



Polychaete community structure in the South Eastern Arabian Sea continental margin (200–1000 m)

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ABSTRACT

Macrofaunal polychaete communities ($> 500 \mu\text{m}$) in the South Eastern Arabian Sea (SEAS) continental margin (200–1000 m) are described, based on three systematic surveys carried out in 9 transects (at ~ 200 m, 500 m and 1000 m) between $7^{\circ}00'$ and $14^{\circ}30'N$ latitudes. A total of 7938 polychaetes belonging to 195 species were obtained in 136 grab samples collected at 27 sites. Three distinct assemblages were identified in the northern part of the SEAS margin (10 – $14^{\circ}30'N$), occupying the three sampled depth strata (shelf edge, upper and mid-slope) and two assemblages (shelf edge and slope) in the south (7 – $10^{\circ}N$). Highest density of polychaetes and dominance of a few species were observed in the shelf edge, where the Arabian Sea oxygen minimum zone (OMZ) impinged on the seafloor, particularly in the northern transects. The resident fauna in this region (*Cossura coasta*, *Paraonis gracilis*, *Prionospio* spp. and *Tharyx* spp.) were characteristically of smaller size, and well suited to thrive in the sandy sediments in OMZ settings. Densities were lowest along the most northerly transect (T9), where dissolved oxygen (DO) concentrations were extremely low ($< 0.15 \text{ ml l}^{-1}$, i.e. $< 6.7 \mu\text{mol l}^{-1}$). Beyond the realm of influence of the OMZ (i.e. mid-slope, ~ 1000 m), the faunal density decreased while species diversity increased. The relative proportion of silt increased with depth, and the dominance of the aforementioned species decreased, giving way to forms such as *Paraprionospio pinnata*, *Notomastus* sp., *Eunoe* sp. and lumbrinerids. Relatively high species richness and diversity were observed in the sandy sediments of the southern sector (7 – $9^{\circ}N$), where influence of the OMZ was less intense. The area was also characterized by certain species (e.g. *Aionidella cirrobranchiata*, *Isolda pulchella*) that were nearly absent in the northern region. The gradients in DO concentration across the core and lower boundary of the OMZ, along with bathymetric and latitudinal variation in sediment texture, were responsible for differences in polychaete size and community structure on the SEAS margin. Spatial and temporal variations were observed in organic matter (OM) content of the sediment, but these were not reflected in the density, diversity or distribution pattern of the polychaetes.

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1. Introduction

Continental margins are geologically complex and hydrodynamically active regions of the oceans (Levin and Dayton, 2009; Menot et al., 2010; Levin and Sibuet, 2012), where disproportionately large amounts of organic matter (OM) are deposited and remineralized by benthic organisms (Premuzic et al., 1982; Walsh et al., 1985). The Arabian Sea is one of the most productive regions of the world ocean, as a consequence of intense upwelling during

the southwest monsoon, and reversal in circulation and deepening of mixed layer during the northeast monsoon (Qasim, 1977, 1982). This ultimately leads to a high export flux of particulate organic matter (POM) from the euphotic zone to sub-surface waters (Sen Gupta and Naqvi, 1984; Nair et al., 1989; Haake et al., 1993; Rixen et al., 1996; 2000; Cowie, 2005; Naqvi et al., 2005). The consistently high, albeit seasonally fluctuating, supply of POM, and relatively weak subsurface flow results in the rapid utilization of oxygen and development of an intense oxygen minimum zone (OMZ) in the intermediate waters of the Arabian Sea (Sverdrup et al., 1942; Ryther and Menzel, 1965; Wyrski, 1973; Kamykowski and Zentara, 1990; Olson et al., 1993; Sarma, 2002; Helly and Levin, 2004; Gooday et al., 2010; Hunter et al., 2011). Within

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OMZs, mid-water recycling of organic matter is suppressed, allowing much more of it to sink to the bottom without being recycled (Wyrtek, 1962; Angel, 1984; Haake et al., 1993; Ittekkot et al., 1996; Witte, 2000; Cowie 2005). Over 285,000 km² of continental margin sediments in the Arabian Sea are impacted by the extremely oxygen-deficient water of this OMZ (DO < 0.2 ml l⁻¹), which extends between ~150 and 1500 m depths (Qasim, 1982; Helly and Levin, 2004; Hughes et al., 2009; Hunter et al., 2012).

Recent predictions of OMZ expansion mediated by climate change (Stramma et al., 2010) have made studies of biological communities associated with these zones increasingly relevant. Studies carried out at bathyal and abyssal depths of the western and northern Arabian Sea (Wouds and Cowie, 2009; Levin et al., 2009; Hughes et al., 2009; Murty et al., 2009) have provided a basic understanding of benthic faunas and processes where the Arabian Sea OMZ impinges on the seafloor. These studies underline the importance of the Arabian Sea margin in carbon cycling as well as the role of benthic fauna in ecosystem processes (Lamont and Gage, 2000; Levin et al., 2000; Cowie and Levin, 2009; Gooday et al., 2009; Hughes et al., 2009; Levin et al., 2009; Hunter et al., 2012). Several works have made the observation that OMZ-impacted sediments are dominated by smaller-sized organisms among the macrofauna, which are better suited for oxygen uptake in hypoxic conditions (Levin, 2003; Hunter et al., 2012). Along the eastern Arabian Sea margin, the benthos of the shelf and inshore sediments are relatively well described (e.g., Jayaraj et al., 2008a,b; Joydas and Damodaran, 2009; Musale and Desai, 2010), while beyond 200 m, a few investigations have been carried out on the qualitative and quantitative aspects of macrofauna (Ingole et al., 2010) and their role in biogeochemical cycling under OMZ conditions (Hunter et al., 2012).

Polychaetes are the dominant taxon in continental margin sediments (Grassle and Maciolek, 1992; Blake and Grassle, 1994; Ward and Hutchings, 1996; Levin et al., 2000; 2009; Narayanaswamy et al., 2005; Hughes et al., 2009) and the species assemblage and distribution patterns of this group tend to reflect the distribution patterns of macrofauna as a whole (Fauchald, 1973; Hughes et al., 2009). Detritus feeding polychaetes obtain food directly from the organic matter in sediments, and they are best adapted for the rapid consumption of OM occurring in concentrated patches or delivered in pulses (Van Nuyter et al., 2009). *In situ* deep-sea enrichment experiments have shown that the initial processing of OM is dominated by polychaetes, particularly the surface deposit feeders, which thereby play a vital role in the decomposition of phytodetritus (Aberle and Witte, 2003). Trophic interactions within the sediments result in further mixing of the OM into deeper layers of sediments, which is reported to occur at high rates in continental slope settings (Levin et al., 1997; Witte et al., 2003; Sweetman and Witte, 2008). Apart from their direct role in OM assimilation, the movement and burrowing activities of polychaetes result in redistribution of OM in the sediments, altering its availability for degradation and remineralization by microbial communities (Gilbertson et al., 2012; Laverock et al., 2013). Most polychaetes have pelagic larval stages that enrich the plankton community and form a food source for many organisms in the water column. The key role of polychaetes in the benthic food web, as well as their importance in the pelagic communities as planktonic larvae, makes them of central importance in benthic–pelagic coupling processes. Assimilation and mineralization of organic carbon (C) and nitrogen (N) by benthic communities are strongly influenced by oxygen availability on and within seafloor sediments (Hunter et al., 2012). The Arabian Sea OMZ, which is responsible for the enhanced OM deposition to the sediments below it, also has profound impacts on the distribution and abundance of the fauna that play a vital role in the remineralization of these materials (Helly and Levin, 2004; Cowie and Levin, 2009; Gooday et al., 2009; Hughes et al., 2009; Hunter et al., 2012).

