

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.

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Abstract

Identifying the drivers that shape the biodiversity of a region is important to predict the response of ecosystems to environmental changes. Macrofaunal distribution pattern in the North Indian Ocean has so far been mainly studied considering small geographical areas, and using taxonomic diversity. The present study is a functional trait based approach aimed to identify the environmental drivers of macrofaunal distribution and diversity pattern from the relatively unexplored southern Indian continental margin. A total of 53 stations were sampled along six transects from a depth range of 19–2639 m. Along with taxonomic (α and β -diversity), functional structure was assessed using Biological Trait Analysis (BTA) and multivariate functional indices (richness, evenness, dispersal, divergence and Rao's Entropy). Principal Component Analysis identified a clear depth-related variability in the measured environmental parameters. Alpha diversity of the macrofaunal community decreased with increasing depth, a trend driven by depth related changes in the environmental factors (dissolved oxygen, sediment organic carbon and texture). However, functional diversity was only partially explained by the studied environmental variables which may due to different factors governing the taxonomic and functional diversity pattern of macrofauna. Among the functional indices, only functional richness and evenness showed a clear trend of increase from shallow to deeper depths indicating that biodiversity-environmental relations are complex. Therefore, investigating the response of macrofaunal community using multiple measure of diversity (α , β - and, functional diversity) was useful for providing an understanding of macrofaunal diversity pattern. The results of our study contribute to the growing knowledge on large-scale diversity gradients for marine macroinvertebrates, which may be critical for understanding ecological patterns and its responses to both habitat and climatic change.

Keywords: Biological Trait Analysis, coastal, deep-sea, α and β -diversity, functional diversity, macrofauna, North Indian Ocean.

Introduction

Marine systems are subjected to a variety of natural, anthropogenic and climate-change induced pressures. An important challenge is to understand how marine biodiversity and ecosystem functioning will be affected by these continuous changes. Understanding the factors that shape spatiotemporal variation in species diversity patterns remains one of the major issues confronting ecologists. Although a great deal of research have been carried out to understand the causes of species distribution and diversity pattern, little is known about the effects of environmental variables on species functional diversity and how they influence the marine ecosystem functioning. Knowledge of the relationship between biodiversity and ecosystem functioning is crucial for understanding the functioning of our biosphere (Danovaro et al. 2008).

Studies on the biodiversity-ecosystem functioning relation have mainly carried out in the terrestrial and freshwater habitat or through experimental research, and these studies have shown that biodiversity is crucial for ecosystem functioning (Bonada et al. 2006; Bremner et al. 2006; Statzner & Bêche 2010; Belly & Snelgrove 2018). The functional composition and diversity of communities changes along environmental gradients (Bremner et al. 2006; Statzner & Bêche 2010; Baldrighi & Manini 2015; Belly & Snelgrove 2018). However, little is known about the influences of local and large-scale environmental factors such as latitude, sediment type, or climatic changes on the functional pattern of marine communities. Therefore in the present rapidly changing environment, it is necessary to understand the role of local and large-scale environmental changes on the functional traits (composition and diversity) and in turn ecosystem functioning. As compared to terrestrial system, only a few studies have attempted to assess the relation between the functional diversity and environmental conditions in marine system (Bremner et al. 2006; Danovaro et al. 2008; Pape et al. 2013; Törnroos et al. 2015; Baldrighi & Manini 2015; Beauchard et al. 2017; Belly & Snelgrove 2018). The realization that functional diversity provides a direct mechanistic link between biodiversity and ecosystem functioning, a growing amount of research in marine studies are using the functional based approach (Bremner et al. 2006; Danovaro et al. 2008; Pape et al. 2013; Törnroos et al. 2015; Baldrighi & Manini 2015; Belly & Snelgrove 2018).

Benthic fauna is an important tool to explore the relationship between biodiversity and ecosystem functioning (Snelgrove 1999). Macrobenthic fauna play a major role in the marine ecosystem functioning, such as food for higher organism including demersal fish, nutrient recycling, and sediment oxygenation (Snelgrove 1999; Meysman et al. 2006). Studies on the macrofaunal functional diversity have often been carried in the coastal waters (e.g. Belley & Snelgrove 2018)

with a few studies in the deep-sea system (Baldrighi et al. 2017; Baldrighi & Manini 2015; McClain et al. 2018).

In contrast to the well-studied coastal and shelf region of the Arabian Sea and Bay of Bengal (Jayaraj et al. 2008; Joydas & Damodaran 2009; 2014; Raman et al. 2014), fundamental questions regarding the distribution and diversity patterns of macrobenthic species from the deep-sea habitats are largely unanswered. Previous studies investigating the deep-sea benthic communities from the region were focused towards the northern, particularly the Oxygen Minimum Zone (OMZ). The OMZ is thicker and intensifies towards the north and is an important region of global biogeochemical processes (Sarma 2003; Banse et al. 2014). Moreover, it is predicted to expand due to climate change (Stramma et al. 2010) resulting in increasing interest to understand the system. Nevertheless, these studies have provided important insights, and documented interesting species new to science indicating that the regions comprise of distinct and diverse biodiversity (Levin et al. 2013; Ingole et al. 2010; Raman et al. 2014).

Currently, the diversity and distribution of macrofaunal assemblages inhabiting the southern Indian continental margin is poorly studied (Abdul Jaleel et al. 2015). Macrofaunal community pattern for the Indian subcontinent is mostly restricted to the northern region and to the depth of <200 m. Further, most of these studies were restricted to taxonomic species composition and α -diversity (species number), limiting the ability to understand the role of the species in the ecosystem functioning. Furthermore, of the few studies that have been published from the Indian continental margin on the macrofaunal functional pattern are on the functional composition and have considered a limited number of functional traits (feeding, size or bioturbation).

Despite the high potential applicability of functional diversity approaches in understanding the marine ecosystem functioning, there are scant studies from the marine benthic system of the North Indian Ocean (Vijapure et al. 2019). The aims of the present study were to (1) compare patterns of taxonomic and functional diversity of macrofaunal species along a depth gradient (19–2639 m), (2) identify the factors governing functional diversity patterns, and (3) find out if the functional diversity responds in the same way as species richness to environmental variation. The functional diversity of organisms can be expressed in several ways (Naeem et al. 1995; Hiddink et al. 2009). The present study uses the Biological Trait Analysis (BTA) and multivariate diversity indices to understand the role of macrofauna functional diversity pattern from the shallow (19 m) to deep sea (2639 m) system of the southern India continental region.

Quantifying pattern of species turnover or species beta diversity (β -diversity) along the environmental gradient is one of the key tools in large-scale ecological studies (McClain & Rex

2015). Given that there are no studies on macrofaunal β -diversity from the region, and it's important to understand the large-scale biodiversity pattern, we also analysed the macrofaunal species β -diversity and the environmental factors governing it in the study area.

Materials & Methods

Study Area: Lakshadweep Sea off the southern margin of India

The North Indian Ocean (NIO) north of 10°S, is amongst the 18 richest multitaxon centers of endemism and at high risk from anthropogenic activities (Roberts et al. 2002). The Indian peninsula divides the NIO into the Arabian Sea (AS) and Bay of Bengal (BoB). Despite located in similar latitudes, the two seas have remarkably contrasting environmental features. As a result the NIO hosts a unique system of interrelated oceanographic, geomorphological and biogeochemical processes, and is characterised by the seasonally reversing monsoon winds (e.g. Shankar et al. 2002; Ittekkot et al. 2003; Prasanna Kumar 2004; Schils & Wilson 2006; Durand et al. 2009; Amol et al. 2012; Rixen et al. 2019). The strong southwest monsoon winds result in an intense upwelling, making the region one of the most productive marine ecosystems in the world oceans. This high productivity and low ventilations due to the closed northern boundaries, sustains the world's thickest oxygen minimum zone (OMZ) in the present day oceans. Further more, the vertical and lateral fluxes in the NIO are highly influenced by the monsoon-induced (southwest and northeast monsoon) temporal and regional variability (Ittekkot et al. 1992, Haake et al. 1993, Rixen et al. 2019). However, on the whole, the biogeochemical processes in the NIO, especially the southern AS and BoB remain poorly understood.

The southern margin of India is unique as it is the conduit between low salinity BoB water entering into the eastern AS during the winter season and high salinity AS water entering into the western BoB during the summers. This exchange of water mass between the AS and BoB, imparts a strong seasonality to the region, off the southern margin of India. A characteristic relict carbonate platform marks the larger part of the shelf in this region. Although the BoB has relatively low productivity compared to AS ($0.1\text{--}8\text{ mg m}^{-3}$), the southern part of the Bay showed high chlorophyll values (upto 2 mg m^{-3}) during northeast monsoon (November–January) due the open ocean upwelling driven by Ekman pumping (Vinayachandran & Mathew 2003; Jyothibabu et al. 2015).

On Board Sampling and Processing

Macrobenthos and environmental samples were collected during the cruises of the project “*Sub-centennial scale quantitative paleoclimatic reconstruction to delineate low frequency natural*

climatic variability". Sampling was conducted on-board RV *Sindhu Sadhana* from 18–26th October 2014 (Fig. 1).

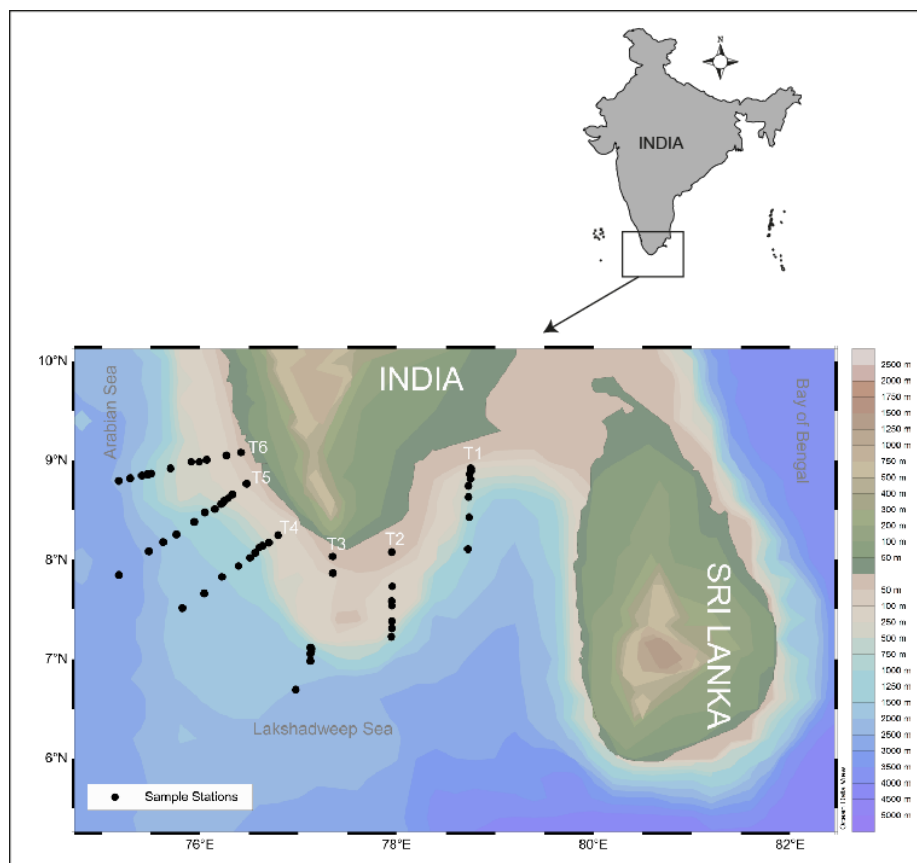


Fig. 1. Map showing the sampling location.

