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Standing stock and composition of macrozoobenthos in the south-eastern Arabian Sea: A revisit after a decade

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ABSTRACT

Changes in macrozoobenthic standing stock and composition along the south-eastern Arabian Sea continental shelf (30–200 m) are investigated, based on data collected from the same sites during the same season 14 years apart (winter monsoon, 1998 and 2012), using the same platform, sampling gear, methods etc. During both surveys, polychaetes dominated among the macrozoobenthos, followed by crustaceans and molluscs. A decline in macrozoobenthic density and biomass with increasing depth was noted in both surveys. Macrozoobenthic density increased significantly between 1998 and 2012, especially in the inner and mid shelf (30–50 m), due to the increase in density of polychaetes and molluscs, while the density of crustaceans decreased. The mean individual body weight of polychaetes decreased between 1998 and 2012, most notably in the inner and mid shelf (30–50 m). This reflected an overall increased dominance of small-sized opportunists such as spionids, magelonids, paraonids, cirratulids and pilargids in 2012 across the entire shelf. Such an increase in dominance of opportunists and decline in abundance of sensitive taxa is indicative of long-term environmental stress and anthropogenic pressure. However, no significant changes were noted in the measured environmental variables which are known to influence benthic faunal distribution in the region, such as sediment nature and oxygen availability. The observed changes may rather be indicative of the long-term effect of intense bottom trawling, which is practiced in the study area year-round. This is the first study of its kind for soft-sediment shelf benthos from the tropical belt.

1. Introduction

Long-term impacts of climate change and anthropogenic disturbances on marine ecosystems are garnering significant attention (Olsson et al., 2013; Birchenough et al., 2015). Assessments of such impacts at any spatial or temporal scale depend on the choice of ecological descriptors (e. g. faunal groups, species, biotic indices) employed, which must be robust and show clear responses to abiotic and biotic factors (Hily et al., 2008). Macrozoobenthic communities are proven to be excellent indicators of overall ecosystem evolution, owing to their ubiquity in marine systems, limited mobility and relatively longer individual lifespans, coupled with their widely documented community-level responses to abiotic and biotic factors (Birchenough et al., 2015; Tsikopoulou et al., 2019).

Broadly, two approaches exist for assessing long-term temporal shifts in benthic communities: (1) the acquisition of long-term time-series data at high or medium frequency which typically focus on one or a few sites, or (2) comparing datasets from two (or more) points in time (usually widely separated), but on a larger spatial scale and covering more sites. While the former provides the advantage of accuracy over time and enables understanding of forcing mechanisms, the spatial limitations in sampling prevent extrapolation of results and conclusions. The latter approach provides a better picture of overall changes in communities over a large area, although it may not explain the exact drivers of the aforementioned changes (Hily et al., 2008). This approach hinges on several factors, including the availability and quality of historic datasets, employment of similar gears and methodologies across surveys, as well as consistency in taxonomic identification (Frid et al., 2000; Olsgard et al., 2003; Quijón and Snelgrove, 2006).

The south-eastern Arabian Sea (SEAS) is among the most biologically productive regions of the world ocean, owing to seasonal coastal upwelling during the summer monsoon (June–September). The seasonal

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pulse of organic particle flux to the bottom supports high benthic biomass and substantial fishery resources (Harkantra et al., 1980; Parulekar et al., 1982; Joydas and Damodaran, 2009; Madhupratap et al., 2001). Although some work had been published on macrozoobenthos of the SEAS shelf, these were mostly limited in scope or in spatial coverage (e. g. Harkantra et al., 1980; Jayaraj et al., 2007, 2008; Musale and Desai, 2011). The most comprehensive dataset on macrozoobenthic standing stock and community composition for the eastern Arabian Sea was generated through high-resolution sampling (30–200 m depth) undertaken in 1998 on-board the Fishery Oceanographic Research Vessel *Sagar Sampada* (FORVSS) as part of the Marine Living Resources Program of the Ministry of Earth Sciences, Government of India. These surveys led to the detailed description of spatial patterns in standing stock and community structure by Joydas and Damodaran (2009, 2014). Analysis of this dataset proved that spatial patterns in macrofaunal polychaete communities are conserved at coarser (family level) taxonomic resolution in the eastern Arabian Sea (Joydas et al., 2009; Joydas and Damodaran, 2013). More recently, short-term variations in macrozoobenthic communities in response to seasonal oceanographic processes in the SEAS have also been described (Abdul Jaleel et al., 2015, 2021; Naidu et al., 2018).

As a consequence of terrestrial runoff, high production and strong stratification during the south-west monsoon, seasonal hypoxia occurs in the sub-surface waters of the SEAS (Naqvi et al., 2009); and there are concerns over the spatial and temporal expansions of both natural and human-induced hypoxia as a result of global climate change (Rabalais et al., 2009). These, along with anthropogenic pressure from intense fishery activities over several decades and substantial modification of coastal ecosystems through developmental activities also pose threats to marine ecosystems (Levin et al., 2009; Kaiser et al., 2006; Tillin et al., 2006). The present study is the first attempt of its kind for the Indian seas to test for long-term changes in standing stock and qualitative composition of macrozoobenthos in the SEAS by examining data collected 14 years apart. Original data from 5 bathymetric transects (10–14°N and 30–200 m depths) in the 1998 surveys (Joydas and Damodaran, 2009, 2013, 2014) was used to compare with data from a 2012 revisit of the same sites. The revisit was undertaken in the same season (February), using the same platform (FORVSS), sampling gear and methodologies. Foreseeing challenges in comparing species-level data, due to the availability of better identification tools and advancement in taxonomic knowledge (revisions, better descriptive accounts etc.), compounded by individual taxonomic bias (Tsikopoulou et al., 2019), overall comparisons of community composition were done using family-level data of polychaetes and order-level data for crustaceans. This is supported by the earlier studies for the region, which prove that community traits are conserved at coarser taxonomic resolution (Joydas et al., 2009; Joydas and Damodaran, 2013). Despite criticism against the 'taxonomic sufficiency' concept (Maurer, 2000), it can be asserted that this approach may be used if its applicability is tested for the concerned taxa, study area and scale of influencing factors (Quijón and Snelgrove, 2006; Tsikopoulou et al., 2019).

The analysis is undertaken with the following objectives: (i) testing for long-term changes in macrozoobenthic standing stock and composition on the SEAS shelf, (ii) testing for changes in composition and distribution of the most numerically abundant macrozoobenthic taxa, polychaetes (>500 um) at coarser taxonomic resolution, (iii) to identify probable causes for any observed changes.

2. Materials and methods

2.1. Sample collection and analysis

Macrozoobenthic samples were collected in February 2012 on-board Fishery Oceanographic Research Vessel *Sagar Sampada* (FORVSS 295), from 20 sites between 30 and 200 m depth along 5 bathymetric transects (T1–T5, ~10–14°N). These represented the same sites surveyed in February 1998 (FORVSS 162) (Joydas and Damodaran, 2009), and the same methodology for collection and analysis were followed (Table 1, Fig. 1). Hydrographic parameters of bottom water (salinity, temperature and dissolved oxygen) were recorded using a Seabird CTD (SBE-911) at all sites, simultaneous with sample collection.