Based on the current understanding of OMZ-impacted benthic communities, the following hypotheses are set in this study. (a) There exists significant spatial (bathymetric and latitudinal) and temporal heterogeneity in the polychaete community structure in the South Eastern Arabian Sea (SEAS) margin. (b) The community changes are affected by gradients in environmental factors, particularly oxygen availability, sediment nature and OM. Based on a detailed investigation of benthic polychaete communities in the SEAS continental margin (200–1000 m), we test the aforementioned hypotheses by (i) characterization of the benthic environment and its spatio-temporal variations, (ii) describing the macrobenthic polychaete assemblages, (iii) elucidating the major factors structuring the polychaete communities, and (iv) examining the role of Arabian Sea OMZ and sediment characteristics in determining the distribution and body size of polychaetes. This is the first study of this kind to employ consistent and repeated sampling in this relatively sizeable area.

2. Materials and methods

2.1. Study area and sampling design

The continental margin of the eastern Arabian Sea is characterized by a wider shelf in the north that gradually narrows to the south, while the slope is narrow in the north and wider to the south (Paropkari et al., 1993; Rao and Wagle, 1997). The area under investigation is located between 6° 57' N and 14° 32' N latitude and 72° 58' E and 77° 20' E longitude with depths ranging from 188 to 1100 m. Sampling was carried out at three depths (~200 m, 500 m and 1000 m) along nine bathymetric transects, about 1° apart, designated as T1–T9 (Fig. 1, Appendix A). Macrofauna were collected from the 27 sites, each visited three times between December 2003 and May 2007 during cruises of the Fishery and Oceanographic Research Vessel *Sagar Sampada* (FORVSS 219, 225, 228, 233 and 254). Sea water conductivity (salinity) and temperature in relation to depth were recorded using a Sea-bird CTD rosette. Water samples from the CTD were used to determine dissolved oxygen via Winkler's titration (Strickland and Parsons, 1972).

A Kahlsico No. 214 WA250 modified Smith-McIntyre grab (specially designed for deep-water operations) having a bite area of 0.2 m² was used for collecting sediments. Sediment samples, collected in duplicates, were sieved using a 500 µm mesh and residual sediments along with the organisms were fixed in 5–7% (neutral) formalin (buffered using borax) containing Rose Bengal stain. In the shore laboratory, the samples were again sieved; the polychaetes were separated and identified up to species level. The taxonomic keys of Fauvel (1953) and Day (1967) were primarily used for identification, supplemented with more recent publications (e.g. Fauchald, 1977; Maciolek, 1985; Imajima, 1990). Validity and taxonomic status of species were checked and updated from the World Register of Marine Species (WoRMS, www.marinespecies.org).

2.2. Sediment analysis

Approximately 200 g of sediment was taken from each grab for sediment analysis and dried at 55 °C. The sediment texture was analyzed using a particle size analyzer (Sympatec). The relative composition of each textural class, expressed as percentage of sand (> 63 µm), silt (4–63 µm) and clay (< 4 µm), was calculated. Organic carbon was estimated by wet oxidation method (El-Wakeel and Riley, 1957), which measures the quantity of chromic acid required to oxidize the organic matter in a known quantity of sediment. The sediment (0.2 g) was incubated at 100 °C for ~15 min with a fixed volume (10 ml) of chromic acid; subsequently it was cooled and added to 200 ml of distilled water.

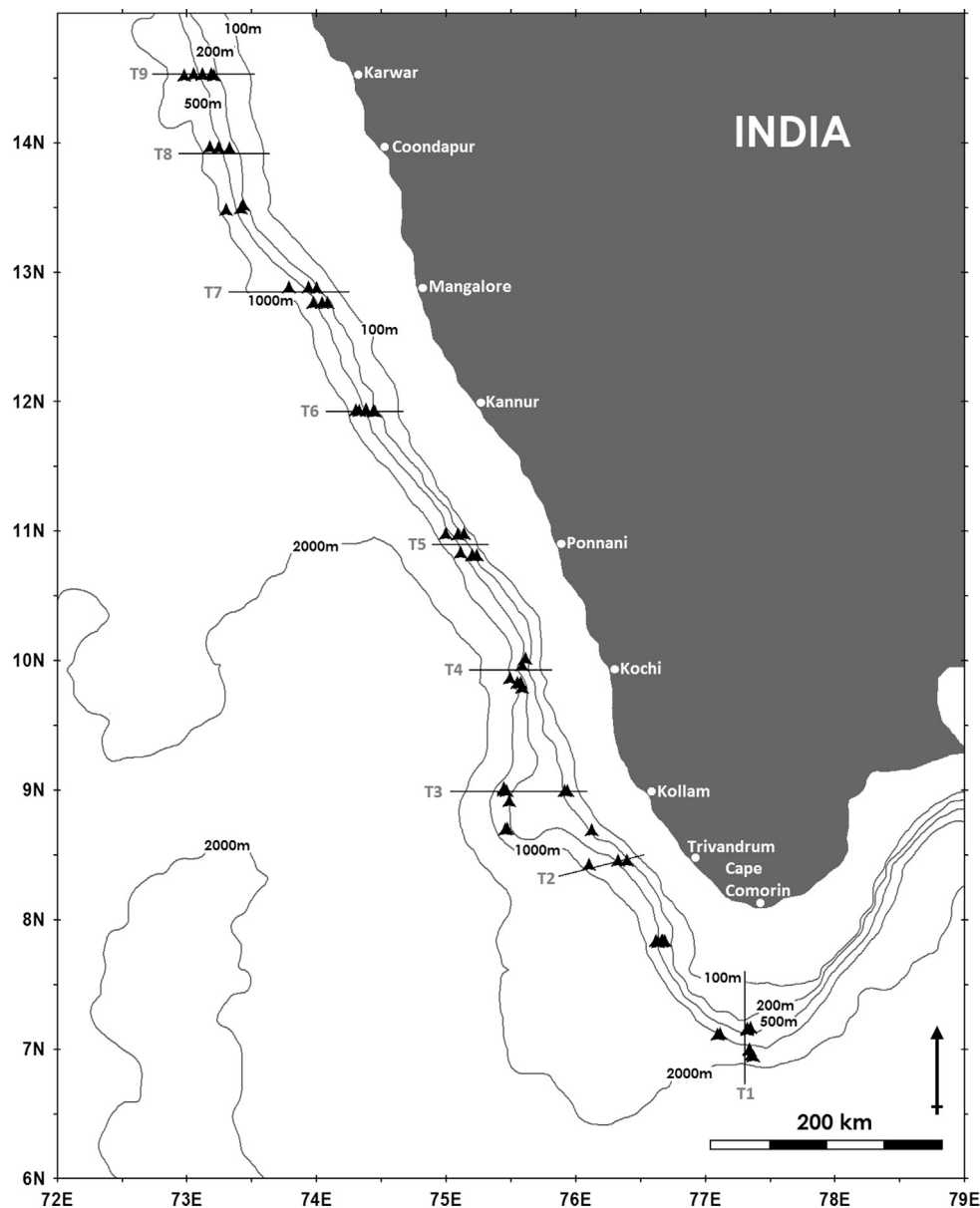


Fig. 1. Map of the South Eastern Arabian Sea continental margin indicating bathymetry, location of transects and sampling sites.

The volume of chromic acid remaining was measured by titration against 0.2 mol l^{-1} ferrous ammonium sulfate solution with phenanthroline indicator. The procedure was simultaneously repeated without the sediment sample, in order to determine blank value. Deducting the titer value of the sample from the blank indicates the volume of chromic acid utilized. The organic carbon content is calculated from this, based on the equivalence of 1 ml of 0.2 mol l^{-1} ferrous ammonium sulfate to $1.15 \times 0.6 \text{ mg}$ of organic carbon (El-Wakeel and Riley, 1957). The values obtained were converted to organic matter (OM) by multiplication with the conversion factor (1.725) provided by Trask (1939), and expressed as percentage of sediment dry weight.

