg m\(^{-2}\)) was found at the middle station along 15°N. This latitudes were influenced by a subsurface cold core eddy, which was centered around 15°N, 84°E and the signatures were evident up to 40m depth. However in other latitudes (11, 13, 17, and 19°N) the eddy signatures were found at much deeper depths and hence could not influence the biology of the upper euphotic column. Subsurface eddies in the Bay of Bengal were reported earlier by Swallow (1983) and Babu et al., (1991). Normally, eddies lead to an enhancement of biological production through the rectified upwelling of nutrients (McGilligcudy & Robinson, 1997 and Oschiles & Garcon, 1998). In addition the eddy transfer heat which results in shallowing of mixed layer which in turn can lead to bloom through biota experiencing more light (Levy et al., 1999). But this is particularly significant when upwelled nutrients are available in the surface layers.
During the season, primary production at the surface waters varied from 1 – 10.5 mgC m\(^{-2}\). Maximum primary production was found at the coastal station along 15\(^{\circ}\)N where the cold core eddy signatures were present and maximum average primary production also was along 15\(^{\circ}\)N. Here the eddy signatures were found at relatively shallower depth and were prominent up to 40m depth along this transect. Maximum average primary production value was present along 15\(^{\circ}\)N where cold core eddy signatures where prominent at relatively shallow depth. But the enhanced biological production observed in the present study at the location of the eddy (16 mg m\(^{-2}\)) was moderate compared to the other productive regions of the Indian Ocean like the upwelling regions of the west coast (88 mg m\(^{-2}\)) and winter convective regions (34 mg m\(^{-2}\)) of the northwest coast of India (Bhattathiri et al., 1996). The moderate level of biological production may due to the fact that the eddy was prominent in the subsurface waters, which could not bring considerable amount of nutrients in to the surface waters (upper euphotic column) where sufficient amount of solar radiation is present. Vertical distribution of PP during the season showed higher values below the surface (10m depth) in most of the stations. This observation overrules the opinion of Qasim (1977) that through out the year maximum primary productivity in the Bay of Bengal is seen at the surface due to the lack of photo inhibition. Average mesozooplankton biomass during the period was maximum (776 mgC m\(^{-2}\)) among different seasons. During the study, maximum zooplankton biomass was found in the southern region and that could be due to the relatively higher primary production and chlorophyll \(a\) biomass existing in the region during the season. Higher average zooplankton biomass observed in the coastal stations along the southern region and that might be due to the river water plumes as suggested by Madhupratap et al., (1993).

### 7.2.2. Spring intermonsoon

It is interesting to note that during inter monsoon spring, chlorophyll \(a\) at the surface varied from 0.01 – 0.03 mg m\(^{-3}\), which is relatively lower than the other two seasons and this could be mostly due to the strong and extended stratification in the surface layers during the season. Chlorophyll \(a\) data derived from satellite
presented by Gomes et al., (2000) clearly indicated very low concentration in the offshore regions of the BOB. Except along 20.5°N, chlorophyll a concentration was relatively less and the maxima found were at deeper depths (50 – 75m). Gomes et al., (2000) presented almost similar seasonal vertical distribution pattern of chlorophyll a and he found subsurface chlorophyll (SCM) maxima at 60 – 80 m depth during inter monsoon spring especially in the offshore stations and the measurements using radiometer clearly indicated that effective solar radiation during inter monsoon spring was optimum compared to the other two seasons. Murty et al., (2000), also found subsurface chlorophyll maxima at 50 – 100m depth during the period in the offshore regions of the study area. Latitudinal variations of chlorophyll a and primary production were minimum during the season, which further indicate the lack of strong physical processes that could alter the stratification of the surface waters. Primary production values at the surface varied from 1-12.3 mgC m⁻³ d⁻¹. Like winter monsoon, upper 20m water column had maximum primary production.

In general, during inter monsoon spring zooplankton biomass was considerably less in the entire study area (Avg. 406 mgC m⁻²) and this could be explained by the hypothesis by Cushing (1989) and subsequently supported by Yentch and Phinney., (1989 and 1995) based on the observations on the seasonal variations in the cell size of phytoplankton from the tropical regions using Flow cytometry. They proposed that in strongly stratified water column, phytoplankton with smaller cell size contribute majority of the standing stock and is important in tropical regions including northern Arabian Sea (Yentch and Phinney, 1995). This hypothesis has particular significance in Bay of Bengal due to the oligotrophic nature around the year as result of stratification, which is maximum during spring inter monsoon. This was clearly indicated in the vertical distribution of physical and chemical parameters during the present study. Hence majority of phytoplankton in Bay of Bengal during spring intermonsoon could be contributed by smaller sized phytoplankton.
The observations of Marshall (1973) that copepods and other zooplankton are unable to crop the smaller sized algae efficiently point out the intermediate role played by the microzooplankton in transferring primary biomass to mesozooplankton (Pathway 2). When considering the trophic transfer efficiencies of Cushing (1975), the energy, which transferred from primary level to the mesozooplankton, is less in Pathway 2 compared to Pathway 1. Hence it can be hypothesized that due to strongest stratification during spring intermonsoon, Pathway 2 may be dominant over pathway 1 and hence less amount of primary energy reaches mesozooplankton and this could be the reason for the low mesozooplankton biomass during the period.