Macrozoobenthic samples were collected in duplicate at each site using a Smith-McIntyre grab (0.1 m^2), and sieved using a 500 μm mesh, followed by preservation in 5% Rose Bengal-formaldehyde solution. Aliquot samples for analysis of organic matter content were also collected from the same grab (before sieving) and frozen immediately. The preserved samples were again washed through a 500 μm mesh in the shore lab and sorted into taxonomic groups (i. e. polychaetes, crustaceans, molluscs, echinoderms and other groups), followed by enumeration and weighing of biomass (wet-weight) of each group using a high-precision electronic balance of ±0.1 mg accuracy (Mettler Toledo ML204). The density and biomass were expressed in no.m^{-2} and gm^{-2} respectively. The mean individual body weight (MIBW) of polychaetes (the most numerically abundant taxa) at each site was calculated as the ratio of total biomass to total density at that site. The polychaetes in each sample were then sorted to the family level following Fauchald (1977) and crustaceans were sorted to order level. After drying the frozen sediment samples, organic matter content was estimated using the wet oxidation method of El Wakeel and Riley (1957) and expressed as % of sediment dry weight following Trask (1955). For sediment texture analysis, 10 g of dried samples were accurately weighed using a high-precision electronic balance of ±0.1 mg accuracy (Mettler Toledo ML204), treated with hydrogen peroxide to remove organic matter and dispersed using sodium hexametaphosphate. The percentage composition of sand (grain size >63 μm), silt (4–63 μm) and clay (<4 μm) was then elucidated using a CILAS 1180 Particle Size Analyser.

2.2. Data analysis

The data on environmental parameters (bottom water salinity, temperature, dissolved oxygen, sediment texture and organic matter content), standing stock of faunal groups (density and biomass), family-level density of polychaetes and order-level density of crustaceans during the 1998 survey (Joydas and Damodaran, 2009; data archived at FORV Data Centre, CMLRE) were compared with that of 2012. Spatial and temporal differences in these variables were tested for statistical significance using the PERMANOVA+ add-on in PRIMER-6 (Anderson et al., 2008), employing collection, latitude and depth category as fixed factors, with interactions being included in the analysis and with 999 permutations per test. Site-wise data was used for the analysis, with

Table 1
Details of sampling sites visited during the 1998 and 2012 surveys.

Transect No.	Depth (m)	Latitude (N)	Longitude (E)
T1	33	09°56.53′	76°00.85′
T1	51	09°52.89′	75°52.70′
T1	101	09°45.80′	75°41.18′
T1	202	09°41.39′	75°38.69′
T2	31	11°21.20′	75°34.28′
T2	50	11°19.50′	75°21.28′
T2	102	11°17.75′	74°56.85′
T2	219	11°18.97′	74°51.83′
T3	202	11°43.19′	74°33.64′
T3	102	11°44.97′	74°40.81′
T3	51	11°56.14′	75°00.86′
T3	31	11°59.11′	75°05.09′
T4	31	12°52.68′	74°40.67′
T4	51	12°49.20′	74°32.49′
T4	101	12°44.14′	74°14.02′
T4	205	12°43.89′	74°06.45′
T4	31	12°52.68′	74°40.67′
T4	51	12°49.20′	74°32.49′
T4	101	12°44.14′	74°14.02′
T4	205	12°43.89′	74°06.45′

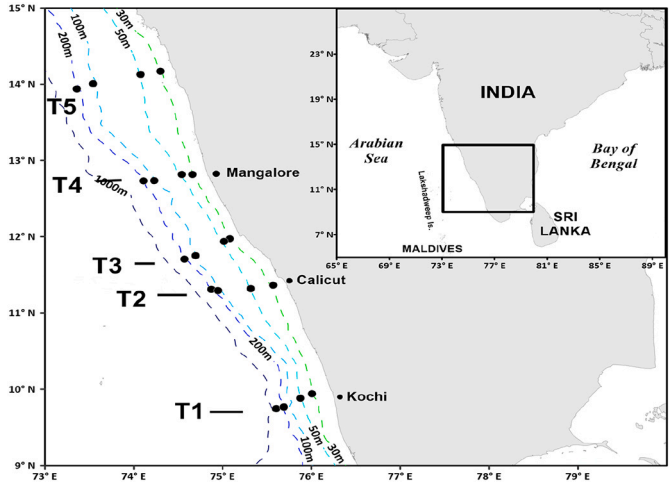

Fig. 1. Map of the study area showing the locations of sampling sites visited in 1998 and 2012.

replicate biological samples being averaged to obtain site-wise density and biomass data. Each environmental parameter was treated separately, except the sediment texture parameters (percentages of sand, silt and clay) which were treated together. Biological variables were grouped as follows: density of faunal groups (polychaetes, crustaceans, molluscs, echinoderms and 'other groups'), biomass of faunal groups (polychaetes, crustaceans, molluscs, echinoderms and 'other groups'), family-wise density of polychaetes (total 35 families) and order-wise density of crustaceans (seven orders). Spatial and temporal variations in environmental parameters were examined using a Principal Component Analysis (PCA) in PRIMER-6. Families which contributed to dissimilarity between the surveys were identified through a SIMPER analysis in PRIMER-6. For the above statistical techniques, square-root transformation and Bray-Curtis similarity index was employed for biological data, while log-transformation, normalisation and Euclidean distance was employed for environmental parameters. Strength of correlations (Pearson's coefficient, r) between individual biological and environmental variables were tested using IBM SPSS 20. The map of the study area was generated using SURFER 11.

3. Results

3.1. Environmental parameters

Among the hydrographic parameters of bottom water, only dissolved oxygen (DO) exhibited significant temporal differences (Table 2). Values were significantly higher in the inner and mid shelf (30–50 m) during the 2012 survey (pseudo-F = 60.141, $P = 0.001$). DO followed a significant decreasing trend with increasing depth in both surveys ($r = -0.961$, $p = 0$), and the values from both surveys were comparable at the shelf edge. Significant bathymetric variations were also recorded for salinity (pseudo-F = 43.141, P = 0.001) and temperature (pseudo-F = 836.03, P = 0.001). Salinity increased with increasing depth ($r = 0.509$, $p = 0.022$) up to the outer shelf, but dropped at the shelf edge. During both surveys, temperature showed a strong negative correlation with depth ($r = -0.962$, p = 0). No significant variations were noted between transects for any of the hydrographic parameters ($P > 0.05$). However, at all depths, a slight increase in salinity was noted with increasing latitude.