Sediment samples were collected along six transects (T) perpendicular to shore, in the Lakshadweep Sea (from 5° 49' N and 78° 25' E) and south-eastern Arabian Sea (8°06' N and 78° 43' E). Sampling depth ranged from 19–2639 m. Sediment samples were collected in replicates (n=2–4) using a multi-corer (internal \varnothing 10 cm). A van Veen grab (12x12") was operated at the shallow depths as it was difficult to recover undisturbed sediment after repeated operation using the multi-corer. Water overlying the core was gently siphoned onto a 300 μ m sieve to retain all the macrobenthic fauna. The core was sectioned at 0-2, 3-5, 5-10, 10-15 and 15-20 cm intervals and fixed in 5% neutral formalin rose-Bengal stain solution.

The water overlying from one of the cores was immediately collected for dissolved oxygen (DO) and photosynthetic pigments (Chlorophyll-a and Phaeopigment) analysis. The surface water samples were collected using a bucket for Chlorophyll-a (Chl-a) and phaeopigment (Phaeo) analysis.

Temperature and salinity of surface and core water were measured by using the multi-parameter probe.

Processing of Environmental and Biological Samples

Sediment for organic matter, and photosynthetic pigments were collected (top 2 cm) and frozen at -20°C. About 1–2 g of sediment was fixed with 10 ml of 90% acetone and incubated for 24 h at 4°C, and then the supernatant was analyzed before and following the acidification using a spectrofluorometer (Holm-Hansen & Reimann 1978). The sediment was dried and weighed in order to standardize pigment concentrations per gram of sediment. For water Chl-a and Phaeo analysis, surface water (2 l) and core water (1 l) was filtered through GF/F filters (pore size 0.45 µm). The phytoplankton biomass retained on the filters was extracted after 12h of incubation with 10 ml of 90% acetone at 4°C and analysed on a spectrofluorometre (Holm-Hansen & Reimann 1978). The core water DO was analyzed following the Winkler's titration method using automated titration unit (Metrohm-Switzerland). Once in the laboratory, all the macrofauna samples were sieved on 300 µm mesh, sorted and preserved in 5% buffered formalin till further analysis. Fauna were identified up to the lowest possible taxonomic level and counted (ind. m⁻²). Biomass was estimated by wet weight method and expressed as g m⁻².

For organic carbon analysis, a small aliquot of sediment was freeze-dried. The dried sediment was finely powdered and used for total and inorganic carbon analysis. The total carbon was measured by using a 'Thermo Flash 2000' elemental analyser and the inorganic carbon was analysed by using a 'UIC CM 5015 CO₂ coulometer'. The organic carbon was estimated by subtracting the inorganic carbon from the total carbon. A part of the freeze-dried sediment was also used for grain-size analysis. The dry sediment was weighed and soaked overnight. Subsequently, the overlying water was decanted and the wet sediment was poured into a 63 µm sieve. The sediments were thoroughly washed to remove all the fine particles (silt and clay). The material retained on the sieve (>63 µm, coarse fraction) was transferred to pre-weighed glass beakers and dried overnight. The dried coarse fraction was weighed to estimate the percentage of coarse fraction in the sediments. The percentage of fine particles was calculated by subtracting the coarse fraction from the weight of sediments.

Data Analysis

The multivariate Principal Components Analysis (PCA) was used to determine the most important environmental gradients in the study area. Pearson's correlation was performed on the environmental data before the PCA analysis, to check for the correlation between the environmental data. Since

surface water photosynthetic pigments were significantly correlated with core water and sediment pigment and C_{org} , it was not considered for the analysis. The software package Statistica 12.0 was used for the Pearson correlation and PCA.

The non-metric multidimensional scaling (nMDS) ordination was performed using the Bray–Curtis similarity measure, after $\log(x+1)$ transformation. The Similarity of Percentage (SIMPER) analysis was used to determine the macrofaunal species that structured the clusters and which contributed to dissimilarity. A species with large $\bar{\delta}_i/SD(\bar{\delta}_i)$ ratio and percentage similarity contribution are considered as ‘good’ discriminating species (Clarke & Warwick 2001). The univariate indices such as total species number (S or α diversity), Margalef’s species richness (d), Pielou’s Evenness (J'), Shannon species diversity (H' , \log_2) and Hurlbert’s expected number of species ES (50) were also calculated using PRIMER-E software (Clarke & Warwick 2001; Clarke & Gorley 2015).

The beta diversity (β) was estimated using the multiplicative formula $\beta_w = \gamma/\alpha$ (Whittaker 1960; 1972) and using similarity matrix. The β diversity using similarity matrix was estimated using the Kulczynski similarity coefficient (Barwell et al. 2015), and the result displayed as an nMDS plot. The diversity was calculated for (1) all pairwise combinations, (2) between transects, (3) within transects and (4) between stations at the same depth.

Functional traits, Biological Trait Analysis and Functional Diversity Indices

For each species, we measured a total of nine functional traits and 47 modalities that were selected from Törnroos & Bonsdorff (2012; Table 1). We focused on traits of macrofaunal species that are functionally important for the ecosystem services. For example, feeding traits (Feeding position and habit and resource capture) is related to elemental cycling, production and decomposition (Törnroos & Bonsdorff 2012). Data on species functional trait were taken from published literature and online databases (MarLIN 2006, Macdonlad et al. 2010, Quierós et al. 2013, Jumars et al. 2015). In cases where no species-specific data was available, we applied the values of the closest taxonomic level. Taxa with incomplete trait data were excluded from analyses to ensure consistency in the analysis. We did not consider the reproduction traits due to lack of information for many of the taxa. Therefore, based on species abundance (those species that contributed to >5% of the total abundance) and species trait data availability, the final data included 67 taxa. In the reduced data, 72 % of taxa were identified to Species/Genera, 18% to Family (Amphipoda, Bivalvia), 4% to Order (Harpacticoida, Isopoda and, Tanaidacea), 2 % to Class (Oligochaeta, Ostracoda) and, 4% to Phyla (Nemertea, Nematoda, Sipuncula and, Priapulida) level. Therefore, trait information was taken

accordingly. Further, a few Polychaeta genera (*Magelona*, *Prionospio* and *Aricidea*) had four, four and, three unidentified species, respectively; hence data for these genera were pooled.

BTA method was used to analyse how the macrofaunal functional trait composition varies in the study area. Including as many traits as possible for the BTAs, increases the general information about the changes in functional trait distribution (Bremner et al. 2006). The fuzzy coding procedure was applied for the traits with values from 0 to 3, where 0 represents no affinity, and 3 full affinity to the expresses category (Chevenet et al. 1994). Trait category scores for each taxon present at a station were multiplied by their abundance at that station. The trait category scores were then summed over all taxa present at each station, resulting in a station by trait table containing the overall frequencies of occurrence of biological traits at each station (Charvet et al. 1998). Following the methods used to analyse the taxon spatial pattern, log transformed, Bray-Curtis similarities and nMDS analyses were applied to the table of trait frequencies. The SIMPER routine was used to identify the biological trait that contributed to the similarity within the group.

Table 1. List of biological traits and modalities

	Trait	Modalities	Codes	Function
Morphology/ Physiology	Protection	No Protection	NP	Elemental cycling
		Tube	TU	Decomposition
		Burrow	BU	Production
		Softshell	SS	
		Hard shell	HS	
	Size	Small	SM	Production
		Small-Medium	SMD	Elemental cycling
		Medium	MD	Respiration
		Medium-large	MDL	
		Large	LA	
Degree of Dependency	Low		LO	Elemental cycling (pelago-benthic)
		Permanent	PT	Elemental cycling (within benthos)
		Temporary	TM	
Behavior	Bioturbation	No Bioturbation	NB	Elemental cycling (within benthos)
		Biodiffusor	BDF	Decomposition
		Upward/Downward Conveyor	UC/DC	
		Upward Conveyor	UC	
		Downward Conveyor	DC	
		Surficial	SR	

		Epifauna	EF	
Movement	Mobility	Mobile	M	Production
		Discretely Mobile	DM	Elemental cycling
		Sedentary	SD	
Living	Habit	Free	F	
		Tube dweller	TD	
		Burrow dweller	BD	
		Commensal	CM	
		Attached	AT	
Feeding	Feeding Position	Selective Particle Feeder	SPF	Elemental cycling (pelago-benthic and within benthos)
		Surface Deposit Feeder	SDF	
		Sub-surface Deposit Feeder	SSDF	
		Filter feeder	FF	
		Miner	MN	
	Feeding Habit	Carnivore	CA	Production
		Omnivore	OM	
		Detritivore	DT	
		Scavenger	SC	
				Contd.

Table 1. contd.

