CHAPTER V

DISCUSSION
Prior to the present study, published informations are very few on the macrofauna in the Central Indian Ocean (Parulekar et al., 1982, 1992; Ingole et al., 1992, 2000, 2001; Ingole, 2003; Ingole et al., 2005a). Further, most of the work in the past has been restricted to the group level. Thus, this is the first attempt to study the macrofaunal community structure in a broader perspective, considering the spatial as well as temporal changes.

5.1 Macrofaunal community structure

5.1.1 Faunal composition and abundance

As in most of the benthic sedimentary habitat, the faunal composition was dominated by the polychaetes and nematodes with mean macrofaunal density of 30 no.m$^{-2}$ and 44 no.m$^{-2}$ for March 2003 and April 2005 studies, respectively. Parulekar et al. (1992), studied the benthos of the Western and the Central Indian Ocean and reported a mean macrobenthic density of 105 no.m$^{-2}$ and 92 no.m$^{-2}$ in water depths of 5000-5499 and 5500-5999 m respectively. Further, Ingole (2003), found an average macrofaunal density of 376 no.m$^{-2}$ from 56 stations in the depth range of 1254-6005 m, and the mean biomass value was 1.0 g wet wt m$^{-2}$. All the above studies reported higher macrofaunal density and biomass compared to the present study. This was mainly due to the inclusion of some shallower stations from the Exclusive Economic Zone of Mauritius and Seychelles. However, the dominance of polychaetes in the macrofauna has been reported in all the deep-sea studies. Though Ingole (2003), considered nematodes among the macrofauna, their density were very low (4%) compared to the present study. Similar to the present study, lower macrofaunal densities (88 no.m$^{-2}$) have been reported in the Pacific Ocean on the Cape Verde Abyssal plain (Sibuet et al., 1993). The low density in the abyssal CIOB was probably due to the lower primary productivity (PP) in the surface water. The PP values reported by Matondkar et al. (2005), in the CIOB, ranged between 9.06 mg C m$^{-2}$d$^{-1}$ to 103.4 mg C m$^{-2}$d$^{-1}$. Similar values
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of PP had also been reported earlier in the CIOB by Krey (1973) and Krey and Babenerd (1976). Likewise, Holmes (1961), Ryther (1969) and Kolbentz – Mishke et al. (1970), reported PP of 150 mg C m$^{-2}$d$^{-1}$ for South Pacific Ocean and were in close agreement with the values obtained by Matondker et al. (2005), in the CIB. Further, the PP values in CIB were higher than those reported for the equatorial Pacific (Malone, 1971; El-Sayed and Taguchi, 1979; mean: 10 mg C m$^{-2}$d$^{-1}$). It has been observed that there is a variation in the density and composition of the macrofauna due to the water depth with a difference of even 500 m. Rowe et al. (1974), observed a density of 785 no.m$^{-2}$ and biomass of 0.69 g.m$^{-2}$ at 2425 to 3923 m depth and lower values were obtained for depth range between 4901 and 4950 m (density: 175 no.m$^{-2}$ and biomass: 0.22 g m$^{-2}$), in the northwestern Atlantic Ocean. In the present study, the water depths ranged from 4810 to 5693 m (Table 1), with an exception of one station (BC-37) located at 4252 m, which is a seamount location. Thus, most of the earlier deep-sea macrofaunal studies showed a much higher density compared to the present study. It is important to note that, very few studies have depths similar to the present work (Rowe et al., 1974; Smith, 1978; Sibuet, et al., 1989). Moreover, nearly all the earlier investigations are restricted at around 4000 m water depths and have used different sieve size for separating the macrofauna (0.25-0.5 mm). Therefore, it did not offer a true comparison with the present study.

Deep-sea macrofauna is known to feed either on matters available in the interface water (filter-feeders), or ingest bulk sediment from the sediment surface or from deeper sediment layers (deposit-feeders). Some act as predator/scavenger (predating, e.g. on meiofauna; Flach et al., 1999), but majority of the deep-sea macro-invertebrates are known to be deposit feeders (Sanders, 1958; Rhoads, 1974; Gray, 1981).