The sediment texture (Table 2), measured as percentage composition of sand (grain size >63 μm), silt (4–63 μm) and clay (<4 μm) did not exhibit significant variation between the 1998 and 2012 surveys ($P > 0.5$). However, at the 50 m depth site off T1, sediment texture changed from sandy in 1998 to silty sand in 2012. Significant bathymetric variations were observed in sediment texture during the surveys (pseudo-F = 27.796, P = 0.001). The sediments of the inner shelf (30 m) characteristically were dominated by finer fractions (silt and clay), with the notable exception at T1 (~95% sand in both surveys). Along the middle and outer shelf, as well as shelf edge (50, 100 and 200 m depths), the sediments were predominantly sandy, with higher silt than clay content. In the outer shelf (100 m) off T5, the texture was silty sand; and towards the shelf edge (200 m), the dominance of silt increased further and clay content was also high. Sediment texture also showed significant latitudinal variations (pseudo-F = 27.796, $P = 0.001$), but without any discernible pattern. Organic matter content (OM) was high in the sediments during both surveys (1998: 1.35–6.71%, 2012: 0.36–8.57%), and values were noticeably lower in the 2012 survey (pseudo-F = 23.803, $P = 0.002$), especially from the inner shelf to the shelf edge (50–200 m depths). In both surveys, the OM values showed some spatial variations (Table 2); strongly correlating with the content of finer sediment (silt and clay) fractions ($r = 0.573$, $p = 0$).

The PCA of hydrographic and sediment characteristics graphically resolved the differences in the environmental conditions of the sampling sites. The PC Axis 1 (eigenvalue = 3.11) explained 44.5% of variance among sites, based on the sediment characteristics (texture and OM); while axis 2 (eigenvalue = 1.99) explained 28.4%, corresponding to variations in hydrographic parameters (Table 3). The ordination of sites in the PCA biplot reveals the clustering of stations primarily based on

Table 3
Results of the Principal Component Analysis (PCA) of environmental variables (Coefficients in the linear combinations of variables making up Principal Components).

Variable	PC1	PC2
Salinity	0.195	0.212
Temperature	−0.178	−0.645
Dissolved Oxygen (DO)	−0.196	−0.655
Organic Matter content (%OM)	−0.386	0.223
Sand (%)	0.512	−0.103
Silt (%)	−0.442	0.195
Clay (%)	−0.534	0.112

Table 2
Mean (±SD) values of environmental variables at each depth during the 1998 and 2012 surveys.

Depth	30 m		50 m		100 m		200 m	
Year	1998	2012	1998	2012	1998	2012	1998	2012
Dissolved oxygen (ml/l)	3.28 ± 0.26	4.07 ± 0.09	3.21 ± 0.16	3.95 ± 0.32	2.13 ± 0.57	2.54 ± 0.40	0.08 ± 0.05	0.15 ± 0.07
Salinity	34.694 ± 0.404	34.580 ± 0.322	34.862 ± 0.356	34.713 ± 0.202	36.214 ± 0.667	35.786 ± 0.184	35.226 ± 0.068	35.235 ± 0.088
Temperature (°C)	28.98 ± 0.47	28.56 ± 0.22	29.07 ± 0.15	28.44 ± 0.26	26.65 ± 2.05	25.93 ± 0.57	13.83 ± 0.60	15.14 ± 0.50
Sand (%)	21.7 ± 41.5	20.8 ± 41.3	76.4 ± 16.3	49.1 ± 18.0	62.6 ± 22.1	68.1 ± 17.5	63.0 ± 36.5	50.7 ± 28.2
Silt (%)	43.7 ± 24.5	61.0 ± 32.7	17.4 ± 11.9	40.8 ± 18.3	32.2 ± 21.5	26.9 ± 16.0	27.2 ± 27.2	40.0 ± 21.1
Clay (%)	34.6 ± 21.1	18.2 ± 8.6	6.2 ± 4.5	10.1 ± 3.5	5.3 ± 1.4	5.0 ± 2.6	9.8 ± 9.5	9.4 ± 7.1
Organic matter content (%)	4.7 ± 2.0	4.4 ± 3.3	3.7 ± 1.4	2.2 ± 0.6	3.6 ± 0.4	1.7 ± 0.4	4.2 ± 1.0	2.4 ± 1.12

depth, indicating that the measured environmental variables were more or less similar at each depth, irrespective of the survey (Fig. 2). The exceptions to this clustering were the sites where sediment texture showed variations from other isobathic sites (30 m of T1, 50 and 200 m of T5).

3.2. Standing stock of macrozoobenthos

During the 1998 survey, the mean density and biomass of macrozoobenthos in the region were 918 ± 720 no.m^{-2} and 4.58 ± 3.34 gm^{-2}, respectively, while in the 2012 survey, these were 1273 ± 1234 no.m^{-2} and 3.73 ± 2.57 gm^{-2} respectively. Polychaetes dominated in terms of density and biomass during both surveys, followed by crustaceans and molluscs (Table 4). The density of polychaetes and molluscs increased at most sites in the 2012 survey, while that of crustaceans decreased (Table 4, Fig. 3); and the resulting minor increase in macrozoobenthic density was statistically significant (pseudo-F = 6.5615, P = 0.003). Echinoderms were represented in low numbers at a few sites during both surveys, with ophiuroids being most common. While asteroids and echinoids were recorded in the 1998 surveys, only one site in the 2012 survey yielded echinoids (*Clypeaster rarispinus*). Temporal changes were not reflected in biomass ($P > 0.05$); although a marginal decrease in biomass of both polychaete and crustaceans was noted in the 2012 survey (Table 4). In both the surveys, faunal density and biomass decreased with increasing depth ($r = -0.342$, $p = 0.031$ and $r = -0.462$, $p = 0.003$ respectively). This trend was prominent in the biomass of the polychaetes ($r = -0.467$, $p = 0.002$). The mean individual body weight (MIBW) of polychaetes decreased considerably from 1998 to 2012 (Fig. 4), particularly in the inner and mid-shelf (30 and 50 m depths). Bathymetric variations in polychaete MIBW were significant in the 1998 survey (pseudo-F = 3.824, P = 0.027) but not in the 2012 survey (P > 0.05).