	Trait	Modalities	Codes	Function
		Parasite	PA	
		Herbivore	HB	
	Resource Capture	Pharynx without Jaws	PX-J	Elemental cycling
		Pharynx with Jaws	PX-UJ	Decomposition
		Tentacles	TN	Production
		Jaws and mandibles	JW	
		Siphon	SP	
		Radula	RA	
		Net	NET	

The multivariate functional indices were calculated to assess different components of the functional diversity, namely Functional richness (FRic), Functional evenness (FEve), Functional Dispersal (FDis), Functional Divergence (FDiv) and Rao's Entropy (Rao Q). FRic is defined as "the amount of functional space filled by the by the community" (Villéger et al. 2008), while FEve "describes the evenness of abundance distribution in a functional trait space" (Mason et al. 2005). Like FEve, FDiv taken into account species relative abundance. Since both the indices reflect the distribution of species abundance in the functional space, thus the contribution of each species to FEve and FDiv is proportional to its abundance (Villéger et al. 2008). FDis is defined as the "mean distance of individual species to the centroid of all species in the community (Laliberté & Legendre

2010). Rao's Q expresses the mean distance between two randomly selected individuals (Botta-Dukát 2005). The indices were calculated on the basis of the fuzzy matrix of functional traits with the R-based software package FDiversity (Casanoves et al.2011).

To test the agreement in the multivariate patterns between two similarity matrices we used the non-parametric Mantle-type test, the RELATE analyses. The analyses use the Spearman's rank correlation (ρ) to determine the significant relation between the two similarity matrices. The test was carried out between (1) Bray-Curtis similarity matrices of total species abundance data and reduced species data, and (2) Bray-Curtis similarity matrices species abundance data and BTA data.

To find the relation between environmental variables and macrofaunal taxonomic and functional diversity, and BTA, non-parametric multiple regression analysis was used, with the DISTLM forward routine (McArdle & Anderson 2001). The analysis was based on Euclidean distances for the functional diversity indices and on Bray-Curtis when species abundance was considered. The forward selection of the predictor variables was carried out using 999 permutations of raw data for the marginal tests, while for all of the conditional tests; the routine used 4999 permutations of residuals under a reduced model.

Result

Environmental Data

The physicochemical (temperature, salinity and DO), biological (Chl-a and Phaeo) features of water, and sediment (texture, Chl-a and Phaeo) are summarised in Table 2. The bottom water DO decreased from shallow to mid depth (<100 m), and increased thereafter (<1000 m) with values that ranged from 0.41 to 4.52 ml l⁻¹. Sediment Chl-a and Phaeo did not show any clear trend from the easternmost transect to the southeastern Arabian Sea. The highest Chl-a (37.20 ug g⁻¹) was detected at T4 (764 and 970 m) and lowest value (0.15 ug g⁻¹) was at T3 2080m. Sediment Phaeo ranged between 0.34 (T6 19 m) and 16.54 (T4 970 m). Sediment C_{org} contents in the studied samples range from 0.02–10.52% with the lowest values in the shallow depth dominated by sand, while the highest values were in T4 (764 and 970 m). The highest coarse fraction (> 80%) was in the shallow depth stations and all the stations of transect 6 (19–1414 m). The fine fractions were highest in the mid to deeper depth (>200–2639 m; Table 2).

Table 2. Range value of environmental variables across each transect						
	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6
Depth (m)	58-1550	110-225	25-2080	60-970	48-2639	19-1414
Surface Water						
Temperature (°C)	28.1-28.92	27.86-28.33	28.21-29.39	28.31-28.95	28.29-28.83	28.1-28.8
Salinity	33.52-36.02	35.55-35.72	33.58-35	34.34-34.98	34.62	34.65-34.9
DO (ml l ⁻¹)	4.58-4.64	4.58-4.63	4.52-4.64	4.53-4.54	4.54-4.56	4.54-4.56
Chl-a (µg l ⁻¹)	0-4.4	0.24-0.58	0-0.72	0.29-1.45	0.18-0.63	0-0.59
Phaeo (µg l ⁻¹)	ND	ND	0-0.78	0-0.11	0-0.81	0-0.6
Core water						
Temperature (°C)	4.09-25.96	4.1-27.42	2.58-27.45	3.57-26.32	3.05-26.19	3.16-27.61
Salinity	34.85-35.18	35.04-35.08	34.77-35.19	34.97-35.12	34.80-35.12	34.89-35.17
DO (ml l ⁻¹)	0.17-2.22	1	0.71-2.58	0.92-1.12	0.56-3.24	0.69-2.78
Chl-a (µg l ⁻¹)	2.5-8.0	0.49	1.03-10.9	4.42-4.2	0.49-2.9	0-2.5
Phaeo (µg l ⁻¹)	0-32	0	0-3.3	0.43-0.43	0-0.21	0-0.14
Sediment						
C _{org} (%)	1.52-6.6	4-6	0.8-8.6	1.03-10.5	0.14-6.1	0.02-4.6
Chl (µg g ⁻¹)	1.87-16.22	NA	0.15-1.86	1.96-37.20	0.47-20.8	0-10
Phaeo (µg g ⁻¹)	1.67-15.45	NA	0-1.01	0.93-16.54	0-16	0.34-15.9
Coarse fraction (%)	3.3-30	91.69-91.87	7.5-94	24.6-94	5.3-97	6-98
Fine fraction (%)	70-97	8.12-8.30	92.4-5.7	75.3-5.7	3-95	2-94

Multivariate PCA of environmental parameters

PCA has been widely used to identify the most variable environmental factor contributing to the differences in a study area (Fig. 2). Based on the Kaiser criterion, the first three PC explained 61 % of the environmental variability. The first PC (35%) showed a high positive loading (>0.7) with depth, organic matter, and fine fraction, and negative loading with coarse fraction and core water temperature and salinity. The first PC also had a moderate positive loading (0.5) with core water Chl-a. A clear spatial trend was observed from the factor scores on PC1. The PC1 separated the deeper stations of T1, 3–5 (200–2639 m) from the shallow depth stations (28–100 m) of T2–5 and all the stations of T6, except deeper depth (1414 m). The second PC (15%) was associated with photosynthetic pigment (Chl-a and Phaeo) in the sediment (positive loading). The factor scoring revealed that sediment Chl-a and Phaeo were high in stations with depth range of 110–1414 (T1–2 and 4–6). The third PC (11%) had moderate (0.58) loading of core water DO. Stations within T1 (152 and 510 m), T3 (1327 m) and T4 (764 and 970 m) scored high on this PC axis.

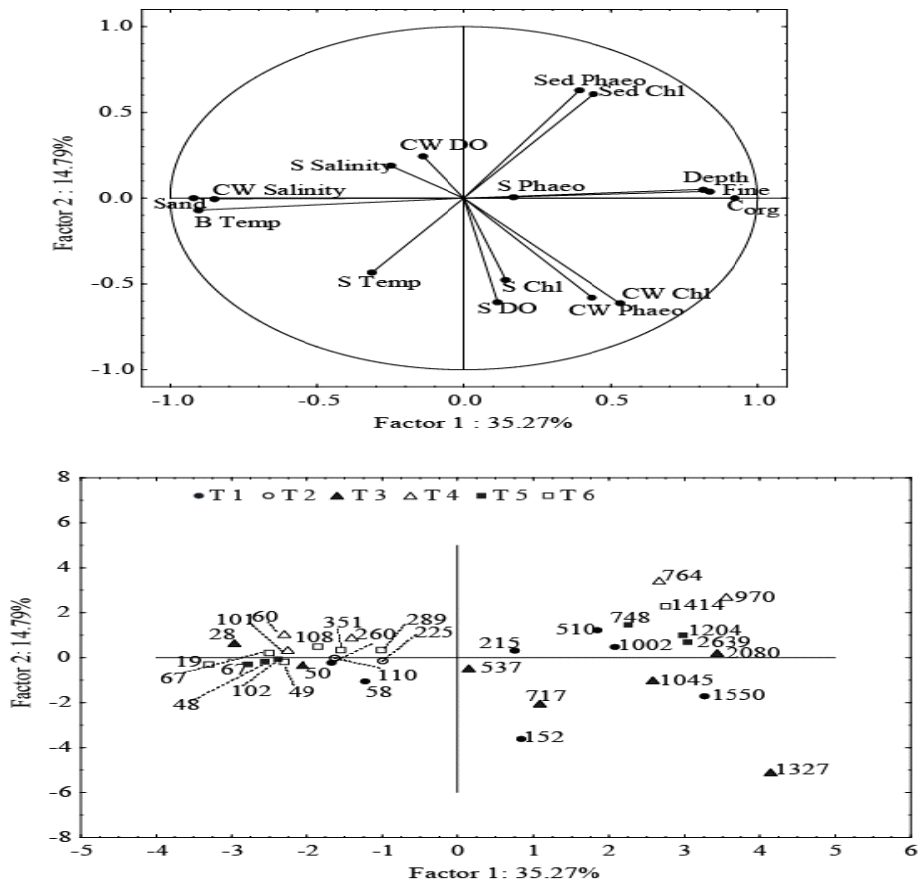


Fig.2. PCA biplot illustrating the variability in the environmental parameters(a) and station distribution in the plot (b). CW core water; S surface; Sed sediment.

Macrobenthic Community

The macrofaunal biomass at T1 and T6 showed decrease from shallow to deeper depth. In the other transects, the depth related gradient in biomass was not very clear. Macrofaunal biomass was highest at T3 717 m (55.15 g m^{-2}) and T5 120 m (41.3 g m^{-2}). Low values were recorded mostly at the deeper stations. In general, biomass showed a decline from shallow to deep locations with marginal increase after 700–1000 m at most transects. The macrofaunal abundance of the study region was represented by 178 taxa belonging to 26 taxonomic groups. The abundance ranged from 446–18980 ind. m^{-2} . The highest count was recorded in T1 (58 m depth) and lowest values were recorded in T3 (1327 m). Overall, macrofaunal abundance showed a decrease from T1 to T6 and, with depth. Macrofaunal abundance at T6 was low (510–2845 ind. m^{-2}) and did not follow the depth related decline found in the other transects. Polychaetes dominated the macrofaunal community at most stations. However, Amphipoda and Sipuncula were the dominant group at shallow stations of T1 and 2, respectively.

The Bray-Curtis analysis was performed on the total species data and reduced species data. RELATE analysis confirmed that the two similarity matrices showed similar multivariate pattern (Rho= 0.98; $p=0.1\%$). The nMDS plot for the reduced species data showed five groups and three outliers, except for few stations, most of the groupings were based on depth (Fig. 3a). Group I clustered the deeper depths (1327–2639 m) of T1, 3, 5, and 6 and 700m depth stations of T 3 and 4. SIMPER analysis identified unidentified Harpacticoida, *Prionospio* spp. unidentified Cumacea and Isopoda, with 57% similarity as the distinguishing species in the group (Table 1S). Group II consisted mostly the shallow stations (19-110 m) of all the six transects and the intermediate depths of T 3 (537 m) and T 5 (748 m). Unidentified Nemertea, *Mediomastus* sp., *Linopherus* sp., unidentified Nematoda, *Monticellina* sp., and *Micronephthys* sp., which together contributed to 38% of the similarity within the group. Group III grouped the deeper depth stations of T3 (1327 m) and 6 (1414 m) with *Cossura* sp., and *Prionospio* spp. (100 %). Stations from T 1 (152 and 510 m) and T 6 (289 and 351 m) formed the fourth group and the characteristic species included Unidentified Oligochaeta, Nemertea and, Nematoda species, *Monticellina* sp., *Prionospio* sp. 2, *Cossura* sp., and, *Exogone* sp.