7.2.3. Summer monsoon

During summer monsoon, chlorophyll $a$ at the surface was relatively higher and varied from 0.09 - 0.8 mg m$^{-2}$ and higher concentration was found in the surface layers and below 20m there was a decrease with increasing depth. Gomes et al (2000) found nearly a five-fold increase in offshore chlorophyll $a$ value
compared to the intermonsoon spring. During the season, maximum column chlorophyll $a$ was found along 15°N where upwelling was found towards the coastal region. During the season, maximum surface production varied from 1 – 45.8 mgC m$^{-3}$ d$^{-1}$ and maximum (45.8 mgC m$^{-3}$ d$^{-1}$) was found at the coastal stations along 19°N. Column production also was maximum (556 mgC m$^{-2}$ d$^{-1}$) at the coastal station along 19°N followed by the coastal station along 15°N (470 mgC m$^{-2}$ d$^{-1}$). It is interesting to note that the column chlorophyll $a$ maximum and primary production maximum did not exactly match each other. Gomes et al., (2000) observed similar situations along the upwelling stations of the Bay of Bengal and this anomalous feature could be due to the limitation of light. During the season, higher primary production was found in the surface layers and below 20m there was a marked decrease. In the northern region (from and north of 15°N) all the stations showed maximum PP at the surface.

The phytoplankton standing stock and primary production observed at the location of upwelling during the present study (45.8 mg m$^{-3}$ and 470 mgC m$^{-2}$ d$^{-1}$ respectively) was considerably lower than the upwelling regions of the Arabian Sea during the same period (88 mg m$^{-3}$ and 1760 mgC m$^{-2}$ d$^{-1}$) (Bhattathiri et al., 1996). This indicates that the intensity of upwelling and its manifestations on biological productivity is considerably less along the east coast of India compared to the Arabian Sea.

The lack of deep subsurface chlorophyll $a$ maxima during summer and winter monsoon could be due to the limitation of light on phytoplankton growth and production. Light limitation may partly due to the thick cloud coverage and increased suspended sediments through river discharge during the season. During the present study the mean attenuation coefficient of the water column during summer (0.084) and winter monsoon (0.070) were considerably higher than spring intermonsoon (0.048) when BOB is under optimum illumination by solar radiation illuminated by optimal solar radiation. The effect of light as a limiting factor on phytoplankton growth in the BOB had been the subject of discussion even in the past. Qasim (1977) suggested that intense cloud cover over the BOB might explain
the absence of photo inhibition at the surface. Similar findings were discussed by Radhakrishna et al. (1978 a & b) and they reported maximum productivity at the surface compared to the other depths sampled in the euphotic zone, which indicated the absence of photo inhibition at the surface waters. They also reported reduced euphotic zone in the inshore areas of BOB that ranged from 6 – 40 m and 40 – 75m in the offshore during summer monsoon, indicating the extend of light limitation during the season. In the present study also euphotic zone showed considerable variations during different seasons. Average coastal and offshore euphotic zone depths were considerably lower during summer monsoon and this was maximum during spring intermonsoon. Gomes et al., (2000) and Madhu et al., (2001) showed the lack of deep subsurface chlorophyll a maximum during summer and winter monsoon in the BOB. Similar to the present study, their study showed maximum chlorophyll a at much shallower depths during winter and summer monsoon (generally with in the upper 50m water column). Gomes et al., (2000) also calculated the primary production per unit chlorophyll a (mgC mg Chl a⁻¹ d⁻¹) and found that it was lower during summer and winter compared to spring intermonsoon. The surface irradiation measurements using radiometer clearly indicated that effective solar radiation during summer and winter monsoon is lower than intermonsoon spring. Average mesozooplankton biomass during the season was 676 mgC m⁻² and relatively higher biomass was found in the northern region and this could be due to the influence from river water plumes as suggested by Madhupratap et al., (1993) and Parson & Kessler (1986).

7.3. Microzooplankton

7.3.1. Biocomposition

During the study, microzooplankton community was composed of both protozoans and some larval stages of invertebrate metazoans. Protozoans were the most dominant group in terms of abundance and biomass. Protozoans present in the samples were heterotrophic dinoflagellates, ciliates, acantherians, radiolarians and foraminifers. Among these protozoans, heterotrophic dinoflagellates and ciliates were the most common and the individual contributions of sarcordines
(radiolarians, acantharians and foraminifers) were minor. Mangesh et al., 1996 & Mangesh, 2000) found a similar biocomposition for the microzooplankton community in the northern Arabian Sea.

