

Composition of macrobenthos from the Central Indian Ocean Basin

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The deep sea is well known for its high faunal diversity. But the current interest in its abundant polymetallic nodules, poses a threat to the little known benthic organisms surviving in this unique environment. The present study is the first attempt to document the Indian Ocean abyssal benthic diversity of macroinvertebrates and to investigate its relation to the surface primary production (chl-*a*), sediment labile organic matter, organic carbon and texture. The present study is based on 87 individuals. Altogether 39 macroinvertebrate genera were obtained from water depths of 4500–5500 m from 23 box cores. Reduction in macrobenthic density was seen towards the southern latitudes. The area was dominated by deposit feeding macrobenthos. Vertically, the fauna was distributed down to 30 cm depth, with the highest faunal density in the top 2–5 cm sediment section. The values for population density were strongly correlated with surface water chl-*a* and sediment protein, indicating supply of fresh organic matter as a critical factor for maintaining the deep sea benthic diversity and abundance.

1. Introduction

Although the deep sea is one of the most remote and least known environments, it has not been spared from human interference. Due to depleting resources, mankind is looking towards the ocean as an alternative source of hitherto land-based minerals. The deep sea is also known to have large deposits of sulphides, polymetallic nodules and gas hydrates. There are discussions on a global level for commercial mining of these resources in future, which implies a tremendous threat to the deep sea organisms, some even new or little known to science. The Central Indian Ocean Basin (CIOB) is covered with dense polymetallic nodules and is considered to have a high quality of commercial grade nodules (Prasad 2007). However, of the three oceans, the Indian Ocean is the least studied in terms of deep sea fauna.

Benthic organisms play an important role as food for large carnivores and some sediment-dwelling

forms influence the mixing of organic and inorganic matter in the upper sediments through bioturbation. Macrobenthos is also known to control the concentration and accretion of metals in the deep sea, helping indirectly in the nodule growth (Riemann 1983).

Only 1–3% of the surface production is known to be available to these deep sea organisms as food. In the deep sea environment, specialist carnivores become increasingly scarce with depth, presumably because of the decreasing food supply (Gage and Tyler 1991). The small size of many deep sea species may allow them to select individual particles (Jumars and Penry 1989). Macrobenthos density and biomass in the deep sea are related to the carbon deposition flux, whereas, meiofaunal assemblages are more linked to the local bacterial production and sediment characteristics (Vanreusel *et al* 1995; Flach *et al* 2002). In deep-sea sediments bacteria are suggested to represent an important storage of living and readily

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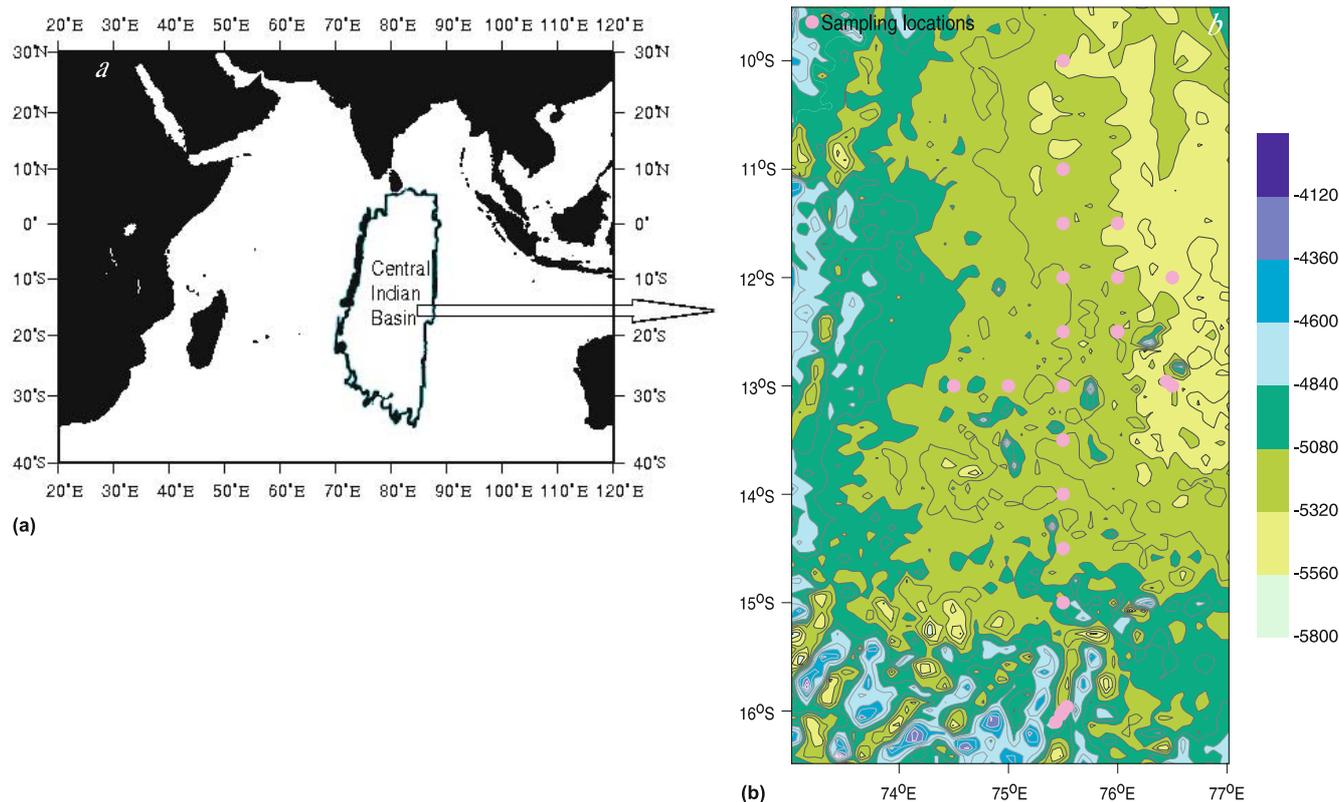


