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Trait-based and taxonomic macrofauna community patterns in the upwelling ecosystem of the southeastern Arabian sea

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ABSTRACT

Coastal upwelling that occurs in the eastern Arabian Sea (EAS) drive the complex dynamics of the food chain. Macrofauna plays a key role in the functioning of coastal ecosystems, but few studies explored the taxonomic and functional patterns of macrofaunal communities under the influence of upwelling. These patterns have been investigated in this study by sampling macrofauna and environmental variables during March–December 2012 across six depths (13–100 m) over the continental shelf off Kochi, south EAS. Upwelling, set over outer shelf prior to March, occupies the entire shelf by May, peaked during June–July and withdrew rapidly by September.

A total of 203 macrofaunal taxa were collected in this study. Multivariate analysis revealed that the macrofaunal composition showed a spatiotemporal variation. Taxonomic diversity increases from nearshore to mid shelf whereas abundance and biomass decreased. Macrobenthic functioning, assessed through Biological Trait Analyses, displayed similar trait modalities between depths and seasons but abundance driven differences in trait expression revealed important habitat filtering. Increase in organic matter and decrease in dissolved oxygen influenced by upwelling and the spatial variation in sediment texture were the strongest drivers of the macrofaunal taxonomic pattern. We suggest that taxonomic and biological trait information needs to be considered in ecological studies as it provides a better understanding of how biodiversity responds to and interacts with environmental changes.

1. Introduction

Coastal and continental shelf ecosystems exhibit marked spatio-temporal patterns in their environmental and biological communities, which are in turn related to natural variability (e.g., upwelling and oxygen minimum zones) and anthropogenic activities (Fajardo et al., 2018; Quintana et al., 2015a; Sivadas et al, 2016, 2020). The coastal upwelling ecosystem is subject to large water chemistry variations when sub-surface waters enter the surface. The upwelling decreases water temperature, dissolved oxygen (DO), and pH, while concentrations of inorganic nutrients and dissolved inorganic carbon (DIC) increases (Bhavya et al., 2017; Gupta et al, 2016, 2021). These nutrient-rich upwelled waters significantly enhance plankton biomass and primary production (Gupta et al., 2016; Prasanna Kumar et al., 2001).

Macrofaunal communities in the coastal upwelling areas experience major changes associated with upwelling-induced environmental variations (Blanchette et al., 2009; Fajardo et al., 2018; Fréon et al., 2009; Hernández-Miranda et al., 2012; Pacheco et al., 2011; Quintana et al., 2015a). These changes include a decline in species richness, diversity, total abundance, and biomass. Changes in species composition, enhancement of small-sized opportunistic species, and decrease in the large-sized polychaetes and carnivore species have also been reported (Fajardo et al., 2018; Hernández-Miranda et al., 2012; Quintana et al., 2015a). The main factors driving low species richness and the strong

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dominance of polychaetes in the coastal upwelling areas are related to the enrichment of the sedimentary organic matter and reduced dissolved oxygen concentration.

Studies addressing the dynamics of macrofaunal communities to upwelling events focussed on the traditional taxonomic patterns (abundance, biomass, and diversity) (Abdul Jaleel et al., 2021; Hernández-Miranda et al., 2012; Quintana et al., 2015a). However, studies exploring the functional response of communities to upwelling are still relatively few and mostly restricted to the eastern boundary upwelling systems (Blanchette et al., 2009; Bon et al., 2021; Fréon et al., 2009). These studies noted that variability in the functional diversity was mainly driven by dissolved oxygen concentration changes. Higher functional diversity occurred when oxygen concentration was higher (normoxic) and, during hypoxia, the macrofaunal community shifted to hypoxia-tolerant communities with low functional diversity (Bon et al., 2021; Pacheco et al., 2011).

While traditional measures of biodiversity give only limited information on ecosystem functioning, trait-based studies can provide additional information as they reflect mechanisms underlying community responses to environmental drivers (Poff, 1997; Statzner and Bêche, 2010). The Biological Trait Analysis (BTA) is one such approach that uses a range of biological traits of the organisms to assess how functioning varies between communities (Bremner et al., 2003). The BTA has proven to be a powerful tool for describing the spatial and temporal patterns of benthic functioning and its response to environmental changes due to natural events and anthropogenic activities (Beauchard et al., 2017; Bremner, 2008; Bremner et al., 2003; Pacheco et al., 2011; Sivadas et al., 2020).

The southeastern Arabian Sea (SEAS) is one such system that undergoes pronounced seasonal upwelling variability with consequent biogeochemical changes in both, water column and seafloor. The SEAS experiences coastal hypoxia during the southwest monsoon when cold, nutrient replete, and hypoxic/suboxic waters from the Arabian Sea Oxygen Minimum Zone upwells onto the coast (Gupta et al, 2016, 2021). The resultant high primary production is supported mainly by upwelled nutrient-rich waters and, to some extent, by terrestrial runoff fuelling a rich secondary production. Subsequently, microbial respiration and decomposition of the sinking organic matter further deplete oxygen resulting in hypoxia (Banse, 1959; Bhavya et al., 2017; Gupta et al, 2016, 2021, 2016; Naqvi et al., 2009; Sudheesh et al, 2016, 2020a).

On the other hand, the high biological production, along with sustaining the pelagic system, supports the commercially important fishery (e.g., *Sardinella longiceps*, *Rastrelliger kanagurta,* and *Cynoglossus macrostomus*) of the SEAS and enriches the benthic system through high levels of sinking organic matter (Banse, 1959; Vivekanandan et al., 2005; Reddy, 2003). The hypoxic condition and the sinking organic matter flux alter the benthic faunal abundance and species composition. The community in such an environment is dominated by benthic infauna that is tolerant of these conditions (Fajardo et al., 2018; Gray et al., 2002; Kodama et al., 2012). The potential for sulfides accumulation in the sediment could also negatively impact benthic communities as even low micromolar concentrations of dissolved sulfides can impair respiratory functions (Bagarinao, 1992; Janas et al., 2004; Vaquer-Sunyer and Duarte, 2010).

In this study, we investigated the macrofaunal communities from the Kochi Shelf of SEAS. While a substantial number of studies have focussed on the macrofaunal communities inhabiting the EAS coastal and shelf regions, less effort has been made to understand the response of macrofauna to coastal upwelling (Abdul Jaleel et al., 2021; Ingole et al., 2016; Naidu et al., 2018; Parameswaran et al., 2018). These studies showed a relationship between changes in taxonomic composition, abundance, and diversity of the macrobenthic community and environmental parameters. During upwelling, the macrobenthos community was characterised by a high abundance of few opportunistic species (*Paraprionospio* sp., *Magelona cincta*, and *Heteromastus* sp.), while species diversity showed a significant increase during the non-upwelling period (onset of monsoon, winter monsoon, and spring inter-monsoon). However, the functional diversity pattern and the factors determining the distribution pattern over the SEAS remain largely unknown. Few studies explicitly investigated macrofaunal functional diversity patterns along the Indian coast (Sivadas et al., 2020; Vijapure et al., 2019). Upwelling being an important driver governing the spatiotemporal patterns of benthic communities, understanding upwelling-related environmental changes on the macrofaunal communities is necessary as they play an important role in various ecosystem processes, including biogeochemical cycles and energy pathways (Dimitriou et al., 2017; Karlson et al., 2007). In order to address the same, the present study was undertaken (1) to describe the taxonomic and functional patterns of the macrofaunal community in the SEAS, and (2) to evaluate how environmental variables influence observed patterns. The present work is part of a larger study (Kochi time-series, KoTS) to understand the effects of upwelling on the SEAS coastal ecosystem.

2. Materials & methods

2.1. Study area

Coastal upwelling during the summer monsoon is the main process that regulates the biogeochemistry and biology of SEAS shelf (Gupta et al., 2016, 2021; Sudheesh et al., 2016, 2020). The dynamics of upwelling from its evolution to decay and the associated nutrient biogeochemistry and net ecosystem metabolism from the Kochi Timer Series have been recently documented in detail by Gupta et al. (2016). The biogeochemistry of SEAS is closely linked to the seasonally reversing coastal currents during winter and summer monsoons, while the periods of intermonsoons experience transitional conditions. Although peak upwelling lasts for about three months during the summer monsoon (June–August), its signals from onset to offset last for about nine months over this shelf (Gupta et al., 2016). Peak upwelling enriches the SEAS shelf with nutrients resulting in significantly high plankton production (Jyothibabu et al., 2008; Madhupratap et al., 2001) and influences fishery production of the region (14.5% of the marine fish catch of India) (Banse, 1959; Vivekanandan et al., 2005). Upwelling also significantly fuels coastal hypoxia, as they are sourced by oxygen minimum zone waters which are further depleted by the decomposition of sinking organic matter (Gupta et al., 2016, 2021), resulting in sediment denitrification especially in the shallow regions (Sudheesh et al., 2016, 2020).

In addition to upwelling, the western shelf also receives substantial amounts of nutrients through terrestrial input, which also influence the biogeochemistry and ecology of the region. Many small and medium rivers flow across the coastal plain and drain into the southwest of India. Cochin (Kochi) estuary, the largest estuarine system on the southwest coast of India, is a highly eutrophic system impacted with anthropogenic activities and debouches directly into the adjoining present study site (Fig. 1). Recent studies have shown that the Kochi Estuary acts as a heavy sink zone due to high turnover rates of nitrogen; hence its export impact on coastal biogeochemistry is mainly limited to the nearshore region (Bhavya et al., 2017; Gupta et al., 2016). The recent isotopic studies of particulate matter also evidently proved that regions beyond the nearshore along the west coast of India, including off Kochi, are least impacted by terrestrial inputs (Gupta et al., 2021).

2.2. Sample collection and analysis

The continental shelf off Kochi was sampled between March and December 2012 at 30–45 days interval onboard FORV *Sagar Sampada* (Tables 1S and 2S). Environmental and benthic samples were collected from six stations at a depth of 13, 20, 30, 40, 50, and 100 m (Stns. 1–6, Fig. 1). These stations were classified as nearshore (Stn. 1), inner shelf (Stns. 2 and 3), mid shelf (Stns. 4 and 5), and outer shelf (Stn. 6) (Gupta et al., 2016). The sampling months were classified into four seasons:

Fig. 1. Map showing the study site across the Kochi shelf in the southeastern Arabian Sea.

spring intermonsoon (SIM: March to April), summer monsoon (SM: June to September), fall intermonsoon (FIM: October), and winter monsoon (WM: November to January). May represents the pre-SM period.

Temperature and salinity data were collected using a conductivity-temperature-depth (CTD) profiler (SBE 11 Plus, Sea-Bird, USA). Surface and bottom water samples were collected from each station using 5 L Niskin samplers mounted on the CTD rosette for analysis of dissolved oxygen (DO), nutrients (nitrate, nitrite, ammonium, phosphate, and silicate), particulate organic matter (POM), chlorophyll *a* (Chl*a*), and Phaeopigment (Phaeo). Analysis of DO and nutrients were carried out onboard following standard methods (Grasshoff et al., 1983). Samples for Chl*a* were filtered onboard, through Whatman GF/F filters under gentle vacuum and kept at −20 °C until analysis. Chl*a* was extracted with 90% acetone at 4 °C in the dark for 12 h and measured fluorometrically (JGOFS, 1994). Phaeopigments were also measured by adding 1N HCl to the chlorophyll extract immediately after the Chl *a* measurement. POM was characterized by its carbon (POC), nitrogen (PN) content, and their respective isotopic composition ($\delta^{13}C_{POC}$ and $\delta^{15}N_{PN}$). Samples for POM were filtered through pre-combusted 47 mm GF/F filters (400 °C for 4 h) and dried overnight at 50 °C. The filters were acidified overnight using concentrated HCl to remove inorganic carbon and further dried at 50 °C. N and C isotopic composition of POM was analysed using a continuous-flow isotope ratio mass spectrometer (Thermo Delta V Plus) attached to an elemental analyser (Flash 2000). IAEA CH-3 cellulose ($\delta^{13}C_{V\text{-}PDB} = -24.7‰$ and C content = 44.4%) and IAEA-N-2 ammonium sulfate ($\delta^{15}N = 20.3‰$ and N content = 21.1‰) was used as standard with an isotopic reproducibility of <0.10‰ and < −0.3‰ for C and N, respectively.