Heterotrophic dinoflagellates were the most abundant group of organisms, which contributed maximum in the microzooplankton community irrespective of the seasons. Its percentage contributions to the total abundance of microzooplankton ranged between 62 and 77%, 48 and 75% and 57 and 73% during winter, inter and summer monsoon respectively. Maximum average contribution of dinoflagellates was during winter (69%) followed by summer (65%) and the least (60%) during inter monsoon season. Earlier Mangesh et al., (1996) and Mangesh (2000) found that the heterotrophic dinoflagellates were the most dominant organisms contributing up to 64% of the community but he did not address the taxonomic composition of this important group. He expressed the need for including this important group in future studies of microzooplankton from these regions. Information is also available on the importance of heterotrophic flagellates as a major component of microzooplankton from the other parts of the world ocean. Earlier work on microzooplankton has shown that heterotrophic dinoflagellates form 40% to 70% of the total standing stock in the coastal regions of northern Atlantic Ocean (Gaines and Elbrachter, 1987; Hansen, 1991a) and subtropical waters (Lessard, 1991). In the review on this group, Lessard (1991) calculated that heterotrophic dinoflagellates accounted for 22 – 67 % of the protozoan biomass in the subtropics and 75 – 97 % in polar waters. The present observations in which heterotrophic dinoflagellates found between 48 and 75% compromises with Lessard’s data and slightly higher than the data reported in Arabian Sea (Mangesh, 2000). Similar ranges were also recorded by Burkill et al., (1993a) in northeastern Atlantic Ocean, which varied between 50 and 75%. This in turn suggests that the relative contribution of heterotrophic dinoflagellates to the protozooplankton may become progressively important in higher latitudes and open tropical waters although this may not be the case in estuaries (Mangesh et al., 1996). In the present study, altogether 12 genera and 57 species of heterotrophic dinoflagellates were
identified and the photomicrographs are presented as Plates and are first of its kind from the Indian waters. *Dinophysis*, which instead attaches a peduncle to the ciliate and its karyosomes, is a member of the Centropyxis group. The ciliate *Dinophysis*, which instead attaches a peduncle to the ciliate and its karyosomes, is a member of the Centropyxis group.

During the present study on microzooplankton it was found that the dinoflagellates contributed about 65% of the total numerical abundance. However, no serious attempts have been made to discuss their mode of nutrition and its ecological advantage. Considering the relatively high numerical abundance of the study area, it will be worth discussing on the different modes of nutrition of this group. Bay of Bengal often reported to be a low productive system is considered in this context. Organisms that are able to withstand or overcome the oligotrophic condition may possibly have a better chance of survival in these regions. Most of the oceanic dinoflagellates are colourless heterotrophic forms (Taylor *et al.*, 1987). Recent studies on heterotrophic dinoflagellates showed that they could use numerous specialized mechanisms for heterotrophy (reviews by Kimor, 1981; Gains and Elbrachter, 1987; Hansen, 1991a; 1992; Lessard, 1991). In addition to uptake of dissolved organic substances (Droop, 1959 a & b; Lee, 1977; Morril & Loeblich, 1979) there are at least three types of dinoflagellate phagotrophy (uptake of particulate food). Some dinoflagellates ingest entire cells, resulting in prey organisms (often other dinoflagellates) being visible inside of, and digested with in the predatory dinoflagellate (Norris, 1969; Smetacek, 1981; Uhling and Sahling, 1990; Strom & Busky., 1991; Nakamura *et al.*, 1992). Other dinoflagellates exude an extracellular pseudopodial pallium, which captures diatoms and other prey outside the dinoflagellate cell (Jacobson & Anderson, 1986). Prey is often larger than the dinoflagellate predator, but they are digested extracellularly with prey cell contents transported through the membranous pallium to the dinoflagellate (Gains and Taylor, 1984). A third type of dinoflagellate heterotrophy is where prey cell contents are sucked out through an extruded peduncle (feeding tube), which the dinoflagellates attach to the prey (Spero & Moree, 1981; Spero, 1982; Hansen, 1991b). In the case of two heterotrophic species of the dinoflagellates genus *Dinophysis* (Hansen, 1991b), the dinoflagellate can attach a peduncle to the ciliate *Tiarina fuscus* which itself feeds up on autotrophic species of Dinophysis by
engulfing them. In an apparent case of mistaken identity, the ciliate attempts to ingest the heterotrophic *Dinophysis*, which instead attaches a peduncle to the ciliate and kill it by vaccuming out its cell contents. Thus, the initially predatory ciliate becomes the prey of the dinoflagellates it tried to eat. In another example of dinoflagellate predation up on ciliates, Bockstahler and Coats (1993) found that three species of red tide forming dinoflagellates from the Chesapeake Bay are frequent predators of oligotrichs and other ciliates, diatoms and other dinoflagellates. Perhaps, the most interesting example of dinoflagellate heterotrophy yet revealed is that of an undescribed "phantom" dinoflagellate from estuarine waters of North Carolina (Burkholder *et al.*, 1992). These dinoflagellates remain encysted in sediments until live fish or fish excreta are present. The dinoflagellates then excyst as motile photosynthetic vegetative cell that kills fish with powerful toxins. While doing so it completes its sexual cycle, with gametes encysting and sinking back to the sediments after fish are no longer present. However, while still in the ephemeral motile stage, the dinoflagellates extrudes a peduncle which it uses to feed on bits of sloughed off tissue from dead or dying fish.