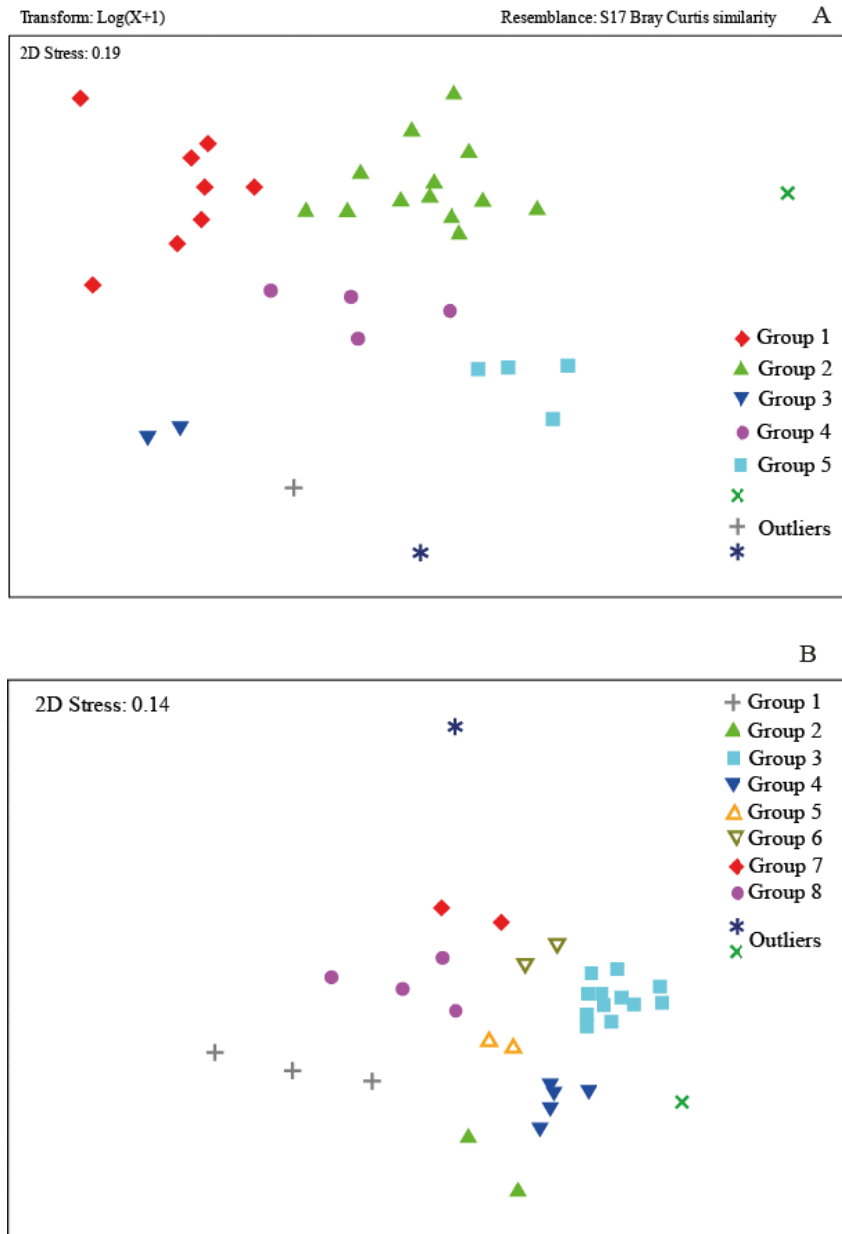


Fig. 3. Non-metric scaling (nMDS) of log transformed abundance based on Bray-Curtis similarity for (A) reduced species data and (B) functional trait frequency data.

Species Diversity

The highest species number was recorded at station T5 102m (75 taxa) and lowest at T3 28m (3 taxa). Similarly, species richness (0.2), evenness (0.4), Shannon Weaver diversity (0.76), Simpson's dominance (0.3) and ES_{100} (2.29) was lowest at T3 28m stations. While high values were recorded at stations T5 102m. Species richness was 8.6, evenness 0.97, Shannon Weaver diversity 5.4, Simpson's dominance 0.9 and $ES(100)$ was 41.

β Diversity

The spatial pattern of β -diversity showed similar trends along the depth gradient: lower at shallow depths (1.5–3) and intermediate to high values in the deeper depth stations (5–20). The nMDS of all stations shows that stations from adjacent transect and similar depths are close together (Fig. 4). The β diversity was high at all levels (expressed as coefficient of similarity values) between transect (26-82%), within transect (T1 4-40%; T2 3-35%; T3 2-50%; T4 7-45%; T5 5-55%; T6 6-46%). The highest similarity were seen between adjacent transects and depth. β diversity also showed major differences between stations at same depth of different transect. The similarity values ranged from 3-55%, 3-45%, 7-46% and 4-53% for the depths of < 100 m, 100-500 m, 500-1000 m and > 1000 m, respectively.

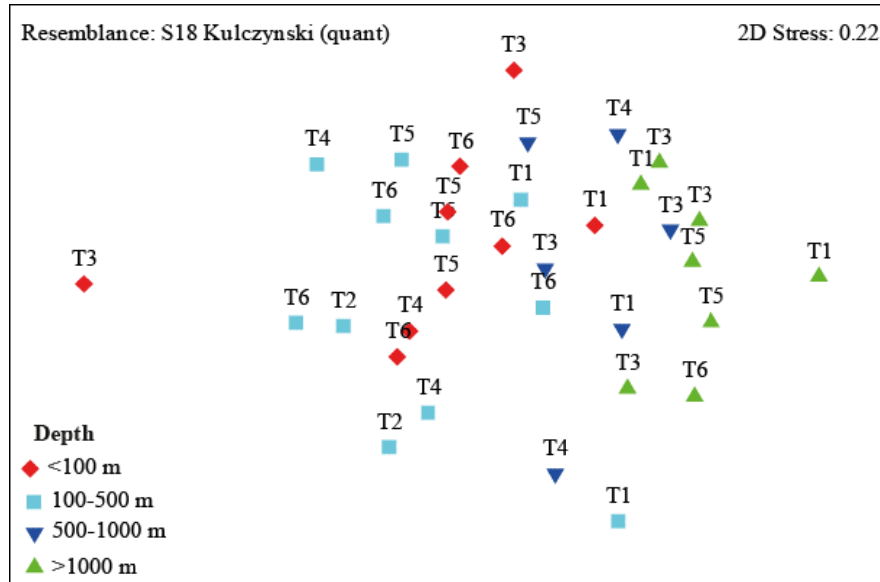


Fig. 4. nMDS plots of macrofauna community structure on the basis of abundance data and Kulczynski similarities between all pairs of data sets

BTA Analysis

In agreement with the species abundance grouping, the samples locations based on functional trait grouped according to depth; however, the number of groups increased (eight groups). Like the species abundance data, functional cluster showed grouping of shallow depth stations. However, some of the deeper station clustered with this group, while some shallow depths formed a separate group. Similarly, the deeper stations formed smaller groups. As seen in the Fig. 3b, functional trait data revealed eight groups and two outliers. The SIMPER

analyses revealed the functional trait modalities that accounted for the differences in the groups (Table 2 S). The deep depth stations formed three separate groups. Group 1 (T6 1414, T3 1327, and T4 970 m) had low abundance (382–637 individual m⁻²) and functional traits that were present in higher abundance were the SSDF (feeding position), and UC and biodiffusor (bioturbators). The dominance of free-living (habit), carnivorous, mobile, method of resource capture by jaw and mandible, and absence of subsurface deposit feeders separated the deeper station group II from rest of the deeper station (Group 1 and 4; Fig. 3b).

Group 3 grouped mostly the shallow and a few deeper depth stations (T1 510 and 152 m, T3 537 and T5 748 m). Functional traits associated with the Group 3 were small to large size (size), mobile and discrete mobility (mobility), burrowers (protection), burrowers and tube (habit), omnivorous, filter feeders and carnivorous (feeding habit), selective particle feeders and deposit feeder (Feeding position), temporary (Degree of Dependency) and jawed and unjawed pharynx (resource capture) and surficial, surface and subsurface (feeding position), and surficial and biodiffusor (bioturbators). The functional trait modalities, medium size and low degree of dependency were exclusively present in Group 4. Group 5 was characterized by temporary (Degree of Dependency), burrower (Protection), unjawed pharynx and small-medium functional modalities. Group 6 (T 6 289 and 351 m) was also represented by small to medium, tube dwelling, sedentary and biodiffusors. Carnivorous and SDF, small to large sized with biodiffusor and surficial modifiers dominated Group 7 (T1 215 and T4 101 m). Group 8 (T2 225, T4 260, T5 190 and T6 108 m) had lower abundance and the functional traits of upward conveyor and hard shell was exclusively present in this group. In general, most of the shallow depth stations, all the T6 stations and some deeper depth stations (T3 1045 and 2080 m, T4 64, T5 748 and 1204 m) in which sediments were mainly coarser with low C_{org} showed higher functional traits. Along with the discretely mobile types, mobile type was high. Although burrowers were the dominant habitat traits, tube and free-living type were well represented. The upward/downward conveyors and UC were other prominent bioturbation types. Along with deposit feeders, carnivorous and filter feeders were equally dominant in the shallow depth stations.

Station T3 28m was an outlier due the dominance of biodiffusor bioturbator, medium sized, discretely mobile, burrow dwelling, omnivorous feeding habit, and resource capture by unjawed pharynx. While the outlier T3 1045m station was represented by a community dominated by medium to large sized, soft shell (protection), mobile (mobility), low (degree of dependency) free living (habit), downward conveyor (bioturbation), and resource capture by

jaws and mandibles. RELATE analysis showed that the species abundance and BTA matrices showed correlation of $Rho= 0.64$ at $P=5\%$.