Smith-McIntyre Grab (0.1 m^2) was employed for sediment sampling. A single grab per sampling site and cruise was collected. Surface sediment was stored at −20 °C for the determination of texture, organic carbon (SOC), nitrogen (SN), and isotopic signatures ($\delta^{13}C_{sed}$ and $\delta^{15}N_{sed}$). Sediment texture was analysed by the sieving method (Boggs, 2009), followed by laser refraction using particle size analyzer (Malvern Mastersizer 2000). Samples for isotopic analysis were oven-dried at 50 °C, grounded, acidified, and analysed as described above for particulate samples.

The sediment samples for macrofauna were washed and sieved through a 500 μm mesh sieve, fixed and preserved using a 4% buffered Rose Bengal formalin solution onboard. In the laboratory, the samples were re-washed and sorted. Macrofauna was counted (ind. m^{-2}) and identified to the lowest possible taxa using available literature (e.g., Day, 1967; Fauvel, 1953; Sendall and Salazar-Vallejo, 2013). Biomass was estimated as wet weight and converted to g m^{-2}.

2.3. Biological traits analysis

We included four functional traits in the analysis: trophic group, mobility, protection, and bioturbation (Table 1). Trait information was compiled from literature and online trait databases (Jumars et al., 2015; Macdonald et al., 2010; MarLIN, 2006; Queirós et al., 2013), and when data was not available, we considered the information of the closest taxonomic level.

Table 1
List of functional traits and modality used.

Functional Trait	Modalities	Codes	*Function
Trophic group	Surface deposit feeder	SDF	Energy transport: production from pelagos elemental cycling/ production bentho-pelagos elemental cycling within benthos, decomposition
	Subsurface deposit feeder	SSDF	
	Filter feeders	FF	
	Carnivore	C	
Mobility	Motile	M	Production, elemental cycling
	Discretely motile	D	
	Sedentary	S	
Protection	No Protection	NP	Proxy for palatability (production)
	Tube	TU	
	Burrow	BU	
	Soft shell	SS	
	Hard shell	HS	
Bioturbation	Surficial modifier	Sm	Habitat modification, bioturbation, elemental cycling within benthos
	Biodiffusors	Bd	
	Upward conveyors	UC	
	Downward conveyors	DC	
	Epifauna	E	

*Source Weigel et al. (2016)

2.4. Data analysis

The variation in environmental parameters was evaluated using the Principal Component Analysis (PCA). The environmental variables were normalized (subtracted by mean and divided by standard deviation) before the PCA analysis.

Three univariate diversity indices were calculated: Pielou's Evenness (J′), Shannon diversity (H′, log_2), and Hurlbert Index ES (50). Pielou's Evenness measures the equality of the community based on abundance. Shannon diversity has been widely used in ecological literature to characterize species diversity. Hurlbert Index ES (50) measures the expected number of distinct species in a randomly selected subset of individuals, e.g., 50 in this study, hence ES (50).

The fuzzy coding procedure was applied for the traits (Chevene et al., 1994). The scoring values ranged from 0 to 3, where 0 represent no affinity and 3 full affinities. For example, *Paraprionospio* sp. are mostly surface deposit feeders but may also filter feed, so they were coded 2 for SDF and 1 for FF for the trait 'trophic group'. Trait category scores for each taxon were multiplied by their abundance for each sample. The trait category scores were then summed for all taxa present in each sample, resulting in a station by trait table containing the overall frequencies of occurrence of biological traits (Charvet et al., 1998).

Multivariate Non-Metric Multidimensional Scaling (nMDS) ordination was performed based on the Bray-Curtis similarity matrices on the log transformed macrofauna abundance and trait modality data. In order to identify the taxa and trait modalities that contributed to the dissimilarity among the samples, a two-way crossed Similarity Percentage (SIMPER) analysis of depth and season was performed. Relationships between environmental variables, macrofaunal taxa, and biological trait were investigated using the distance-based linear model (DISTLM) (McArdle and Anderson, 2001). All statistical analysis omitted samples that had <10 individuals. The statistical analyses were performed with Primer -E and Statistica 8 statistical packages.

3. Results

3.1. Environmental parameters across the shelf

The sea surface temperature (SST) exhibited progressive warming between January (>28 °C) and April (>30 °C), cooled down to as low as 26 °C between May and September when upwelling was strongest, and again warmed till December. The surface salinity was lowest at the nearshore in September (31.6) while it was highest at the outer shelf in July (34.9); rest of the year, salinity was stable (32.6–35.4). Bottom salinity did not show much variation and ranged from 35 to 36 throughout the study period.

Upwelling waters are associated with depleting DO concentration, and together with the terrestrial runoff, and decomposition of sinking organic matter resulted in hypoxic (<50 μM) to sub-oxic (8–10 μM) conditions in the study area. The surface water oxygen ranged from 106 to 222 μM during the non-upwelling periods (FIM, WM, and SIM). The bottom DO of the entire shelf varied from 11.5 to 112 μM and 7.7–187 μM during upwelling and non-upwelling periods, respectively. The outer shelf sustained consistent low bottom oxygen concentrations (14–132 μM) below the permanent pycnocline throughout the year.

The surface Chl*a* concentration in all the stations peaked during SM upwelling and reached a maximum of 9.50 mg m^{-3} in the nearshore waters during September, coinciding with the nutrient enrichment. Bottom Chl*a* ranged from 0.01 to 8.3 mg m^{-3} and 0.05–3.6 mg m^{-3}during the upwelling and non-upwelling periods, respectively. In general, Phaeo followed a similar trend to that of Chl*a* with high concentrations during upwelling and low and stable values during the non-upwelling periods.

3.2. Elemental and isotopic composition of organic matter

The surface (4.1–74.1 μM) and bottom water (2.3–52.2 μM) POC concentrations decreased from nearshore to outer shelf. The nearshore and inner shelf surface POC showed an increase from SIM (8.3–16.9) to September–October (66.2–74.0 μM). The $\delta^{13}C_{POC}$ followed the temporal trend of POC at all the locations. It ranged from −25.3 (Stn. 3 March) to −17‰ (Stn 2 October) with an average of −22.6 ± 1.6‰. The PN in the surface and bottom ranged from 0.6 to 12.3 μM and 0.09–6.1 μM, respectively. Temporally, the highest surface PN was recorded during SM (July) in the nearshore and inner shelf, but it was high in the bottom during SIM and pre-SM. In the deeper depths (mid shelf and outer shelf), high PN concentrations were recorded during SIM. The surface and bottom $\delta^{15}N_{POM}$ ranged from 0.1 to 9.8‰ and 1.7–17.2‰, respectively (overall 6.4 ± 4.0‰). The $\delta^{15}N_{POM}$ in the nearshore and inner shelf showed two peaks, each during SIM (6.1–6.82‰) and SM (4.6–7.7‰), whereas it was high during SM in the mid shelf. The highest $\delta^{15}N_{POM}$ was recorded at the outer shelf during SIM (15.8‰) and SM (17.2‰).

Sediments in the nearshore and inner shelf had higher amounts of silt, while mixed sediment was prevalent in the mid shelf and outer shelf. Temporal variation in sediment texture was observed only in the inner shelf (Stn 2) with sand, silt, and clay ranging from 1 to 74%, 23–91%, and 1–7%, respectively. In general, the sand and silt contents ranged from 37 to 73% and 12to 91%, respectively of the total sediment. Sediment organic carbon (SOC) was higher (3–5%) in the nearshore and inner shelf with the highest observed during June–July. A decrease in SOC was observed from nearshore to mid shelf, and then an increase in the outer shelf. The $\delta^{13}C_{sed}$ ranged from −20.0 to −26.1‰ (mean ± SD: −21.77 ± 1.35‰) with the highest and lowest values in the outer shelf (April) and nearshore (June), respectively. Sediment nitrogen (SN) ranged from 0.01 to 0.29%, while it's $\delta^{15}N$ ranged from 2.17 to 7.37‰ (6.06 ± 1.41‰). Sediment C/N ratios ranged from 16 to 42, with the highest values recorded at the inner shelf station 3 in April. The correlations among the bottom water and sediment variables were analysed and presented in Table 3S.

3.3. Principal component analyses of environmental variables

The PCA analysis revealed a clear spatiotemporal trend of environmental variables in the study area (Table 2 and Fig. 2a). The first three

Table 2
PCA loading of water and sediment parameters. Bold values are strong loading. SW- surface water; BW- bottom water; Temp- temperature; Sal- Salinity; Sed sediment.

	Factor 1	Factor 2	Factor 3
Eigenvalue	7.02	4.78	2.59
% Total	35.11	23.89	12.93
Cumulative (%)	35.11	58.99	71.92
SW Temp	0.23	**0.79**	0.29
SW Sal	0.50	0.02	0.18
SW DO	0.49	0.54	−0.57
SW NO_3	−0.38	−0.59	0.53
SW pH	0.54	0.57	−0.50
BW Temp	−0.44	0.77	0.32
BW Sal	0.05	0.10	0.09
BW DO	0.02	**0.78**	0.45
BW NO_3	0.55	−0.59	−0.41
BW pH	0.15	**0.79**	0.36
BW Chl*a*	**−0.78**	−0.33	0.27
BW Phaeo	**−0.77**	−0.41	0.04
Depth	**0.88**	−0.10	−0.04
SOC	**−0.84**	0.18	−0.13
Sed_$\delta^{13}C$	0.68	0.26	−0.10
Sed N	**−0.86**	0.16	−0.14
Sed_$\delta^{15}N$	−0.35	0.57	0.29
Sand	**0.71**	−0.32	0.50
Clay	**−0.71**	0.25	−0.55
Silt	**−0.71**	0.32	−0.50

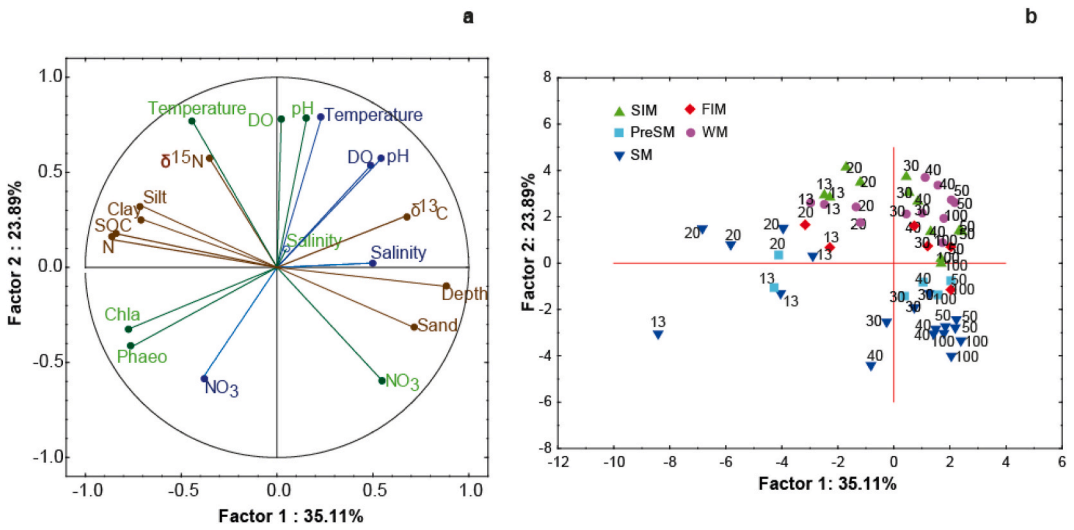

Fig. 2. PCA biplot showing variation in the environmental variables (a) and samples (b). DO dissolved oxygen; SOC sediment organic carbon; Chl*a* Chlorophyll *a*. Blue: surface water variables; Green: bottom water variables; Brown: sediment variables. Numbers in right panel represent the sampling depth. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

PCs were retained based on the Kaiser Criterion (Kaiser, 1960), which explained 72% of the total variance. PC1 accounts for 35% of the total variance in the environmental variables and has strong loading (>0.7) for sediment variables (SOC, SN, sand, silt), bottom Chl*a* and Phaeo, and depth. Therefore, this axis (PC1) represents the spatial variation and separates the nearshore and inner shelf (Stn. 2) from mid shelf and outer shelf as the former is characterized by silty-clay and sand was predominant in mid shelf and outer shelf (Fig. 2b).