Among the polychaetes, family Ampharetidae and Spionidae (*Prionospio sp.*) were the most dominant in March 2003 and April 2005 (Fig. 4.1.a and 4.2.b).
Most of the members belonging to these two families are surface deposit feeders (Fauchald and Jumars, 1979) and known to dominate the deep-sea macrofauna (Wilson and Hessler, 1987). Furthermore, these polychaete families are well represented bathyally where food is sparse (Hartman, 1965; Hessler and Jumars, 1974). Thus, their dominance in the abyss of CIOB which is sustained by low surface primary productivity (Matondkar et al., 2005) is not surprising. During March 2003, the surface deposit feeders constituted 71.4% of the polychaetes, while the carnivorous and the subsurface deposit feeders constituted 14.3% each (Fig. 5.1). Similar results were obtained during April 2005, with 68.8% of deposit feeding polychaetes, 18.8% carnivores and 12.5% of subsurface deposit feeders (Fig. 5.2). Only 3 species of carnivores were obtained in the present study viz., Glycera sp., Glycine sp. and Euphrosine myrtosa. On morphological grounds, it is postulated that the carnivorous habit is the primary feeding mode among the Glycera sp., and that an unknown, probably small number of species have become detritivores. It is further suggested that, bathyal and abyssal glycerids can use both modes (Fauchald and Jumars, 1979) and hence are capable to adapt the less productive CIOB for their survival. The Euphrosinidae (Euphrosine myrtosa) are also carnivorous in nature and in the deep-sea their major diet is known to be foraminiferans (Fauchald and Jumars, 1979). The surface deposit feeding stratagem of deep-sea Hesionidae family, Flabelligera sp., Brada sp., Lumbriconeris latreilli, Sabellidae family, Exogone sp. and Eunicidae were investigated and documented by Fauchald and Jumars (1979) and Thistle (1979). These surface deposit feeders also contributed substantially to the polychaetes composition in the CIOB (Fig. 4.1.a and 4.2.b). The subsurface deposit feeders belonging to family Maldinidae were observed in March 2003 as well as in April 2005. The subsurface deposit feeding nature of Maldinidae family (Axiothella sp. and Maldane sp.) and Aricidae wassi, were confirmed by Fauchald and Jumars (1979). Maldanids are known to build tubes throughout their life, and hence move slowly from one location to another. It suggests that species with poorly constructed tubes and all deep-water species have this capability. It is unlikely
that forms living in food-rich environments, will keep on constructing tubes for an extended time. According to Fauchald and Jumars (1979), maldanids are capable of continuous tube building. The experimental studies have also confirmed the amount of food available and the tube-building activity of maldanids. Studies of some smaller macrofauna have revealed a response where the organism, by means of a relatively simple change in behavior, may change to feeding on suspended particles rather than on particles lying on the sediment surface. These interface feeders can switch to suspension feeding, depending on flow energy, by a simple re-orientation of feeding appendages into the overlying water (Taghon et al., 1980; Dauer et al., 1981).

Among all the polychaetes the deposit feeders showed a wide spatial distribution in CIOB, wherein Brada sp., was the most widely distributed (11.5° S to 15° S), followed by Prionospio sp., (latitude 12° S and 16.1° S) and Ampharetidae family (10.2° S to 13° S) (Fig. 4.3.a). These surface deposit-feeding polychaetes are known to survive well in the food limited deep-sea habitat (Wilson and Hessler, 1987).

During March 2003, 60% of the nematodes were omnivores-carnivores/facultative predators; the remaining 40% belonged to the selective deposit feeders (Fig. 5.1), while during April 2005, nematodes belonging to four different feeding types were obtained (62% were omnivores-carnivores/facultative predators, 14 % selective deposit feeders, 14% epigrowth feeders and 10% non-selective deposit feeders; Fig. 5.2). The most dominant omnivores-carnivores/facultative predators were Viscosia sp., Polygastrophora sp. and Dolicholaimus sp., followed by Filoncholaimus sp., Adoncholaimus sp., Calyptronema sp., Belbolla sp., Metacylicolaimus sp. and Trileptium sp., while Leptosomatum sp. and Halalaimus sp., were the most dominant selective deposit feeders. The dominant Viscosia sp., showed a wide spatial distribution between latitude 11.23° S to 16° S (Fig. 4.3.b). Cephalanticoma sp. and Sabatieria sp. are
the non-selective deposit feeders, while, *Comesa* sp. and *Phanoderma* sp. are the epigrowth feeders. The feeding type categorization is based on the shallow water feeding strategies described by Wieser (1953) and Tietjen and Lee (1977). However, the predator-prey encounter in the deep-sea would be very less compared to the coastal environment; hence, the feeding strategy might vary in the deep-sea. It also depends on the strike rate of the predator and their success in predation (Moens et al., 1999).

In an experimental study, Moens et al. (2000) demonstrated low predatory efficiency in nematode *Adoncholaimus fuscus*, which is a known omnivores-carnivores/facultative predator and has low strike rates. Even when the environment was devoid of other food, *A. fuscus* did not increase its predation efficiency. It has been demonstrated elsewhere that, oncholaimid nematodes preferentially feed in organically enriched microhabitats, probably utilizing a mix of particulate and dissolved compounds, and that predation is merely a facultative strategy (Lopez et al., 1979; Moens et al., 1999). Eventhough, the knowledge about the biology of other deep-sea species is limited, similar stratagem might be adapted by the other deep-sea nematodes, which result in their dominance in the deep-sea macrofauna.

Furthermore, the feeding behaviors have not been directly studied on the deep-sea tanaid, harpacticoids, isopods and bivalves and little is known about the ecology of tanaids except for a few littoral species (Holdich and Jones, 1983a). Among tanaids, *Leptognathia* sp. (Fig. 4.1.c and 4.2.c) was the dominant tanaid in the present study. Most of these leptognathiids are no smaller than others in the continental shelf (Holdich and Jones 1983a,b). Nevertheless, small size may be an advantage to species competing for minimal resources (Thiel, 1975; 1979), and the study of mouthparts of these species suggests that they feed on micro-organism/detritus aggregates. These could be the probable reason for their high
density and wide spatial distribution (latitude 11.5° and 16.2° S; Fig. 4.3.d) of
Leptognathia sp., in the CIB.