Figure 1. (a) CIOB and (b) depth contours (meters) and box core locations in the CIOB.

available organic carbon (Danovaro *et al* 1995), and might represent a major trophic link to the meiofauna.

All impact studies need a sound basis against which impacts originating from experiments or commercial actions may be assessed. The present study was aimed at providing baseline data on the density, diversity and distribution of macrobenthos in the Indian Ocean. Earlier studies on macrobenthos in the Indian Ocean were largely confined to group level identification (Ingole *et al* 2005 and references therein). Recently, Pavithran *et al* (2007) studied these organisms up to family/genus level. However, the macrobenthic diversity was related only to organic carbon. The current investigation provides the faunal data up to family/genus/species level and their relation with the biogeochemical parameters. The documentation of the deep-sea biodiversity will be useful in understanding the global species distribution and their role in different ecological habitats. In addition, inventorization of macrobenthos can be used as reference information for biodiversity conservation of the less known abyssal fauna of the Indian Ocean. However, owing to the comparatively small sample size – a problem frequently faced in deep-sea studies, the results of the current study should be treated with caution.

2. Materials and methods

2.1 Sampling and analysis

Twenty three box cores were sampled onboard R.V. *Akademic Boris Petrov* in April 2005 from the Central Indian Ocean Basin (CIOB: figure 1a), sampling depths ranging between 4500 to 5500 m (figure 1b) between latitudes 10°–16.1°S and longitudes 74.5°–76.5°E. Sediment samples were collected with a 0.25 m⁻² spade box corer (50 × 50 × 50 cm size). The subsamples for macrobenthos were taken with the help of a PVC core tube (12 cm dia. 50 cm length from each box core) and quadrant (15 × 15 × 10 cm, 3 subsamples for each box core). The PVC core samples were subsectioned at 0–2, 2–5, 5–10, 10–15, 15–20 cm depth through the complete core length. Sub-sectioning of the core sample was done with the help of a locally developed core cutter. All the sub-samples were preserved in neutralized 5% formalin-Rose bengal solution prepared in filtered sea water. These samples were later sieved using 0.5 mm stainless steel sieves and the organisms retained on the sieves were collected and sorted groupwise.

Surface water chl-*a* data was extracted in individual locations in February–March 2005 from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS-weekly data), considering that the