2.3. Data analysis

Prior to community analysis, the sufficiency of sampling was tested using a species accumulation curve (Appendix B). This curve plots the numerical addition of species with the addition of each sample and reaches its asymptote when no new species are added with the addition of samples. Various species estimators, which

predicted the number of species likely to be encountered as the number of samples tends to infinity, were also employed, namely Chao1 (Chao's estimator based on numbers of rare species), Chao2 (Chao's estimator utilizing presence-absence data), Jackknife1 (based on species that occur only on one sample) and Bootstrap (based on proportion of quadrants containing each species).

Polychaete assemblages were characterized using univariate diversity measures, which were analyzed to determine spatio-temporal variations in community structure. The number of species in each sample (S) was used as a direct measure of species richness. This was complimented with the Shannon–Wiener Diversity Index (H'_2), which also takes into account the relative abundance of species within the samples, and is widely used as an absolute measure of diversity when comparing different samples, sites or geographic areas (Magurran, 2003). A graphical visualization of species dominance in each depth category was obtained using k -dominance curves. Mean individual biomass of polychaetes at each station was calculated by dividing the biomass of polychaetes in each sample with their abundance; this value was used as an index of body size of polychaetes. Pearson's correlation

coefficient (r) was used to test the significance of relationship between biological parameters of the polychaete communities (density, species richness, diversity and mean individual biomass), environmental variables (temperature, salinity, DO, OM, sand, silt and clay), depth and latitude.

The significance of spatio-temporal variations in the polychaete abundance was tested using Analysis of Similarity (ANOSIM in PRIMER6) employing average ranked values of Bray–Curtis similarity in square root-transformed species abundance data. The ordination of the sites according to this similarity matrix was visualized by non-metric multi-dimensional scaling (nMDS) using PRIMER package (Clarke and Gorley, 2006). ANOSIM was further employed to confirm the significance of the groups obtained in the nMDS. The percentage contribution of species (through incidence or abundance) towards similarity within the nMDS clusters and dissimilarity amongst them was quantified using the SIMPER procedure; and a step-wise search for combinations of species responsible for the observed ordination was also carried out (BVSTEP in PRIMER6). Correlations between the distribution and abundance of these selected species and environmental variables were tested by Canonical Correspondence Analysis (CCA) using CANOCO 4.5 (ter Braak and Smilauer, 2002).

3. Results

3.1. Environmental parameters

Temperature of bottom water (Fig. 2a) decreased considerably with depth ($r=0.943$, $p<0.01$); while there were no marked temporal and latitudinal distinctions. Variations in salinity with depth and latitude, although minor (34.95–35.42), were found to be consistent. Salinity increased progressively from south to north ($r=0.776$, $p<0.01$), and higher salinity was recorded around 500 m depth in all transects (Fig. 2b). Bottom water DO concentrations (range 0.149 ml l^{-1} at T9 to 1.2 ml l^{-1} in T2, Fig. 2c) increased with depth ($r=0.387$, $p<0.01$). Consistently low DO was recorded at the shelf edge ($0.395 \pm 0.165 \text{ ml l}^{-1}$) and intermediate depth (500 m, $0.49 \pm 0.172 \text{ ml l}^{-1}$), with higher value at the deeper sites (1000 m, $0.667 \pm 0.217 \text{ ml l}^{-1}$). DO concentration decreased considerably ($r=-0.26$, $p<0.05$) from the south (T1) to north (T9). According to the varying proportion of its components (sand, silt, clay), five textural classes of sediments could be recognized from the SEAS continental margin; these were sand, silty sand, sandy silt, clayey sand and a homogeneous admixture of sand, silt and clay. The proportion of sand was high at the 200 m sites of all transects (Fig. 2d), and decreased progressively towards deeper sites ($r=-0.66$, $p<0.01$). The finer fractions (silt and clay) contributed over 80% in the deeper sediments (500 and 1000 m). A clear latitudinal distinction was observed in sediment texture, with the relative proportion of sand being higher ($>70\%$ at 200 m and $>50\%$ at 500 m) at the three southern transects (T1–T3) compared to isobathic sites in the north (T4–T9). Total OM content showed significant bathymetric variation, with high values at 1000 m on all transects, but no latitudinal trends were observed. Temporal variations were also significant for OM content, with peak values being recorded during the May 2007 survey (Fig. 2d). The OM had a strong positive correlation with silt content ($r=0.567$, $p<0.01$), which in turn was strongly correlated with depth ($r=0.655$, $p<0.01$).

3.2. Density and diversity of polychaetes

Mean density of polychaetes was the highest at 200 m ($835.4 \pm 534.9 \text{ ind. m}^{-2}$) and decreased significantly ($r=-0.59$, $p<0.01$) with depth ($251.6 \pm 155.7 \text{ ind. m}^{-2}$ at 500 m and

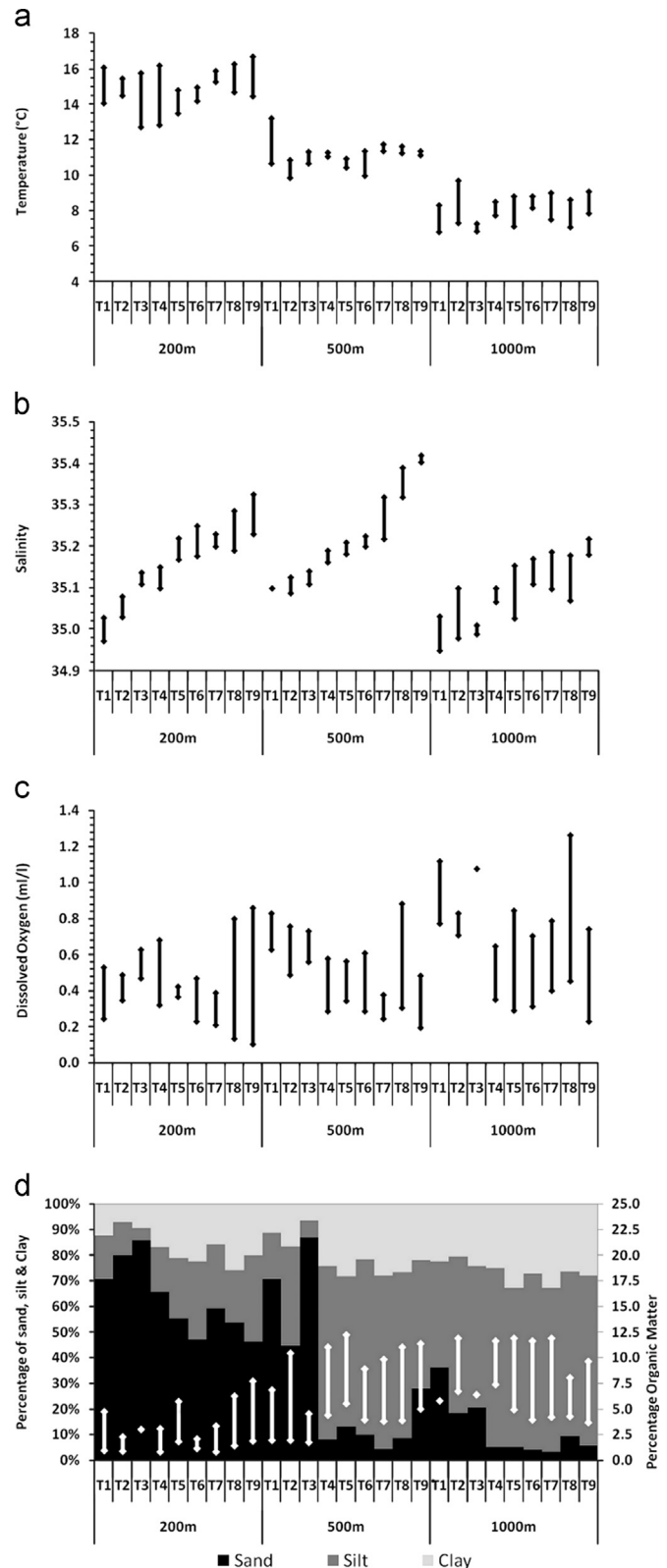


Fig. 2. Range of environmental factors in the 27 sampling sites of the SEAS margin. (a) Temperature ($^{\circ}\text{C}$), (b) salinity, (c) dissolved oxygen (ml l^{-1}), and (d) sediment texture (vertical stack showing percentage composition of sand, silt and clay) and organic matter (white).