Harpacticoids were the dominant crustaceans obtained in the present study. Generally free-living harpacticoid copepods are known to feed on organic detritus particles and mucus (Rudnick, 1989; Rieper et al., 1991; Ingole, 1994a), some feed on microalgae (Ingole, 1982; Rieper, 1985; Decho, 1988; Ingole, 1994b), protozoans (Rieper and Flotow, 1981) and many species are believed to feed on bacteria which are attached to detritus or to mucus films (Rieper, 1978; Hicks and Coull, 1983). Studies have shown that Pseudobradya pulchella (Ectinosomatidae) feeds on diatoms Navicula directa and N. pelliculosa, ciliates and bacteria (Coull and Dudley, 1976), while carnivory has been demonstrated for two species of Ectinosoma (Ectinosomatidae). Because of their wide distribution and their large number of species, Ectinosomatidae are called the 'jacks of all habitats' (Hicks and Coull, 1983). Scottolana longipes (Ingole, 1994a) and Amphiascoides subdebilis (Ingole, 1994b) are known to feed extensively on diatoms and ciliates under the laboratory conditions. However, these particular genuses were not obtained in the present study. Overall, it can be concluded that most of the harpacticoid species in the present study are either detritivorous or bacterivorus, since the deep-sea environment is generally food limited.

Among crustaceans, Isopoda was the least abundant during both the study periods and was represented by only two families' viz. Macrostylidae and Haploniscidae (Fig. 4.1.c and 4.2.d). Several studies have treat the gut contents of deep-sea isopods (Svavarsson et al., 1993; Gudmundsson et al., 2000) and revealed foraminifers as important food source for some species. Some other deep-sea isopods, Echinozone arctica and lyarachna Bergendali are reported to be mainly feeding on the deep-sea foraminifera. Even then their guts composed of only 5% of the diatoms (Gudmundsson et al., 2000). In the current study, high density (30 no.m⁻²) of isopods were observed at station BC-37 (Fig. 4.2.e), which could be
no.m$^{-2}$) of isopods were observed at station BC-37 (Fig. 4.2.e), which could be due to the high amount of benthic foraminiferal ooze which was observed at this station. Agglutinated foraminiferans found in the sediments of the deep-sea are known to be a favourite prey item for deep-sea isopods (Svavarsson et al., 1993; Schmiedl et al., 1997; Gudmundsson et al., 2000). This station is located at the seamount summit and had relatively low amount of organic carbon (0.09%) in the sediment compared to the other stations in the adjoining abyssal plain (Fig. 4.2.f). Also, Heinz et al., (2004) observed lower levels of surficial sedimentary organic carbon at the summit of the Great Meteor Seamount than in the slopes and the adjacent abyssal plain and suggested that this may be due to an accumulation of material from the top during lateral and vertical transport and resuspension processes.

According to various studies, the structure of the macrofauna depends on the feeding modes of the various species present, which in turn depend on the quality of available food (Dauwe et al., 1998; Wieking, 2002). Fresh organic matter will result in abundance of species mainly feeding at the sediment surface or in the benthic boundary layer, while refractory organic matter will enhance subsurface deposit feeders and predators. Some studies show that under ‘normal’ conditions, the potential food of deposit feeders seems to be an unpromising mixture of lithogenic and biogenic particles. These have very low refractory organic carbon content and sparse populations of micro-organisms (Jannasch and Wirsen, 1973; Sorokin, 1978; Deming and Colwell, 1982; Tabor et al., 1982). However, the organic carbon content in the CIOB varied between 0.14 to 0.46% (Fig. 4.1.e) and 0.07 to 0.41% (Fig. 4.2.f) during March 2003 and April 2005 respectively (Nath et al., 2005, 2006). The rain of labile organic material from the overlying water column and the transformation of refractory organic matter into labile organic matter by sediment bacteria are thought to be the two processes that provide food for deep-sea benthic fauna (Richardson and Young (1987). The labile part of the organic matter consists of major fraction of carbohydrates and proteins, which are
assumed to be easier to digest and assimilate by the benthic consumers (Fichez, 1991; Danovaro et al., 1993; Fabiano et al., 1995; Tselepides et al., 2000; Raghukumar et al., 2001), whilst, the refractory matter are composed of complex substances like humic acids and fulvic acids which is slowly broken down by bacteria (Henrichs, 1992; Danovaro et al., 2001). Bacteria transform refractory material into more labile forms prior to its use by surface deposit feeders. The deep-sea sediment in CIOB had a mean bacterial density of 1.43E+08 (Table 4.1.b) and 1.35E+08 no.g\(^{-1}\).dry wt (Table 4.2.b) during the March 2003 and April 2005, respectively (Lokabharathi et al., 2005, 2006), which is probably sufficient for the processing of refractory matter. Infact, bacteria are known to sustain a much greater biomass in abyssal sediments than metazoa because of their ability to degrade aged organic material as well as their capacity to survive starvation (Witte, 2003a). Rex et al. (2006), reported a significant decrease in animal abundance with water depth where bacterial abundance was constant. Bacteria may enhance the nutritional value of refractory organic matter by converting it into bacterial biomass or degrading the complex detritus into simpler, more readily assimilable compounds. In either case, bacteria regulate this food source to deposit feeders according to their rate of transformation. The sedimentary proteins and carbohydrates in the present study were 0.7 mg.g\(^{-1}\) and 0.3 mg.g\(^{-1}\) (Fig. 4.1.f) during March 2003, while the values were 1.0 mg.g\(^{-1}\) and 0.4 mg.g\(^{-1}\) (Fig. 4.2.g) during April 2005, respectively (Lokabharati et al., 2005 and 2006). Present study reveals that CIOB has higher content of fresh organic matter, since higher sediment proteins were recorded compared to the carbohydrates. This indicates the possibility of flux of fresh organic material to the benthic environment. However, it could not be confirmed in the absence of flux data. Accordingly, a stipulated investigation leading to long-term flux measurement in CIOB would be vital. Availability of sedimentary proteins may be an important factor regulating the abundance of deep-sea benthic consumers (Deming and Barross, 1993). Since, the lower protein to carbohydrate ratio indicates the presence of aged organic matter (Danovaro et al., 1993) and higher ratio indicate
the presence of fresh flux and appears to be the most probable reason for abundance of surface deposit feeding fauna in the CIOB.