Functional Diversity

The functional diversity values are represented in Table 3. The Rao Q ranged from 12–42 at stations T6 1414m and T5 102 m, respectively. FRich ranged between 0.01 (T2 110m) and 120 (T1 1550 m). FEve was the highest at T4 970 m (0.88) and lowest was recorded at T4 260 m (0.36). FDiv varied between 0.74 (T4 101 m) and 0.95 (T1 215 m) and FDis ranged from 3.3 (T6 1414 m) and 6.35 (T3 1045 m). Only FEve showed a significant variation with depth ($F= 4.64$; $p=0.02$). A general trend observed was that the functional diversity indices were higher at both the shallow (<100m) and deeper depths (<1000 m) with low values mostly recorded between 200–1000m depth stations.

Table 3. Summary of the functional indices					
	Rao	FRic	FEve	FDiv	FDis
T 1	23-37	17.70-120	0.61-0.75	0.85-0.95	4.48-5.99
T 2	26-27	0.01-42	0.5-0.65	0.81-0.84	4.82-5.07
T 3	20-41	7.87-76.97	0.59-0.84	0.82-0.92	4.30-6.35
T 4	17-37	0.92-88.51	0.36-0.88	0.74-0.92	3.72-5.92
T 5	24-42	0.88-71.43	0.56-0.87	0.87-0.93	4.81-6.35
T 6	12-41	0.1-17	0.52-0.72	0.79-0.91	3.3-6.34

Relating macrofaunal assemblages to environmental variations

To determine the environmental features that influence the macrofaunal assemblages, the DISTLM analysis was carried out. DISTLM constructed the best combination of environmental variables that accounted for the variation seen in the biotic community. The model revealed that sediment C_{org} , sediment texture, DO, salinity and depth were the factors explaining the depth-related changes in the macrofaunal composition (Table 4). The species abundance pattern showed a significant relation with depth, surface salinity, core water DO, C_{org} , and grain size (Table 4). Bottom water Chl-a and Phaeo was also related to the macrofaunal species abundance, however not statistically significant ($p > 0.01$). The shallow depths stations which formed the largest group (Group IV; Fig 3) were dominated by sand and low organic matter.

Table 4. Result of DISTLM forward analysis. Only the significant ($p \leq 0.01$) results are given. CW core water; Sed sediment				
Variable	SS(trace)	Pseudo-F	P	Prop.
Species Abundance				
Depth	15680	6.08	0.001	0.16
CW DO	7359.1	2.59	0.002	0.07
C _{org}	10740	3.93	0.001	0.11
Coarse fraction	18438	7.40	0.001	0.19
Fine fraction	18438	7.40	0.001	0.19
Biomass				
CW Temperature	9773.70	7.89	0.005	0.21
CW Salinity	6952.50	5.22	0.01	0.15
Sed Chl	6446.90	4.78	0.01	0.14
Sed Phaeo	6920.50	5.19	0.005	0.15
C _{org}	9974.70	8.10	0.001	0.21
Coarse fraction	9836.20	7.95	0.003	0.21
Fine fraction	9836.20	7.95	0.002	0.21

In the coastal regions, the southwest monsoon upwelling induced increased primary productivity, eventually contributes to fresh organic matter to the shallow benthic system. The input of fresh organic matter (Chl-a and Phaeo) along with sediment type supports the high macrofaunal abundance and diversity, separating the shallow sites from the shelf and deeper sites. The stations in the depth range of >200–1000 m (except for T6) which exhibited high organic matter content, fine sediment fraction and low DO, were characterised by low macrofaunal abundance and species diversity. The deeper stations formed two separate groups (Fig. 3a) as Group I was dominated by *Prionospio* spp. and *Cossura* sp., while Group VI was dominated by unidentified Harpacticoida, Bivalvia, Amphipoda, Cumacea, and *Prionospio* spp. Although, the environmental variable was similar in both the locations, the differences were observed in the community. DISTLM showed significant effects of depth, bottom water temperature, salinity and, Phaeo, sediment photosynthetic pigments, C_{org} and sediment texture on biomass.

Overall the most important environmental factors that influenced the macrofauna diversity were depth, bottom water factors, C_{org} and heterogeneity of the substrate (Table 5). However, compared to most diversity indices, ES (50) were related to fewer factors (Table 5) with H' (\log_2) not showing any significant relation with any of the variables. The significant environmental parameters that described the β -diversity were water depth, bottom water variables (temperature, salinity, DO, and Chl-a), C_{org} and sediment texture (Table 5).

Table 5. Result of DISTLM forward analysis. Only the significant ($p \leq 0.01$) results are given. CW core water.				
Variable	SS(trace)	Pseudo-F	P	Prop.
Species Number (S)				
Depth	8.87	11.76	0.00	0.27
CW Temp	13.21	21.35	0.00	0.40
CW Salinity	8.66	11.38	0.00	0.26
Pielou's Evenness				
Depth	7.31	9.10	0.01	0.22
CW Temp	8.56	11.21	0.00	0.26
CW Salinity	6.90	8.46	0.01	0.21
CW DO	5.52	6.43	0.01	0.17
CW Chl	7.83	9.95	0.01	0.24
C_{org}	6.98	8.59	0.01	0.21
Coarse fraction	5.80	6.82	0.01	0.18
Margalef's Species Richness				
Depth	7.99	10.22	0.01	0.24
CW Temp	12.28	18.97	0.00	0.37
CW Salinity	7.73	9.79	0.00	0.23
Coarse fraction	6.27	7.51	0.01	0.19
Fine fraction	6.27	7.51	0.01	0.19
ES (50)				
Depth	7.18	8.90	0.00	0.22
CW Temp	8.22	10.61	0.00	0.25
CW Salinity	5.94	7.03	0.01	0.18
β diversity				
Depth	12101	3.81	0.001	0.10
CW Temp	13028	4.13	0.001	0.11
CW Salinity	10098	3.11	0.001	0.08
C_{org}	10477	3.24	0.002	0.09
Coarse fraction	16858	5.56	0.001	0.14
Fine fraction	16858	5.56	0.001	0.14

Drivers of functional diversity

Unlike taxon assemblages, the macrofaunal functional trait responded to only a few environmental variables. The functional traits showed a significant relation with depth and sediment texture (Table 6). Spearman's correlation was also carried out between the environmental parameters and all the functional trait modalities (data not presented). Overall, a large number of trait modalities showed a significant positive relation with sand, and negative with depth. The organic matter content was negatively correlated with size trait. Tubicolous macrobenthic fauna showed reverse relation with core water DO. Discretely mobile showed a significant positive relation with sand. Sediment Phaeo were negatively related to the bioturbation modalities (UC/DC and Biodiffusor), while DC showed a positive relation. Only FRic and FEve shared a significant relation with environmental variables (Table 6). FRic and FEve exhibited strong relation with depth, core water temperature and salinity, C_{org} and, sediment texture.

Table 6. Result of DISTLM forward analysis. Only the significant ($p \leq 0.01$) results are given. CW core water.				
Variable	SS(trace)	Pseudo-F	P	Prop.
BTA				
Depth	1250.4	5.90	0.006	0.16
Coarse fraction	824.74	3.66	0.01	0.10
Fine fraction	824.74	3.66	0.01	0.10
F Ric				
Depth	9.6	13.1	0.00	0.3
CW Temp	8.3	10.8	0.00	0.3
CW Salinity	8.8	11.6	0.00	0.3
C_{org}	6.8	8.3	0.00	0.2
Coarse fraction	5.9	6.9	0.00	0.2
Fine fraction	5.9	6.9	0.00	0.2
FEve				
CW Temp	4.0	4.4	0.00	0.1
CW Salinity	4.9	5.6	0.00	0.1
CW Chl	4.3	4.8	0.00	0.1
C_{org}	4.4	4.9	0.00	0.1
Fine fraction	3.6	4.0	0.00	0.1

Discussion

Environmental factors in the study area

The PCA provides a robust overview of the environmental variability in the study area (Fig. 2). PCA extracted sediment texture, organic matter content (C_{org} , Chl-a, and Phaeo), bottom water DO, and depth as the key environmental factors influencing the region. The shallow depth and all the T6 stations were separated from the deeper locations due to higher coarse fraction (PC 1). Terrestrial runoff brings coarser particles and a majority of it is debouched in the inner shelf leading to increased abundance of coarser fraction on the shelf. The finer particles are carried to the deeper region in suspension and subsequently deposited on the slope and further into the deeper regions. Differences in the water and sediment photosynthetic pigments, mainly determined the segregation of stations on the second PC. The negative relation of sediment photosynthetic pigments and C_{org} with coarse fraction and positive with fine fractions confirms that the accumulation of C_{org} in the sediment is associated with fine particles (Meyers 1994; Hedges & Keil 1995).

The third PC separated the stations with low DO from rest of the locations. The low DO was recorded mostly in the depth range of >100–1000 m. In the AS, a well-developed OMZ is located at mid-water depth between ~100–1100 m (Naqvi 1987; Warren 1994), resulting in the greater proportion of the continental slope being exposed to hypoxic (<0.5 mL/L O_2) to anoxic condition. In the BoB, the low oxygen zone was reported at ~70–550 m (Sarma et al. 2013). Sarma et al. (2013) also observed that OMZ occurs closer to the coast in the north region compared to the southern region. However, the present sampled area reported higher DO as compared to those observed in the northern part of the AS and BoB (Ingole et al. 2010; Sarma et al. 2013; Abdul Jaleel et al. 2014), confirming the gradual deepening of OMZ from south to north in both the seas. The oceanographic features, increase in vertical stratification, and biological production could be attributed to the formation of intense OMZ towards the north (Sarma et al. 2013; McCreary Jr. et al. 2013).

The OMZ also coincides roughly with maxima in sediment organic carbon content and the preservation of highly labile organic compounds including photosynthetic pigments (Cowie et al. 1999; Shankle et al. 2002; Woulds & Cowie 2009). Although C_{org} was high at stations with low DO, some of the deeper depth stations beyond the core OMZ also had high C_{org} (4–6%). A similar trend was also observed in the northern BoB (Raman et al. 2014), while in the northern AS higher C_{org} was found in OMZ (Ingole et al. 2010; Joydas & Damodaran 2014). Cowie (2005) reported maxima C_{org} within the core OMZ (200–1000 m)

towards the northern AS (16 to 18° N). However, major variability in C_{org} was observed at similar depths to the north of their sampling location and in the shelf sediments (Cowie 2005) which was attributed to hydrodynamic equivalence of OM and fine sediment and/or to sorption of organic matter onto finer particles (Cowie 2005). On the other hand, off the Pakistan margin of AS, the highest and lowest C_{org} occurred within the OMZ (Levin et al. 2000; Cowie and Levin 2009). In the Peru slope and Chilean margin, C_{org} showed a reverse pattern with bottom water DO (Levin et al. 2002; Sellanes et al. 2010). Therefore, the relationship between sediment organic matter content and DO may not be a simple linear reverse relationship (Calvert 1995; Cowie 2005).