There are other reports of dinoflagellate predation up on metazoans, or at least their reproductive products. Dinoflagellate of the genus *Noctiluca* is well-known phagotrophic predators of phytoplankton and microzooplankton (Anderson & Sorensen, 1986 and Elbrachter, 1991), and they also ingest copepod eggs (Kimor, 1979 and Daan, 1987). In some cases it has been estimated that half to three fourths of the reproductive output of a copepod population was consumed by *Noctiluca* (Sekiguchi & Kato, 1976 and Daan, 1987). Since copepods are among the most frequent predators of dinoflagellates, it is ironic that a dinoflagellate may be a major predator up on the progeny of its most likely predator. From the above discussion it becomes obvious that the dinoflagellate can feed on a variety of organisms including bacteria, phytoplankton, heterotrophic protists and even metazoans and this could enable them to become abundant and ubiquitous protists in marine environments. Furthermore many of the dinoflagellates can live by
establishing symbiotic associations with cyanobacterial cells called ‘phaeosomes’ (Taylor, 1982 & 1990). This diverse mode of nutrition of dinoflagellates may be the reason for their higher abundance in the study area. It is felt that the role of advantageous modes of nutrition discussed in the present study for the abundance of dinoflagellates in the Bay of Bengal merit more detailed studies targeting its ecological significance.

In the present study, ciliates were the second dominant group of organisms in the samples. Its percentage contribution varied 4 - 33%, which was close to the ranges obtained from off southern California (18 – 32%, Beers and Stewart, 1967; 1970) and lower than Northern Adriatic (12-52%, Revelante and Gilmartine, 1983). However, Mangesh et al., (1996) showed relatively higher contribution of ciliates (24 – 58%) during his studies in the Arabian Sea and that could be due to the higher phytoplankton standing stock in the Arabian Sea. Leaky et al., (1996) found a general relationship between ciliate biomass and phytoplankton biomass in the Arabian Sea and he explained that many ciliates are herbivorous, feeding on both cyanobacteria and algae (Pierce & Turner, 1992; Bernard and Rassoulzadegan, 1993). Indeed, ciliates and phytoplankton biomass have been shown to be positively correlated in marine waters (Lynn & Montagnes, 1991). Although some smaller ciliates may graze picoplankton-sized cells (Rassoulzadegan et al., 1988 and Sheer and Sherr, 1987), ciliates are not considered to be major bacterivores in oceanic waters (Pierce & Turner, 1992). The correspondence between ciliate biomass and bacterial biomass and production is therefore likely to reflect their common utilization of phytoplankton derived food and substrate. However it may also reflect an indirect predator prey relationship between ciliates and bacteria via grazing on bacterivorous nanoflagellates (Verity, 1986a).

During the study, tintinnid ciliates were the most dominant groups among ciliates followed by aloricates. Tintinnid ciliates had representation from 35 genera with 78 species. Literature available on nutritional requirements of tintinnids, shows that they mostly feed on pico and nanoplankton groups. Aloricate ciliates were numerically less compared to tintinnid ciliates and represented by 5
genera and 12 species. Dominance of loricate ciliates (tintinnids) over aloricate ciliates were contrary to the results obtained by Leaky et al., (1996) and Mangesh et al., (1996) in the Arabian Sea and they found that the aloricate ciliates represents maximum in the samples followed by tintinnids. Leaky et al., (1996) further observed that the abundance of ciliates were considerably less in low productive areas of the study region and showed clear dependency of microzooplankton on phytoplankton biomass. However Mangesh (2000) found strong positive relationship between bacterial and aloricate abundance suggesting bacterivorous feeding habit to aloricates. But it is a known fact that phytoplankton biomass in the Bay of Bengal is considerably less compared to the Arabian Sea throughout the year. In the present observation the total microzooplankton abundance in the Bay of Bengal was considerably less than that of the Arabian Sea, which may be directly linked to the low productivity of the BOB throughout the year. This information infers that the low concentration of phytoplankton standing stock may be the reason for the observed low aloricate abundance during the study. Another reason for the low densities of aloricates in the Bay of Bengal could be due to the low salinity observed at the surface layers. Low salinity is reported as an important factor, which decrease aloricate ciliates in the estuaries where their abundance is lower than tintinnids (Mangesh, 2000). Bay of Bengal is known for its low saline waters at the surface and the northern part of the Bay of Bengal is particularly is a semi-estuarine system. In addition to this, the regions all along the coast are influenced by the freshwater influx from various rivers.