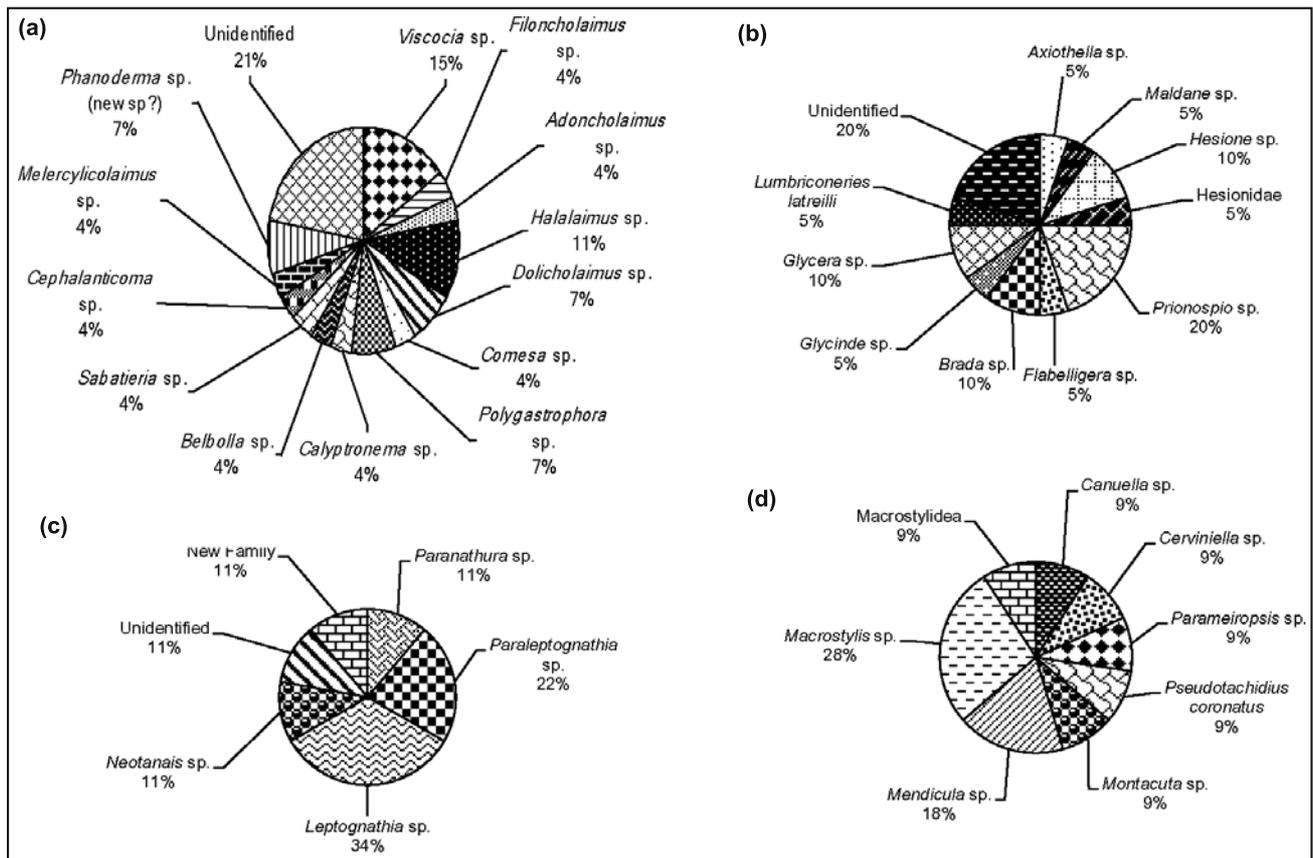


Figure 2. Composition of macrobenthos (a) Nematodes, (b) Polychaetes, (c) Tanaids, and (d) other dominant groups.

surface particles will take, on an average, 40–48 days to reach the seabed (Lampitt and Antia 1997). Sediment organic carbon estimation was carried out using wet oxidation method (El Wakeel and Riley 1957). For the estimation of sediment protein and carbohydrate, air-dried sediment samples were homogenized using a mortar and pestle. Protein estimation was carried out using the Folins-phenol method (Lowry *et al* 1951) using Bovine serum albumin as the standard. Carbohydrates were estimated by phenol-sulphuric acid method using glucose as the standard (Kochert 1978). For sedimentological studies, the sand content was determined after wet sieving through a 63 μm sieve. The silt (63–20 μm) and clay (< 20 μm) contents were determined following the standard pipette analysis method (Folk 1968).

2.2 Data analysis

Subsequently, all the macrobenthic specimens were identified to the lowest possible level under a stereoscopic microscope. All unidentified specimens are referred to by their generic/family names and were considered in single taxonomic category.

All data were subjected to Shapiro-Wilks test to check for normality. All environmental

parameters were subjected to factor analysis. Spearman's coefficient was used to detect significant correlations between parameters.

3. Results

3.1 Faunal composition and abundance

The data presented in this study is based on 87 individuals collected from 23 box cores. The low abundance probably resulted from the sampling artifact, where 69 quadrants (15 \times 15 \times 10 cm) were sub-sampled. A total of seven macrobenthic groups were obtained from the 23 deep-sea sediment samples. Large sized (> 0.5 mm) nematodes were the most diverse group with 14 species (figure 2a). It was followed by polychaetes with 11 species (figure 2b). Crustacea was represented by 12 species, of which Tanaidacea had six species (figure 2c), Harpacticoida had four species and Isopoda had two species (figure 2d). Mollusca were represented by two species, both belonging to the order Veneroida (bivalves; figure 2d). In terms of composition, Nematoda constituted 40% of the total fauna followed by Polychaeta (29%), Tanaidacea (13%), Isopoda (6%), Harpacticoida (6%), Veneroida (4%) and Nemertina (1.5%).

Table 1. Composition (%) of polychaetes and nematodes based on their feeding pattern.

Taxa	Feeding type	%
Polychaetes	Surface deposit feeders	70
	Subsurface deposit feeders	13.33
	Carnivores	16.66
Nematodes	Predatory omnivores	61.54
	Selective deposit feeders	19.23
	Non-selective deposit feeders	7.69
	Epigrowth feeders	11.54

Among the identified nematodes, *Viscosia* sp. (15%) was the most dominant, while the polychaete community was dominated by *Prionospio* sp. (20%). Among tanaiids, *Leptognathia* sp. constituted 34% to the tanaidacea community, followed by *Paraleptognathia* sp. (22%). Other dominant macrobenthos comprised of harpacticoids, bivalves and isopods. Similar to the nematodes, a substantial number of large sized harpacticoids were encountered on the 0.5 mm mesh sieve. A total of four harpacticoid species were obtained viz., *Canuella* sp., *Cerviniella* sp., *Parameiropsis* sp., *Pseudotachidius coronatus* each contributed 9% to the macrobenthic community. Between the two species of Veneroidea, *Mendicula* sp. (18%) was the dominant one followed by *Montacuta* sp. (9%). *Macrostylis* sp. (28%), was the dominant Isopoda, while the contribution by an unidentified isopod species (family Macrostylidae) was 9%. The total density of macrobenthos ranged between zero and 133 ind·m⁻², with a mean density of 44 ± 43 sd ind·m⁻², n = 23. The polychaete community in CIOB was dominated by deposit feeding polychaetes (68.8%), carnivores (18.8%) and subsurface deposit feeders (12.5%; table 1). Only two carnivore species were obtained in the present study viz., *Glycera* sp. and *Glycinde* sp. Nematodes belonging to four different feeding types were obtained (62% were predatory omnivores, 14% selective deposit feeders, 14% epigrowth feeders and 10% non-selective deposit feeders) in the current study. The dominance of deposit feeders over carnivore macrobenthos means that organic matter is the main food for the macrobenthic community in the CIOB. However, very little is known about the trophic roles of other deep-sea macrobenthos, hence feeding type categorization was limited to polychaetes and nematodes.