PC2 (24% of the total variance) showed strong positive loading of bottom DO and pH, and surface and bottom temperature, and moderate (>0.5) negative loading of surface nitrate. This axis thereby discriminates the SIM and WM from the SM due to higher DO, pH, and temperature (Fig. 2b). PC3 (14%) showed a positive loading of surface nitrate, and negative loading for surface DO, reflecting the peak upwelling (SM).

3.4. Spatiotemporal patterns of macrofaunal abundance and biomass

Macrofaunal abundance showed a temporal and spatial variation (Fig. 3). In general, macrofaunal abundance was highest at the shallow region with the highest abundance (17560 ind. m^{-2}) recorded at the inner shelf (stn. 3) compared to the deeper stations (stn. 4 to 6) during the SM monsoon. The abundance at nearshore ranged from 260 to 9110 ind. m^{-2}, with the lowest and highest observed during May and July, respectively (Fig. 3a). Polychaeta and Mollusca dominated the macrofaunal community in the nearshore. Macrofaunal abundance at stn. 2 ranged from 330 (SM) – 6210 ind. m^{-2} (WM) and was dominated by Polychaeta (Fig. 3b). At the inner shelf (stn. 3), macrofauna showed an increase from May (11,677 ind. m^{-2}), peaked during June–July (10,780–17,560 ind. m^{-2}), and declined from September (5550 ind. m^{-2}) with Polychaeta dominating during all the seasons (Fig. 3c). Although the nearshore abundance was highest during upwelling, it was lower than the mid shelf during the rest of the period. The abundance in the deeper sites showed 2–3 peak periods throughout the year. At the mid shelf, the abundance showed three peaks each in SIM (340–3290 ind. m^{-2}), SM (980–5130 ind. m^{-2}) and WM (1430–4540 ind. m^{-2}; Fig. 3d and e). At the outer shelf, it peaked during the WM (2320 ind. m^{-2}) followed by SIM (1030–1850 ind. m^{-2}) and declined during upwelling (545–1503 ind. m^{-2}). The deeper stations were dominated by Polychaeta followed by Crustacea (Fig. 3f).

The macrofaunal biomass showed a different trend from that of abundance (Fig. 4). The biomass showed a peak (79 g m^{-2}) in SM (June) at the nearshore station but in SIM and Pre-SM (35–75.6 g m^{-2}) at the inner shelf (Stn 2). At Stn. 3 biomass was highest during Pre-SM followed by SM (June; Fig. 4). Biomass fluctuated throughout the year at the mid and outer shelves with the highest value recorded at Stn 4 (37.2 g m^{-2}) in SM (September), Stn 5 (21 and 20 g m^{-2}) in FIM and WM, and Stn 6 (15.3 g m^{-2}) in SM (September). The dominant group that contributed to the macrofaunal biomass also showed a spatiotemporal variation. In the nearshore (Fig. 4a), high biomass was due to the dominance of Mollusca, except during SM (July) and WM when Polychaeta dominated. Others (Echinodermata, Nemertea, Nematoda, Sipuncula, Echiuroidea, Cephalochordata, Phoronida, Cnidaria, Scaphopoda) followed by Mollusca and Polychaeta dominated the macrofaunal biomass at the inner shelf (Stn 2), during different periods (Fig. 4b). Polychaeta was the most dominant group (31–98%) in the inner shelf (Stn 3; Fig. 4c) and the mid shelf (24–100%; Fig. 4d). Stn 5 and outer shelf were dominated by Crustacea and Polychaeta (Fig. 4 e and f).

The ordination of species composition using nMDS based on the log transformed macrofaunal abundance showed that all four regions (nearshore, inner shelf, mid shelf, and outer shelf) during upwelling remained separate, reflecting the dissimilarity of the entire shelf with respect to the species composition and abundance (Fig. 5). The non-upwelling samples of the nearshore and inner shelf stn. 2 are similar, yet quite dissimilar to the stn. 3 (inner shelf). The separation of stn. 3 during non-upwelling (FIM, WM, SIM, and Pre-SM) indicates variation in its species composition compared to the nearshore and inner shelf. However, the pre-SM samples of stn. 3 overlapped with most of the mid shelf samples but was dissimilar from those of the outer shelf.

Two-way crossed SIMPER analysis shows that the observed dissimilarity of samples was mainly attributed to the successive replacement and coverage variation of different taxa (Table 4S). In general, a higher abundance of *Magelona* sp., *Ethminolia* sp., and *Paraprionospio* sp. separated the nearshore and inner shelf from the other samples. Most of the mid shelf samples were separated due to the higher abundance of Amphipoda, *Neomediomastus* sp., and *Sigambra* sp.1. The polychaetes, *Kirkegaardia* sp., *Ceratonereis* sp., and Oligochaeta dominated the outer shelf samples.

3.5. Spatiotemporal pattern of macrofaunal diversity

A total of 203 taxa belonging to 16 groups represented the macrofaunal community (Table 5S). The number of taxa was highest in the mid

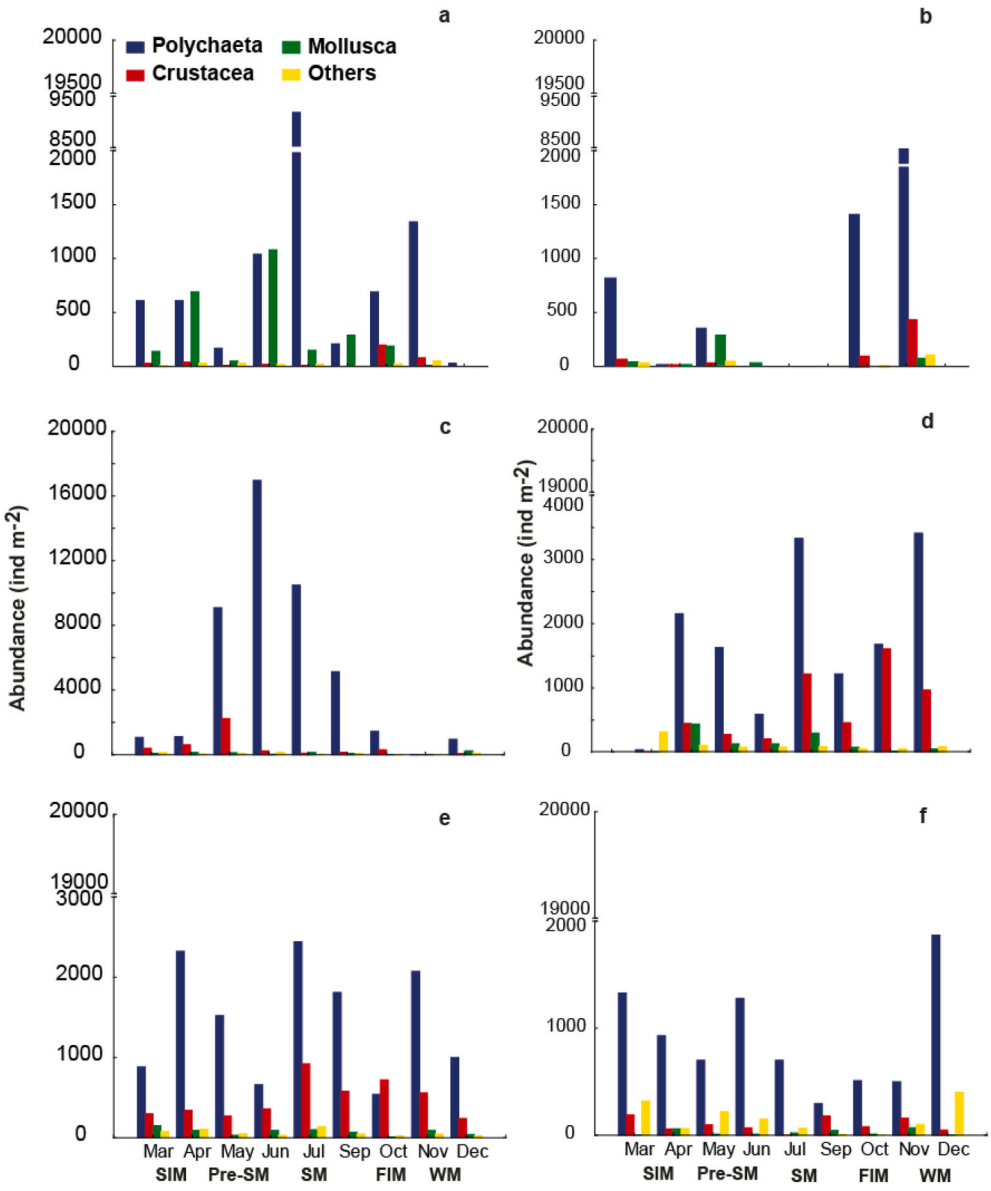

Fig. 3. Spatiotemporal variation in abundance for different macrofaunal taxonomical groups.

shelf (136 and 138 taxa) and lowest in the nearshore (54 taxa; Fig. 6). Except for nearshore station, the number of taxa was high during the non-upwelling period. Evenness was highest (0.70–0.90) in the mid shelf, and the lowest (0.09–0.80) were in the nearshore. Evenness showed temporal variation at only the nearshore and inner shelf stations, with low values recorded during the SM period. Changes in the Shannon diversity (0.29–3.67) and ES (50) (2.94–27.47) followed the same pattern as number of taxa with highest values at mid shelf. Lowest values of Shannon diversity (1.2–3.6) and ES (50) (7–14) were recorded in the nearshore. Temporally, Shannon diversity and ES were low during the upwelling period at all the sites, while high values were observed during SIM and WM.

3.6. Biological trait analysis (BTA)

As seen from the nMDS plot, biological trait composition showed similar separation across the depths and seasons for taxonomic composition, although separations were less well defined (Fig. 7). The spatial segregation was visible as some of the inner and nearshore samples (stn. 2) and the mid shelf formed separate groups. When compared by seasons, nMDS showed that the functional traits of macrofauna in the nearshore and inner shelf differed from the other region during SM, but less so during the other seasons. The composition of modalities for each trait was almost same at all the stations and seasons, but the abundance differed, which led to the observed differences among the samples (Fig. 8). Based on the two-way crossed SIMPER analysis (Table 6S), the combination of the biological trait that contributed to the differences between the shallow (nearshore and inner shelf) and deeper (mid shelf) stations include the dominance of SDF (feeding), sedentary (mobility), soft shell (protection), and epifauna and surficial modifier (bioturbators) in the shallow sites. The differences during the seasons were evident with the higher composition of traits during the non-upwelling periods (SIM, FIM, and WM) relative to the upwelling period.