$134.7 \pm 154.2 \text{ ind. m}^{-2}$ at 1000 m). Polychaete density did not show any significant latitudinal ($r=0.133$, $P=11\%$) or temporal ($r=0.061$, $P=0.6\%$) trends (Fig. 3). The 136 grab samples collected from 79

stations in the SEAS yielded a total of 195 polychaete species belonging to 107 genera and 37 families. The species accumulation plot (for individual stations) approached the upper asymptote, indicating that the study area was sampled sufficiently (Appendix B). Species estimators calculated using Chao1, Chao2, Jackknife1 and Bootstrap were 195, 220, 236 and 244, respectively. In the present investigation, 80–90% of the estimated numbers of species were obtained. The numerically dominant species in the study area were *Tharyx dorsobranchialis* (11.1% of total polychaetes), *Levinsinia oculata* (8.2%), *Prionospio polybranchiata* (7.9%), *Cossura coasta* (7.7%) and *Tharyx annulosus* (7.6%). Other species represented were *Prionospio*

cirrifera (4.2%), *Paraonis gracilis* (4.1%), *Tharyx sp. 1* (3.9%) and *Paraprionospio pinnata* (3.6%).

Species richness (S) showed no significant bathymetric or temporal trends (Fig. 4); however, southern transects (T1–T3) were more species rich than those of the north. Spatial variations in species diversity (H') were prominent (Fig. 4); the values increasing with depth ($r=0.223$, $p<0.05$) and towards south ($r=0.44$, $p<0.01$). The depth-associated trend in diversity (H') was a reflection of the high dominance at the 200 m sites, and an increase in evenness with depth (Fig. 5). At the 200 m sites, 80% of polychaete abundance was represented by 11 species, while the same proportion of abundance was accounted by nearly 30 and 40 species at 500 m and 1000 m, respectively. Species diversity decreased progressively to the north, with the lowest values in T9 ($H': 2.37 \pm 1.07$). Exceptionally low density, richness and diversity were observed in T4 ($N: 252.8 \pm 515 \text{ ind. m}^{-2}$, $S: 10.66 \pm 2.69$, $H': 2.8 \pm 0.52$) despite prevailing environmental conditions, which were similar to adjacent transects.

3.3. Polychaete assemblages

Multivariate analysis of the dataset revealed bathymetric (ANOSIM $r=0.571$, $P=0.1\%$) as well as regional distinctions in polychaete assemblages while temporal variations were not significant ($r=0.017$, $p=16.7\%$). The species abundance data from the three surveys were therefore pooled for each site (27 sites with 6 samples each) and subjected to ANOSIM and non-metric multi-dimensional scaling (nMDS) analyses. Pair-wise ANOSIM test (Appendix C1) revealed that differences were significant between the 200 m and 500 m assemblages ($r=0.851$, $P=0.2\%$), and also between the 200 m and 1000 m assemblages ($R=0.864$, $P=0.2\%$). Five significant assemblages ($P<0.05$) were obtained in the nMDS ordination at 35% similarity (Fig. 6a). Along the northern transects, three distinct assemblages occupied the three depth strata (groups A–C), while towards the south, they were grouped into shallow (group D) and deep (group E) assemblages. The biological characteristics of these assemblages, along with the prevailing environmental conditions, are detailed in Table 1. In the northern sector (groups A–C), there was a progressive decline in total polychaete abundance with increasing depth, while richness remained more

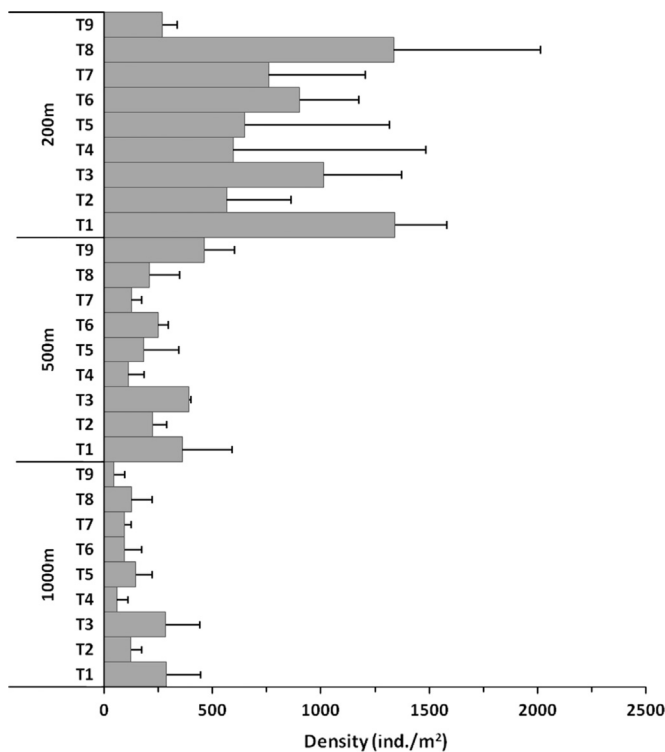


Fig. 3. Density of polychaetes (mean $\pm$ SD) at the 27 sampling sites of the SEAS margin.

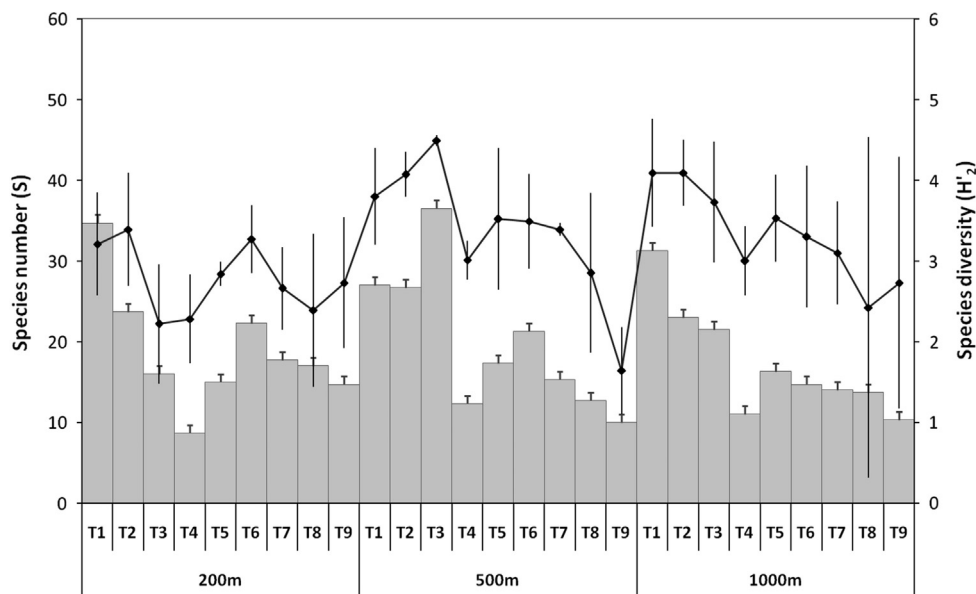


Fig. 4. Diversity indices of polychaetes at the 27 sampling sites of the SEAS margin: species number, S (vertical bars $\pm$ SD) and Shannon–Wiener Diversity, $H' \log_2$ (line graph $\pm$ SD).

or less unchanged. The higher polychaete abundance in group A was a result of dominance of small-sized species (e.g. *P. polybranchiata*, *P. gracilis*, *L. oculata*, *Tharyx* spp. and *C. coasta*) on the shelf edge (Fig. 6b), which resulted in low diversity in the region. The deeper sites were dominated by malidanids, capitellids, lumbrinerids, terrellids and ampharetids, which are characterized by larger body size. A similar depth-associated distinction was observed in the southern sector (groups D & E), where density decreased and diversity increased with depth. However, the occurrence of characteristic species unique to the southern transects (*Aonidella cirrobranchiata*, *Aricidea capensis* and *Isolda pulchella*), and high species richness, caused these assemblages to be distinct from isobathic assemblages in the north. The species contributing to the distinction among these assemblages were identified using SIMPER tool and detailed in Appendix C2.