3.2 Relationship between macrobenthic density and sedimentary environment parameters

Although there was high variability among stations, the macrobenthic density appeared to

be positively correlated with organic carbon (p = 0.002; figure 3a), sediment protein (p = 0.05; figure 3b) and chl-*a* (p = 0.02; figure 3c). It appears that, the macrobenthic density augments with increase in these parameters. In contrast a significant negative trend of macrobenthos (p = 0.009; figure 3d), organic carbon (p = 0.01; figure 3e) and chl-*a* (p = 0.002; figure 3f) was observed with increasing latitude in the southern hemisphere. It suggests a decreasing trend of these parameters with increasing latitude southwards.

Significant positive correlation was observed between chl-*a* and organic carbon (p < 0.05; figure 4). Hence, an increase in chl-*a* enhances the sediment organic carbon and labile organic matter content in the seabed. However, sediment carbohydrate did not show a significant correlation with chl-*a*. Silt-clay-sand (%) did not show any correlation with macrobenthic density, sediment organic carbon, sediment protein and carbohydrate.

Unrotated factor analysis reduced the seven sediment and biological variables to three factors with eigene values greater than 1.0 (table 2). Factor loadings express the relative contributions of original variables to the derived factors. Using a correlation (loading) of 0.7 or greater to indicate a strong contribution to a factor, it is evident that factor 1 was mostly influenced by chl-*a* and organic carbon (figure 5). Factor 1 explained 39% of the total variance of the original measures. Factor 2 explained 31% of the total variance and was influenced mainly by clay, silt and sand. Factor 3 contained 15% of the total variance and was influenced by sediment protein and CHO. Factor 1 through 3 accounted for 85% of the total variance explained by these factors.

3.3 Vertical distribution of macrobenthos

Vertically, fauna was observed down to 30 cm sediment depth (figures 6 and 7a). Highest density was observed at the sediment depth of 2–5 cm (21 ind·m⁻²) whereas the top 0–2 cm had lower density (11 ind·m⁻²; figure 6). Generally, the higher species diversity was in the 2–5 cm sediment section with six species, while the top 0–2 cm had only two species and 5–10 cm section had only four species. The lower 10–30 cm section showed the presence of six species (figure 6). *Capitella minima* and *Odanticoma* sp. were present at greater (15–20 cm) sediment depth.

Sediment organic carbon showed decreasing trends with increasing sediment depth (figure 7b). A similar trend was also observed for sediment protein and carbohydrate. Overall, the top 2 cm sediment section had higher protein value (1.0 mg g⁻¹ dry wt), and below 2–10 cm the values were low (figure 7c). Similar results were observed for CHO