3.3. Composition of polychaete families

The study area yielded 30 polychaete families during the 1998 survey, and 33 families during the 2012 survey. During the first survey, the most abundant families were Spionidae, Magelonidae, Pilargidae and Lumbrineridae, while in the 2012 survey, Paraonidae and Cirratulidae also contributed significantly to polychaete density (Table 5). A small but statistically significant difference was noted in the composition of polychaete families between the two surveys (pseudo-F = 3.4507, P = 0.008). A SIMPER analysis revealed an overall increase in abundance of some families such as spionids, magelonids, paraonids, cirratulids and pilargids in the 2012 survey (Table 5, Fig. 5). The mean density of spionids was nearly unaltered at 30 m, while it increased noticeably at all other depths. Mean density of magelonids was highest at 50 m in both surveys, and at this depth, was considerably higher in 2012, with a dense assemblage along T5 (4240 no.m^{-2}, ~70% of polychaetes at this site). Along the 30 m contour, this family recorded a small decline, while its density was relatively unchanged at 100–200 m. Cirratulids and paraonids recorded a more or less consistent increase in mean density at all depths, while pilargids increased marginally at the 30 and 50 m depths. There was a considerable decline in density of capitellids at 30 m; but while they were sparsely represented at 50 m and altogether absent at 100–200 m in 1998, they were collected at several stations along these contours in 2012. Hesionidae and Chrysopetalidae, which were not recorded at all in the 1998 survey, were observed at low densities in most of the sites between 30 and 100 m depths in 2012. Other families like Aphroditidae, Syllidae, Phyllodocidae and Nereididae, which were sparsely represented (2–3 incidences) in 1998, were encountered more frequently in 2012.

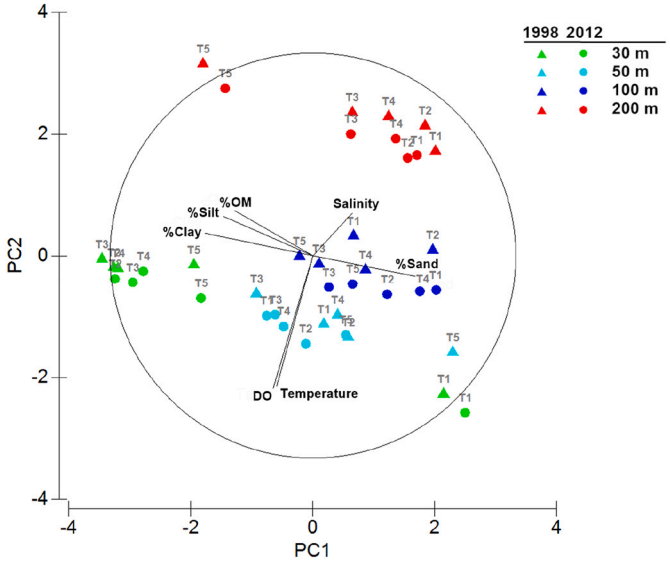

Fig. 2. Principal Component Analysis of environmental variables in the study area during the 1998 and 2012 surveys (DO = dissolved oxygen of bottom water, %OM = organic matter content of sediments).

During both surveys, bathymetric variations were noted in the composition of polychaete families (pseudo-F = 5.8407, P = 0.001), while latitudinal variations were not ($P > 0.05$). During both surveys, the spionids were most abundant and magelonids occurred at low densities at 30, 100 and 200 m (~31–53%); while the latter family accounted for nearly 50% of polychaetes at 50 m (Table 5). Density of cirratulids and paraonids increased with increasing depth, and that of pilargids and lumbrinerids decreased in both surveys.

3.4. Composition of crustacean groups

Decapods and amphipods were the most abundant crustacean groups; while tanaids, cumaceans, ostracods and isopods were also well represented (Table 5). The relative abundance of these groups displayed minor but significant temporal (pseudo-F = 5.7453, R = 0.003) as well as bathymetric (pseudo-F = 2.6552, p = 0.006) variations, while latitudinal differences were absent (P > 0.05). An overall decline in density of most groups led to the prominent decrease in total crustacean density. Isopods, which were represented in most stations in 1998 were sparsely recorded in 2012. Similar sharp declines were noted for amphipods, except at 50 m. At the same depth, the density of decapods decreased appreciably. In the case of cumaceans, which only contributed significantly to density at 50 m, no temporal changes were observed. In general, temporal changes in density of crustacean groups were most prominent at the 30 m contour.

4. Discussion

The environmental parameters known to influence benthic fauna and their community structure in the EAS margin include oxygen availability, sediment nature and sedimentary organic matter content (Jayaraj et al., 2007, 2008; Joydas and Damodaran, 2009, 2014; Abdul Jaleel et al., 2015, 2021). None of these factors showed any substantial change between the 1998 and 2012 surveys. In the SEAS shelf (up to ~100 m depth), bottom water DO is known to show strong seasonal cyclicity; with intense hypoxia associated with the summer monsoon upwelling (June–September), and well-oxygenated conditions during the winter monsoon (November–February) season (Banse, 1959; Gupta et al., 2016). The present surveys, conducted during the winter monsoon season (February of 1998 and 2012), both recorded high DO levels in the inner and mid-shelf (30 and 50 m depths). Although the values were higher in the 2012 surveys at this depth, they fell well within the range of values previously recorded in the same region during the winter monsoon season (Parameswaran et al., 2018). In both surveys, DO decreased substantially with increasing depth, falling below 0.2 mll^{-1} at

Table 4
Mean (±SD) density (no.m^{-2}) and biomass (gm^{-2}) of total macrozoobenthos and constituent groups at each depth during the 1998 and 2012 surveys.

Depth		30 m		50 m		100 m		200 m	
Year		1998	2012	1998	2012	1998	2012	1998	2012
Density (no.m^{-2})	Polychaetes	964 ± 1002	933 ± 433	781 ± 685	1946 ± 2361	426 ± 196	927 ± 302	243 ± 0	599 ± 0
	Crustaceans	168 ± 172	68 ± 33	151 ± 104	110 ± 64	180 ± 62	128 ± 70	87 ± 2	35 ± 3
	Molluscs	88 ± 131	50 ± 50	15 ± 15	45 ± 42	2 ± 4	21 ± 17	2 ± 0	4 ± 0
	Echinoderms	8 ± 18	1 ± 2	15 ± 17	2 ± 4	2 ± 4	15 ± 19	0	0
	Other groups	178 ± 81	17 ± 13	110 ± 98	48 ± 53	28 ± 18	53 ± 64	57 ± 0	12 ± 0
	Total density	1406 ± 1146	1069 ± 444	1072 ± 638	2151 ± 2370	638 ± 256	1144 ± 410	389 ± 2	650 ± 3
Biomass (gm^{-2})	Polychaetes	1.61 ± 0.90	1.65 ± 1.10	3.80 ± 2.26	3.10 ± 2.21	0.88 ± 0.47	1.71 ± 0.41	0.42 ± 0.27	0.82 ± 0.47
	Crustaceans	1.32 ± 1.78	0.87 ± 0.83	0.74 ± 0.55	0.72 ± 0.77	2.20 ± 1.93	3.03 ± 2.79	1.50 ± 2.17	0.77 ± 3.11
	Molluscs	3.44 ± 4.71	0.38 ± 0.32	0.17 ± 0.18	0.31 ± 0.32	0.01 ± 0.01	0.205 ± 0.25	0.01 ± 0.01	0.08 ± 0.27
	Echinoderms	0.63 ± 1.32	0 ± 0	0.10 ± 0.20	0.02 ± 0.04	0.01 ± 0.01	0.12 ± 0.17	0	0 ± 0.07
	Other groups	0.98 ± 1.51	0.45 ± 0.30	0.43 ± 0.34	0.35 ± 0.23	0.10 ± 0.08	0.16 ± 0.18	0.12 ± 0.05	0.14 ± 0.11
	Total biomass	7.97 ± 4.27	3.35 ± 2.09	5.24 ± 2.55	4.50 ± 2.84	3.20 ± 1.80	5.23 ± 2.623	2.05 ± 2.14	1.81 ± 3.16