The sediment organic carbon observed in the present study is comparable to reported values of CIOB (Gupta and Jauhari, 1994; Pattan et al., 2005) as well as that of the global average for the deep-sea sediments (0.2 wt%; Degens and Mopper, 1976). The low organic content in the CIOB is attributed to low sediment accumulation rates (Pattan et al., 2005) that allow more remineralization at the sediment water interface. The higher water depth (mean: 5187 m) in the present study may also facilitate extensive remineralization of organic matter during settling through water column, resulting in a low organic carbon content (Pattan et al., 2005). The low organic content in the CIOB indicates a well-oxidized environment. Such a situation may be possible due to the influx of Antarctic Bottom Water (AABW) into the Central Indian Basin through the saddle at around 5°S along the Ninety East Ridge (Warren, 1982). The AABW enriched in the dissolved oxygen helps the organic carbon to get oxidized.

5.1.2 Macrobenthic biomass

Among deep-sea organisms, both gigantism and dwarfism occur, evolutionary trends that can be explained by selection on optimal foraging strategies (Gage and Tyler, 1991). A foraging animal may adapt to low food levels by increasing its size or decreasing its maintenance costs (decrease in size; Carney et al., 1983). Sibuet et al. (1993) observed (in the north-east tropical Atlantic) a relatively smaller impact of decreasing food input on the smaller organisms and a sharper decrease in large organism abundance when food diminished. In general, a decrease in average body-size with depth is reported for most faunal components. This appears to be caused by a replacement of larger species by smaller ones (Carney et al., 1983). Thiel (1975; 1979) and Rex et al. (1999; 2006) showed a decrease in average organism size with depth. Similar observation was made by
Gage and Tyler (1991), wherein deep-sea invertebrate fauna had a small size in most species compared to their shallow water counterparts.

Most investigators report only the faunal densities because the biomass measurement of small animals is technically difficult and the taxonomic value of deep-sea specimens precludes bulk ash-free dry weight determination (Richardson and Young, 1987). Hence, deep-sea macrobenthic biomass is usually given as wet weight (Kröncke and Türkay, 2003). But AFDW are estimated using conversion factors given by McIntyre and Eleftheriou (1968). Since AFDW excludes ash weight, it is more reliable for comparison among taxa (Rowe, 1983). Kröncke et al., (2003) recorded biomass values ranging between 2-94 mg (ww) 0.25m^-2 in the Mediterranean deep-sea. The mean biomass values, however, in the present study were 0.5 mg AFDW.m^-2 (Table. 4.1.a) and 0.6 mg AFDW.m^-2 (Table 4.2.a) during the March 2003 and April 2005, respectively. Similar values are reported in the northeast Pacific Ocean in the depth range of 3570 to 5900 m, where biomass ranged between 0.001 to 0.3 g AFDW m^-2 (Smith, 1987; Murray and Kuivila, 1990). Extensive study on abyssal macrofaunal biomass in North West Atlantic Ocean was reported by Smith (1978), where all the area was within the distance of less than 1000 km from the shore. Hence, as reported by Parulekar et al. (1982) such areas will obviously have higher primary productivity leading to higher sediment organic matter and macrofaunal density as well as biomass. Remoteness of the present study area from the major landmasses (Matondkar et al., 2005), does not allow the comparisons with most of the other studies.