During the present study Genus Tintinnopsis was the most dominant form among the loricate ciliates in the coastal waters, because this genus requires fine sand grains or mineral flakes for constructing loricae. However, abundance of these particles generally decreases as they move away from the shore (Mangesh, 2000). Other protozoans present in the samples belong to three different groups namely radiolarians, acantharians and foraminifers. Collectively their numerical abundance was 9% during winter monsoon, 8% during inter monsoon and 7% during summer monsoon.
7.3.2. Temporal and spatial (vertical) variations

During the present study, maximum average column density of microzooplankton was observed during spring intermonsoon (701 x 10^4 m^-2) followed by summer (575 x 10^4 m^-2) and winter monsoon (350 x 10^4 m^-2). Column biomass showed similar distribution with maximum biomass (228 mgC m^-2) during inter monsoon followed by summer (152 mgC m^-2) and winter monsoon (103 mgC m^-2). This seasonal pattern of distribution was similar to the observation made by Mangesh et al., (1996) along the western Arabian Sea and Revelante and Gilmartin (1983) in the northern Adriatic Sea and found great variability in abundance between relatively mixed and stratified periods as observed in the present study. In their studies abundance of microzooplankton during stratified condition was much higher than the mixed period. A study by Suzuki and Taniguchi (1998) also reported large temporal and spatial variability in abundance of microzooplankton in the western Pacific. Suzuki and Taniguchi (1998) also reported great temporal variability in microzooplankton abundance in north Pacific, Subtropical North Pacific and off eastern Australia. Availability of food concentration as well as the temperature is reported to be the key factors, which influence microzooplankton distribution (Heinbokel 1978 b; Taniguchi & Kawakami 1983; Verity 1986 b; Godhantaraman, 2001). During the present study maximum sea surface temperature was found during spring intermonsoon. However, phytoplankton standing stock during the period (Avg.13.8 mg m^-2) was lesser than summer monsoon (18.14 mg m^-2). Hence, higher average microzooplankton abundance during spring intermonsoon could be explained by the higher temperature and increased abundance of smaller phytoplankton during strongly stratified periods as suggested by (Cushing, 1989; Yentch & Phinney (1995); Aksnes and Egge, (1991); Pomeroy, 1974; Johnson and Sieburth (1979); Platt (1983); Li et al., 1983). During spring intermonsoon stratification of water column in the Bay of Bengal was maximum and 1µM contour of nitrate was found below 50m. According to the recent understanding, this is the ideal condition where cyanobacteria and smaller diatoms dominate the phytoplankton standing stock and
Pathway 2 of the food web substantially dominates over pathway 1 (Figure 7.1). Two blooms of cyanobacterium, *Trichodesmium erythraeum* observed in the oceanic regions of the Bay of Bengal during the present study give biological evidence for the strong stratification prevailed during the period. Marked increase in the ciliate abundance during spring intermonsoon compared to the other two seasons provide further support to the observation by Cushing, 1989, Yentch and Phinney (1995) that during stratified conditions smaller sized diatoms and cyanobacteria dominate the phytoplankton standing stock which result in the increase of microzooplankton. Available information on the feeding requirement suggests that ciliates could not feed efficiently on large sized phytoplankton and usually prefers phytoplankton, which is smaller than their loria diameter (<40μm) (Revelante & Gilmartin (1983), Paranjape (1990), Rassoulzadegan et al., (1981). A recent study by Bernard and Rassoulzadegan (1993) observed that many tintinnid ciliates consume mostly *Synechococcus* (cyanobacteria), nanoplankton and picoflagellates for their nutrition. Hence optimum temperature and availability of smaller phytoplankton during the period could be the reason for the observed increase of microzooplankton abundance during spring intermonsoon. But confirmation of this hypothesis can only be done after the seasonal measurement of phytoplankton cell size using Flow cytometry.