Among the feeding types, SDF was highly abundant in all habitats and seasons, particularly during the upwelling period (Fig. 8a). The SSDF and carnivores showed a similar pattern but showed an increase from shallow to mid shelf and during the non-upwelling period. Discretely mobile forms dominated the mobility trait at all depths and seasons (Fig. 8b). Regarding the bioturbation trait, surficial modifiers

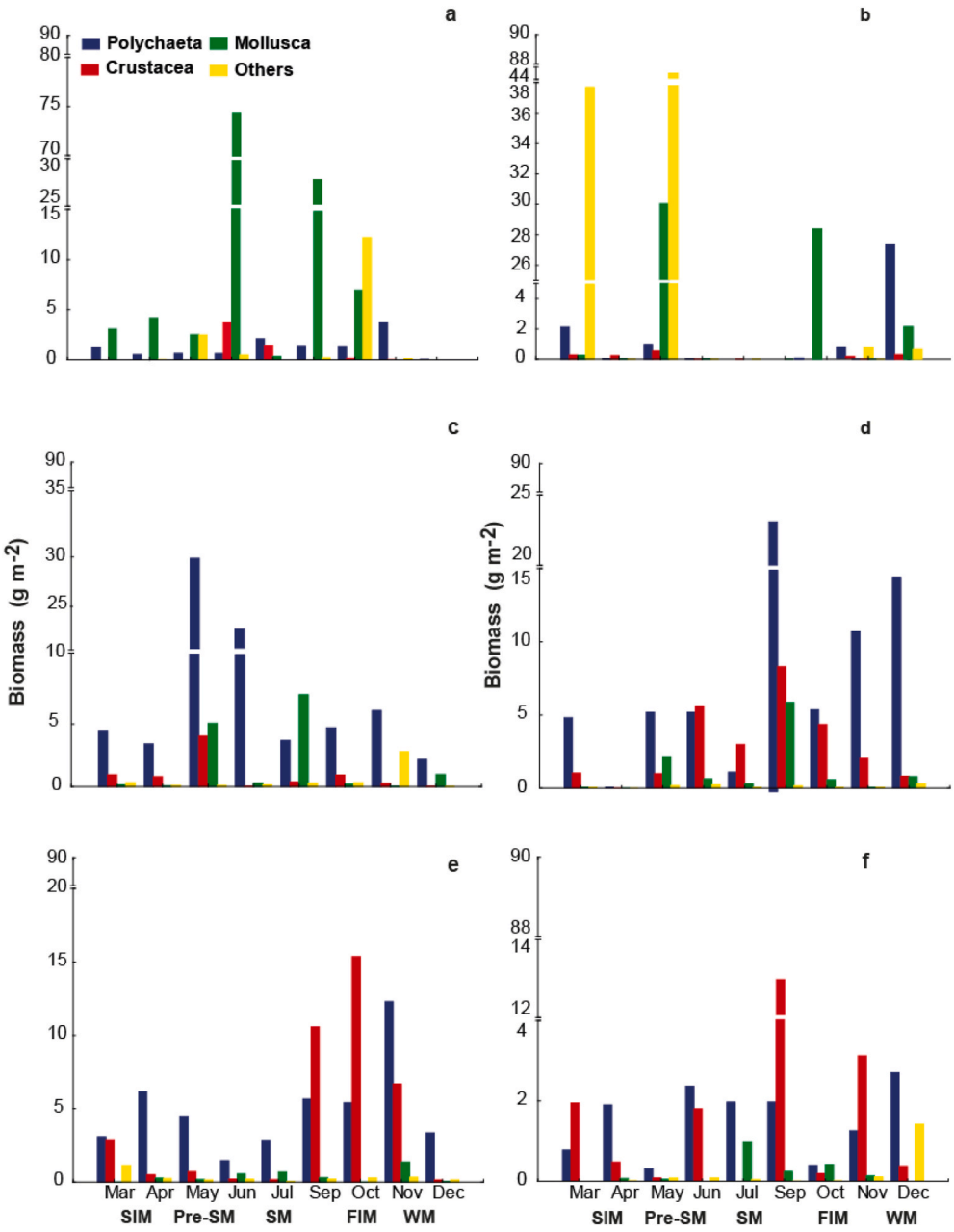

Fig. 4. Spatiotemporal variation in biomass for different macrofaunal taxonomical groups.

dominated the shallow depths during upwelling and upward/downward conveyor during the rest of the period (Fig. 8c). Although surficial modifiers dominated the mid shelf, other modalities were also abundant, which showed an increase after upwelling. The outer shelf showed a similar trend to that of mid shelf in terms of bioturbator trait. The trait protection and burrowing forms were common at all depths and seasons, but their abundance showed a spatiotemporal variation. The nearshore was dominated by burrowers, tubiculous and hard-shells during different seasons (Fig. 8d). Tubiculous was dominant during most of the seasons in the inner shelf. Most of the protection trait modalities were present at mid shelf with a temporal variation. Although burrowing organisms dominated, other protection modalities were also present in an almost equal percentage at the outer shelf.

The variation in macrofaunal abundance was related to eight environmental variables, including depth (Table 3), whereas biomass correlated strongly to only four parameters. Species number showed a significant relation with bottom $\delta^{13}C_{POM}$, Chl*a*, and Phaeo. The Shannon diversity was related only to the bottom Chl*a* and Phaeo. The biological trait was related to changes in sediment variables (SOC, SN, and texture), bottom POC, Chl*a*, Phaeo, and depth (Table 3).

4. Discussion

4.1. Environmental settings over the shelf

The natural coastal process (e.g., upwelling), land runoff, and the adjacent estuarine system influnec the sediment and water quality of the coastal system aas in the case of the SEAS. The most notable anthropogenic activities in the estuarine and coastal areas of Kochi are industries and port activities. This is in addition to domestic sewage from the Kochi city and the remote areas through river runoff, aquaculture, agriculture, and aqua-tourism (Balachandran et al., 2006; Martin et al., 2013). During the summer monsoon, large amount of fresh water is brought to the adjoining Arabian Sea, altering the environmental

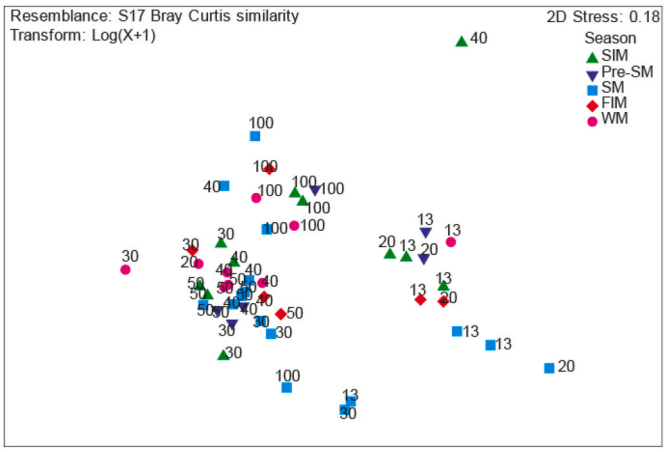

Fig. 5. Nonmetric multidimensional scaling (nMDS) based on Bray-Curtis similarity matrix of log transformed abundance data. Numbers are sampling depths.

features of the water column. Therefore, seasonal variation in precipitations imposes a substantial impact on river discharge and, consequently, on the environmental variables of the estuarine and adjacent coastal waters. It is widely accepted that increased river flow results in increased organic matter, sediment, and contaminants from the estuary to the coastal waters of Kochi. However, the impact of river discharge is mostly confined up to the nearshore region (up to 5 km), while the shelf system beyond this is influenced largely by coastal upwelling (Bhavya et al, 2017, 2018; Gupta et al., 2016; Sudheesh et al., 2016), which was also confirmed by isotopic studies of particulate matter (Gupta et al., 2021).

The nearshore region influenced by upwelling and runoff from the adjacent estuarine system had a higher amount of mud, SOC, SN, and pigments, especially during the SM compared to the deeper stations. The inner shelf (Stn. 3), mid shelf, and outer shelf separated from the nearshore and inner shelf (Stn 2) due to higher sand content and lower bottom Chl*a* and Phaeo (Fig. 2; PC1). Silt content decreased with depth, and coarse sand dominated the mid shelf, confirming the earlier report (Rao and Wagle, 1997). The mud content in the shallow depths increased after the SM, confirms that nearshore sediments in the

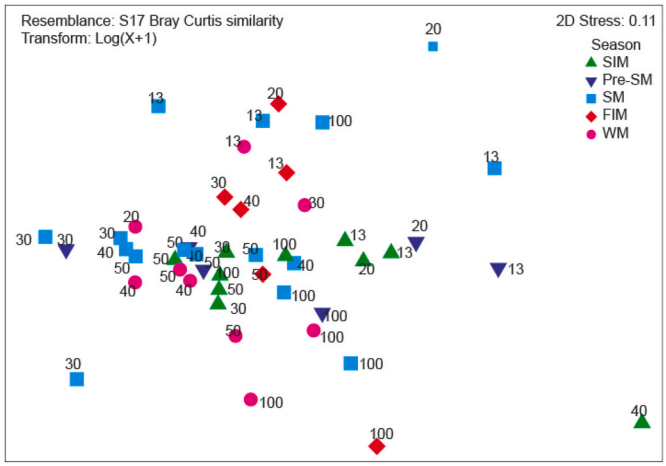

Fig. 7. Nonmetric multidimensional scaling (nMDS) based on Bray-Curtis similarity matrix of log transformed trait categories abundance.

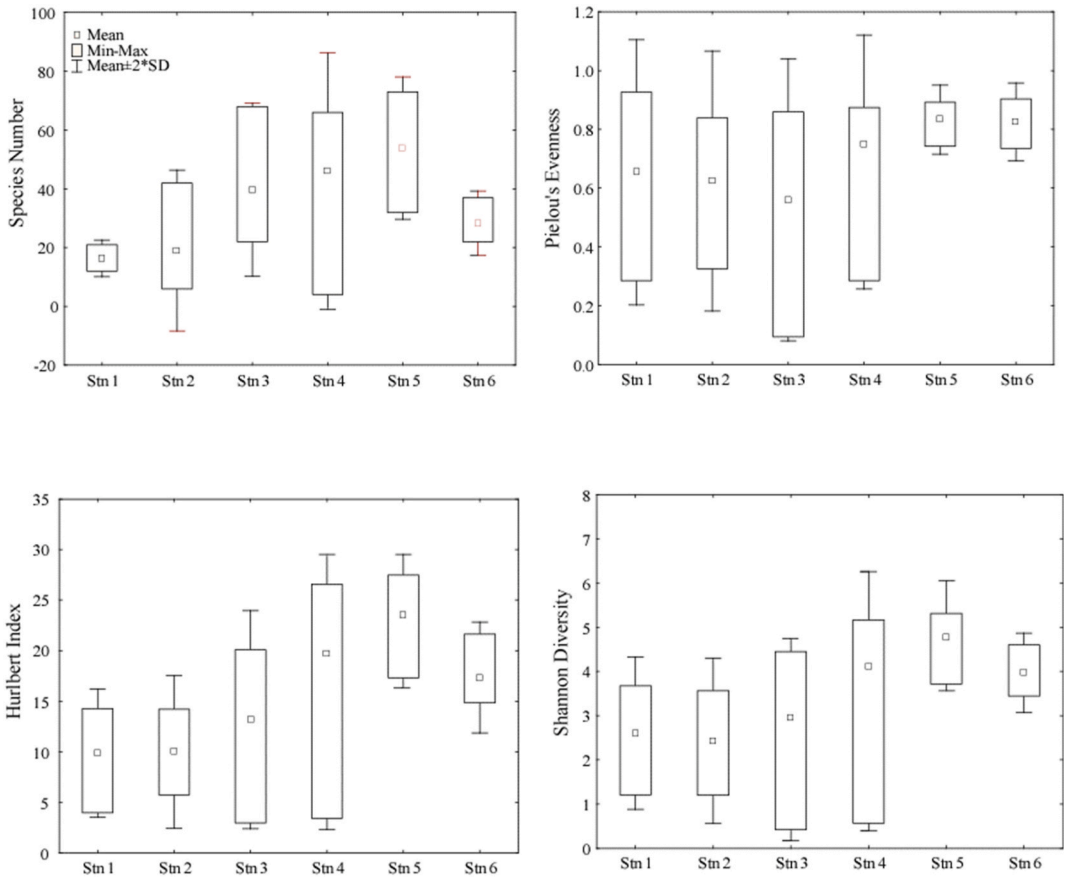

Fig. 6. Variation in the macrofaunal univariate diversity indices.