3.4. Relating assemblages to environmental variations

Polychaete density and species richness were positively correlated with sand content ($p < 0.001$), which decreased towards higher depths. Species diversity (H') showed a weak positive correlation with depth ($p < 0.05$), but was not significantly

correlated with sediment characteristics ($p > 0.05$). Species richness (S) and diversity were positively correlated with DO level ($p < 0.05$), which decreased considerably from south to north (Table 2). Individual polychaete biomass was positively correlated with depth, silt content and OM ($p < 0.001$), and negatively correlated with sand content ($p < 0.001$). Comparison of nMDS ordinations of species abundance and environmental data revealed that the pattern of species distribution corresponded well to the patterns of variations in the measured environmental parameters (Fig. 6a, b).

The Canonical Correspondence Analysis (CCA) ordination (Tables 3 and 4, Fig. 7) shows the extent of inter-dependence between environmental factors and how they influence the distribution of 35 selected species (identified using SIMPER and BVSTEP). The CCA axes 1 and 2 explained 27% and 22% of variation in species distribution, respectively (Table 3). Axis 1 (eigenvalue 0.403) showed a strong negative correlation with salinity and weak positive correlation with sand content. Both these factors showed latitudinal trends in the SEAS. However, all other factors, which contributed very little to this eigenvector, did not show significant latitudinal trends. Axis 2 (eigenvalue 0.327), which was strongly correlated with depth, and the bathymetric variations in temperature, sediment texture, OM and DO, contributed significantly to this eigenvalue. CCA axes 3 and 4 together explained 13.3% of differences among the sampling sites (eigenvalue 0.231 and 0.200, respectively). Species such as *Isolda pulchella*, *Aonidella cirrobranchiata*, *Aricidea capensis* and *Aricidea* sp. 1 were characteristic of the sandy sediments along the southern SEAS shelf edge. Towards the north, salinity increased at this depth contour, along with silt and OM content, and *Tharyx* spp. and *P. cirrifera* showed strong affinity to these conditions. Silt, OM and DO progressively increased with increasing depth. A latitudinal distinction was also evident on the upper slope (500 m), as a result of the strong salinity gradient. At this depth *Magelona cincta*, *Spiophanes bombyx*, *Spiophanes* sp. 1, *Goniada eremita*, *Aricidea* sp. 2 and *Laonice cirrata* were characteristic forms in the south, while *P. pinnata*, *Tharyx marioni*, *Prionospio ehlersi*, etc. typified the assemblages in the north. At 1000 m depth, salinity was relatively low throughout the study area (no latitudinal trend), and finer sediment fractions, along with OM and DO, were highest. Typical deep-water species, such as *Notomastus* sp., *Sigambra constricta* and *Lumbrineris* spp., showed affinity to these conditions. Some species such as *C. coasta*, *Poecilochaetus serpens*, *Amphitrite rubra* and *Aglaophamus dibranhis* were apparently not influenced by any of the environmental factors included in the analysis, and were found ubiquitously throughout the SEAS margin.

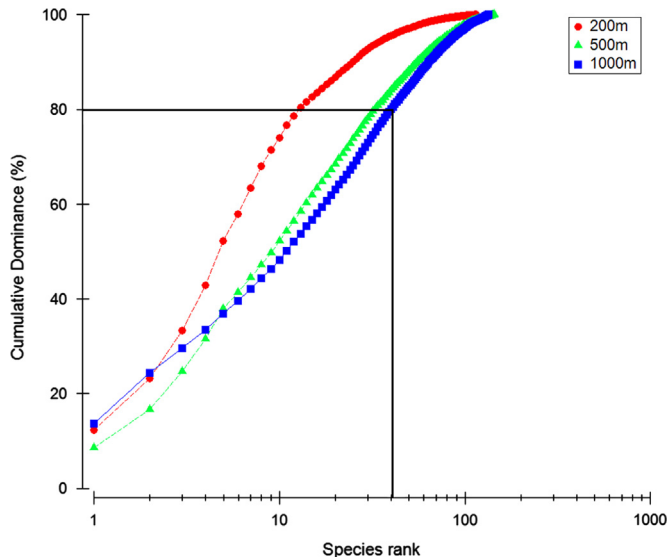


Fig. 5. Species rank-accumulation (k-dominance) curves for polychaetes at 3 depth categories of SEAS margin, using pooled data from 9 transects.

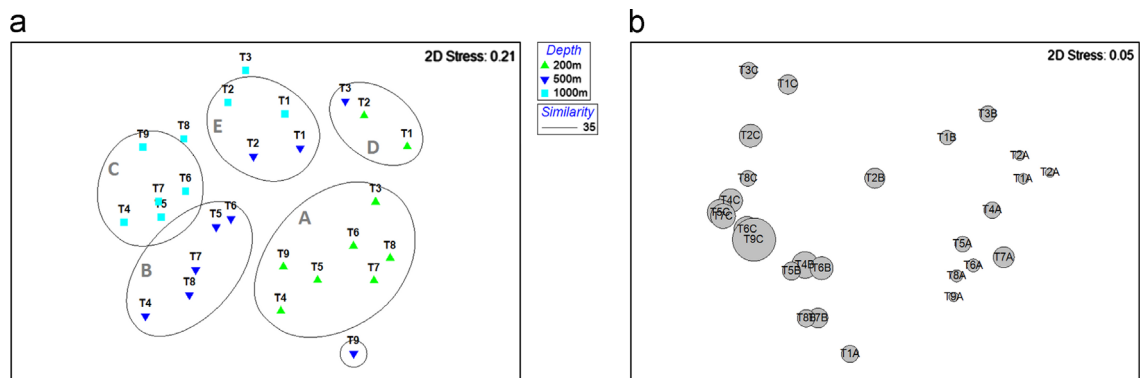


Fig. 6. Two-dimensional MDS plots. (a) Polychaete assemblages (A–E) of the SEAS margin using square root transformed species abundance data (Bray–Curtis similarity) and (b) environmental factors (temperature, salinity, DO and composition of sand, silt, clay & organic matter), using log-transformed and normalized data from 27 sampling sites (Euclidean distance), with superimposed bubbles indicating mean body size of polychaetes at each site. Samples are labeled by transect (T1–T9) and depths (A: 200 m, B: 500 m, and C: 1000 m).

Table 1
Biological characteristics of the five assemblages identified from the SEAS continental margin and the prevailing environmental conditions of the respective regions.