Summer monsoon showed higher surface density of microzooplankton (Avg. 175 x 10^4 m^{-2}) compared to inter monsoon (Avg. 43 x 10^4 m^{-2}) and winter monsoon (Avg. 43 x 10^4 m^{-2}). Surface biomass of microzooplankton also showed similar trends with higher concentration during summer (46 mgC m^{-2}) followed by spring intermonsoon (17 mgC m^{-2}) and winter monsoon (13 mgC m^{-2}). During summer, phytoplankton biomass was mostly confined to the surface layers due to light limitation and relatively higher temperature and this could be the reason for the higher abundance of microzooplankton at the surface during the season. But due to limitation of light, phytoplankton biomass in the deeper depths were considerably less during the period and this in turn resulted in low microzooplankton abundance at deeper depths. On the contrary during winter,
microzooplankton abundance decreased considerably in the surface layers of the northern region even though the phytoplankton biomass at the surface was relatively higher than spring intermonsoon. This could be due to the low temperature at the surface layers of the northern transects. Temperature limitation on the abundance of microzooplankton is mainly reported from the temperate regions. Recently, Godhantaraman et al., (2001) found that 6°C temperature drop during winter compared to the summer resulted in substantial reduction in the ciliate abundance in the Japanese waters. Though, the SST in the northern region showed only around 3°C drop at the surface during winter compared to the other seasons, it caused considerable reduction in the abundance of ciliates. Low temperature (3 - 4°C drop compared to the other season) in the surface along with low phytoplankton standing stock in deeper waters could be the reason for the low microzooplankton column abundance and biomass in the northern region which ultimately resulted in low average values for the entire area.

It is logical to consider that during summer monsoon higher density of microzooplankton at the surface was due to the increased phytoplankton biomass and optimum temperature at the surface. This means that the two key factors, which are reported to be limiting microzooplankton distribution, were optimum during the season. Decrease in microzooplankton abundance towards depth is apparently due to the low concentration of phytoplankton biomass due to the limitation of light.

A study by Leaky et al., (1996) described that ciliate abundance was largely dependant on phytoplankton standing stock in the central and northwestern Arabian Sea. If this happens during winter monsoon, naturally microzooplankton abundance in the northern Arabian Sea (north of 17°N) would be high due to the higher phytoplankton biomass existing in that region resulting from winter convection. Interestingly, Mangesh (2000) reported only an average minimum of microzooplankton column density in the AS especially in the northern region during winter monsoon. This conveys the fact that temperature limitation on microzooplankton abundance is also apparent in the northern regions of the Arabian Sea during winter.
Generally, vertical distribution of microzooplankton during different seasons showed high concentrations in the upper layers (75m - surface). With in the upper layers clear seasonal fluctuations were found, which was corresponding to the distribution of phytoplankton standing stock. During summer and winter monsoon higher numerical abundance was found at the upper 20m water column below which it decreased with increasing depth. This could be due to the concentration of phytoplankton biomass in the surface layers during the season. During inter monsoon higher microzooplankton abundance and biomass was found at relatively deeper depths (50 – 75m) and was corresponding to the higher phytoplankton standing stock at respective depths. Close associations between vertical distribution of ciliate abundance and phytoplankton chlorophyll a was reported globally by many earlier researchers (Beers and Stewart 1970 & 1971, Lynn and Montagnes, 1991), which support the present observation. Statistical analysis showed that during different seasons number of species of ciliates decreased steadily from spring intermonsoon to winter through summer reducing to nearly 50 % of the species, with 62 % richness, 67 % concentration, and 78% species diversity.

Vertical distribution of different groups of microzooplankton showed variations during different seasons. During winter and summer monsoon dinoflagellates showed a decreasing trend from the surface. This indicates the higher range of tolerance of dinoflagellates to temperature during winter. Interestingly, ciliates showed more or less uniform distributional pattern during winter with very low abundance in the surface layer, which points out that during the season ciliate distribution in the surface layers were severely limited by the relatively low temperature particularly in the northern regions. Numerical abundance of ciliates during the season were comparable with the densities of other protozoans and micro metazoans, which usually represented in very low densities through out the study. During summer monsoon ciliates showed a decreasing trend in abundance from surface to bottom in almost all the stations. This could be due to the higher concentration of phytoplankton biomass at the surface layers.
Distribution of dinoflagellates showed increased densities in the subsurface layers during spring inter monsoon compared to the other two seasons. But the change in the distribution of ciliates was more prominent during the period. During the season ciliate concentration in the 20 - 75m water column increased considerably compared to the other seasons. At many stations other protozoans and micrometazoaans also showed higher densities in the subsurface layers. This apparently is due to the higher concentration of phytoplankton biomass at the deeper depths.

Inferences from statistical analysis shows that maximum number of species, diversity and concentration of microzooplankton was during spring intermonsoon. This supports the general pattern of microzooplankton distribution during spring intermonsoon.