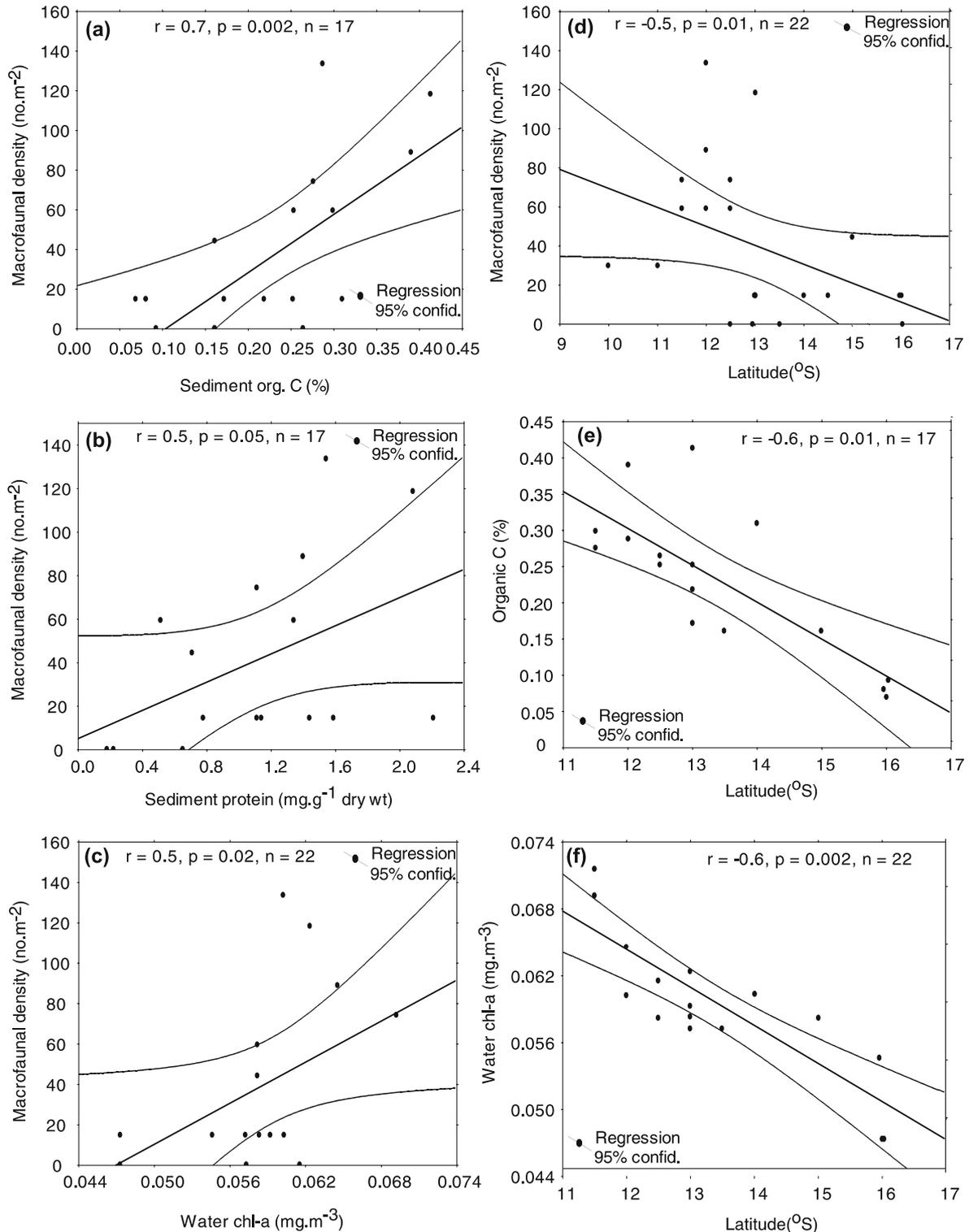


Figure 3. Relationship of macrobenthos and latitude with sediment organic carbon, protein and water chl-*a*.

with higher values in the top 0–2 cm (0.41 mg g⁻¹ dry wt) and low CHO concentrations in 2–10 cm sediment depth (figure 7c). Macrobenthic density showed a significant correlation with sediment protein ($r = 0.8$, $p = 0.03$, $n = 7$) and carbohydrate ($r = 0.8$, $p = 0.02$, $n = 7$) through sediment depth.

4. Discussion

4.1 Faunal composition and abundance

As in most of the benthic sedimentary habitats, the faunal composition was dominated by the

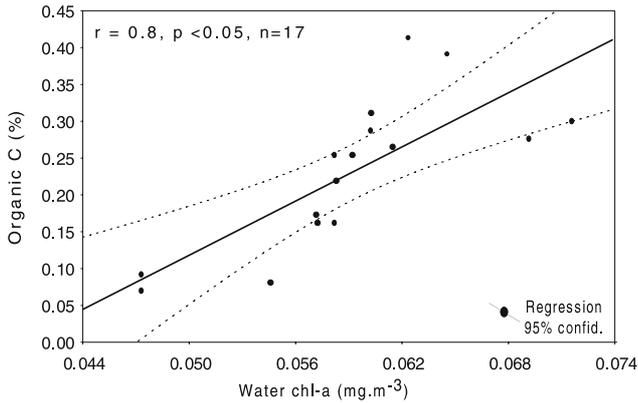


Figure 4. Relationship between water chl-a and sediment organic carbon.

Table 2. Eigene values for the seven environmental variables studied in the CIOB.

Factors	Eigen value	% total variance	Cumulative eigen value	Cumulative %
1	2.71	38.76	2.71	38.76
2	2.20	31.38	4.91	70.14
3	1.03	14.66	5.94	84.80

nematodes and polychaetes with mean density of $44 \text{ ind}\cdot\text{m}^{-2}$. The low density in the abyssal CIOB was probably due to the lower primary productivity (PP) in the surface waters. According to Matondkar *et al* (2005) the surface water PP values in CIOB ranged between $9.06 \text{ mg C m}^{-2}\text{d}^{-1}$ and $103.4 \text{ mg C m}^{-2}\text{d}^{-1}$, which is considerably lower than in the other oceans (table 3). Similarly, organic carbon values seem to be the lowest in Central Indian Ocean in comparison with other known deep-sea areas. The low organic content in the CIOB (0.07 to 0.41% in the present study) is attributed to low sediment accumulation rates (Pattan *et al* 2005) that allow more remineralization at the sediment water interface. However, comparisons between different deep-sea macrobenthic studies poses a problem due to the varying sieve sizes used (table 3). Kröncke *et al* (2003) used a sieve size similar to that of the present study and reported a very low density ($15 \text{ ind}\cdot 0.25 \text{ m}^{-2}$) of macrobenthos in the deeper stations in the eastern Mediterranean. These values were comparable with those of other studies from Indian Ocean (Ingole *et al* 1992; Pavithran *et al* 2007). In contrast, work carried out by Sibuet *et al* (1989) using a sieve size of 0.25 mm reported a very high density of macrobenthos ($95\text{--}2159 \text{ ind}\cdot\text{m}^{-2}$) from the Atlantic Ocean. Comparatively in studies by Glover *et al* (2002) in the Pacific Ocean with a sieve size of 0.3 mm, the polychaete density, which is the dominant macrofauna group, ranged between 9 and $84 \text{ ind}\cdot 0.25 \text{ m}^{-2}$. Though the macrofaunal density