the 200 m depth sites, where the perennial Arabian Sea oxygen minimum zone (ASOMZ) impinges on the EAS margin (Ingole et al., 2010; Abdul Jaleel et al., 2014). A decrease in bottom DO as well as temperature with increasing depth is well recorded along the EAS shelf (Jayaraj et al., 2007; Joydas and Damodaran, 2009, 2014; Parameswaran et al., 2018). During both surveys, bottom water salinity was low in the inner and mid-shelf (30–50 m depths), which is attributed to the intrusion of low-salinity Bay of Bengal water from the south during the winter monsoon (Prasannakumar et al., 2004), which also creates a weak latitudinal trend (Parameswaran et al., 2018).

The nature of sediments in the study area showed overwhelming bathymetric variations, without any temporal changes between the two surveys. The SEAS shelf, between 10 and 15°N receives substantial terrestrial inputs via several rivers, the largest of which are the Periyar, Bharathapuzha, Chaliyar, Korapuzha, Valapattanam, Chandragiri and Netravati. The west coast of India being a passive margin, most of these river-mouths typically form estuaries, some of which are large and extensive. These estuaries and adjacent coastal areas (up to ~10 m water depth) are reported to trap coarser sediment particles, which leads to the deposition of finer sediments (silt and clay) in the inner shelf (up to ~40 m depth) (Jayaraj et al., 2008; Rao and Wagle, 1997; Joydas and Damodaran, 2009; Parameswaran et al., 2018). Beyond this region, the surface sediments are sandy with a mixture of silt and low quantities of clay (Rao and Wagle, 1997; Parameswaran et al., 2018). At the shelf edge, the sands are known to be relict and composed of coarser particles (Rao and Wagle, 1997; Abdul Jaleel et al., 2014). Some exceptions to this general pattern were noted in the present study, which are attributed to localized factors. For example, the inner shelf sediments (30 m) off Kochi (T1) were characterised by high sand content, owing to the proximity to the mouth of the complex Cochin Estuary system, which is subjected to intense navigational dredging (Rehitha et al., 2017; Abdul Jaleel et al., 2021). The sediment organic matter content was higher in the inner shelf (30 m) and was lower beyond this depth (Parameswaran et al., 2018). This indicates the close relationship between OM content and proportion of finer sediments (Abdul Jaleel et al., 2021).

The standing stock of macrozoobenthos are among the most useful indices for ecological change in marine soft-sediments (Labrune et al., 2007; Hily et al., 2008; Bonifácio et al., 2018; Grebmeier et al., 2018; Tsikopoulou et al., 2019; Manushin et al., 2020). In the SEAS margin, macrozoobenthic density showed significant change between 1998 and 2012. This reflected changes in standing stock of the major constituent groups – the polychaetes and crustaceans. The density of polychaetes increased significantly beyond the inner shelf (50–200 m), while that of crustaceans decreased substantially at all depths. However, these were not accompanied by corresponding changes in biomass of these groups, which indicates an overall decrease in average body size. In the case of crustaceans, a decline was noted in the density of dominant groups like amphipods and isopods. A decline in amphipod density was reported in the northern Bering Sea, which was attributed to declining food supply or increasing predation (Coyle et al., 2007; Grebmeier et al., 2018). In both surveys of the present study, faunal density was higher in the inner and mid-shelf (30–50 m), compared to the outer shelf and shelf edge (100–200 m). Several environmental factors, most notably sediment nature and oxygen concentration in bottom water, are known to cause shifts in macrozoobenthic community structure along bathymetric gradients in the SEAS margin (Jayaraj et al., 2008; Joydas and Damodaran, 2009, 2014; Abdul Jaleel et al., 2015, 2021). Joydas and Damodaran (2013), based on an extensive polychaete species distribution dataset from the eastern Arabian Sea, demonstrated that these distribution patterns are adequately detected even at generic and family levels. Surface deposit feeders like spionids (*Paraprionospio* sp. and *Prionospio* spp.) dominate in the silty sediments (with high deposition rates) of the inner shelf (30 m) along with pilargids (*Sigambra* sp.). Relatively diverse assemblages occur in the sand-dominated sediments beyond this depth, comprising surface and sub-surface deposit feeders (spionids, magelonids, paraonids etc.) as well as predators/omnivores such as lumbrinerids and glycerids (Joydas and Damodaran, 2009; Abdul Jaleel et al., 2021). At the shelf edge, where the ASOMZ impinges on the continental margin, the abundance and relative dominance of deposit feeders such as paraonids, cirratulids and cossurids were higher (Abdul Jaleel et al., 2014), and this was more pronounced in the 2012 survey.

An assessment of mean individual body weight (biomass: density ratio) indicates an overall reduction in size of polychaetes in the 2012 dataset, which was most prominent in the inner and mid shelf (30–50 m depths). This was a result of an increase in abundance of smaller-sized taxa belonging to families such as Spionidae, Paraonidae and Cirratulidae. These, along with a few other families are known to constitute the bulk of macrozoobenthic polychaetes in the SEAS margin, being well adapted to the high biological productivity and the fluctuations of environmental factors associated with summer monsoon upwelling (Joydas and Damodaran, 2009, 2014; Abdul Jaleel et al., 2015, 2021). Similar increases in small-sized and short lived opportunistic macrofaunal taxa have been reported from the North Sea and Bohai Sea, and have been attributed primarily to anthropogenic perturbations (Zhou et al., 2007; Kraan et al., 2011; Kröncke et al., 2011; Johansen et al., 2018). The aforementioned small-sized taxa are dominant on the shelf-edge of the SEAS, which is impinged with the ASOMZ (Ingole et al., 2010; Abdul Jaleel et al., 2014). On the shelf, they are known to attain dominance during the summer monsoon, as they are adapted to tide over the hypoxic conditions existing over the shelf during this season (Abdul Jaleel et al., 2015, 2021). With the abatement of seasonal hypoxia (post monsoon period), communities become more taxonomically and functionally diverse during the winter monsoon season (Joydas and Damodaran, 2009, 2014; Naidu et al., 2018). Seasonal fluctuations notwithstanding, the present work records an increase in the abundance of these taxa across the entire shelf within the winter monsoon season itself, over the span of a decade (1998 to 2012).