Assemblage	Northern sector shelf edge Group A 200 m: T3–T9	Northern sector upper slope Group B 500 m: T4–T8	Northern sector mid-slope Group C 1000 m: T4–T9	Southern sector shelf edge Group D 200 m: T1–T2 500 m: T3	Southern sector upper and mid-slope Group E 500 m: T1–T2 1000 m: T1–T3
Sediment texture	Clay: 18.7% Silt: 22.3% Sand: 59%	Clay: 25.8% Silt: 65.4% Sand: 8.8%	Clay: 28.6% Silt: 66% Sand: 5.4%	Clay: 8.8% Silt: 12.9% Sand: 78.3%	Clay: 18.6% Silt: 42.1% Sand: 39.3%
DO	0.423 ± 0.286 ml l ⁻¹ (18.87 ± 12.76 μmol l ⁻¹)	0.449 ± 0.169 ml l ⁻¹ (20.01 ± 7.54 μmol l ⁻¹)	0.586 ± 0.250 ml l ⁻¹ (26.14 ± 11.15 μmol l ⁻¹)	0.465 ± 0.148 ml l ⁻¹ (20.74 ± 6.60 μmol l ⁻¹)	0.805 ± 0.183 ml l ⁻¹ (35.90 ± 8.16 μmol l ⁻¹)
OM (%)	2.7 ± 1.8	7.3 ± 2.9	7.5 ± 2.8	2.4 ± 1.6	6.4 ± 2.8
Density (ind./m²)	747 ± 440	213 ± 148	176 ± 92	767 ± 181	254 ± 148
Species number	16 ± 6	16 ± 6	13 ± 7	31 ± 9	26 ± 9
Diversity (H')	2.63 ± 0.64	3.25 ± 0.63	3.01 ± 1.07	3.56 ± 0.75	3.97 ± 0.48
Dominant and characteristic species (density %)	<i>Cossura coasta</i> (14%) <i>Prionospio cirrifera</i> (10%) <i>Tharyx dorsobranchialis</i> (10%) <i>Prionospio polybranchiata</i> (9%) <i>P. pinnata</i> (8%) <i>Tharyx annulosus</i> (3%) <i>Nephtys dibranchis</i> (2%)	<i>Prionospio pinnata</i> (13%) <i>P. ehlersi</i> (11.5%) <i>Laonice</i> sp. (7%) <i>Lumbrineris meteorana</i> (7%) <i>Spiophanes</i> sp. 1 (6.7%)	<i>Cossura coasta</i> (18%) <i>Notomastus fauveli</i> (9%) <i>Tharyx dorsobranchialis</i> (8.5%) <i>Notomastus aberans</i> (8%) <i>Nereis</i> spp. (6%) <i>Sigambra parva</i> (5%)	<i>Aonidella cirrobranchiata</i> (9%) <i>Tharyx dorsobranchialis</i> (6.3%) <i>Magelona cincta</i> (6.2%) <i>Aricidea belgicae</i> (6.2%) <i>Laonice cirrata</i> (5%) <i>Isolda pulchella</i> (2%) <i>Cirrophorus branchiatus</i> (1.5%)	<i>Notomastus aberans</i> (9%) <i>Cossura coasta</i> (7%) <i>Prionospio</i> spp. (5%) <i>Notomastus</i> sp (4%) <i>Onuphis holobranchiata</i> (4%) <i>Lumbrineris tetraura</i> (2%) <i>Diopatra neapolitana</i> (1%)

Table 2
Pearson correlation of biological parameters with environmental variables. OM: organic matter, DO: dissolved oxygen, N: density, S: species number, H': Shannon–Wiener diversity (log₂), MIBW: mean individual body weight. Numbers in bold indicate significance level < 0.01 and numbers in italics indicate significance level < 0.05.

	Depth	Clay	Silt	Sand	OM	Temperature	Salinity	DO	Transect
N	-0.595	-0.336	-0.530	0.524	-0.418	0.650	-0.043	-0.067	-0.118
S	-0.084	-0.266	-0.392	0.393	-0.231	0.055	-0.461	0.233	-0.536
H'	0.223	-0.114	-0.022	0.051	0.118	-0.262	-0.393	0.264	-0.440
MIBW	0.353	0.216	0.323	-0.322	0.258	-0.336	-0.011	-0.132	0.172

Table 3
Results of Canonical Correspondence Analysis (CCA).

Axes	1	2	3	4	Total inertia
Eigenvalues	0.401	0.324	0.224	0.196	6.157
Species–environment correlations	0.852	0.796	0.689	0.750	
Cumulative percentage variance:					
Species data	6.5	11.8	15.4	18.6	
Species–environment relation	27.2	49.1	64.3	77.6	
Sum of all eigenvalues	6.157				
Sum of all canonical eigenvalues	1.476				

4. Discussion

4.1. Hydrographic and environmental settings – spatial and temporal trends

Over a third of the sites on the SEAS margin recorded DO values below 0.5 ml l⁻¹, chiefly representing the shelf edge and upper slope, and reflecting the impingement of the Arabian Sea OMZ on the continental margin (Naqvi et al., 2009; Levin et al., 2009; Joydas and Damodaran, 2014). The lower boundary of this OMZ was encountered around the 1000 m depth, where DO levels began to rise (Helly and Levin, 2004; Woulds et al., 2007). Increase in bottom DO at comparable depths below the OMZ 'core' has been reported on the Indian (Ingole et al. 2010; Hunter et al. 2012),

Table 4
Subset of polychaete species used for Canonical Correspondence Analysis (CCA).

Species	Abbreviation	Species	Abbreviation
<i>Sigambra constricta</i>	(S.con)	<i>Tharyx annulosus</i>	(T.ann)
<i>Sigambra parva</i>	(S.par)	<i>Tharyx dorsobranchialis</i>	(T.dor)
<i>Nephtys dibranchis</i>	(A.dib)	<i>Tharyx</i> sp. 1	(T.fil)
<i>Glycera longipinnis</i>	(G.lon)	<i>Tharyx marioni</i>	(T.mar)
<i>Goniada emerita</i>	(G.eme)	<i>Poecilochaetus serpens</i>	(P.ser)
<i>Diopatra neapolitana</i>	(D.neo)	<i>Aricidea fauveli</i>	(A.fav)
<i>Onuphis holobranchiata</i>	(O.hol)	<i>Aricidea</i> sp. 1	(Ari.1)
<i>Lumbrineris</i> sp. 1	(Lum.1)	<i>Aricidea (Allia) belgicae</i>	(Ari.2)
<i>Ninoe</i> sp.	(N.sp)	<i>Aricidea capensis</i>	(A.cap)
<i>Aonidella cirrobranchiata</i>	(A.cirr)	<i>Levinsonia oculata</i>	(L.ocu)
<i>Laonice cirrata</i>	(Lao.c)	<i>Paraonis gracilis</i>	(P.gra)
<i>Paraprionospio pinnata</i>	(P.pin)	<i>Cossura coasta</i>	(C.cos)
<i>Prionospio cirrifera</i>	(P.cirr)	<i>Notomastus fauveli</i>	(N.fav)
<i>Prionospio ehlersi</i>	(P.ehl)	<i>Ampharete</i> sp. 1	(Amp.1)
<i>Prionospio polybranchiata</i>	(P.pol)	<i>Amphiteis gunneri</i>	(A.gun)
<i>Spiophanes bombyx</i>	(S.bom)	<i>Isolda pulchella</i>	(I.pul)
<i>Spiophanes</i> sp. 1	(Sph.1)	<i>Amphitrite</i> sp. 1	(A.rub)
<i>Magelona cincta</i>	(M.cin)		

Pakistan (Gooday et al., 2009; Hughes et al., 2009) and Oman (Levin et al., 2000) margins. Relatively high DO was observed towards the southern transects (T1–T3), where the hydrodynamic conditions differ from those of the north, with intrusion from the Equatorial Indian Ocean and Bay of Bengal (Prasanna Kumar et al., 2004).