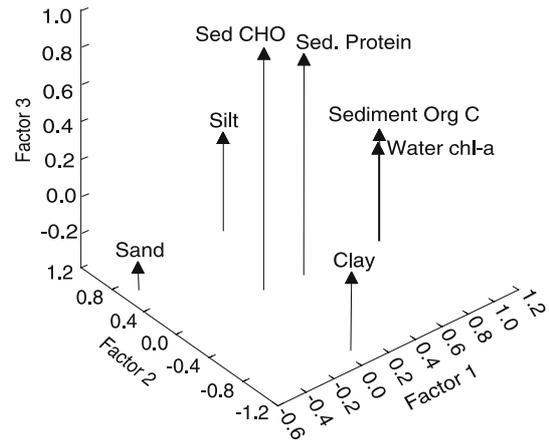


Figure 5. Factor analysis of water and sediment parameters.

in the CIOB is very low compared to the above-mentioned studies it can be attributed to the difference in sieve sizes. However, all the studies point towards the fact that macrobenthic abundance is related to the overhead production (table 3). Hence the possibility of low abundance of macrobenthos in the CIOB can be due to a combination of the above discussed factors.

Deep-sea macrobenthos are known to be filter feeders, deposit feeders or predator/scavenger (predating, e.g., on meiofauna), but the majority of them are known to be deposit feeders. The feeding type of the dominant groups, nematodes and polychaetes suggests that the area is dominated by deposit feeders.

Among the polychaetes, *Prionospio* sp. was the most dominant, because they are opportunistic deposit feeders (Fauchald and Jumars 1979; Santosa *et al* 2009). 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 could adapt to the less productive CIOB for their survival.

In the present study, the feeding type categorization of nematode is based on the basis of shallow water feeding strategies described by Wieser (1953) and Tietjen and Lee (1977). The most dominant predatory omnivores were *Viscosia* sp., *Polygastrophora* sp. and *Dolicholaimus* sp., followed by *Filoncholaimus* sp., *Adoncholaimus* sp., *Calyptonema* sp., *Belbolla* sp., *Metacylicolaimus* sp. and *Trileptium* sp., *Leptosomatium* sp. and *Halalaimus* sp. were the most dominant selective deposit feeders. *Cephalanticoma* sp. and *Sabatieria* sp. were the non-selective deposit feeders, while *Comesa* sp. and *Phanoderma* sp. were

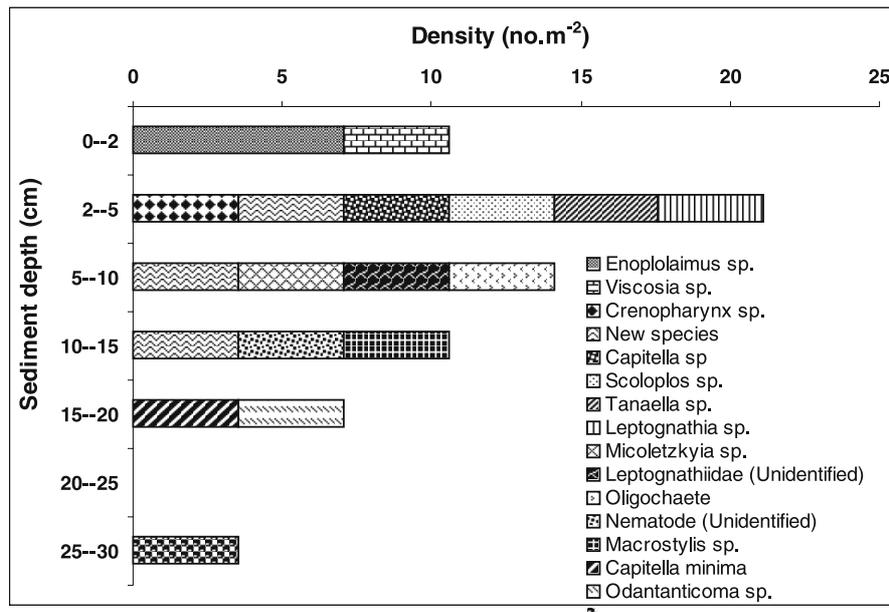


Figure 6. Vertical distribution of macrobenthos in the sediment.

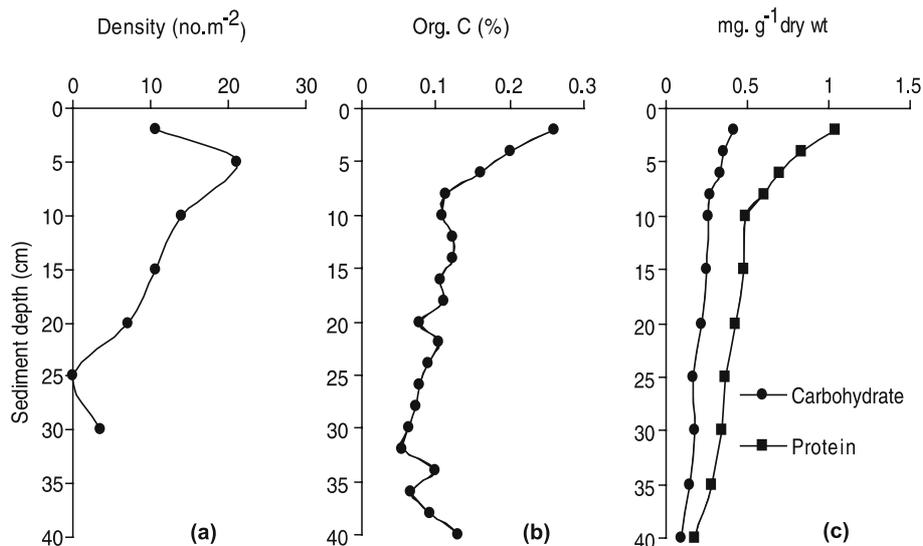


Figure 7. Vertical distribution of (a) macrobenthos density, (b) sediment organic carbon and (c) sediment protein and carbohydrate.

the epigrowth feeders. However, the predator-prey encounter in the deep sea would be much less than that of the coastal environment; hence, the feeding strategy might vary in the deep sea. It would also depend on the strike rate of the predator and their success as predators in the deep sea (Moens *et al* 1999).