Long-term changes in benthic communities have been examined in

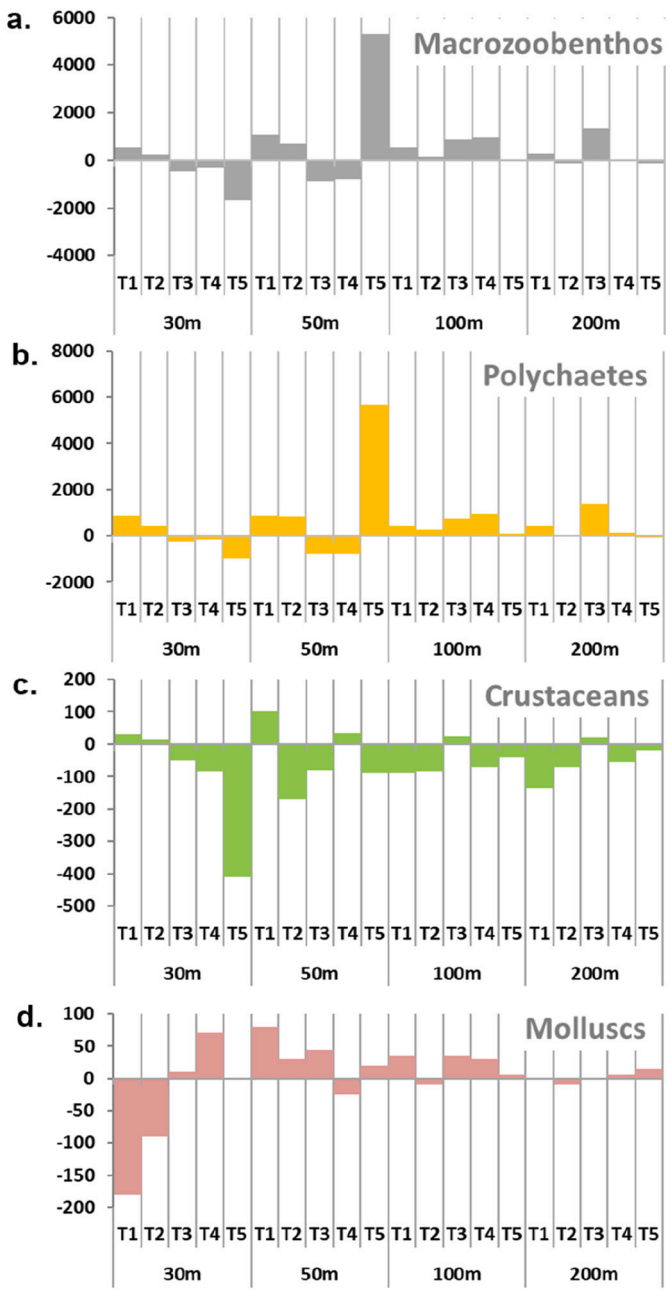

Fig. 3. Plot showing change (increase/decrease) in density of (a) macrozoobenthos, (b) polychaetes, (c) crustaceans and (d) molluscs at each site between 1998 and 2012.

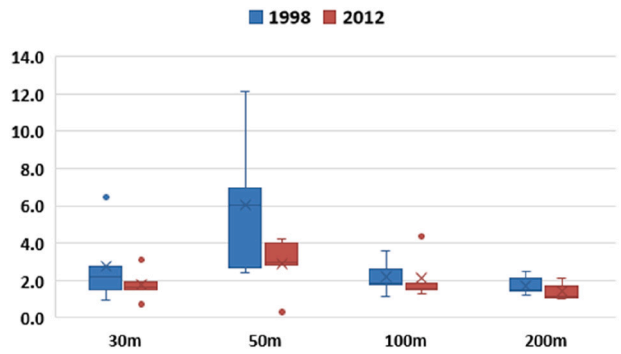

Fig. 4. Mean individual body weight (biomass: density ratio) of polychaetes (mean ± SD) at each depth during the 1998 and 2012 surveys.

many parts of the world, with many studies employing the 'revisit' approach particularly in intertidal areas and estuaries (e. g. Hong and Yoo, 2001; Kraan et al., 2011). Diverse responses have been recorded in macrofaunal communities of polar and temperate margins in response to long-term changes in biotic and abiotic factors as well as to anthropogenic stressors. In polar regions, long-term community changes have been attributed to several factors, such as warming of the water column (and its variability), declining sea-ice cover and long-term (decadal scale) climate oscillations (e. g. Blanchard, 2015; Grebmeier et al., 2018; Manushin et al., 2020). In temperate waters the key factors identified include ocean warming, changes in sediment texture, anthropogenic disturbances (coastal modification, bottom trawling etc.), as well as long-term climactic oscillations (e. g. Grémare et al., 1998; Labrune et al., 2007; Zhou et al., 2007; Hily et al., 2008; Kröncke et al., 2011; Bonifácio et al., 2018; Tsikopoulou et al., 2019; Xu et al., 2020). The 'revisit' approach has rarely been employed in tropical areas, and no studies have been reported beyond estuaries and coastal embayments (Raut et al., 2005; Yan et al., 2017; Dash et al., 2021). The present study uses this approach to investigate spatial as well as temporal changes in macrozoobenthic fauna the eastern margin of the Arabian Sea, which is a highly productive region in the tropical belt with distinct ecological features (seasonal coastal upwelling and hypoxia, impingement of ASOMZ etc.).

In the SEAS shelf, while variations in sediment texture and oxygen availability resulted in the widely-documented bathymetric trends in faunal distribution (Joydas and Damodaran, 2009, 2014; Parameswaran et al., 2018), these factors did not vary significantly between the 1998 and 2012 surveys. The observed temporal changes in polychaete communities, chiefly the increase in abundance (and even dominance) of smaller-sized taxa, thus, cannot be directly attributed to changes in these measured variables. In general, increased dominance of small-sized opportunistic taxa among macrozoobenthos is associated with oxygen-deficient, organic matter enriched sediments which may be indicative of eutrophication (Levin et al., 2009). Although the south-west coast of India is densely populated, with substantial industrial activities, several studies have shown that nutrient loading from anthropogenic sources does not have a significant impact on biogeochemical processes beyond the shore (Bhavya et al., 2017, 2018; Gupta et al., 2021). Gupta et al. (2016, 2021) have also shown that there has been no significant intensification of seasonal oxygen deficiency over the western Indian shelf during the past few decades. Considering this, and the fact that there is no significant variation in bottom water dissolved oxygen concentration between 1998 and 2012, it is unlikely that increase in anthropogenic organic load or oxygen depletion are responsible for the observed increase in small-sized opportunistic polychaetes on the SEAS shelf.