7.3.3. Microzooplankton herbivory

Herbivory studies during winter monsoon at four locations in the surface waters (5m) of southern Bay of Bengal indicated that herbivory ranged between 1.8 – 7.9 µgC l⁻¹ d⁻¹ (Avg.5µgC l⁻¹ d⁻¹), which indicated that major portion of (average 72%) of the phytoplankton standing stock was grazed by microzooplankton. In deeper depths (40m), herbivory ranged between 3.3 – 4.8 µgC l⁻¹ d⁻¹ (Avg. 4µgC l⁻¹ d⁻¹) and on an average 63% of the phytoplankton standing stock was grazed daily by microzooplankton. This result agrees with the earlier works from the different parts of the world oceans, which revealed that microzooplankton grazing is highly important for the transfer of primary organic material to the higher trophic levels.

James and Hall (1998) studied the grazing rates of microzooplankton on total phytoplankton, picophytoplankton and bacteria in Sub Tropical, Sub Tropical Convergence and Sub Antarctic waters in winter and spring of 1993. They found that the grazing impact on total chlorophyll a standing stock and phytoplankton production ranged from 10 - 92% in winter and 4 - 57% in spring, respectively. The abundance of microzooplankton was generally higher in spring than winter. Grazing by microzooplankton is known to be quantitatively significant (Burkill et
al.; 1993 a & b; Verity, 1990; 1993 a&b) because of their key role in the microbial system where they graze on particles of varying sizes. This allows the incorporation of a greater proportion of the primary production into the food chain. Microzooplankton is capable of consuming a significant proportion of primary production (Frost, 1991), which is reported to be of 40-70% of the total primary production (Riley et al., 1965; Beers and Stewart, 1970) in the tropical Pacific. Indeed, field experiments have demonstrated that microzooplankton consumes between 10 and 75% of daily primary production (Garrison, 1991; Pierce and Turner, 1992). Similar studies (Capriulo and Carpenter, 1983; Cosper and Stepieen, 1982) have shown that certain components of the microzooplankton community alone would have consumed 20-100% of primary production. Burkill (1982), Capriulo and Carpenter (1983) and Verity (1987) found that the tintinnids are responsible for the consumption of ~30% of the annual primary production, a value of the same order of magnitude as those consumed by copepods. In the present study the relationship between ambient chlorophyll a concentration and herbivorous activity showed a linear relationship (r = 0.921, n = 8, p < 0.05), which indicates the dependency of microzooplankton on phytoplankton biomass.

7.3.4. Some ecological aspects of microzooplankton

7.3.4.1. Relationship with phytoplankton standing stock

In the present study, correlation between microzooplankton biomass and chlorophyll a during different seasons showed significant linear relationship (p < 0.05) during all the seasons. During all the seasons dinoflagellates and ciliates had linear relationship to phytoplankton biomass and the magnitude changed during different seasons. During winter and summer monsoon when higher concentration of chlorophyll a was available in relatively shallower depth, dinoflagellates were more closely related to phytoplankton biomass compared to the ciliates. Higher linear relationship between ciliates and phytoplankton during spring intermonsoon could due to the increased abundance of smaller phytoplankton during the season, which is proved as the preferential food of ciliates. During the present study, dinoflagellates were relatively more concentrated in the surface layers through out
the year. But ciliates proliferate in deeper depths when sufficient phytoplankton biomass is available in deep, which was clear from the vertical distribution during spring intermonsoon.

7.3.4.2 Symbiotic associations with cyanobacteria

Symbiotic associations were found in three genera of dinoflagellates namely *Ornithocercus*, *Histioneis* and *Parahistioneis*. These dinoflagellates hosted clusters of cyanobacteria - rod, ovoid or spherical shaped (*Synechococcus* and *Synechocystis*, Norris 1967 and Taylor 1982 & 1990) located between the 'lists' the cells. Normally *Synechococcus* and *Synechocystis* (Cyanobacteria) inhabit extracellularly is referred as phaeosomes (Taylor, 1982; Norris, 1967). But the ecological advantage of these associations in the waters of nitrogen limitation received scientific attention recently (Gordon, 1994).

During the present study, the percentage occurrence symbiotic association was maximum (97%) during spring intermonsoon, relatively less during winter (13%) and summer (11%). More over the abundance of these heterotrophic genera increased five times during spring intermonsoon compared to the other season. This seasonal shift in the frequency of occurrence of this association is directly linked to the oligotrophy of the water column arisen from strong and prolonged stratification during intermonsoon. In the Bay of Bengal, stratification of water column is maximum during spring intermonsoon where nitracline was usually below 50m depths.

Normally cyanobacterial cells dominate in the nitrate depleted (strongly stratified) environment (Gordon, 1994; Johnson and Sieburth, 1979; Platt, 1983) and *Trichodesmium* is one among them, which proliferate in such environments. During the present study also, two blooms of *Trichodesmium erythraeum* were observed at different regions of the study area, which is an indication of the oligotrophic nature of the water column.