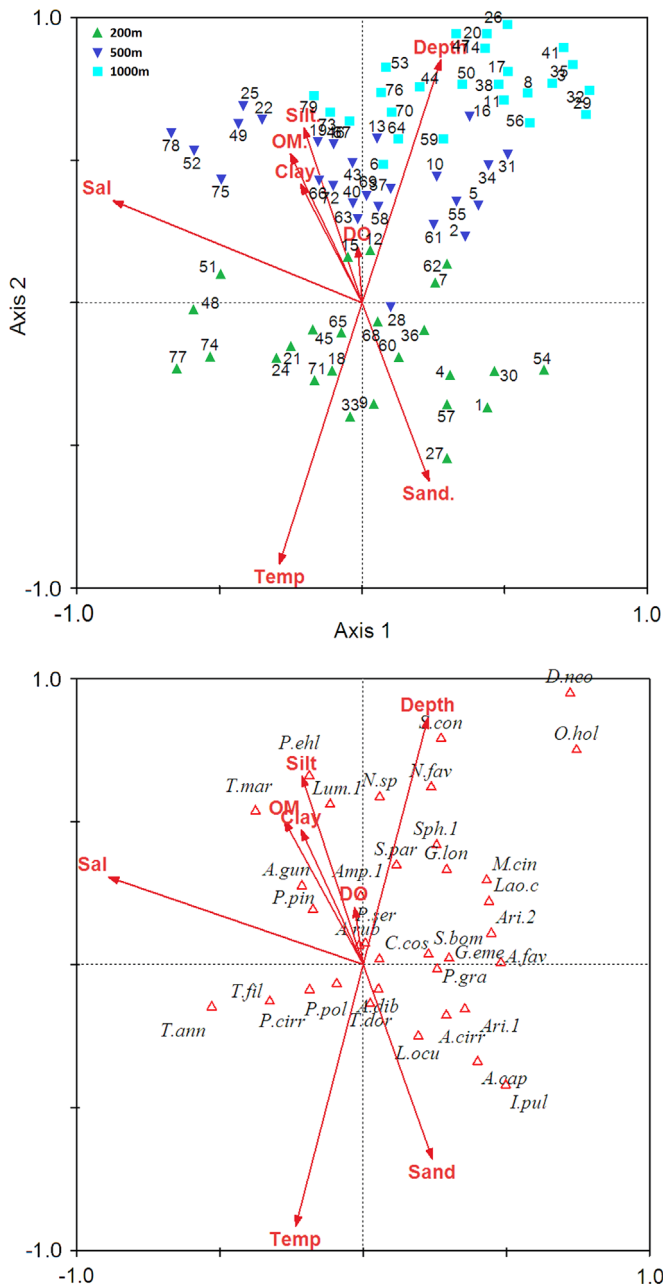


Fig. 7. Canonical Correspondence Analysis (CCA) showing (a) scatter plot for 79 stations (see Appendix A) in the SEAS and (b) CCA bi-plot showing ordination of 35 most important infaunal species. List of important species and abbreviation given in Table 4.

Lowest oxygen values were observed at the shelf edge of the northern-most transect (T9).

The 200 m sites are located close to the highly productive coastal upwelling zone of the SEAS (Madhupratap et al., 2001; Shankar et al., 2002; Smitha et al., 2008). Coupled with the suppressed mid-water recycling of OM within the OMZ (Angel, 1984; Haake et al., 1993; Cowie, 2005), high POM flux to the bottom can be expected in the region. Despite this, OM content was lower in the sandy sediments of the shelf edge when compared to the deeper regions (500–1000 m). Retention and burial of OM in deeper levels of sediments may be limited in the shelf edge due to the high sand content, while the prevailing dynamic hydrography (currents, turbidity flow, etc.) leads to redistribution and re-suspension of OM, making them more readily available for degradation (Naidu, 1993). This may result in

further depletion of oxygen from the OMZ-impacted bottom waters of the SEAS shelf edge. Additionally, it is reported that down-slope movement of sediment on the western Indian slope, by turbidity flow and re-suspension, hinders the settlement of organic matter and foraminiferal shells (mainly planktonic), especially on the upper part of the slope (Naidu, 1993). The retention of OM in the mid-slope (500–1000 m) sediments may be higher, owing to the higher proportion of fine particles or minerals, along with depth-related settling fluxes of OM to the sea floor (Calvert et al., 1995; Paropkari et al., 1992; Keil et al., 1994). Other works on the Arabian Sea OMZ also report similar organic carbon (OC) maxima in the mid-slope (Goody et al., 2009; Ingole et al., 2010). In general, retention of OM in slope sediments is strongly influenced by a combination of factors, including production in the overlaying waters, currents, DO levels and sediment texture. In the present study, OM maxima were observed in April–May, during which period the SEAS is characterized by massive phytoplankton (e.g. *Trichodesmium* sp.) blooms (Padmakumar et al., 2010) and more or less weak circulation (Sarma, 2002). On all transects in the present study, the 500 m sites recorded the highest salinity. The values increased from south to north, reaching up to 35.4 at 500 m in T9. In the eastern Arabian Sea, patches of high saline water are reported at 180–600 m depths, hugging the shelf break and slope (Shenoi et al., 2004), as a result of intrusion from the Red Sea and Arabian Gulf (Rochford, 1964; Shenoi et al., 1993). Similarly, high salinity at ~500 m (35.2–35.3) was recorded by Ingole et al. (2010) and Hunter et al. (2012) in the eastern Arabian Sea margin.

4.2. Zonation of polychaete assemblages and structuring factors

On the SEAS margin, polychaete density decreased with depth between 200–1000 m, while diversity increased, and distinct assemblages were characteristic of the three depth strata (200 m, 500 m and 1000 m). Apart from the depth-associated differences, polychaetes were more abundant in the southern sector, where assemblages were also species rich and more diverse when compared to the north. In the northern sector, shelf edge assemblages were characterized by high density and low diversity, with dominance of deposit feeders belonging to families Spionidae, Cirratulidae, Paraonidae, Cossuridae, etc. These families dominate macrofaunal communities of the bathyal and abyssal sea floor across the world (Quiroga et al., 2005; Palma et al., 2005; Levin et al., 2000; Hughes et al., 2009) and in the eastern Arabian Sea margin as well (Ingole et al., 2010; Hunter et al., 2012; Joydas and Damodaran, 2014). Similar observations of low species richness and high dominance have been reported under OMZ settings throughout the world (Thistle et al. 1985; 1991; Levin, 2003; Gallardo et al., 2004; Hughes et al., 2009). With increasing depth, as the OMZ conditions began to ease, the dominance of these forms decreased and diversity was higher.

The assemblages of the south were distinguished with high species richness and diversity, having nearly twice the number of species as the north, but comparable densities. The region harbored a number of characteristic species, which were nearly absent in the north. In the deeper regions of the southern sector, the relative abundance of the characteristic species was low, and typical deep-water forms such as *Notomastus* sp. and *C. coasta* were found in good numbers, along with malidanids, capitellids, *Ninore* sp., nereids and lumbrinerids. The mid-slope (500–1000 m) region of the southern sector was biologically similar to that of the north, but the higher faunal density in the south, coupled with the occurrence of some characteristic species resulted in higher species richness and diversity. Thus, a regional north–south distinction could be observed, even at 1000 m depth where the environmental conditions were not significantly different. The use

of different sieve sizes makes it impossible to compare our polychaete densities with those from previous studies conducted on the Oman, Pakistan and Indian margins of the Arabian Sea.

The bathymetric zonation of polychaete assemblages and their latitudinal distinction in the SEAS margin are attributed to gradients in environmental parameters, particularly DO and sediment texture (Pearson and Rosenberg, 1978; Warwick, 1988; Snelgrove and Butman, 1994; Diaz and Rosenberg 1995; Laine, 2003; Wei et al., 2010). The impingement of the Arabian Sea OMZ resulted in significant bathymetric and latitudinal gradients in bottom water DO. Similarly, the nature of substrate also showed spatial heterogeneity in the SEAS margin, being influenced by the physical dynamics of bottom water (Gray, 1974; Buchanan, 1984; Snelgrove and Butman, 1994; Jayaraj et al., 2008b). These factors influence the biology of polychaete species and their ecological interactions (Rex, 1976; Levin, 2003; Carney, 2005), thereby affecting their distribution patterns. The seasonal peak and bathymetric gradient in OM content did not appear to have any direct influence on density, species richness and diversity of polychaetes. In other words, it is apparent that food availability (quantity of OM) is not a limiting factor for polychaete density and diversity in the SEAS margin.