Another anthropogenic factor which is known to cause widespread changes in benthic ecosystems is bottom trawling (Jennings and Kaiser, 1998; Frid et al., 2000; Kaiser et al., 2002). The physical disturbance caused directly by bottom trawling causes alteration in seabed morphology, damage or destruction of biota etc., which ultimately lead to substantial, long-term changes in benthic community structure and food webs (Kaiser et al., 2002; Zhou et al., 2007; Hinz et al., 2009). High trawling intensity over long periods of time is known to reduce the abundance of larger and more common but vulnerable species (e. g. echinoderms), and lead to increased abundance of small-sized, burrowing opportunists (e. g. *Prionospio* spp.) (Zhou et al., 2007; Hinz et al., 2009; De Juan et al., 2011; Jørgensen et al., 2016). The continental shelf off the west coast of India, particularly between ~30–100 m depths, is an area with intense fishing activity, particularly bottom trawling for crustaceans and demersal finfishes. Over the study period (1998–2012), there have been substantial changes in the fishery practices in the region, such as an increase in number of mechanised trawlers and operations (e. g. from single-day to multi-day), as well as improved gear efficiency (Vivekanandan et al., 2010). Trawling activities occur year-

Table 5
Mean (±SD) density (no.m^{-2}) of polychaete families and crustacean groups at each depth during the 1998 and 2012 surveys.

	Depth	30 m		50 m		100 m		200 m	
	Year	1998	2012	1998	2012	1998	2012	1998	2012
Polychaetes	Ampharetidae	0	4 ± 9	10 ± 12	13 ± 9	6 ± 9	25 ± 29	8 ± 11	28 ± 57
	Amphinomidae	0	0	12 ± 16	2 ± 4	6 ± 9	8 ± 9	0	3 ± 7
	Aphroditidae	0	0	2 ± 4	1 ± 2	0	3 ± 4	0	4 ± 4
	Capitellidae	96 ± 193	8 ± 13	2 ± 4	15 ± 18	0	15 ± 12	0	11 ± 24
	Chaetopteridae	0	0	0	0	0	0	0	1 ± 2
	Chrysopetalidae	0	0	0	3 ± 4	0	3 ± 4	0	1 ± 2
	Cirratulidae	4 ± 5	27 ± 27	10 ± 7	162 ± 167	27 ± 30	65 ± 31	54 ± 45	149 ± 208
	Cossuridae	16 ± 26	35 ± 46	6 ± 5	10 ± 9	8 ± 11	10 ± 17	20 ± 19	49 ± 101
	Dorvilleidae	0	0	2 ± 4	1 ± 2	0	0	0	0
	Eunicidae	2 ± 4	0	17 ± 16	93 ± 79	6 ± 9	10 ± 12	0	3 ± 7
	Flabelligeridae	0	2 ± 2	0	1 ± 2.2	0	0	0	0
	Glyceridae	19 ± 23	11 ± 11	19 ± 25	38 ± 39	26 ± 17	43 ± 4	8 ± 8	6 ± 9
	Hesionidae	0	6 ± 6	0	9 ± 15	0	6 ± 9	0	0
	Lacydoniidae	6 ± 13	8 ± 8	2 ± 4	34 ± 60	0	0	0	0
	Lumbrineridae	112 ± 100	81 ± 101	82 ± 53	73 ± 74	28 ± 11	39 ± 30	0	4 ± 9
	Magelonidae	68 ± 104	33 ± 56	384 ± 664	961 ± 1843	18 ± 16	43 ± 56	5 ± 11	5 ± 11
	Maldanidae	2 ± 4	4 ± 5	42 ± 61	12 ± 11	2 ± 4	6 ± 5	0	5 ± 7
	Nephtyidae	50 ± 32	16 ± 19	20 ± 16	36 ± 46	12 ± 13	16 ± 14	2 ± 4	5 ± 11
	Nereididae	0	10 ± 17	0	7 ± 7	10 ± 22	21 ± 24	0	5 ± 11
	Onuphidae	2 ± 4	6 ± 13	11 ± 7	8 ± 8	0	24 ± 31	0	1 ± 2
	Opheliidae	0	1 ± 2	0	0	0	1 ± 2	0	0
	Orbiniidae	2 ± 4	3 ± 4	7 ± 16	14 ± 31	6 ± 5	2 ± 3	0	0
	Paraonidae	27 ± 42	52 ± 35	16 ± 18	98 ± 75	37 ± 39	55 ± 46	18 ± 13	76 ± 121
	Pectinariidae	0	0	2 ± 4	0	0	0	0	0
	Phyllodocidae	0	3 ± 4	4 ± 9	6 ± 9	0	3 ± 4	0	3 ± 4
	Pilargidae	192 ± 198	222 ± 157	29 ± 31	69 ± 100	9 ± 15	14 ± 5	0	3 ± 4
	Poecilochaetidae	0	3 ± 7	18 ± 40	4 ± 7	6 ± 9	3 ± 4	0	0
	Sabellidae	0	0	4 ± 5	8 ± 15	4 ± 5	10 ± 8	36 ± 49	1 ± 2
	Scalibregmidae	0	0	2 ± 4	0	0	0	0	0
	Serpulidae	0	0	2 ± 4	2 ± 3	0	0	0	0
	Spionidae	343 ± 408	290 ± 56	49 ± 42	178 ± 142	203 ± 145	495 ± 237	92 ± 53	233 ± 171
	Sternaspidae	5 ± 7.	98 ± 219	6 ± 5	1 ± 2	2 ± 4	0	0	0
	Syllidae	0	5 ± 11	4 ± 9	8 ± 8	4 ± 9	5 ± 5	0	2 ± 4
	Terebellidae	4 ± 9	4 ± 5	4 ± 5	62 ± 59	4 ± 5	2 ± 4	0	1 ± 2
	Trichobranchidae	10 ± 12	1 ± 2	0	17 ± 38	0	0	0	0
	Unidentified polychaetes	4 ± 9	0	13 ± 19	0	2 ± 4	0	0	0
Crusraceans	Amphipoda	87 ± 118	25 ± 24	34 ± 76	46 ± 39	46 ± 28	24 ± 29	17 ± 21	10 ± 20
	Cumacea	0	4 ± 7	12 ± 13	9 ± 10	2 ± 4	2 ± 4	4 ± 5	0
	Decapoda	44 ± 61	33 ± 17	78 ± 79	25 ± 15	70 ± 38	87 ± 70	48 ± 40	23 ± 30
	Isopoda	31 ± 10	0	6 ± 5	2 ± 4	38 ± 58	1 ± 2	18 ± 14	0
	Ostracoda	2 ± 4	2 ± 2	9 ± 12	11 ± 15	20 ± 28	3 ± 7	0	0
	Stomatopoda	0	0	10 ± 14	5 ± 11	2 ± 4	6 ± 13	0	1 ± 2
	Tanaidacea	4 ± 9	4 ± 5	2 ± 4	12 ± 13	2 ± 4	5 ± 6	0	1 ± 2

round except for a 45- to 60-day 'closed fishing period', concurrent with the summer monsoon (June–July). The silty sand sediments of the study area prove ideal for bottom trawl operations. While studies have shown that short-term impacts of trawling may be modest in such sediments (Hinz et al., 2009), the changes could potentially accumulate over longer periods of time (e. g. on decadal scales). The observed changes in the macrozoobenthic communities between 1998 and 2012, i. e. the substantial increase in small-sized opportunistic taxa among polychaetes, as well as decline in populations of echinoderm (Parameswaran et al., 2018) and crustaceans (e. g. amphipods) may indicate the cumulative impact of physical disturbance caused by intense trawling. As a result, macrozoobenthic communities in the SEAS shelf (up to 100 m) shifted from relatively diverse, larger-sized taxa to relatively opportunist-dominated, becoming more similar to the OMZ-impacted shelf-edge communities in terms of mean body size.