According to various benthic studies, the structure of the macrobenthos depends on the feeding modes of the species present, which in turn depend on the quality of available food (Dauwe *et al* 1998; Wieking 2002; Kröncke *et al* 2003). Fresh organic matter will result in abundance of species mainly

feeding at the sediment surface or in the benthic boundary layer, while subsurface deposit-feeders and endobenthic predators have been found to be related to total organic carbon levels (Gaston 1987; Maurer *et al* 1994; Dauwe *et al* 1998) or to sediments with more refractory material (Flach and Heip 1996; Gutiérrez *et al* 2000; Kröncke *et al* 2003).

In the present study, the sedimentary proteins (mean: $1.0 \text{ mg} \cdot \text{g}^{-1}$) were higher than the carbohydrates ($0.4 \text{ mg} \cdot \text{g}^{-1}$). Higher protein to carbohydrate ratio indicates the presence of fresh flux (Danovaro *et al* 1993) and appears to be the most

Table 3. Comparison of macrobenthic data between different deep-sea areas.

Area	Depth (m) mean	No. of box cores	Sieve size (mm)	Abundance per 0.25 m ²	Total number		Polychaete density/0.25 m ²	Polychaete (no. of sps.)	OC (%)	PP (gCm ⁻² yr ⁻¹)
					Species	Groups				
Eastern Mediterranean										
Me 25/1 ¹	4580	4	0.5	60 ± 30	20	-	33 ± 31	9	0.48	-
Me 40/3 ¹	4366	8	0.5	15 ± 13	8	-	13.5 ± 13	5	0.53	-
Northeast Atlantic										
Cape Verde Abyssal Plain ²	4600	5	0.25	232 [•]	-	-	~50	39	0.29	120 [*]
Vema Fracture Zone ³	5100	8	0.25	860 [•]	-	-	-	-	17# and 5.5 ^{***}	-
Demerara Plain ³	4420	8	0.25	2159 [•]	-	-	-	-	50# and 5.5 ^{***}	-
Cape verde Basin ³	5190	6	0.25	100 [•]	-	-	-	-	13# and 2.5 ^{***}	-
Cape verde Basin ³	4950	7	0.25	95 [•]	-	-	-	-	16# and 2.5 ^{***}	-
Western Atlantic										
Venezuela Basin ⁴	5050	-	0.3	238 [•]	-	-	-	-	0.59-0.85	150-250 ^{**}
Pacific Ocean										
EQPAC 0°N ⁵	4300	3	0.3	-	-	-	84 ± 27.9	73	-	230
EQPAC 2°N ⁵	4400	4	0.3	-	-	-	60 ± 6.4	82	-	200
EQPAC 5°N ⁵	4400	3	0.3	-	-	-	80 ± 19.1	76	-	155
EQPAC 9°N ⁵	4900	3	0.3	-	-	-	13 ± 2.3	23	-	140
HOT 23°N ⁵	4800	4	0.3	-	-	-	9 ± 1.7	14	-	105
DOMES A ⁵	5100	47	0.3	-	-	-	16 ± 0.8	104	-	140
PRA ⁵	4800	16	0.3	-	-	-	65 ± 16.8	100	-	130
ECHO 1 ⁵	4500	15	0.3	-	-	-	42 ± 5.5	113	-	135
Indian Ocean										
Southwest Indian Ocean ⁶	4349	8	0.5	79 [•]	-	10	56 ± 9 [•]	-	-	-
Central Indian Ocean ⁷	5322	6	0.5	48-704 [•]	-	9	54.6 ± 63.5 [•]	-	0.28-0.4	76.5-103.4 ^{**}
Central Indian Ocean ⁸	5150	26	0.5	30 ± 21 [•]	27	12	12 [•]	11	0.2	-

• Macrobenthic density (ind·m⁻²); * PP values (gCm⁻²yr⁻²); ** PP values (mg C m⁻² d⁻¹); # C flux (mg·m⁻²·yr⁻¹); *** POC mg·g⁻¹.
References: ¹Kröncke et al (2003); ²Cosson et al (1997, 1998); ³Sibuet et al (1987); ⁴Richardson and Young (1987); ⁵Glover et al (2002); ⁶Ingole et al (1992); ⁷Ingole et al (2001); ⁸Pavithran et al (2007).

probable reason for the relative abundance of surface deposit feeding fauna in the CIOB and lower ratio indicates the presence of aged organic matter (Danovaro *et al* 1993). Thus, availability of sedimentary proteins is an important factor regulating the abundance of deep sea benthic consumers. The labile part of the organic matter consists of the major fraction of carbohydrates and proteins, which are assumed to be easier to digest and assimilate by the benthic consumers, whilst, the refractory matter is composed of complex substances like humic acids and fulvic acids which is slowly broken down by bacteria into more readily assimilable compounds (Danovaro *et al* 2001).