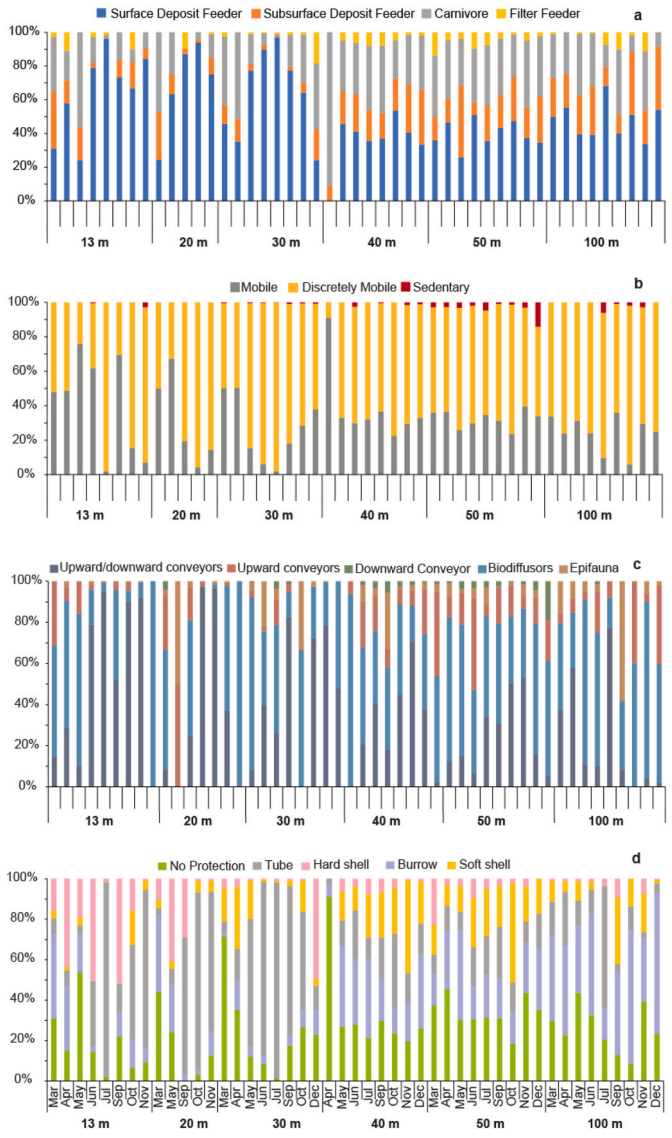

Fig. 8. Spatiotemporal variation in the abundance of the trait modalities of the (a) trophic group; (b) mobility traits; (c) bioturbation, and (d) protection trait.

Relationships between macrofaunal community and environmental variables.

southwest coast of India are influenced by estuarine inputs (Abdul Jaleel et al., 2015; Joydas and Damodaran, 2009).

The relatively higher $\delta^{13}C_{POM}$ during upwelling compared to the rest of the seasons over the entire shelf shows the dominance of upwelling-derived phytoplankton during SM, except the nearshore in June (Gupta et al., 2021). Overall, during SM upwelling, the shelf was enriched mainly by upwelling derived phytoplankton with a minor contribution of inputs from the Kochi estuary limited to the nearshore region, whereas autochthonous phytoplankton prevailed during the rest of the year. The high concentration of surface nitrate, chlorophyll concentration and low surface DO reflect the environmental conditions during peak upwelling (Fig. 2).

Sediment organic carbon followed the distribution pattern of Chl*a*, with the highest values recorded at shallow depths during the upwelling. This trend reflects the influence of an upwelling-induced increase in primary production and subsequent flux of fresh organic matter to the benthic system (Quintana et al., 2015a). The relatively high $\delta^{13}C_{sed}$ and $\delta^{15}N_{sed}$ also indicate the dominance of marine phytoplankton-derived organic matter in the benthic system. The observed $\delta^{13}C_{POM}$ values of −16 to −25‰ are signatures for marine phytoplankton (Khan et al., 2015; Rolff, 2000). The strong positive correlation among POM, Chl*a*, Phaeo, and SOC (Table 3S) confirms that the massive upwelling phytoplankton blooms in surface water produces a substantial amount of organic matter, which is transported to the benthic system, suggesting an important link in the benthic-pelagic coupling over this shelf. The accumulated organic matter forms a source of high-quality food for benthic organisms. The benthic-pelagic coupling is a complex process, particularly in the highly productive coastal areas, and the spatiotemporal variability in the flux of organic matter from the surface water to the seafloor will influence the community structure and functioning of benthic community.

Table 3
Result of DISTLM analysis. Only the significant correlations are given. BW-bottom water; Sed sediment.

	Variable	SS (trace)	Pseudo-F	P (perm)
Abundance	BW POC	4326.2	1.72	0.05
	BW$\delta^{13}C_{POM}$	5004.7	2.00	0.02
	BW PON	4686.2	1.87	0.03
	BW Chl*a*	5660.5	2.28	0.01
	BW Phaeo	4404.3	1.75	0.05
	Depth	5413.2	2.18	0.01
	SOC	4800	1.92	0.03
	Sed N	4766.2	1.90	0.03
Biomass	BW POC	5723.8	1.74	0.04
	BW Chl*a*	5573.8	1.69	0.04
	BW Phaeo	5393.7	1.63	0.05
	SOC	6061.5	1.85	0.03
Species number	BW $\delta^{13}C_{POM}$	468.6	4.97	0.03
	BW Chl*a*	663.54	7.42	0.02
	BW Phaeo	493.68	5.27	0.03
Shannon Diversity	BW Chl*a*	1183.1	5.19	0.05
	BW Phaeo	895.61	3.81	0.05
BTA	SOC	677.16	6.06	0.002
	Sed N	637.12	5.65	0.001
	BW PON	684.33	6.13	0.002
	BW Chl*a*	305.96	2.52	0.078
	BW Phaeo	401.27	3.38	0.044
	Depth	412.97	3.48	0.024
	Sand	919.04	8.71	0.001
	Clay	970.4	9.31	0.001
	Silt	911.5	8.62	0.001

4.2. *Influence of upwelling on macrofaunal community pattern*

Macrofaunal abundance and biomass decreased from shallow to deeper depths during both upwelling and non-upwelling periods, albeit their magnitude was higher during the former period. However, the macrofaunal species diversity indices showed a reverse trend to that of abundance and biomass. The upwelling fuelled organic matter supply to the benthic system, and sediment texture constitute the strongest environmental drivers of macrofaunal pattern in the study area, as evident from the DISTLM (Table 3). High abundance and biomass in the nearshore during the SM upwelling when primary production and organic matter were the highest indicates that quantity and quality of food is an important factor in influencing the macrofaunal pattern in the coastal upwelling areas (Bonsdorff et al., 2003; O'Brien et al., 2003; Sellanes et al., 2007).

The nearshore and inner shelf regions of the Kochi shelf influenced by upwelling displayed macrofaunal community patterns similar to those reported for the SE coast of India (Abdul Jaleel et al., 2021; Ingole et al., 2016; Naidu et al., 2018) and elsewhere (Dauwe et al., 1998; Gutierrez et al., 2000; Sellanes et al., 2007; Villnäs et al., 2011). Macrofaunal community along the SE coast of India during the SM period was dominated by few species but with high abundance and biomass. High abundance in the nearshore and inner shelf was contributed by the polychaetes, *Magelona* sp. and *Paraprionospio* sp. which together accounted for >70% of the total abundance. These two genera were also recorded in other hypoxic habitats as they are adapted to low oxygen

conditions (Fajardo et al., 2018; Levin et al., 2009; Pacheco et al., 2011). Adaptations in these organisms include increased respiratory movements to enhance oxygen uptake, changes in circulation, modulation of oxygen binding by respiratory pigments, reduced oxygen consumption and overall energy expenditure, as well as fermentation pathways for ATP synthesis (Grieshaber et al., 1994). The high abundance of these two polychaetes, dominated by juveniles, possibly indicates that the recruitment of these species seems to be tied to the upwelling period when fresh organic matter input is increased. At the same time, hypoxia reduces competition and predation (Levin, 2003), which made the environmental conditions more favourable for these two polychaete species. Although polychaetes dominated in terms of abundance, the gastropod *Ethminolia* sp., contributed to high biomass in the nearshore during peak upwelling. *Ethminolia* sp. is primarily a deposit feeder (Herbert, 1992), so abundant food in the sediment during the upwelling supports the high abundance and biomass.

Polychaeta, Mollusca, and Crustacea dominated macrofaunal communities in the mid shelf. The abundance of Crustacea, dominated by Ampeliscidae amphipods, was highest at the mid shelf, and the abundance of Ostracoda increased after upwelling. As crustaceans are sensitive to low DO (Gray et al., 2002), they are replaced by more tolerant macrofauna during upwelling. The outer shelf stations influenced by the long period of low oxygen conditions (~8 months; Gupta et al., 2016) were characterized by overall low macrofaunal abundance and dominated by polychaetes, *Kirkegaardia* sp., *Ceratonereis* sp., and Oligochaeta. High tolerance to organic enrichment and reduced oxygen level allows oligochaetes to increase under unfavourable conditions (Caspers, 1980).

Unlike the spatiotemporal variability observed in the macrofaunal abundance and biomass, the diversity indices showed a different pattern. The number of taxa (54–138) reported is higher than those reported by Hernández-Miranda et al. (2012), Ingole et al., (2016), and Naidu et al. (2018) but lower than that reported by Abdul Jaleel et al. (2021) and Sivadas et al. (2020). The Shannon diversity ranged from 0.29 to 3.67, which is similar to those reported by Hernández-Miranda et al. (2012) and Ingole et al., (2016) but lower than that reported by Sivadas et al. (2020) and Soto et al. (2017). The DISTLM analysis between the environmental variables with macrofaunal species diversity indices showed that only species number and Shannon diversity appeared to relate to environmental variables such as bottom $\delta^{13}C_{POM}$, Chl*a*, and Phaeo (Table 3). These variables are tracers of fresh organic carbon and high-quality food in the coastal sediments (Fry, 2006; Le Guitton et al., 2015; Rodil et al., 2020). Since the amount of quality organic matter reaching the coastal sediment is mostly associated with the upwelling, the most plausible environmental factor explaining the relation between the diversity indices and bottom $\delta^{13}C_{POM}$, Chl*a*, and Phaeo, is the upwelled-driven primary productivity. The high correlation between $\delta^{13}C_{POM}$, Chl*a*, and Phaeo, and the macrofaunal diversity indices is probably because the high organic matter allows few species to dominate, i.e., the macrofaunal community is characterised by high abundance and few taxa. This pattern of high abundance of few species and low diversity is consistent with the highly productive coastal regions of Chile (Hernández-Miranda et al., 2012; Sellanes et al., 2007; Soto et al., 2017). Most benthic studies concluded that trophic resources and substrate type are important factors influencing the macrofaunal diversity (Gallardo et al., 2004; Joydas and Damodaran, 2014). Macrofaunal diversity indices in this study are weakly correlated with sediment texture; such a weak relationship is arguably governed by the measured variables of fauna and environment, and is often context-dependent, which is in line with observations elsewhere (Bremner et al., 2006; Coll et al., 2010; Pape et al., 2013).