Further, the range of sediment C_{org} and photosynthetic pigments recorded in the investigated samples were higher as compared to those reported from the northern AS and BoB (Cowie 2005; Ingole et al. 2010; Raman et al. 2014) and other region (Pedrosa-Pàmies et al. 2015) and comparable to the Oman margin (Pedersen et al. 1992). A relatively high concentration of sedimentary organic matter in the present study and previous studies from the region (Abdul Jaleel et al. 2015; Sivadas et al. communicated) is attributed to the strong upwelling induced sinking flux that enriches the sediments in the region. The sediment organic matter content (C_{org} , Chl-a, and Phaeo) is the measurement of the food availability for the benthic organism and along with sediment and DO, it may act as a major factor controlling the distribution of macrobenthic assemblage. As most deep sea communities are food-limited, the vertical flux of organic carbon from the surface production strongly influences these communities and ecosystem functioning (Smith et al. 2008, Corliss et al. 2011; Baldrighi et al. 2014).

Macrofaunal Abundance

Macrofaunal abundance decreased from T1 (easternmost transect) to T6 (southeastern Arabian Sea) for 19-764 m depth, while the deeper depths (> 1000 m) did not show any variation among transects. Although macrofaunal distribution was previously reported from the southern India shelf, there are no macrofaunal sampling carried out covering the shelf to deeper regions (T1 and 3). Previous studies in the southern AS were restricted between 6° N to 77° E (Abdul Jaleel et al. 2014; 2015). The BoB studies were mainly limited to 10° N (Ansari et al. 1977; Harkantra et al. 1982; Ganesh & Raman 2007; Raman et al. 2014). All these and other studies carried out were from <200 m depth, and reported an increase in macrofaunal abundance from north to south (Ingole et al. 2010; Abdul Jaleel et al. 2014; 2015; Joydas & Damodaran, 2014; Sivadas et al., 2016). The highest abundance found

in the shelf (>200m) is higher as compared to the values recorded towards the north (Ingole et al. 2010; Raman et al. 2014) and comparable to 140 m depth of Pakistan margin (10,945–15,909 ind. m⁻²)(Hughes et al. 2009). As compared to the BoB, macrofaunal abundance was higher in the AS (Ansari et al. 1977; Harkantra et al. 1982; Ganesh & Raman 2007; Raman et al. 2014).

Total macrofaunal abundance also decreased with depth, confirming previous studies from the region (Gooday et al. 2009; Levin et al. 2001; 2013; Ingole et al. 2010; Abdul Jaleel et al. 2015; Raman et al. 2014) and other seas (Rowe 1983; Rex et al. 2006; Nephin et al. 2014). The lowest abundance was mostly recorded at 500–1000 m depth coinciding with low bottom-water oxygen. The abundance again was higher as compared to the northern region (Ingole et al. 2010; Levin et al. 2013; Raman et al. 2014). However, Levin et al. (2000) reported the highest macrofaunal abundance (16383–19183 ind. m⁻²) in the middle of the OMZ (700–850 m) off Oman margin. A similar higher abundance of macrofauna has been reported from the Chilean Shelf (Gallardo et al. 1995; 2004) and north off Peru (Levin et al. 2003). However, this depth-related decrease in the macrofaunal abundance is not uniform (Gage 2003) and regions with high productivity have higher abundance, regardless of depth (Rex & Etter 2010). This observation is also supported by our findings, as some of the 500–1000 m stations had higher abundance.

Macrofaunal Species Composition and Structure

As noted in other studies, the macrofaunal abundance tended to be dominated by a few polychaete families (Spionidae, Cossuridae, Cirratulidae, Paranoidae, Pilargidae, and Capitellidae) (Gooday et al. 2009; Ingole et al. 2010; Gunton et al. 2015; Abdul Jaleel et al. 2015; Raman et al. 2014). Species of the family Spionidae, Cossuridae, Cirratulidae, Paranoidae, Pilargidae, and Capitellidae have been previously reported as dominant species in the coastal, OMZ and deep sea habitat (Gutiérrez et al. 2000; Gooday et al. 2009; Hughes et al. 2009; Abdul Jaleel et al. 2015; Ramana et al. 2014). Species belonging to those families are considered to be opportunistic and, hence, highly adaptable to varying food and low oxygen conditions (Gutiérrez et al. 2000; Gooday et al. 2009; Gunton et al. 2015). However, species belonging to the family Amphinomidae and Ampharetidae was equally dominant in the shallow depths of some transect (T1 58 m, T2 225 m, T3 28 m, T4 60 m, and T5 48 m). The Amphinomidae, *Linnopherus* sp. dominated under low-oxygen conditions off Pakistan margin (Levin et al. 2009; Gooday et al. 2009). However, in our study *Linnopherus* sp. was either absent or found in low abundance (31–177 ind m⁻²) at stations with low oxygen. Their

highest abundance was recorded at T3 28 m and T5 48 m and is in concordance with earlier reports from the region (Joydas & Damodaran 2009; Abdul Jaleel et al. 2014). Gunton et al. (2015) also reported a high abundance of Amphinomidae in the western branch of Whittard Canyon, NE Atlantic.

Although the group Polychaeta was dominant at most of the stations, other groups such as Amphipoda, Sipuncula, Priapulida, Nematoda and Nemertea dominated at some of the stations. The Amphipoda families (Oedicerotidae and Ampeliscidae) dominated the community with highest abundance recorded at T1 (58 and 152 m) and T3 (50 m). Although ampelsicid amphipods, appears to be an important component of OMZ fauna (Levin & Gage 1998; Levin et al. 2000), in the northern BoB higher abundance were found, above and below this zone (Raman et al. 2014). In the present study, although amphipods were recorded at all depths, their abundance was highest in the shallow depth.

Oligochaeta abundance was high at T1 (152 m), T2 (110 m), T5 (102 and 190 m) and T6 (108–351 m). All these transect also recorded low DO (0.17–0.9 ml l⁻¹). Similar dominance of oligochaetes in the low oxygen levels have been reported in the northern Arabian Sea (Ingole et al. 2010; Sivadas et al. in preparation), off Pakistan margin (Gooday et al. 2009), off Peru (Levin et al. 2002) and over the Chile margin (Gallardo et al. 2004; Palma et al. 2005). A very high abundance (5132 ind m⁻²) of Sipuncula was registered at T3 28 m. A high abundance of Nematoda was recorded at 200–500 m depth and at T3 2080 m. Nemertea abundance was high in the shallow depth (<100m) of most transects. A similar dominance of Sipuncula, Nemertea, and Nematoda has been reported to the north of the present investigated area (Sivadas et al., communicated). Similar observations of dominance of groups other than Polychaeta were reported from other seas (Sorbe & Galil 2002; Galil 2004; Baldrighi et al. 2014). Priapulida abundance was the highest at T1 58 m and is reported for the first time from the region.

The macrofaunal assemblages of the southern Indian continental margin showed a spatial variability. Depth related environmental gradient influenced the macrofaunal assemblages which were confirmed by the DISTLM models. DISTLM constructed the best combination of environmental variables that accounted for the variation seen in the biotic community (Table 4-5). The model revealed that sediment C_{org}, sediment texture, DO, salinity and depth were the factors explaining the depth-related changes in the macrofaunal abundance and biomass (Table 4). The significant role that sediment, depth, DO and food availability (C_{org} and photosynthetic pigments) play in structuring the macrofaunal

community distribution pattern has been noted by a number of studies across different seas (Gallardo et al. 2004; Levin et al. 2001; 2003; Joydas & Damodaran 2014; Ramana et al. 2014; Gunton et al. 2015).

The macrofaunal species diversity indices (species number, richness, Shannon diversity and ES 50) declined from shallow to upto 1000 m and showed a marginal increase after 1000 m depth. Previous studies from the region and other seas have reported a general decline in the macrofaunal diversity with increasing depth (Ingole et al. 2010; Raman et al. 2014; Abdul Jaleel et al. 2015; Baldrighi et al. 2014).

The 178 macrofaunal taxa reported from the present study is higher than previously reported from India, both along the BoB (Raman et al. 2014) and AS (Ingole et al. 2010) and similar to the previous observation in the region (Abdul Jaleel et al. 2015). However, the species number could be higher, as some species were identified to higher taxonomic level. Lack of taxonomic expertise and updated literatures remains a major limitation to advancing our knowledge of marine biodiversity of India. Due to which many of the studies, especially from the deep seas lacked detailed taxonomic identification for many macrobenthic groups (Ingole et al. 2010). For example, although tanaids, isopods, amphipods, cumaceans, and harpacticoids, are frequently reported, it is often reported only up to Order in many studies (Pavithran et al. 2007; 2009 a; Ingole et al. 2010). This was also the case in the present study, where these crustacean groups dominated at some of the deeper depth stations.

Same is true for other phyla like Sipuncula, Nemertea and Priapulida. In fact, Priapulida is reported for the first time from the region. Since some of the locations were sampled for the first time, chances of new records and species are high. Such lack of knowledge of taxa is not exclusive to the region, and is often observed in many marine areas, due to the small size of the taxonomic community available to study them (Bouchet 2006; Giere 2009). Even in the present study many of the unidentified species were rare making identification difficult. The effect of taxonomic sufficiency on the biodiversity pattern is a highly debated topic. However, identifying taxa to the lowest possible taxa may provide significant insight into the biodiversity pattern, especially in large-scale studies, which is a significant challenge to ecologist.