The meiofaunal density in the CIOB is very low (Ingole *et al* 2005) and no correlation exists between macro- and meiofaunal abundances (Pavithran 2008). Hence, meiofauna being directly consumed by macrofauna as a major food source appears uncommon in CIOB. Further, the dominance of deposit feeders over carnivore macrobenthos means that organic matter is the main food for the macrobenthic community in the CIOB. A similar result was documented by Iken *et al* (2001) in the Porcupine Abyssal Plain region, showing a dominance of deposit feeders over predators/scavengers.

4.2 Relationship between macrobenthos and sedimentary environmental parameters

Organic matter is known to be the first order parameter to control the faunal distribution in the deep sea (Danovaro *et al* 2001; Kröncke *et al* 2003). The macrobenthic density tends to show a significant correlation with the sediment organic carbon content (figure 3a) and this pattern is well established for the Indian Ocean (Ingole *et al* 1992; Pavithran *et al* 2007). Positive correlation of macrobenthos and sediment protein (figure 3b) and no correlation between macrobenthos and CHO could be due to the dependence of these organisms on fresh organic matter. The significant positive correlation between surface water chl-*a* and organic carbon (figure 4) as well as macrobenthos and chl-*a* (figure 3c), reveals that the euphotic primary production contributes a major fraction to the available organic matter reaching the abyssal depths and hence providing food to the deep-sea macrobenthos in CIOB. Furthermore, macrobenthic abundance did not show any relation with sediment texture, which could be due to the smaller depth differences between the sampling stations.

An inverse relationship of macrobenthos, sediment organic carbon and surface water chl-*a* with latitude (figure 3d-f) also advocates the importance of surface productivity and sediment organic matter to the macrobenthos. It indicates that

food available for benthos decreases with increasing latitudes and corresponds with the decrease in macrobenthos. In the study area, the influence of landmasses decreases considerably towards the south; 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 phytoplankton and 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). 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 ($76.26 \text{ mg C m}^{-2}\text{d}^{-1}$) 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 ($103.4 \text{ mg C m}^{-2}\text{d}^{-1}$). This confirms that the surface production decreases with increasing latitude southwards in the CIOB, ultimately responsible for the observed latitudinal variation of macrobenthos. Latitudinal species diversity has been studied by Rex *et al* (1993), in the S. Atlantic wherein a poleward decrease in diversity of isopods, gastropods and bivalves has been observed. Lambshead *et al* (2000) reported an increase in nematode diversity towards higher latitudes in N. Atlantic. Similarly, in the S. Atlantic, mollusk showed a significant decrease in diversity towards higher latitudes whereas the crustaceans like isopods did not show any significant pattern (Stuart *et al* 2003). While discussing the global patterns of benthic standing stock, Rex *et al* (2006) opined that decline in benthic abundance is related to the distance from productive coastal waters and to the rate and seasonal pattern of nutrient input from overhead production (Falkowski *et al* 1998; Rex *et al* 2000).

4.3 Vertical distribution of macrobenthos

Generally the macrobenthos are dominant in the top 0–1 cm sediment depth (Witte 2000), however in the present study a peak in density as well as diversity was obtained in the 2–5 cm sediment depth. This could be due to the surface and sub-surface deposit feeders moving to the lower depth from the upper sediment layer probably due to the disturbance caused by the box corer during sampling. This can be further confirmed from the work carried out by Witte (2000), wherein it has been argued that the recovery layer of the organisms need not necessarily represent the layer of main activity of the individual, particularly those with vertical tubes, which may feed and live on/in the

surface layer but escape into deeper layers when disturbed by the box corer. 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 (Ingole *et al* 2005).

It is also known that, some macrobenthos 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 (Jumars *et al* 1990; Flach *et al* 1999). Macrobenthic infaunas, especially deposit feeders, are the major agents of particle mixing, also known as bioturbation. Bioturbation leads to increased oxygenation and mineralization rates in sediments (Aller 1994). Dauwe *et al* (1998) found that sediments containing intermediate quantity and quality of organic matter displayed a higher diversity of trophic groups and a deeper distribution of infauna and that minimal potential mixing was associated with the highest quality of organic matter. Consequently, bioturbation not only affects the vertical distribution of organic matter along the sediment profiles, but also potentially increases the available food concentration at depths within the sediment (Ingole 2004).

Capitellid polychaetes, which are subsurface deposit feeders, were observed in the upper sediment layer of 2–5 cm as well as at greater sediment depths (25–30 cm) (Hayashi 1988; D'Andrea and Lopez 1997). The values of organic carbon, protein and carbohydrate in the present study decreased with increasing sediment depth (figure 7), 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 *et al* 2000). 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, 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 a large predominance of carbohydrates and possibly different adaptive mechanisms to optimize the exploitation of this trophic source.

5. Conclusions

From the current study it can be concluded that CIOB is mainly dominated by deposit feeding polychaetes and predatory omnivorous nematodes, since the macrobenthic distribution depends on the availability of surface primary production and their abundance is strongly related to

sedimentary organic matter. Vertically, the presence of fauna at deeper sediment depths could be due to the transport of organic matter by the bioturbators hence facilitating the distribution of fauna in deeper depths.

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