The biogeochemical processes that operate in the benthic realm are crucial for the cycling of energy and nutrients in aquatic ecosystems, and are therefore integral to ecosystem functioning and biological production. Functional diversity in faunal assemblages is critically important for the maintenance and resilience of ecosystem functions. Alterations in benthic faunal composition as well as species functional traits in an area will affect biogeochemical cycling and trophic transfer, and also have cascading impacts on ecosystem function (Kristensen et al., 2014). In the SEAS, regions with high benthic standing stock and diversity are associated with rich and diverse demersal fishery resources (Parulekar et al., 1982). In the present study, benthic communities exhibited a long-term shift from diverse to opportunist-dominated ones, with an overall decline in body size. Even though there is a poor understanding of the exact relation between benthic faunal composition and specific fishery resources in the SEAS, the changes observed in the present study are likely to have significant long-term impacts on the fishery resources of the region. Along the south-west coast of India, fisheries provide food, food security and livelihoods to a substantial human population, and contribute significantly to the regional economy. Any changes in ecosystem function which can impact regional fish and shellfish stocks, will therefore also have far reaching economic implications.

5. Conclusion

There are growing concerns about the long-term impact of climate change and anthropogenic disturbances on marine benthic communities across the world. However, there are few studies on community shifts in soft sediment benthos, and none from the tropical belt, even though macrozoobenthos are considered as excellent indicators of ecological change. The present study is a first attempt to test for long term changes in macrozoobenthic communities in the tropical continental margin of the south-eastern Arabian Sea, based on spatially resolved data collected from the same sites during the same season 14 years apart (1998 and

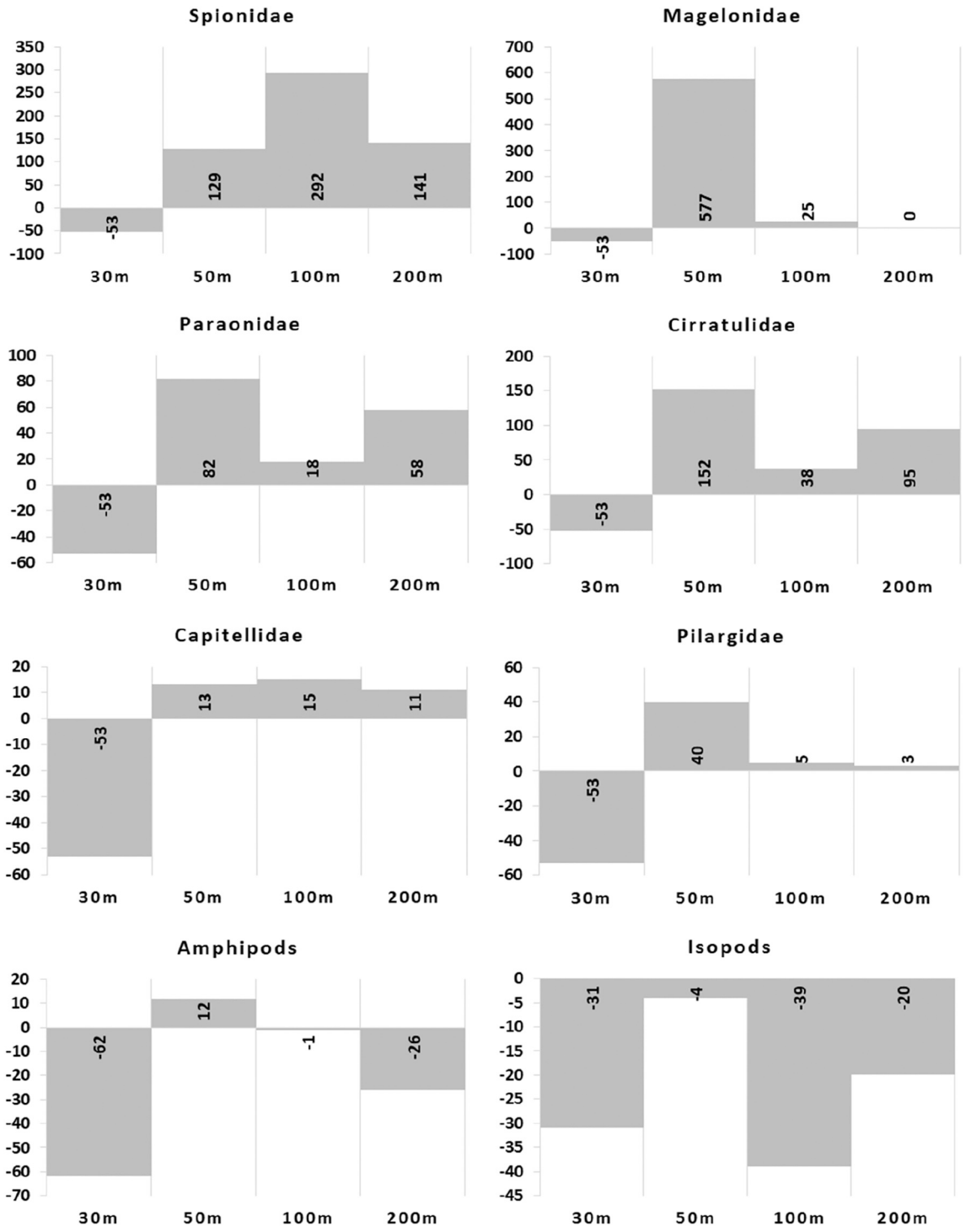

Fig. 5. Changes in mean density of selected polychaete families and crustacean groups in the study area between the 1998 and 2012 surveys.

2012), and following the same protocols. Subjective bias in species identification has been circumvented by undertaking the comparison at coarser taxonomic resolution. Over the study period, the macrozoobenthic communities became dominated by small-sized opportunistic taxa, most particularly the spionid, magelonid and paranoid polychaetes, with a decline in ecologically sensitive groups like crustaceans and echinoderms. Increased dominance of opportunists is usually indicative of overall environmental degradation, which may be caused by anthropogenic or natural disturbances. In the present study, no significant changes were noted in the measured environmental variables which are known to influence benthic faunal distribution in the region, such as nature of substrate and oxygen availability. The most significant change in the study area with respect to the seafloor habitat is the intensification of mechanised trawling activity. Increased dominance of opportunists and decline of sensitive taxa will have far-reaching impacts on marine food webs and on the integrity of the ecosystems.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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