5.1.3 Correlations

As shown in fig. 4.1.1 and fig. 4.2.m, the macrofaunal density was significantly correlated with the sediment organic carbon content. Such correlation has also been reported by Sibuet et al. (1989), in the Atlantic Ocean and Kroncke and Turkay (2003) in deep Angola Basin of the Atlantic Ocean. The positive

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relationship between the amount of organic matter reaching the seafloor and standing stocks of benthic fauna is well established (Rowe, 1983; Thiel, 1983; Richardson et. al., 1985; Ingle, Ingole et al., 1992). This is because, the organic matter is known to be the first order parameter to control the faunal distribution in the deep-sea. Carbon is mainly important for basic metabolism (calorimetric needs) and even refractory organic matter seems to be sufficient to fulfill energetic requirements (Tenore, 1983; Tenore and Chesney, 1985). A positive correlation of macrofauna and sediment protein (Fig. 4.1.m and 4.2.n) and no correlation between macrofauna and CHO (Table. 4.1.c and 4.2.c) reveal that deep-sea benthic communities in the CIOB feed on the fresh organic matter. Similarly, there is no correlation of organic carbon with protein and CHO (Table. 4.1.c and 4.2.c). This is because, organic carbon contains the labile and refractory fraction, and the benthic consumers utilize both this fractions, while, the protein and CHO contains a meager fraction of the surface production.

The significant positive correlation between surface water chl-a and organic carbon (Fig. 4.1.s and 4.2.s) as well as chl-a and macrofauna (Fig. 4.1.n and 4.2.o), reveals that the euphotic primary production contribute a major fraction to the available organic matter reaching the abyssal depths and hence providing food to the deep-sea macrofauna in CIOB. The sediment texture did not show much variation spatially. Furthermore, sediment texture did not show any relation with macrofauna, organic carbon and labile organic matter (Table. 4.1.c and 4.2.c), which could be due to the similarity in sampling depths with very minor variation.

An inverse relationship of macrofauna (Fig. 4.1.o and 4.2.p), sediment organic carbon (Fig. 4.1.p and 4.2.q), and surface water chl-a (Fig. 4.1.r and 4.2.r) with latitude also advocate the importance of surface productivity and sediment organic matter to the macrofauna. It indicates that, food available for benthos decreased with increasing latitudes and it corresponded with the decrease in macrofauna. In the study area, towards the south, the influence of landmasses decreases considerably, hence, the surface production is also seen to decrease.
Moreover, the CIB region is totally isolated from the mainland and the only source of iron (Fe) is dust from islands or landmasses around the Indian Ocean (Matondkar et al., 2005). Iron is generally required for the growth of the phytoplankton and recently it has been shown that in the equatorial Pacific where wind-borne dust is as negligible as the source, adding iron to the surface waters stimulates the growth of phytoplankton (Coale, et al., 1996; Fitzwater et al., 1996). Matondkar et al. (2005) reported a low concentration of Fe (154.74 mg m$^{-2}$) at around 13.5°S and this was found to affect the rate of primary productivity, which was 76.26 mg C m$^{-2}$d$^{-1}$ in the euphotic zone of the CIOB. However, at around 10.5°S, high content of Fe (562.75 mg m$^{-2}$) was found to enhance the primary productivity (103.4 mg C m$^{-2}$d$^{-1}$). This confirms that, the surface production decreases with increasing latitude southwards in the CIOB, ultimately showing a latitudinal variation of macrofauna and their food material. This is further confirmed by Rex et al. (2006), wherein a decline in benthic abundance is also related to the distance from productive coastal waters.

During March 2003, stations BC-7 and BC-22 had 100% similarity because of the similar densities and presence of only one common species, *Haploniscus* sp., while the similarity of station BC-17 with BC-25 can be attributed to their comparable densities and the presence of common (*Macrostylis* sp.) species. Further, analogous faunal density and diversity at BC-4 and BC-24 lead to their similarity of 58.58%. Comparable results were obtained for the macrofaunal biomass (Fig. 4.1.h). During April 2005, similarity between TVBC-26 and BC-38 was because of the low densities in the two stations and presence of unidentified polychaetes. The similarity of station TVBC-25 with TVBC-8R was due to the low densities. Th *Viscosia* sp. *Mendicula* sp. was present both at TVBC-19 and TVBC-13, leading to 50% similarity (Fig. 4.2.i).
5.1.4 **Vertical distribution of macrofauna**

Generally, the abundance and biomass of deep-sea macrofauna is highest in the top 0-5 cm sediment section (Ingole et al., 1992, 1999, 2001, 2005a). A peak in the density, biomass and diversity obtained in the 5-10 cm and 2-5 cm sediment depth during the March 2003 (Fig. 4.1.u and 4.1.w) and April 2005 (Fig. 4.2.u and 4.2.w) could be due to the presence of surface and sub-surface deposit feeders. In the food limited areas, even the surface deposit feeders occupy the lower depths of the sediment layer to compensate for the low food availability and to avoid predation from larger carnivores (Ingole et al., 2005a). This is observed in the present study also, wherein the ampharetid polychaetes, which are surface deposit feeders, were present at 5-10 cm and 10-15 cm sediment depth (Fig. 4.1.u). Fauchald and Jumars, (1979) indicated that most ampharetids have very long tubes, compared with the length of the specimens. Their experimental study on intertidal ampharetid (*Hobsonia* sp.) revealed that worms maintained without additional food added markedly to their tubes. Continuous tube building may represent a form of locomotion in ampharetids and certain other tube-building polychaetes. Further, the orientation of tubes, horizontally or vertically, may depend on the amount of food available for each individual. It is also known that, some macrofauna can gather as much food as possible in a short time (possibly during high pulse rate), bury it out of the reach of the small fauna and live on it until the next pulse arrives. Many of the surface deposit feeders possibly live in the deep sediment layers (Jumars et al., 1990; Witte, 2000; Ingole, 2005a), hence most organisms might be living deeper in the sediment at locations where food is scarce. Macrobenthic infaunas, especially deposit feeders, are the major agents of particle mixing (Rhoads, 1974), also known as bioturbation. Bioturbation leads to increased oxygenation and mineralization rates in sediments (Aller, 1994; Andersen and Kristensen, 1991). Consequently, bioturbation not only affects the vertical distribution of organic matter along the sediment profiles, but also
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potentially increases the available food concentration at depth within the sediment (Rice and Rhoads, 1989; Ingole, 2004).