4.3. Faunal responses to oxygen gradients (OMZ) and changes in sediment characteristics

Along the SEAS shelf edge, where DO levels fall below the threshold of 0.45 ml l^{-1} ($20 \mu\text{mol l}^{-1}$) suggested by Levin and Gage (1998), the sandy substrate, which offers ample interstitial space, and the availability of fresh organic matter in the benthic boundary layer supports the proliferation of relatively small-sized interface feeders with food-gathering tentacles (e.g. *P. polybranchiata*, *P. cirrifer*, *Tharyx dorsobranchialis* and *T. annulosus*). Among the smallest forms found at this depth are *P. gracilis* and *L. oculata*, whose small size offers a higher surface area–volume ratio, which enhances oxygen uptake. Several of the dominant forms, such as *Prionospio* spp. (particularly *P. pinnata* and *P. ehlersi*), also possess extended branchiae for the same purpose (Levin, 2003). Smaller-sized forms are known to be important components of benthic communities located below upwelling regions, which have high productivity–biomass ratios and enhanced nutrient processing (Rowe and Menzel, 1971; Peters, 1983; Levin et al., 2000; 2002; Quiroga et al., 2005). The dominance of the aforementioned small-sized, rapidly colonizing, opportunistic species that tolerate environmental stress (i.e. OMZ) in turn reduces faunal diversity at the shelf edge of the northern sector (Rosenzweig and Abramsky, 1993; Ellis et al., 2000; Levin et al., 2001; 2009; Clarke and Warwick, 2001).

Beyond the shelf edge in the northern sector, oxygen levels rose above the threshold of 0.45 ml l^{-1} , and the quantity of OM was also relatively high. Despite these more favorable conditions, faunal density was relatively lower here than at the shelf edge, owing to depth and depth-associated factors such as low temperature and reduced heterogeneity in substrate and food availability (quality of OM). In the upper slope region (500 m), where silt was the predominant textural class, *P. polybranchiata* and *P. cirrifer* were less abundant. The assemblages in this region were dominated by *P. pinnata* and *P. ehlersi*, along with *Laonice* sp., *Magelona* sp., lumbrinerids, *Spiophanes* sp. 1 and *Amphicteis gunneri*. Studies by Ingole et al. (2010) in the SEAS margin, corresponding to T8 of the present study, also revealed similar low species richness and diversity, with dominance of *P. pinnata* at 500 m. This species is known to prefer silty sediments with high OM (Sukumaran and Sarladevi, 2009), and is also well suited to thrive under low-oxygen conditions (Levin, 2003). This region represents a ‘transition zone’ in the SEAS, with a lower degree of

stress from the OMZ but where dominance of opportunistic species is still observed, albeit at lower densities (Ellis et al., 2000). The abundance of these species decreased at the 1000 m depth, where the higher oxygen levels, coupled with the silty nature of the bottom and relatively stable hydrodynamic conditions, support a diverse assemblage of polychaetes. Sediments in the southern sector were characterized by higher sand content at all depths (relative to the north) and smaller-sized forms were favored, with higher diversity owing to the relatively higher DO concentration (i.e. weak influence of Arabian Sea OMZ). Observations on body size distribution in the SEAS margin, therefore, indicate that the key factor influencing size in the region is sediment texture (sand content). Smaller size is well suited for the sandy, OMZ-impacted shelf edge sediments, as well as the southern sector.

On the shelf edge of the northernmost transect (T9, off Karwar), the lowest polychaete density was recorded in December (2003) and May (2007), along with extremely low DO levels ($< 0.15 \text{ ml l}^{-1}$ or $< 6.7 \mu\text{mol l}^{-1}$). Woulds et al. (2007) established a threshold of $5\text{--}7 \mu\text{mol l}^{-1}$ ($0.11\text{--}0.16 \text{ ml l}^{-1}$), based on studies in the Arabian Sea OMZ, above which metazoan macrofauna (including polychaetes) were able to take advantage of the abundant OM and dominate OM uptake, but below which OM processing was dominated by foraminiferans. This could explain the paucity of polychaetes in this region in May and December collections, as well as the relatively high density and diversity during the southwest monsoon (October 2005), when DO rose above 0.8 ml l^{-1} ($35 \mu\text{mol l}^{-1}$). Despite the extremely low densities at the shelf edge, the diversity was higher here than at the upper slope, where a single species (*Tharyx marioni*) dominated. The density and diversity in the upper slope (T9) thereby resemble shelf edge (200 m) sites of the SEAS margin, where DO levels were also of the same range. In the deeper region (1000 m) of this transect, DO was appreciably higher during spring inter-monsoon and southwest monsoon seasons ($0.58\text{--}0.74 \text{ ml l}^{-1}$), but decreased to 0.23 ml l^{-1} during the winter monsoon. Coincidentally, the species richness dropped from 12 (southwest monsoon) to 2 (winter monsoon). These observations indicate that under the influence of the Arabian Sea OMZ, depth or an associated factor exerted greater control over polychaete distribution.

The macrofaunal community off Kochi (T4) was atypical and distinct from the communities of neighboring transects. The region was species poor and characterized by the dominance of *C. coasta*, along with capitellids and spionids in very low abundance, which are adapted to adverse environmental conditions. Discharges from the Cochin Estuary and Kochi metropolitan area (Balachandran et al., 2006; Martin et al., 2008) cause reduced species richness in the shelf sediments of this region (Joydas and Damodaran, 2009). The adverse effects of pollution and sedimentation may be acting even beyond the shelf (Menot et al., 2010) owing to the steeper continental slope off Kochi (Rao and Wagle, 1997), which may cause sediment instability and reduced habitat heterogeneity, thereby further depressing species diversity (Levin et al., 2001). The species that dominate along the shelf edge (Cossurids, $> 60\%$) are considered to be an indicator of sediment instability (Ellis et al., 2000) and are also characteristic of bathyal faunas impacted by environmental stress (Levin et al., 1997; Hughes et al. 2009; Ingole et al., 2010) and high sedimentation rates (Blake and Grassle, 1994). *Cossura coasta* was also recorded at high densities along T3, T5 and T9, which are all regions receiving estuarine and river discharges, and therefore likely to have higher sedimentation rates. Comparisons between T4 (Kochi) and T9 (Karwar) indicate that while the communities off T9 are impacted with natural disturbance in the form of hypoxia, it is unclear whether the disturbance off Kochi is natural (sediment instability), anthropogenic (pollution) or a combination of both. Further

studies in the area are necessary to determine the nature and magnitude of ecological disturbances off Kochi.

5. Conclusion

The present study describes the community structure of polychaetes in an ecologically significant area in the South Eastern Arabian Sea margin, which was hitherto poorly studied. The communities in this region were spatially heterogeneous in terms of density and diversity, while temporal variations were not significant. A change in community composition was noticed when moving from the shelf-edge to the mid-slope (1000 m) and also when moving from north to south. The communities at the shelf edge, which are under the influence of the Arabian Sea OMZ, were characterized by high density and low diversity, with dominance of small-sized opportunists such as *Prionospio cirrifera*, *P. polybranchiata*, *Cossura coasta*, *Paraonis* spp. and *Tharyx* spp. These species were well adapted to the low oxygen conditions and also suited for the sandy sediments of the shelf edge. As the stress from the OMZ gradually decreased, a 'transition zone' was noticed, where the opportunistic species were observed at lower densities, along with forms such as *Paraprionospio pinnata* and *Prionospio ehlersi*, which were well suited for the silty sediments of the region. Further increase in DO levels with depth, along with the domination of finer sediment fractions, resulted in the occurrence of more diverse assemblages in the mid-slope, but at lower densities. The southern sector of the study area was relatively less influenced by the OMZ, and sediments were more sandy at all depths, when compared to the north. Some species (*Aonidella cirrobranchiata*, *Isolda pulchella*, *Cirrophorus branchiatus*, *Aricidea capensis*, etc.) were found to be almost exclusive to this region. Thus, in the SEAS margin, the variations in sediment texture and dissolved oxygen of bottom water acting in combination, rather than OM content, played a key role in structuring the polychaete communities. While localized studies in the eastern Arabian Sea reported the near absence of macrofauna in the 200–1000 m depth range, the present study has uncovered the existence of dense and diverse polychaete communities between 7°00' and 14°30'N latitudes in the SEAS.

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Appendix A-C. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2014.07.006>.

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