The possible ecological advantage of the symbiotic association between heterotrophic dinoflagellates and cyanobacterium during prolonged oligotrophic
condition is very significant (Norris, 1967). *Ornithocercus*, *Histeonis* and *Parahisteonis* are heterotrophic organisms, which live osmotrophically (by absorbing dissolved organic compounds) (Droop, 1974). During the period of prolonged nitrogen limitation, abundance of cyanobacterial cells increases in the water column and the dinoflagellates allow them to inhabit between their girdles. By doing this heterotrophic dinoflagellates get organic substances from the cyanobacteria and in turn the latter get a micro environment which is relatively reducing and thought to be advantageous to carry out the nitrogen fixation.

**7.3.5. Comparison with microzooplankton and mesozooplankton biomass**

During the present study, comparison between microzooplankton and mesozooplankton biomass convey some interesting results. During summer and winter mesozooplankton biomass was markedly higher. But during these seasons microzooplankton biomass was relatively less. But during intermonsoon period mesozooplankton biomass was considerably low although microzooplankton biomass was maximum during the season.

Present observation is contrary to the observation by Madhupratap et al., (1996) in the Arabian Sea that high mesozooplankton biomass is supported by increased microzooplankton biomass during spring intermonsoon. But from the
present study it become obvious that, although microzooplankton biomass increases during intermonsoon spring, it is not sufficient enough to support higher mesozoooplankton biomass especially in conditions of strong stratification. A logical reason for the present observation could be drawn from the observations of Cushing (1989) and Yentch & Phinney (1995) (Figure. 7.1) which suggest that in stratified conditions food web is more complex (pathway 2) and hence primary organic carbon reaches higher trophic level less efficiently (Azam et al., 1983). The consequence of pathway 2 is the distribution of photosynthetic carbon at multitrophic levels (widely dispersed) with a long residence time in the upper layers of the ocean. Though the Bay of Bengal is oligotrophic through out the year there are some regions that are moderately productive during summer and winter due to the upwelling process, river runoff and eddies which becomes evident in the present study. But during spring intermonsoon entire region was strongly stratified and hence the latitudinal variations of primary productivity was minimum during the period. From these observations it could be concluded that due to the relatively mixed surface layers during summer and wintermonsoon traditional pathway (Pathway 1) of the food web dominates (Figure 7.1) in the Bay of Bengal (at least in some regions). This results in the efficient transfer of primary food to the mesozoooplankton and could be the possible reason for the higher mesozoooplankton biomass during summer and winter monsoon. Another reason for higher mesozoooplankton biomass during summer and winter may be due to the river water plumes as suggested by Parson and Kessler (1986) and Madhupratap et al (1993). These results suggest that in the Bay of Bengal, microzooplankton could not be considered as an alternative source when phytoplankton biomass and productivity remain low, instead as a key component, which transfers organic carbon from smaller sized phytoplankton and bacteria to mesozoooplankton through out the year but more crucial during spring intermonsoon when water column is strongly stratified. Presently, global implications of the two pathway systems (Figure 7.1) are of major concern to ocean ecologists and geochemists. In regions where pathway two dominates, the transfer of photosynthetic carbon is complex due to the
interactions at the multitrophic levels. The consequence is that carbon becomes widely dispersed with long residence time in the upper layers of the ocean. In regions where pathway 1 dominates, the photosynthetic carbon is transported directly to the primary herbivore in a straight shot.

During the present study microzooplankton density and biomass was maximum during spring intermionsoon (most stratified period). This is a common observation in many other parts of the world ocean during strong and prolonged stratification (Mangesh et al., 1996; Mangesh, 2000; Revelante & Gilmartin, 1983; Suzuki & Taniguchi, 1998). The opinions of Marshall (1973) found that copepods and other zooplankton are unable to crop small sized algae efficiently further signify the trophic importance of microzooplankton in the Bay of Bengal. Results from the grazing studies showed that >60% of the daily primary productions are consumed by microzooplankton during winter monsoon in the southern region. From the above discussion it can be concluded that even though the total abundance and biomass of microzooplankton in the BOB is less compared to AS, the trophic role played by them is crucial by transferring the organic carbon from small sized phytoplankton and bacteria to mesozooplankton which is significant in the context of the general oligotrophy of the BOB. Being the first study on microzooplankton from the open waters of Bay of Bengal, the present observations are also relevant as base line information from these regions. Hence future studies on this subject should include the phytoplankton cell size measurements using Flow cytometry and also the seasonal fluctuations in the grazing pressure of microzooplankton on phytoplankton biomass along with the routine qualitative and quantitative measurements of microzooplankton.