Capetellid polychaetes, which are subsurface deposit feeders, were observed at upper sediment layer of 2-5 cm as well as in the deeper sediment depth of 25-30 cm (Fig. 4.2.u), which indicate their capabilities to build deep tubes. Linke (1939), Schafer (1962) and Jepsen (1965), reported that in the shallower areas, some capitellids build tubes at or near the surface of the sediment, others build horizontal or vertical tubes or burrows stretching up to 15 cm below the surface. These tubes maintain contact with the surface and allow the worm to feed in black, anoxic muds, getting the necessary oxygen from the overlying waters by irrigation of the burrow. Since the abyssal is a food-limited area the tubes of these polychaetes could have been extended deeper down to 30 cm in the present study (Fig. 4.2.u). Experimental work by Witte et al. (2003a), further supports our findings; wherein they found macrofauna in the 5-10 cm layer became labeled with $^{13}$C within few days. Graf (1989), Levin et al. (1997) and Witte et al. (2003b), studied the macrofauna at continental slope depth and showed that macrofauna rapidly subduct labile food down to 5-15 cm depth, where it is degraded quickly by bacteria and deep-dwelling deposit feeders. Most of the stations showed a decrease in values of organic carbon and protein with increasing sediment depth, but the carbohydrate did not show much variation. This could be because carbohydrates might represent the main food source for organisms living in the deeper sediment layers (Dell’Anno’, 2000). As shown in fig. 4.1.v-4a to 4.1.v.4j and 4.2.v-4a to 4.2.v.4k, even though the protein concentration decreased with increasing sediment depth, the protein concentration was never less than 0.2 mg.g$^{-1}$, dry wt. Since the metabolic rates of the deep-sea fauna are low, these amounts of LOM available could be sufficient for the deeper sediment dwelling macrofauna. Subsurface deposit feeders (which usually feed beneath the sediment mixing depth) are known to be constrained by lower amounts of available organic matter, but according to the optimal foraging theory,
Fig. 5.1: Composition (%) of polychaetes and nematodes based on feeding pattern during March 2003

Fig. 5.2: Composition (%) of polychaetes and nematodes based on feeding pattern during April 2005
this is partially compensated by a diminished competition for available resources (Jumars and Penry, 1989). According to Dell’Anno’ et al. (2000) subsurface consumers would also be subjected to a different diet regime characterized by the large predominance of carbohydrates and possibly different adaptive mechanisms to optimize the exploitation of this trophic source. However, it must be kept in mind that the recovery layer of the organisms must not necessarily represent the layer of main activity of the individual, particularly, those with vertical tubes, may feed and live on/in the surface layer but escape into deeper layers when disturbed by the box corer (Witte, 2000), or due to the surface predation pressure (Ingole et al., 2001, 2005a).

5.2 TEMPORAL VARIATION

5.2.1 Temporal variability of macrofauna

In the abyssal environment, the benthic response to temporal changes has been poorly documented, primarily due to the difficulty of sequential sampling. However, the deep-sea macrofauna was sampled on two occasions in the CIOB to study the temporal variation. The macrofaunal density was higher during April 2005 (mean: 57±46sd no.m⁻², n=10) as compared to that during March 2003 (mean: 37±23sd no.m⁻², n=10). Statistically, the variation was not significant. Also, the surface water chl-α (mean: 0.06 mg.m⁻³ for both the years) and sediment organic carbon (mean: 0.3 % for both the years) did not show any significant temporal variation. Similarly, the sediment texture, bacterial density and meiofauna also did not show a significant variation. But, there was increase in sediment protein (Fig. 4.4.f) and CHO (Fig. 4.4.g) during April 2005 with significant variation compared to March 2003. Moreover, nitrogen has also been regarded to be an important factor limiting macrofauna growth (Rice, 1982; Tenore, 1983) and particularly protein uptake seems to be essential for covering the nitrogen demand of macrofauna (Tenore, 1988; Taghon and Greene, 1990).
Proteins are the most important nitrogen source and are utilized at a faster rate than carbohydrates by consumers (Vezzulli and Fabiano, 2006).