4.3. Biological trait analysis

We used biological traits that formed a proxy for mineralization potential (bioturbation and mobility) and link to the food web (protection and trophic guild). We predicted that macrofaunal biological traits would respond to spatiotemporal environmental variations. Environmental variables, including bottom DO, food quality, and sediment composition, explained a significant proportion of the variation in the functional patterns (Table 3). Relation between the DO, organic matter, sediment texture, and bottom water temperature, and macrofaunal functional trait has also been reported from other upwelling regions (Bon et al., 2021; Pacheco et al., 2011).

In this study, it can be concluded that spatiotemporal segregation of macrofaunal community, although weak based on the functional traits, but abundance-driven differences in the trait indicates the importance of habitat filtering. The filtering effect is supported by the observed changes in the number of individuals within trait modalities and was also underpinned by the dissimilarities in trait modalities expression between the samples (Table 6S). For example, the trait "trophic group" was dominated by SDF in the shallow depth habitats during all the seasons, whereas the mid shelf stations were dominated by SDF, FF and SSDF. Among the protection trait modalities, hard shell dominated in the nearshore, burrows, and tube dwellers in the inner shelf, while no protection was dominant in the mid shelf.

The shallow habitat, especially during the upwelling period, was characterized by few trait modalities (Fig. 8), which may be due to the stressful conditions associated with upwelling (low oxygen) and the fine sediment that retains high organic matter. *Magelona* sp. (SDF and burrower) and *Paraprionospio* sp. (SDF and tube-dweller) dominated the shallow regions. The dominance of SDF, which depends upon the pelagic primary production (Kristensen et al., 2014), indicates a strong benthic-pelagic coupling during the SM upwelling. *Paraprionospio* sp. switches from surface deposit-feeding to suspension-feeding based on the food availability (Dauwe et al., 1998). Moreover, through their various activities (feeding, bioturbation), these first colonizers make the shelf habitable for the next community to colonize (Valdemarsen et al., 2018). This is evident from the increase of carnivores and SSDF after the cessation of the upwelling. The presence of carnivores is an indicator of community functioning (high complexity of food web) as they have a higher position in the food web (Muniz and Pires, 1999). Besides, the biological activities of the initial colonizers also transport a fraction of the organic matter to deeper sediment that forms food for the SSDF. The diverse trophic group trait modalities in the mid shelf, the outer shelf, and the shallow depths during non-upwelling periods suggest a varied food source that reflects diverse pathways of energy and matter recycling (Tennenbaum and Ulanowicz, 1988; Ulanowicz, 1997).

Macrofaunal assemblages by their bioturbation activities play an important role in maintaining oxic conditions of the upwelling regions off central Chile (Gallardo et al., 1995; Gutierrez et al., 2000), eutrophication in the eastern Mediterranean Sea (Dimitriou et al., 2017), and the coastal shelf off northern Chile which is characterized by persistent upwelled oxygen-deficient waters (Pacheco et al., 2011). Surficial modifiers (*Magelona* sp. and *Paraprionopsio* sp.) that are weak-bioturbators dominated the nearshore and inner shelf macrofaunal community during upwelling. During non-upwelling periods, upward and downward conveyors and biodiffusors were the dominant bioturbators. Although the surficial bioturbators dominated at the mid shelf and outer shelf, the abundance of the biodiffusors increased from nearshore to outer shelf. Such a shift with depth in the sediment reworking traits was reported off central Chile (Gutierrez et al., 2000). A higher abundance of biodiffusors promotes nutrient retention and removal and enhances sediment oxygen penetration (Villnäs et al., 2019). Regions with high quantity and quality of organic matter are represented by SDF. While sediment with intermediate to low quantity and quality of organic carbon is related to strong bioturbating groups (Dauwe et al., 1998; Gutierrez et al., 2000; Pacheco et al., 2011). Indeed, the bioturbation by small benthic fauna is important for sediment oxidation over the SE Brazilian coastal upwelling system during summer whereas the large-sized species stimulate sediment reoxidation throughout the year (Quintana et al., 2015b).

In the SEAS, the SM upwelling is characterized by high organic

matter and bottom hypoxia/suboxia, which is conducive to the development of reduced sediment conditions (Gupta et al., 2016). Unlike denitrified surface sediments that exist over India's central west coast due to anoxic conditions during SM, the hypoxic/suboxic conditions at Kochi limits denitrification only in the anoxic subsurface sediments (Gupta et al., 2016; Sudheesh et al., 2020; 2016). Accordingly, the benthic bioturbation could be contributing to the release of denitrified gases from deeper sediments to the overlying water column at Kochi. However, due to low benthic faunal abundance, this activity is expected to be insignificant in the anoxic sediment column of the central west coast. Pacheco et al. (2011) also observed that although bioturbation may not be significant when bottom water oxygen is low, however, it may contribute to aerobic functioning at some level even under hypoxic conditions. Bon et al. (2021) suggested that in areas with natural and permanent hypoxia and anoxic conditions, species are adapted to the environmental condition, and the functioning is maintained by few well-adapted taxa.

The observed changes in the diversity and composition of traits influenced by environmental variation over the SEAS are comparable with similar results elsewhere. The shallow and deep habitats off northern Chile characterized by normoxic and hypoxic, respectively, showed different trait expressions (Pacheco et al., 2011). The shallow normoxic habitat was characterised by large and medium (size), omnivore/carnivore (trophic group), motile (mobility), while the deep hypoxic locations were dominated by small (size), filter feeders, subsurface deposit feeders (feeding strategy), and sessile (mobility) community (Pacheco et al., 2011). A nearshore-offshore difference of trait expression was also reported along the Emilia-Romagna coastline, with the nearshore community dominated by moderately mobile vermiform organisms with burrowing or tube-dwelling behaviour, and deposit feeding behaviour (Paganelli et al., 2012). The offshore community was mainly composed of laterally compressed or globose body and tube-dwelling behaviour; filter feeders and deposit feeders were dominant (Paganelli et al., 2012). In the upwelling system of northern Chile, macrofaunal communities were associated with varied feeding, movement types, and living habits. In contrast, the community in the deepest locations were mostly permanent burrowers, subsurface deposit feeders, soft bodies, and small size organisms (Bon et al., 2021). In the SEAS, diverse trait modalities dominated the mid shelf while the hypoxic habitat (shallow stations during upwelling) supported less diverse trait modalities, which can affect the ecosystem functioning (Bon et al., 2021; Fukami et al., 2005; Leibold et al., 2004; Pacheco et al., 2011).

There are limitations to this study, as the macrofauna were identified mostly to the genera level (Polychaeta), family/genera (Crustacean), and higher taxonomic level for other macrofaunal taxa. Moreover, for the biological trait information, we considered the information of the closest taxonomic level. Since data on a biological trait is often not available for all species because it might be difficult to measure specific traits for individual species, time and resources are usually limited, and species might be scarce (Pakeman, 2014). Nevertheless, studies have shown that closely related species may co-occur in a similar environment due to shared traits (Burns and Strauss, 2011), providing evidence for the observed functional pattern. Taxonomic patterns are important tools to understand community changes, and the current study reflected the seasonal changes in the environmental variables. At the same time, functional trait showed a weak spatiotemporal variation, but the abundance-driven differences in the trait modalities confirm the importance of habitat filtering. In the current study, taxonomical and functional approaches revealed different community patterns and hence, highlights the importance of considering both these approaches to describe the effects of the coastal process such as upwelling.

We argue that given the paucity of biological trait data information and lack of taxonomists for most marine invertebrates, improving taxonomy and functional trait information and understanding the contribution of rare species to ecosystem functioning is an essential first step to improve the understanding of the potential role of benthic species in the coastal ecosystem processes.

5. Conclusions

The present study explored how macrofaunal taxonomic and functional composition patterns respond to the environmental changes during the seasonal upwelling in the SEAS. This study suggests that the seasonal changes in the environmental conditions linked to upwelling (SOC, Chl*a*, and Phaeo) and spatial variation (depth and sediment texture) constitute the strongest drivers of macrofaunal taxonomic patterns (abundance and biomass). At the same time, diversity indices responded only to the spatial variation in the environmental factors. On the other hand, the biological trait modalities were distributed similarly in the study area during different seasons, but the differences in the abundance of trait modalities provide evidence for habitat filtering.

Biological trait analysis is useful for characterizing habitat and providing mechanistic explanations to animal-environmental relationships. The current study shows how considering taxonomic and functional approaches can reveal different community patterns. However, the use of macrobenthic communities to understand the tropical marine ecosystem functioning is limited due to the lack of baseline ecological data, insufficient knowledge of fauna, and difficulty in identifying marine invertebrates. Future work on this topic will require extensive sampling and field-based experimental studies, improving marine invertebrate taxonomy and complete trait information, providing better information on the links between biodiversity and ecosystem functioning.

CRediT authorship contribution statement

Sanitha K. Sivadas: Conceptualization, Formal analysis, Investigation, Writing – original draft. **G.V.M. Gupta:** Conceptualization, Writing – review & editing, Supervision. **Sanjeev Kumar:** Formal analysis, (Isotopic analysis), Investigation, Writing – original draft. **Baban S. Ingole:** Writing – review & editing.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2021.105431.

References

Abdul Jaleel, K.U., Parameswaran, U.V., Gopal, A., Khader, C., Ganesh, T., Sanjeevan, V. N., Shunmugaraj, T., Vijayan, A.K., Gupta, G.V.M., 2015. Evaluation of changes in macrobenthic standing stock and polychaete community structure along the south eastern Arabian Sea shelf during the monsoon trawl-ban. Continent. Shelf Res. https://doi.org/10.1016/j.csr.2015.04.011.

Abdul Jaleel, K.U., Parameswaran, U.V., Gopal, A., Khader, C., Sanjeevan, V.N., Vijayan, A., Gupta, G.V.M., 2021. Response of macrozoobenthic communities to summer monsoon upwelling and related hypoxia in the south eastern Arabian Sea shelf. Mar. Environ. Res. 166, 105278. https://doi.org/10.1016/j.marenvres.2021.105278.

Bagarinao, T., 1992. Sulfide as an environmental factor and toxicant: tolerance and adaptations in aquatic organisms. Aquat. Toxicol. 24, 21–62. https://doi.org/10.1016/0166-445X(92)90015-F.

Balachandran, K.K., Laluraj, C.M., Martin, G.D., Srinivas, K., Venugopal, P., 2006. Environmental analysis of heavy metal deposition in a flow-restricted tropical estuary and its adjacent shelf. Environ. Forensics 7, 345–351. https://doi.org/10.1080/15275920600996339.

Banse, K., 1959. On upwelling and bottom-trawling off the southwest coast of India. J. Mar. Biol. Assoc. India 1, 33–49.

Beauchard, O., Veríssimo, H., Queirós, A.M., Herman, P.M.J., 2017. The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. Ecol. Indicat. https://doi.org/10.1016/j.ecolind.2017.01.011.