The greater number of taxa in the region could be indicative of the heterogeneous environment that supports a rich biodiversity compared to the northern region. The benthic biodiversity distribution pattern along the Indian sub-continent, not only shows an east-west

and north-south gradients but also showed a smaller scale with highest species richness recorded in the southern ecoregion (Sivadas & Ingole 2016). The southern tip of the Indian continent is influenced by the BoB, AS and the open Indian Ocean circulation, making it a transition zone and along with the diverse habitat allow different species can co-occur (Rao et al. 2011; Sivadas & Ingole 2016). Similarly, sediment, biological productivity, river runoff, current pattern, intensification of OMZ, temperature and salinity also shows a north-south gradient in both the seas (Rao & Wagle 1997; Rao & Kessarkar 2001; Lévy et al. 2007; Durand et al. 2009; Sarma et al. 2013; Amol et al. 2014; Sivadas & Ingole 2016). Therefore, the environmental heterogeneity in the southern Indian region supports the higher abundance and species rich macrofaunal community. This was also confirmed from the β -diversity pattern. The high β -diversity in the region confirms that heterogeneous distribution of environmental conditions such as those addressed in the present study (depth, bottom water variables, C_{org} , and sediment texture) are the potential drivers of macrofaunal diversity (Table 5). McClain and Rex (2015) in their review article on β -diversity of deep sea benthic community concluded that organic matter flux and depth emerged as the best predictors of β -diversity.

Macrofaunal Functional diversity pattern

The functional approach (BTA and functional diversity indices) can provide information on the role of the macrofaunal community in the ecosystem functioning better than attributes based on community structure or species composition (Bremner 2008; Mestdagh et al. 2018). The study of functional patterns of macrobenthic communities is not novel; what is new in the present study is the use of BTA and functional diversity indices (Rao Q, FRich, FEve, FDis and FDiv) on a benthic system over a range of habitat, from shallow (19 m) to deep sea (2639 m) including the OMZ. Further, this is the first study from the region to use the functional approach to macrofaunal assemblage.

The functional trait in the region was mostly dominated by few modalities. However, there were differences in the relative proportions of functional traits, with some functional trait modalities exclusively present at some locations. Higher functional traits were recorded in the stations with coarse sediment and low C_{org} . Fewer functional trait combinations can be the result of (i.e., the investment in one trait modality leaves fewer resources available for another), spin offs (selection favors traits modalities that act together), result of constraints,

similar responses of species' to an underlying environmental gradient across sites or reduced diversity (Verberk et al. 2013; Valanko et al. 2015; Villnäs et al. 2018).

The feeding traits provide information on the trophic status of an ecosystem and on the structural complexity (Pearson & Rosenberg 1987; Tselepides 2000; Bremner et al. 2003; Törnroos & Bonsdorff 2012). The dominance of different feeding trait from shallow to deeper depth stations observed in the present study was also reported in other regions and was associated with influx of organic matter (Maciolek et al. 1987; Pacheco et al. 2011). In the presence of different feeding traits, more diverse pathways of energy and matter cycling are expected allowing efficient utilization and transfer of organic matter in the benthic system (Ulanowicz 1997; Karlson et al. 2010).

Functional traits like body size, range of protection, degree of dependency, and environmental position indicates prey accessibility and ease of its ingestion (Postel et al. 2000; Norkko et al. 2013; Weigel et al. 2016). The shallow depth community was primarily composed of small to medium-size, burrowers, temporary, discretely mobile fauna that are easily accessible, and carry high energy due to minimal loss during predation (Weigel et al. 2016).

An interesting observation was of the community from the low oxygen zone. Although, each functional trait was dominated by a single modality (Table 2S), the other trait modalities were also well represented in this zone. The dominance of small size, short-lived, burrowing and infauna trait is reported from the deep hypoxic habitat off northern Chile (Pacheco et al. 2011). Small-sized individuals can exploit the high organic matter under low bottom-water oxygen (Warwick 1986; Levin 2003; Pacheco et al. 2011). One possible reason for the diverse functional trait within the low oxygen locations of the present study area is that the sediment was sandy or silty-sand. Gooday et al. (2010) concluded that the habitat heterogeneity within the OMZ is strongly created by bottom-water oxygen gradient, sediment characteristics and organic matter content that in turn influences the macrofaunal assemblages. Sandy sediment can enhance the benthic surface complexity providing habitat for other species and thus having implications on functional diversity of the community. Although our stations had substantial C_{org} content (1.2–6%), the dominance of sandy sediment along with the bioturbating fauna (bioturbators, surficial and UC) may be keeping the sediment sufficiently oxygenated (0.27 to 0.8 ml l⁻¹), supporting a functionally diverse fauna. Although macrofauna from hypoxic regions are usually dominated by weak bioturbators, they contribute to aerobic functioning at some level even in low oxygen environment (Pacheco et

al. 2011). The spatial pattern of functional traits in the present study was controlled by depth, DO, C_{org} , and sediment texture, as revealed by the DISTLM analysis (Table 6). Previous studies have reported that temperature, food availability, hydrodynamic, bottom-water oxygen, and substrate heterogeneity and their interaction are known to regulate the macrobenthic assemblages on large spatial scale including the deep-sea (Levin et al., 2001; McClain & Barry 2010; Bladrgihi et al., 2017).

Drivers of Functional diversity

We found that of the five measured functional diversity indices, only FRic and FEve showed significant relation with environmental variables. FRic and FEve increased with increasing depth, indicating that deep sea allows a broader distribution of traits in the macrofaunal community. These indices also showed strong positive relation with fine sediment and C_{org} , and moderate with bottom water photosynthetic pigments. Although the species number and abundance declined with depth, higher FRic and FEve indicates that the deep sea community of the present study area is represented by fewer species with higher functional evenness.

Higher FD is indicates that the community is dominated by higher number of extreme values, which occurs due to increase in abundance or appearance of species with extreme trait, or decrease in abundance or disappearance of species with more central trait values (de ArrudaAlmeida et al 2018). Any community with higher FDis supports a wider ecological traits and hence diverse ecological functions. The increase in the FEve with depth indicates that the different functional traits are equally represented in the deep sea macrofaunal community that can increase the ecosystem functioning even under reduced species number and abundance. Belly & Snelgrove (2018) reported that the community composed of few species with relatively low abundance could equally contribute to the benthic flux rates. A study in the coastal Skagerrak-Baltic Sea region also suggested that ecosystem processes and functions could potentially be maintained at lower taxonomic richness but similar functional diversity (Törnroos et al. 2015).

The lack of clear pattern in the functional diversity indices, its relation with the taxonomic diversity and the measured environmental variables may be related to the fact that functional traits used in the present study might not encompass the array of functions performed by the macrofaunal community (Pape et al. 2013). Relations between functional traits and environmental condition are complex, often difficult to interpret (Bremner et al.

2006). Additionally, environmental parameters other than those measured during the present study, such as biotic interaction (e.g prey-predator, competition) may also influence the observed pattern that needs to be considered in future studies.

Species diversity vs Functional Diversity

Overall, the functional diversity measures (BTA and functional diversity indices) can provide better insights in the macrofaunal assemblages than indices based only of taxonomic indices or species abundance. Although the species abundance and functional similarity analyses showed similar grouping of the stations, the number of groups increased (eight groups) (Fig. 3). This indicates that the macrofauna showed differences based on the functional traits. Functional indices (FRic and FEve) showed a reverse trend with species number corroborating the results from other regions that the relation between structural and functional diversity is negative (Pape et al. 2013; Baldrighi & Manini 2015). The lack of relationship between taxonomic and functional diversity may be related to the degree of redundancy or the naturally lower diversity of the community (Pape et al. 2013; Baldrighi & Manini 2015). However, a positive relation between species number and the functional diversity have been reported (Schratzberg et al. 2007; Danovaro et al. 2008; Wiedmann et al. 2014). Therefore, comparative studies help in identify patterns, especially for studies that cover large spatial scales or habitat such as the deep sea where studies are limited (Loreau 2008).

Sampling Biases

In the present study, sediment samples were collected by using a multi-corer and a van Veen grab. Moreover, sieve with mesh size of 0.3 mm was used compared to the 0.5 mm that was used in most previous studies from the region (Joydas & Damodaran 2014; Raman et al. 2014; Abdul Jaleel et al. 2014). Previous studies have shown sample biases between different sampling gears (Hughes & Gage 2004; Blake & Narayanaswamy 2004). A perfect sampling is that in which all the samples are collected using a single gear; however due to practical reasons, no single sampling device will perform optimally in different habitat. In the present study, the grab was used in the shallow depth locations (nine stations of T3–6) as the sediment was sandy, and repeated operation failed to retrieve intact cores. The operation either failed, or the sediment penetration was less than 10 cm or, the recovered sediment was highly disturbed. Therefore, in extremely heterogeneous benthic system, sampling using a single benthic sampling gear is practically not possible (Narayanaswamy & Bett 2011). At T1 and T2, all the samples were collected by using the multi-corer which also recorded the

highest macrofaunal abundance and depth related decline in the abundance. Therefore, patterns observed for the macrofaunal abundance may be the trend in the study area.

The effect of sieve mesh size on the macrofaunal pattern is also a well discussed topic (Bachelet 1990; Schlacher & Wooldridge 1996; Gage & Bett 2005). The gear and sieve mesh size had substantial effect on the macrofaunal abundance, modest effect on diversity and limited influence on the biomass and community composition (Gage et al. 2002; Ferraro & Cole 2004; Narayanaswamy & Bett 2011). However, a significant loss in biomass of deep sea macrofauna was reported when larger mesh was used (Pavithran et al. 2009b). In many coastal regions (high biological productive or silty sediment) and deep sea, the macrofaunal community is often dominated by small-size macrofauna, which may be under sampled by bigger mesh sizes, resulting in biased interpretation of the community pattern. The use of smaller mesh sizes allows the retention of juveniles that provided information on the macrofaunal population dynamics. In the present study, the macrofaunal abundance at many of the stations was dominated by the juvenile population indicating the recruitment period for the macrobenthos community in the region. Studies have concluded that the sieve mesh size with 0.1–0.2 mm should be used in studies involving population dynamics of macrofauna, to provide an adequate estimate of abundances of individuals in small size classes (Bachelet 1990; Schlacher & Wooldridge 1996).

The importance of trait information and rare species

A key constraint in the functional based approach is the unavailability of species specific trait information. This is particular true for marine invertebrates, where data is lacking for many of the species. Therefore due to declining taxonomist (discussed above) and inadequate species specific trait information, the focus is on the higher taxonomic ranks and most abundant species which although debated, is widely used in ecological studies, in particularly for marine invertebrates (e.g. Bevilacqua et al. 2012 and references therein). In the present study, of the 178 taxa identified, functional trait information was available for 157 taxa. Out of the 157 taxa, 90 taxa were not considered based on their low abundance (rare taxa). If species are considered rare due to their low abundance, they may not influence the ecosystem functioning (e.g. Smith and Knapp 2003; Gaston 2011; Jane et al. 2013). However, there is evidence that rare species may also contribute to ecosystem functioning (Gascon et al. 2015). Further, it is argued that it is essential to understand the role of rare species as their abundance may increase in response to environmental changes and hence, influence the ecosystem functioning (Jane et al. 2013). Compared to terrestrial plant and soil communities,

significant knowledge gap exist in the understanding of the mechanistic link between traits and ecosystem functioning (Murray et al. 2014). Therefore, marine benthic ecologist needs to focus on obtaining the functional trait information of marine invertebrates that will help in understanding the links between species and ecosystem functioning. It is clear that at present getting information of rare species will remain inherently difficult, therefore generalizing the results from such studies require caution.