Thistle et al. (1991), suggest that deep-sea macrofauna did not present significant differences in abundance over time. Hence, it is assumed that the benthic community is relatively little influenced by seasonal changes in the tropical deep-sea environment (Cosson et al., 1997). Similarly, Drazen et al. (1998) observed that the metazoan density and biomass did not vary consistently with the presence of detrital aggregates in the abyssal North East Pacific. Studies carried out by Smith (1987), during September 1980 and October 1983 at 4900 m water depth in the Central and eastern North Pacific showed that the organic carbon values were 4.2 mg·g⁻¹ and 3.2 mg·g⁻¹, while the sediment total nitrogen was 0.6 mg·g⁻¹ and 0.4 mg·g⁻¹, respectively. Even with higher amounts of organic carbon and nitrogen values, there was a lower macrofaunal density (213 no.·m⁻²) in September 1980 (213 no.·m⁻²) as compared to October 1983 (412 no.·m⁻²). Similarly, Smith et al. (1983), studied the macrofauna at 5900 m during August 1978 and August 1979 in the North Pacific, and reported a density of 201 no.·m⁻² and 584 no.·m⁻² and organic carbon value of 4.2 mg·g⁻¹ and 5.4 mg·g⁻¹, respectively with a constant nitrogen value of 0.5 mg·g⁻¹ during both the years. However, in the present study the organic carbon was more or less constant for both the years, while protein and carbohydrate showed an increase during April 2005. This increase in the labile organic matter must have resulted in comparatively higher density of macrofauna in April 2005. Proteins are preferentially utilized by benthic consumers (Tenore, 1988; Danovaro et al., 1999) and represent the limiting compound in most deep-sea environments (Deming and Baross, 1993).

As far as the community feeding is concerned, it was seen that, surface deposit feeders (78%) and subsurface deposit feeders (22%) dominated polychaete community during March 2003. While in April 2003, polychaetes comprised of the surface deposit feeders (62.5%), carnivores (25%) and subsurface deposit
feeders (12.5 %). During both the study periods, the surface deposit feeders were dominant, but carnivores were present only during the April 2005. This was because; increase in labile organic matter obviously increased the surface deposit feeders, which in turn attracted the carnivorous forms.

5.2.2 Vertical distribution of macrofauna

In the deep-sea environment, where food is limited, fauna was thought to be available only in the top sediment layer. However, recent studies have demonstrated the presence of meio- and macrobenthic organisms in the deeper (>35cm) sediment depths (Ingole et al., 2005 a,b). Even though distributed in the lower sediment depths, all macrofauna require contact with the surface, either constantly or periodically, directly or indirectly through biogenic structures and sediment reworking (Schwinghammer, 1981). Distribution of macrofaunal density and biomass within the sediment column did not show any statistical difference between 2003 and 2005 sampling. However, for the selected stations used for the temporal variability study, during March 2003, the macrofauna was restricted only up to 10 cm sediment depth (Fig. 4.4.aI), whereas in April 2005 the organisms were recorded down to a sediment depth of 30 cm (Fig. 4.4.all), probably due to the increased LOM in April 2005. As shown in fig. 4.4.cl and II, the LOM content in March 2003 was comparatively lower on the surface as well as throughout the sediment depth. Hence, the organisms were, probably, present up to 10 cms during March 2003 (Fig. 4.4.al). One possible explanation is that the higher bioturbation of the top layer of sediment as a result of the increase in the population of megafaunal deposit feeders or predation by large carnivores may have contributed to a downward movement of infaunal organisms in April 2005, seeking to avoid physical disturbance of their habitat (Thiel, 1983; Lambshead et al., 1995). Further, some deep-sea organisms such as ampharetid polychaetes, construct long tubes to store the high particle flux and bury the material out of the reach of competitors and thrive on it until the arrival of pulse in the next season.
Metazoan macrofauna mix surface sediments through bioturbation, thereby burying labile and decomposed organic materials (Nomaki et al., 2005). Bioturbation leads to increased oxygenation and mineralization rates in sediments (Andersen and Kristensen, 1991; Aller, 1994) and alters the geochemistry of the sediment particles and solutes (Aller, 1982). As seen during the present study, bioturbation probably not only affects the vertical distribution of organic matter along the sediment profiles, but also potentially increases the available food concentration at depth within the sediment (Rice and Rhoads, 1989), since organisms in the current investigation are obtained at very deeper sediment depth (>30 cms). Various other studies also detected the bioturbated deeper sediment layers by the macrofauna (Cosson et al., 1997; Witte, 2000; Ingole et al., 2005a). The major fraction of the organic matter is degraded in the water column or at the sediment-water interface, most deposit feeding macrofauna, even in the shallow continental seas, therefore, has to cope up with a highly food-diluted environment (Lopex and Levinton, 1987). Many infaunal organisms are able to immediately detect and respond to a variable food flux by adapting their feeding, growth and respiration rates (Kanneworff and Christensen, 1986; Graf, 1987; Kristensen et al., 1992).
5.3 INFLUENCE OF SIEVE SIZE ON MACROFAUNA