Bhavya, P.S., Kumar, S., Gupta, G.V.M., Sudharma, K.V., Sudheesh, V., 2018. Spatio-temporal variation in δ 13 C DIC of a tropical eutrophic estuary (Cochin estuary, India) and adjacent Arabian Sea. Continent. Shelf Res. 153 https://doi.org/10.1016/j.csr.2017.12.006.

Bhavya, P.S., Kumar, S., Gupta, G.V.M., Sudheesh, V., 2017. Carbon uptake rates in the Cochin estuary and adjoining coastal Arabian Sea. Estuar. Coast 40, 447–456. https://doi.org/10.1007/s12237-016-0147-4.

Blanchette, C.A., Wieters, E.A., Broitman, B.R., Kinlan, B.P., Schiel, D.R., 2009. Trophic structure and diversity in rocky intertidal upwelling ecosystems: a comparison of community patterns across California, Chile, South Africa and New Zealand. Prog. Oceanogr. 83, 107–116. https://doi.org/10.1016/j.pocean.2009.07.038.

Boggs, S.J., 2009. Petrology of Sedimentary Rocks, Petrology of Sedimentary Rocks. The University for Texas, Austin Texas. https://doi.org/10.1017/cbo9780511626487.

Bon, M., Grall, J., Gusmao, J.B., Fajardo, M., Harrod, C., Pacheco, A.S., 2021. Functional changes in benthic macrofaunal communities along a natural gradient of hypoxia in an upwelling system. Mar. Pollut. Bull. 164 https://doi.org/10.1016/j.marpolbul.2021.112056.

Bonsdorff, E., Laine, A.O., Hänninen, J., Norkko, I.V., 2003. Zoobenthos of the outer archipelago waters (N. Baltic Sea) - the importance of local conditions for spatial distribution patterns. Boreal Environ. Res. 8, 135–145.

Bremner, J., 2008. Species' traits and ecological functioning in marine conservation and management. J. Exp. Mar. Biol. Ecol. 366, 37–47. https://doi.org/10.1016/j.jembe.2008.07.007.

Bremner, J., Rogers, S.I., Frid, C.L.J., 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol. Indicat. 6, 609–622. https://doi.org/10.1016/j.ecolind.2005.08.026.

Bremner, J., Rogers, S.I., Frid, C.L.J., 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Mar. Ecol. Prog. Ser. 254, 11–25. https://doi.org/10.3354/meps254011.

Burns, J.H., Strauss, S.Y., 2011. More closely related species are more ecologically similar in an experimental test. Proc. Natl. Acad. Sci. U.S.A. 108, 5302–5307. https://doi.org/10.1073/pnas.1013003108.

Caspers, H., 1980. The relationship of saprobial conditions to massive populations of tubificids. In: Aquatic Oligochaete Biology, pp. 503–505. https://doi.org/10.1007/978-1-4613-3048-6_26.

Charvet, S., Kosmala, A., Statzner, B., 1998. Biomonitoring through biological traits of benthic macroinvertebrates: perspectives for a general tool in stream management. Arch. fur Hydrobiol. 142, 415–432. https://doi.org/10.1127/archiv-hydrobiol/142/1998/415.

Chevene, F., Doléadec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshw. Biol. 31, 295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F.B.R., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglia, C., Galil, B.S., Gasol, J.M., Gertwage, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M.S., Koukouras, A., Lampadariou, N., Laxamana, E., de la Cuadra, C.M.L.F., Lotze, H.K., Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., Vicente, C.S., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., Voultsiadou, E., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PloS One. https://doi.org/10.1371/journal.pone.0011842.

Dauwe, B., Herman, P.M.J., Heip, C.H.R., 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Mar. Ecol. Prog. Ser. 173, 67–83. https://doi.org/10.3354/meps173067.

Day, J.H., 1967. A monograph on the Polychaeta of Southern Africa, Part I (Errantia) and Part II (Sedentaria). Trustees of the British Museum Natural History,, London, pp. 1–878.

Dimitriou, P.D., Papageorgiou, N., Karakassis, I., 2017. Response of benthic macrofauna to eutrophication in a mesocosm experiment: ecosystem resilience prevents hypoxic conditions. Front. Mar. Sci. 4 https://doi.org/10.3389/fmars.2017.00391.

Fajardo, M., Andrade, D., Bonicelli, J., Bon, M., Gómez, G., Riascos, J.M., Pacheco, A.S., 2018. Macrobenthic communities in a shallow normoxia to hypoxia gradient in the Humboldt upwelling ecosystem. PloS One 13. https://doi.org/10.1371/journal.pone.0200349.

Fauvel, P., 1953. The fauna of India including Pakistan, Ceylon, Burma and Malaysia-Annelida Polychaeta, Part I (Errantia) and Part II (Sedentaria). The Indian Press Ltd, India, pp. 1–499.

Fréon, P., Arístegui, J., Bertrand, A., Crawford, R.J.M., Field, J.C., Gibbons, M.J., Tam, J., Hutchings, L., Masski, H., Mullon, C., Ramdani, M., Seret, B., Simier, M., 2009. Functional group biodiversity in Eastern Boundary Upwelling Ecosystems questions the wasp-waist trophic structure. Prog. Oceanogr. 83, 97–106. https://doi.org/10.1016/j.pocean.2009.07.034.

Fry, B., 2006. Stable Isotope Ecology. Springer, New York. https://doi.org/10.1007/0-387-33745-8.

Fukami, T., Bezemer, T.M., Mortimer, S.R., Van Der Putten, W.H., 2005. Species divergence and trait convergence in experimental plant community assembly. Ecol. Lett. 8, 1283–1290. https://doi.org/10.1111/j.1461-0248.2005.00829.x.

Gallardo, V.A., Carrasco, F.D., Cañete, J.I., Roa, R., 1995. Ecological patterns in the benthic macrobiota across the continental shelf off central Chile. Ophelia. https://doi.org/10.1080/00785326.1995.10430583.

Gallardo, V.A., Palma, M., Carrasco, F.D., Gutiérrez, D., Levin, L.A., Cañete, J.I., 2004. Macrobenthic zonation caused by the oxygen minimum zone on the shelf and slope off central Chile. Deep. Res. Part II Top. Stud. Oceanogr. 51, 2475–2490. https://doi.org/10.1016/j.dsr2.2004.07.028.

Grasshoff, K., Ehrhardt, M., Kremling, K., 1983. Methods of Sea Water Analyses. VCH, Wainheins, Germany.

Gray, J.S., Wu, R.S.S., Ying, Y.O., 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps238249.

Grieshaber, M.K., Hardewig, I., Kreutzer, U., Portner, H.O., 1994. Physiological and metabolic responses to hypoxia in invertebrates. In: Reviews of Physiology, Biochemistry, and Pharmacology, pp. 43–147. https://doi.org/10.1007/BFb0030909.

Gupta, G.V.M., Jyothibabu, R., Ramu, C.V., Reddy, A.Y., Balachandran, K.K., Sudheesh, V., Kumar, S., Chari, N.V.H.K., Bepari, K.F., Marathe, P.H., Reddy, B.B., Vijayan, A.K., 2021. Is the world's largest coastal deoxygenation zone not anthropogenically driven? Environ. Res. Lett. https://doi.org/10.1088/1748-9326/abe9eb.

Gupta, G.V.M., Sudheesh, V., Sudharma, K.V., Saravanane, N., Dhanya, V., Dhanya, K.R., Lakshmi, G., Sudhakar, M., Naqvi, S.W.A., 2016. Evolution to decay of upwelling and associated biogeochemistry over the southeastern Arabian Sea shelf. J. Geophys. Res. Biogeosci. 121, 159–175. https://doi.org/10.1002/2015JG003163.

Gutierrez, D., Gallardo, V.A., Mayor, S., Neira, C., Vasquez, C., Sellanes, J., Rivas, M., Soto, A., Carrasco, F., Baltazar, M., 2000. Effects of dissolved oxygen and fresh organic matter on the bioturbation potential of macrofauna in sublittoral sediments off Central Chile during the 1997/1998 El Nino. Mar. Ecol. Prog. Ser. 202, 81–99. https://doi.org/10.3354/meps202081.

Herbert, D.G., 1992. Revision of the umboniinae in southern Africa and Mozambique (Mollusca: Prosobranchia: trochidae). Ann. Natal. Mus. 33, 379–459.

Hernández-Miranda, E., Veas, R., Labra, F.A., Salamanca, M., Quiñones, R.A., 2012. Response of the epibenthic macrofaunal community to a strong upwelling-driven hypoxic event in a shallow bay of the southern Humboldt Current System. Mar. Environ. Res. 79, 16–28. https://doi.org/10.1016/j.marenvres.2012.04.004.

Ingole, B.S., Periasamy, R., De, K., 2016. Macrobenthic community structure response to coastal hypoxia off southeastern Arabian Sea. J. Coast. Zone. Manag. 19, 1–10. https://doi.org/10.4172/2473-3350.1000436.

Janas, U., Wocial, J., Szaniawska, A., 2004. Seasonal and annual changes in the macrozoobenthic populations of the Gulf of Gdańsk with respect to hypoxia and hydrogen sulphide. Oceanologia.

JGOFS, 1994. Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurements. IOC Manual and guides N°. 29, Paris.

Joydas, T.V., Damodaran, R., 2014. Infaunal macrobenthos of the oxygen minimum zone on the Indian western continental shelf. Mar. Ecol. 35, 22–35. https://doi.org/10.1111/maec.12052.

Joydas, T.V., Damodaran, R., 2009. Infaunal macrobenthos along the shelf waters of the west coast of India, Arabian Sea. Indian J. Mar. Sci. 38, 191–204.

Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of polychaete feeding guilds. Ann. Rev. Mar. Sci. 7, 497–520. https://doi.org/10.1146/annurev-marine-010814-020007.

Jyothibabu, R., Asha Devi, C.R., Madhu, N.V., Sabu, P., Jayalakshmy, K.V., Jacob, J., Habeebrehman, H., Prabhakaran, M.P., Balasubramanian, T., Nair, K.K.C., 2008. The response of microzooplankton (20-200 μm) to coastal upwelling and summer stratification in the southeastern Arabian Sea. Continent. Shelf Res. 28, 653–671. https://doi.org/10.1016/j.csr.2007.12.001.

Kaiser, H.F., 1960. The application of electronic computers to factor Analysis. Educ. Psychol. Meas. 20, 141–151. https://doi.org/10.1177/001316446002000116.

Karlson, K., Bonsdorff, E., Rosenberg, R., 2007. The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. Ambio 36, 161–167. https://doi.org/10.1579/0044-7447(2007)36[161:TIOBMF]2.0.CO;2.

Khan, N.S., Vane, C.H., Horton, B.P., 2015. Stable carbon isotope and C/N geochemistry of coastal wetland sediments as a sea-level indicator. In: Handbook of Sea-Level Research. https://doi.org/10.1002/9781118452547.ch20.

Kodama, K., Lee, J.H., Oyama, M., Shiraishi, H., Horiguchi, T., 2012. Disturbance of benthic macrofauna in relation to hypoxia and organic enrichment in a eutrophic coastal bay. Mar. Environ. Res. 76, 80–89. https://doi.org/10.1016/j.marenvres.2011.08.007.

Kristensen, E., Delefosse, M., Quintana, C.O., Flindt, M.R., Valdemarsen, T., 2014. Influence of benthic macrofauna community shifts on ecosystem functioning in shallow estuaries. Front. Mar. Sci. https://doi.org/10.3389/fmars.2014.00041.

Le Guitton, M., Soetaert, K., 2015. Biogeochemical consequences of vertical and lateral transport of particulate organic matter in the southern North Sea: a multiproxy approach. Estuar. Coast Mar. Sci. 165, 117–127. https://doi.org/10.1016/j.ecss.2015.09.010.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. https://doi.org/10.1111/j.1461-0248.2004.00608.x.