Conclusion

To our knowledge, this is the first study to compare the relationship between environmental variables and species diversity (α and β -diversity) and functional diversity along a depth-gradient, from coastal to deep-sea system of the NIO. The results of the study indicate that different environmental factors may be important for different aspects of macrofaunal taxonomic and functional diversity pattern. The present study confirms that focusing only on taxonomic diversity is insufficient if we aim to understand the role of biodiversity in the ecosystem functioning. Much to be gained from consideration of multiple diversity indices, particularly for macrofauna in the NIO where there the environmental heterogeneity is high, and hence, allowing the testing of different environment factors in governing the large-scale biodiversity pattern. Although the present study provides important information on the factors governing the macrofaunal community diversity pattern along a depth gradient, more detailed studies considering the lacunae identified (e.g. species level identification, species specific trait information) are required in order to explicitly test the observed patterns of macrofaunal community in the southern Indian continental margin.

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Table 1S. Result of SIMPER Analysis for macrofaunaltaxa abundance					
Group 1 (Average similarity: 41.14)					
Species	Average Abundance	Average Similarity	Sim/SD	Contribution %	Cum.%
Unidentified Harpacticoida	4.75	6.62	1.53	16.08	16.08
<i>Prionospio</i> spp.	3.64	5.16	0.91	12.53	28.62
Unidentified Cumacea	3.66	4.48	1.02	10.9	39.51
Unidentified Isopoda	3.43	3.74	1.04	9.08	48.6
Phoxocephalidae	3.03	3.51	0.68	8.53	57.13
Group 2 (Average similarity: 43.15)					
Unidentified Nemertea	4.73	4.15	3.94	9.63	9.63
<i>Mediomastus</i> sp.	4.74	3.5	1.96	8.12	17.75
<i>Linopherus</i> sp.	4.11	2.99	1.46	6.92	24.67
Unidentified Nematoda	4.13	2.91	1.37	6.75	31.43
<i>Monticellana</i> sp.	4.01	2.81	1.38	6.51	37.94
<i>Micronephtys</i> sp.	3.35	1.99	1.07	4.6	42.54
Group 3 (Average similarity: 49.44)					
<i>Cossura</i> sp.	5.06	26.6	94	53.8	53.8
<i>Prionospio</i> spp.	4.86	22.84	23	46.2	100
Group 4 (Average similarity: 42.73)					
Unidentified Oligochaeta	6.21	7.63	6.5	17.85	17.85
Unidentified Nematoda	6.16	7.52	6.56	17.59	35.44
Unidentified Nemertea	4.41	5.29	7.31	12.39	47.83
<i>Monticellana</i> sp.	3.74	3.64	0.91	8.51	56.34
<i>Prionospio</i> sp. 2	4.31	3.54	0.9	8.28	64.61
Group 5 (Average similarity: 41.16)					
<i>Magelona</i> sp. 2	4.36	9.58	7.42	23.28	23.28
<i>Monticellana</i> sp.	4.31	8.06	8.92	19.59	42.87
<i>Aricidea</i> sp. 2	3.74	5.26	0.91	12.78	55.65
<i>Paraprionospio</i> sp.	3.15	4.57	0.9	11.1	66.74
Unidentified Oligochaeta	3.69	4.18	0.83	10.16	76.9

Table 2S: Result of SIMPER Analysis on BTA. Codes in Table 1					
Trait	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Group 1 (Avg. similarity: 80.37)					
DM	7.24	6.45	9.25	8.03	8.03
BR	7.14	6.37	9.02	7.92	15.95
TM	7.14	6.37	9.02	7.92	23.86
OM	7.18	6.34	9.18	7.89	31.75
PXUJ	7.25	6.34	9.18	7.89	39.64
SM	7.01	6.14	6.89	7.63	47.27
BD	6.54	5.82	10.8	7.24	54.51
Group 2 (Avg. similarity: 81.79)					
TM	8.08	5.23	11.12	6.39	6.39
SM	8.07	5.1	10.9	6.24	12.63
BR	7.93	5.06	10.8	6.18	18.81
DM	7.3	4.76	11.2	5.82	24.62
BD	7.59	4.76	11.6	5.82	30.44
SPF	7.19	4.76	10.9	5.82	36.26
CA	7.05	4.76	9.89	5.82	42.08
OM	7.69	4.76	10.1	5.82	47.89
UC/DC	6.64	4.48	8.99	5.48	53.37
Group 3 (Avg. similarity: 90.41)					
TM	9.25	3.98	22.75	4.41	4.41
BR	9.14	3.94	17.71	4.36	8.77
DM	9.15	3.92	21.93	4.34	13.1
SM	9.11	3.91	23.12	4.32	17.42
OM	9.1	3.9	21.76	4.32	21.74
PXUJ	8.93	3.83	12.51	4.23	25.97
BD	8.56	3.68	24.59	4.07	30.05
SR	8.55	3.61	18.92	4	34.04
BDF	8.21	3.55	21.76	3.93	37.97
TD	8.32	3.54	17.9	3.92	41.89
SPF	8.18	3.52	20.6	3.89	45.78
CA	8.13	3.49	21.45	3.86	49.63
SSDF	8.07	3.48	11.77	3.85	53.49
Group 4 (Avg. similarity: 91.84)					
TM	8.31	4.44	27.6	4.84	4.84
SM	8.3	4.42	27.08	4.82	9.65
BR	8.17	4.37	24.12	4.75	14.41
OM	8.13	4.35	26.68	4.73	19.14
DM	8.05	4.25	29.9	4.63	23.77
PXUJ	7.78	4.08	18.72	4.44	28.21
SR	7.75	4.08	26.27	4.44	32.65
BD	7.49	3.97	34.74	4.32	36.97

Table 2 S continued					
Trait	Av. Abund	Av. Sim	Sim/SD	Contrib%	Cum.%
JW	7.44	3.92	20.67	4.27	41.23
SDF	7.19	3.79	28.38	4.13	45.36
F	7.19	3.78	21.24	4.12	49.48
M	7.16	3.74	11.57	4.07	53.55
Group 5 (Avg. similarity: 94.86)					
TM	8.15	4.19	20.5	4.41	4.41
BR	8.13	4.18	20.34	4.4	8.82
PXUJ	7.95	4.1	19.59	4.32	13.14
SM	7.94	4.08	20.65	4.3	17.44
OM	7.8	3.98	20.24	4.19	21.63
DM	7.81	3.97	20.89	4.19	25.82
TD	7.21	3.71	17.8	3.91	29.73
SPF	7.24	3.69	18.98	3.89	33.62
H BD	7.29	3.67	21.23	3.87	37.49
BDF	7.27	3.65	21.32	3.85	41.34
CA	7.23	3.65	20.98	3.85	45.19
M	7.2	3.61	17.56	3.81	48.99
SSDF	7.07	3.61	17.05	3.81	52.8
Group 6 (Avg. similarity: 94.16)					
TM	9.01	4.85	14.25	5.15	5.15
OM	9.01	4.84	14.00	5.14	10.29
SM	8.92	4.79	19.62	5.08	15.37
PXUJ	8.88	4.74	18.23	5.03	20.4
DM	8.86	4.73	16.54	5.02	25.42
BR	8.58	4.49	19.65	4.77	30.19
SDF	8.41	4.49	19.48	4.77	34.96
SR	8.27	4.44	18.75	4.72	39.68
F	8.2	4.38	17.5	4.66	44.33
TD	8.18	4.38	17.5	4.66	48.99
UC/DC	7.79	4.07	15.46	4.32	53.31
Group 7 (Av. similarity: 87.45)					
TM	9.5	5.29	13.25	6.05	6.05
BR	9.5	5.28	13.00	6.03	12.09
PXUJ	9.36	5.23	14.25	5.98	18.06
DM	9.34	5.2	15.21	5.94	24
OM	9.32	5.19	14.56	5.93	29.94
SR	8.97	5.03	15.6	5.75	35.69
SM	9.25	5.02	14.23	5.74	41.43
BD	9.07	4.97	13.56	5.69	47.11
SDF	8.51	4.74	12.98	5.41	52.53

Table 2 S continued					
Trait	Av. Abund	Av. Sim	Sim/SD	Contrib%	Cum.%
Group 8 (Avg. similarity: 83.26)					
TM	8.34	5.21	21.11	6.26	6.26
DM	8.32	5.2	20.74	6.25	12.51
OM	8.31	5.2	20.74	6.25	18.76
PXUJ	8.29	5.19	20.08	6.23	25
BR	8.1	5.07	25.04	6.09	31.09
SM	7.98	4.94	25.19	5.93	37.02
SDF	7.73	4.77	12.83	5.72	42.74
SR	7.48	4.71	14.75	5.65	48.39
BD	7.19	4.51	19.58	5.42	53.81

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Table 3 S Result of correlation analysis between environmental variables.												
	Depth	B DO	S Chl	B Chl	S Phaeo	B Phaeo	Sed Chl	Sed Phaeo	Sand	Silt	Clay	Corg
Depth	1.00											
B DO	-0.12	1.00										
S Chl	-0.34	0.29	1.00									
B Chl	0.05	0.21	0.89	1.00								
S Phaeo	0.12	-0.03	-0.06	0.28	1.00							
B Phaeo	0.43	-0.16	0.29	0.57	0.32	1.00						
Sed Chl	0.18	0.49	-0.31	0.40	-0.01	0.32	1.00					
Sed Phaeo	0.13	0.23	-0.22	0.07	-0.34	-0.06	0.65	1.00				
Sand	-0.68	0.16	0.23	-0.20	0.05	-0.60	-0.28	-0.05	1.00			
Silt	0.68	-0.16	-0.19	0.18	-0.05	0.63	0.23	-0.04	-0.98	1.00		
Clay	0.50	-0.12	-0.09	0.33	-0.09	0.58	0.31	0.27	-0.81	0.75	1.00	
Corg	0.77	0.01	-0.11	0.67	0.22	0.79	0.45	0.31	-0.56	0.55	0.54	1.000