Among deep-sea organisms, both gigantism and dwarfism occur, evolutionary trends that can be explained by selection on optimal foraging strategies (Gage and Tyler, 1991). Numerous biological processes have been shown to correlate strongly with individual body size (metabolism, abundance, biomass production, nutrient recycling, home range size etc (Peters, 1983; Schmidt-Nielsen, 1984; Brown et al., 2004; Kaariainen, 2006). Most of the studies have argued that food limitation may act as a major contributing factor in controlling the optimal body size of benthic communities, resulting in smaller body size distribution (Thiel, 1975, 1979; Kaariainen, 2006). In a food limited environment, the advantages of having either larger or smaller body size is explained by Thiel (1975). He elucidated that, although the cost of maintaining a given biomass of smaller organisms is higher than that required to maintain the same biomass of larger organisms, the high individual food demands of larger animals and the requirements to maintain a critical population density for reproduction generally favours smaller body sizes. This hypothesis generally applies to infauna (e.g. meio- and macrofauna) that feeds on the sediment locally. The macrofauna are generally considered as organisms larger than 0.5 mm size, but the phenomenon of miniaturization in the deep-sea have lead to the use of different sieve sizes (0.25 mm to 0.5mm) in the bathyal and abyssal macrofaunal studies. The benthic body size miniaturization hypothesis states that the deep-sea communities are dominated by organisms of smaller body size (Kaariainen, 2006).

The organisms in the deep-sea are suggested adapting to the diminished food levels in one of the two ways. Some taxa [gastropoda (Clarke, 1960); isopoda (Wolff, 1962); amphipoda (Thurston, 1979)] showed a trend towards gigantism, potentially allowing them to forage further in search of limited food resources. On the other hand, meio- and macrofaunal communities have shown tendency towards body size miniaturization with increased water depth. Thiel (1975)
hypothesized that, ‘associations governed by constantly limited food availability are composed of smaller individuals on an average’ and attributed this to the fact that food limitation does not allow the higher energy consumption of larger organisms on a local scale (Thiel, 1979).

Based on the above arguments, use of larger sieve sizes (e.g., 0.5 mm or 1 mm) for separating the deep-sea metazoans could potentially underestimate their densities. As described in the previous chapter, the Central Indian Ocean has very low primary productivity; hence, the food available to the deep-sea communities in the area is also low. The influence of sieve size on the macrofaunal community structure was therefore investigated using mesh of 0.3 and 0.5 mm. As depicted in fig. 4.5.4 I and II and 4.5.c, a loss of macrofaunal species and individuals has been observed using the 0.5 mm sieve. The loss was greater for the polychaetes, nematodes, harpacticoids and isopods both in terms of number of specimens and species obtained (Fig. 4.5.b I and II). Nematodes and harpacticoid copepods are generally considered among the meiofauna, but their presence in the 0.5 mm sieve has lead to their inclusion among macrofauna. As reported by Ingole et al. (2001), the nematodes sometimes outnumber the polychaetes in macrofauna. Also, statistically, there was significant difference between the two sieves for the number of specimens, macrofaunal density and biomass. Vertical distribution of macrofauna showed a marginal increase in density (Fig. 4.5.h) and biomass (Fig. 4.5.i) for finer mesh. The vertical distribution of macrofauna in the CIB did not show any significant variation for the two meshes used.

Gage et al. (2002), argued that leaving aside issues of comparability with previous studies, for the purpose of describing macrobenthic biomass in the deep sea (but not abundance and species richness), a sieve as coarser as 0.5 mm might be used depending on the precision required; sieve size smaller than 0.5 mm add very little to the estimate. Additional number of macrobenthic individuals appear as
more and more juvenile stages are collected in progressively finer meshed sieves in the coastal ecosystem (Schlacher and Wooldridge, 1996), however in the deep-sea these numbers include more of small sized species that have passed through coarser mesh (Gage et al., 2002).

As shown in fig. 4.5.e, the Hulbert’s expected number of species \( E(Sn) \), was highest for finer sieve compared to the coarser sieve. Species richness and diversity was highest for nematodes whereas, the species evenness was lowest for the same in the 0.3 mm mesh. Similar results were obtained for the coarser sieve. The species diversity was roughly constant between the meshes for polychaetes, nematodes and tanaids, while, the diversity was higher for harpacticoids in the coarser mesh (Table 4.5.b). Similarly, the diversity indices \( H', J \) and \( d \) did not vary much between stations (Table 4.5.a). Nevertheless, using the two sieves the overall \( H', d \) and \( E(Sn) \) was higher for finer mesh, while the species evenness was almost constant for the two meshes. Similar trend of varying response on diversity indices of different macrofaunal groups with different sieves was obtained by Gage et al. (2002). In the present study also, the polychaetes, nematodes and crustaceans (harpacticoids and isopods) showed different response to sieve size, when considered separately. It may therefore be unwise that the result of one group can be taken as a proxy for the total assemblage. Hence, the total macrofaunal community as a whole should be studied. However, it is confirmed that a finer mesh (0.3 mm) will retain more macrobenthic organisms from the deep-sea than a 0.5 mm mesh since, higher number of organisms and species were obtained using a finer mesh. Though, it is time consuming, it is recommended to use a smaller mesh size, preferably 0.3 mm for separating deep-sea macrofauna since it results in higher diversity.