Levin, L.A., 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanogr. Mar. Biol. Annu. Rev. 41, 9. https://doi.org/10.1201/9780203180570-3.

Levin, L.A., Ekau, W., Gooday, A.J., Jorissen, F., Middelburg, J.J., Naqvi, S.W.A., Neira, C., Rabalais, N.N., Zhang, J., 2009. Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences 6, 2063–2098. https://doi.org/10.5194/bg-6-2063-2009.

Macdonald, T., Burd, B.J., Macdonald, V.I., Roodselaar, A., Road, W.S., 2010. Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the strait of Georgia , British Columbia Canadian technical report of fisheries and aquatic Sciences 2874. Can. Tech. Rep. Fish. Aquat. Sci. 69.

Madhupratap, M., Nair, K.N.V., Gopalakrishnan, T.C., Haridas, P., Nair, K.K.C., Venugopal, P., Gauns, M., 2001. Arabian Sea oceanography and fisheries of the west coast of India. Curr. Sci. 81, 355–361.

MarLIN, 2006. BIOTIC - biological traits information catalogue. In: Marine Life Information Network. Marine Biological Association of the United Kingdom, Plymouth [Cited 12.2015] Available from. www.marlin.ac.uk/biotic.

Martin, G.D., Jyothibabu, R., Madhu, N.V., Balachandran, K.K., Nair, M., Muraleedharan, K.R., Arun, P.K., Haridevi, C.K., Revichandran, C., 2013. Impact of eutrophication on the occurrence of Trichodesmium in the Cochin backwaters, the largest estuary along the west coast of India. Environ. Monit. Assess. 185, 1237–1253. https://doi.org/10.1007/s10661-012-2628-7.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2.

Muniz, P., Pires, A.M.S., 1999. Trophic structure of polychaetes in the Sao Sebastiao channel (southeastern Brazil). Mar. Biol. 134, 517–528. https://doi.org/10.1007/s002270050567.

Naidu, S.A., Rao, G.D., Vardhan, K.V., Kumaraswami, M., Rao, V.R., Ramu, K., 2018. Impact of natural and anthropogenic disturbances on the benthic ecological quality of the coastal waters of Kochi, southwest coast of India. Int. J. Environ. Res. 12, 861–875. https://doi.org/10.1007/s41742-018-0140-9.

Naqvi, S.W.A., Naik, H., Jayakumar, A., Pratihary, A.K., Narvenkar, G., Kurian, S., Agnihotri, R., Shailaja, M.S., Narvekar, P.V., 2009. Seasonal anoxia over the Western Indian continental shelf. In: Geophysical Monograph Series, pp. 333–345. https://doi.org/10.1029/2008GM000745.

O'Brien, K., Hänninen, J., Kanerva, T., Metsärinne, L., Vuorinen, I., 2003. Macrozoobenthic zonation in relation to major environmental factors across the Archipelago Sea, northern Baltic Sea. Boreal Environ. Res. 8, 159–170.

Pacheco, A.S., González, M.T., Bremner, J., Oliva, M., Heilmayer, O., Laudien, J., Riascos, J.M., 2011. Functional diversity of marine macrobenthic communities from sublittoral soft-sediment habitats off northern Chile. Helgol. Mar. Res. 65, 413–424. https://doi.org/10.1007/s10152-010-0238-8.

Paganelli, D., Marchini, A., Occhipinti-Ambrogi, A., 2012. Functional structure of marine benthic assemblages using biological traits analysis (BTA): a study along the Emilia-Romagna coastline (Italy, North-west Adriatic sea). Estuar. Coast Shelf Sci. 96, 245–256. https://doi.org/10.1016/j.ecss.2011.11.014.

Pakeman, R.J., 2014. Functional trait metrics are sensitive to the completeness of the species' trait data? Methods Ecol. Evol. 5, 9–15. https://doi.org/10.1111/2041-210X.12136.

Pape, E., Bezerra, T.N., Jones, D.O.B., Vanreusel, A., 2013. Unravelling the environmental drivers of deep-sea nematode biodiversity and its relation with carbon mineralisation along a longitudinal primary productivity gradient. Biogeosciences 10, 3127–3143. https://doi.org/10.5194/bg-10-3127-2013.

Parameswaran, U.V., Abdul Jaleel, K.U., Sanjeevan, V.N., Gopal, A., Vijayan, A.K., Gupta, G.V.M., Sudhakar, M., 2018. Diversity and distribution of echinoderms in the South Eastern Arabian Sea shelf under the influence of seasonal hypoxia. Prog. Oceanogr. 165, 189–204. https://doi.org/10.1016/j.pocean.2018.06.005.

Poff, N.L.R., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. J. North Am. Benthol. Soc. 16, 391–409. https://doi.org/10.2307/1468026.

Prasanna Kumar, S., Madhupratap, M., Dileep Kumar, M., Muraleedharan, P.M., De Souza, S.N., Gauns, M., Sarma, V.V.S.S., 2001. High biological productivity in the central Arabian Sea during the summer monsoon driven by Ekman pumping and lateral advection. Curr. Sci. 81, 1633–1638.

Queirós, A.M., Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Van Colen, C., Van Hoey, G., Widdicombe, S., 2013. A bioturbation classification of European marine infaunal invertebrates. Ecol. Evol. 3, 3958–3985. https://doi.org/10.1002/ece3.769.

Quintana, C.O., Bernardino, A.F., de Moraes, P.C., Valdemarsen, T., Sumida, P.Y.G., 2015a. Effects of coastal upwelling on the structure of macrofaunal communities in SE Brazil. J. Mar. Syst. 143, 120–129. https://doi.org/10.1016/j.jmarsys.2014.11.003.

Quintana, C.O., Shimabukuro, M., Pereira, C.O., Alves, B.G.R., Moraes, P.C., Valdemarsen, T., Kristensen, E., Sumida, P.Y.G., 2015b. Carbon mineralization pathways and bioturbation in coastal Brazilian sediments. Sci. Rep. 5 https://doi.org/10.1038/srep16122.

Rao, V.P., Wagle, B.G., 1997. Geomorphology and surficial geology of the western continental shelf and slope of India: a review. Curr. Sci.

Reddy, N.P.C., 2003. Organic matter distribution in the continental shelf sediments, off Kochi, west coast of India. Indian J. Petrol Geol. 12, 41–47.

Rodil, I., Lucena-Moya, P., Tamelander, T., Norkko, J., Norrko, A., 2020. Seasonal variability in benthic–pelagic coupling: quantifying organic matter inputs to the seafloor and benthic macrofauna using a multi-marker approach. Front. Mar. Sci. 7, 404. https://doi.org/10.3389/fmars.2020.00404.

Rolff, C., 2000. Seasonal variation in δ13C and δ15N of size-fractionated plankton at a coastal station in the northern baltic proper. Mar. Ecol. Prog. Ser. 203, 47–65. https://doi.org/10.3354/meps203047.

Sellanes, J., Quiroga, E., Neira, C., Gutiérrez, D., 2007. Changes of macrobenthos composition under different ENSO cycle conditions on the continental shelf off central Chile. Continent. Shelf Res. 27, 1002–1016. https://doi.org/10.1016/j.csr.2007.01.001.

Sendall, K, Salazar-Vallejo, SI, 2013. Revision of *Sternaspis* Otto, 1821 (Polychaeta, Sternaspidae) 286:1–74. Zookeys 286, 1–74. https://doi.org/10.3897/zookeys.286.4438.

Sivadas, S.K., Nagesh, R., Gupta, G.V.M., Gaonkar, U., Mukherjee, I., Ramteke, D., Ingole, B.S., 2016. Testing the efficiency of temperate benthic biotic indices in assessing the ecological status of a tropical ecosystem. Mar. Pollut. Bull. 106 https://doi.org/10.1016/j.marpolbul.2016.03.026.

Sivadas, S.K., Singh, D.P., Saraswat, R., 2020. Functional and taxonomic (α and β) diversity patterns of macrobenthic communities along a depth gradient (19–2639 m): a case study from the southern Indian continental margin. Deep. Res. Part I Oceanogr. Res. Pap. 159 https://doi.org/10.1016/j.dsr.2020.103250.

Soto, E., Quiroga, E., Ganga, B., Alarcón, G., 2017. Influence of organic matter inputs and grain size on soft-bottom macrobenthic biodiversity in the upwelling ecosystem of central Chile. Mar. Biodivers. 47, 433–450. https://doi.org/10.1007/s12526-016-0479-0.

Statzner, B., Bêche, L.A., 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? Freshw. Biol. 55, 80–119. https://doi.org/10.1111/j.1365-2427.2009.02369.x.

Sudheesh, V., Gupta, G.V.M., Naqvi, S.W.A., 2020a. Massive methane loss during seasonal hypoxia/anoxia in the nearshore waters of southeastern Arabian Sea. Front. Mar. Sci. 7 https://doi.org/10.3389/fmars.2020.00324.

Sudheesh, V., Gupta, G.V.M., Naqvi, S.W.A., 2020b. Massive methane loss during seasonal hypoxia/anoxia in the nearshore waters of southeastern Arabian Sea. Front. Mar. Sci. https://doi.org/10.3389/fmars.2020.00324.

Sudheesh, V., Gupta, G.V.M., Sudharma, K.V., Naik, H., Shenoy, D.M., Sudhakar, M., Naqvi, S.W.A., 2016. Upwelling intensity modulates N2O concentrations over the western Indian shelf. J. Geophys. Res. Ocean 121, 8551–8565. https://doi.org/10.1002/2016JC012166.

Tennenbaum, S., Ulanowicz, R.E., 1988. Growth and Development: Ecosystems Phenomenology, Estuaries. Springer-Verlag, New York. https://doi.org/10.2307/1351721.

Ulanowicz, R.E., 1997. Ecology, the Ascendent Perspective. Columbia University Press, New York.

Valdemarsen, T., Quintana, C.O., Thorsen, S.W., Kristensen, E., 2018. Benthic macrofauna bioturbation and early colonization in newly flooded coastal habitats. PloS One 13. https://doi.org/10.1371/journal.pone.0196097.

Vaquer-Sunyer, R., Duarte, C.M., 2010. Sulfide exposure accelerates hypoxia-driven mortality. Limnol. Oceanogr. https://doi.org/10.4319/lo.2010.55.3.1075.

Vijapure, T., Sukumaran, S., Neetu, S., Chandel, K., 2019. Macrobenthos at marine hotspots along the northwest Indian inner shelf: patterns and drivers. Mar. Environ. Res. 144, 111–124. https://doi.org/10.1016/j.marenvres.2018.12.007.

Villnäs, A., Janas, U., Josefson, A.B., Kendzierska, H., Nygård, H., Norkko, J., Norkko, A., 2019. Changes in macrofaunal biological traits across estuarine gradients: implications for the coastal nutrient filter. Mar. Ecol. Prog. Ser. 622, 31–48. https://doi.org/10.3354/meps13008.

Villnäs, A., Perus, J., Bonsdorff, E., 2011. Structural and functional shifts in zoobenthos induced by organic enrichment - implications for community recovery potential. J. Sea Res. 65, 8–18. https://doi.org/10.1016/j.seares.2010.06.004.

Vivekanandan, E., Srinath, M., Kuriakose, S., 2005. Fishing the marine food web along the Indian coast. Fish. Res. 72, 241–252. https://doi.org/10.1016/j.fishres.2004.10.009.

Weigel, B., Blenckner, T., Bonsdorff, E., 2016. Maintained functional diversity in benthic communities in spite of diverging functional identities. Oikos 125 (10), 1421–1433. https://doi.org/10.1111/oik02894.