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ORIGINAL RESEARCH ARTICLE

Do seasonal dynamics influence traits and composition of macrobenthic assemblages of Sundarbans Estuarine System, India?

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Abstract The present study investigates the influence of seasonal dynamics on macrobenthic assemblages in four seasons of 2017—2018 from the central sector of Indian Sundarbans which is under the constant threat of climate change. Besides taxonomic analysis, a trait-based approach has also been applied to assess the change in their ecosystem functioning. The maximum species density (11675 ± 11883.31 ind. m^{-2}) was observed during the spring season which declines considerably in the monsoon season (5875 ± 6224.08 ind. m^{-2}). A total of 95 macrobenthic taxa were recorded from Sundarbans and they were dominated by families like Capitellidae, Donacidae, Magelonidae, Nereididae, Paraonidae and Spionidae. Overall, polychaetes have shown higher taxonomic and functional variation than other groups. Opportunistic polychaete species have shown a prominent compositional shift during post-monsoon seasons. Both the univariate and multivariate analyses have shown a significant relation between macrobenthic composition and environmental parameters. SIMPER has depicted that environmental parameters made the station 4 unique for several types of molluscs like *Acteocina estriata, Stenothyra deltae* and *Meretrix meretrix* during spring. Trait percentages also showed a seasonal succession pattern and among the trait categories, burrowers and deposit feeders dominated the estuary. A gradual increase in suspension feeders in spring has been noticed. RLQ

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approach with fourth-corner analysis was used to unravel the relationship between traits and environmental parameters. Hence, the present study provided a comprehensive idea about the species composition along with their trait categories from such a dynamic habitat. That could be the first stepping stone for a long term monitoring of macrobenthic assemblages from this largest delta on earth.

1. Introduction

An estuary acts as a transitional zone between marine and freshwater domains where it plays a crucial role in controlling fluxes between ecosystems as well as in faunal distribution (Modéran et al., 2010). Being a buffer zone, estuaries share both the characteristics of the river and ocean. It has been continually exposed to various hydrological pressures, which results in a highly dynamic habitat. Moreover, due to high productivity, estuaries serve as breeding and nursery grounds for various faunal communities. However, in recent times, it has become one of the most degraded ecosystems globally (Kennish, 2002). Furthermore, due to various anthropogenic pressures and its proximity to harbours, these areas might be under the threat of bioinvasion (Taupp and Wetzel, 2019).

Macrobenthos are the dominant member of the benthic community and also act as a food source for various demersal predators inhabiting in the same ecosystem (Griffiths et al., 2017). Macrobenthic species perform invaluable ecosystem services during the process of feeding, tube construction and bioturbation which mediates the exchange of energy and matter between sediment and water column (Mestdagh et al., 2018; Rhoads and Young, 1971). Additionally, macrobenthic species can enhance sediment accumulation and thereby protect the habitat from erosion. By their physiological activities, they can also influence benthic-pelagic coupling and perform a crucial role in bioturbation which have been the focal point in major ecological studies (Zhang et al., 2019). Among the macrobenthic community, polychaetes represent as the most dominant and ecologically diverse component and due to their wide range of habitat variation and diverse feeding guild in different trophic level, they can be used as a bioindicator in environmental monitoring programmes (Fauchald and Jumars, 1979).

In general, the macrobenthic assemblages were assessed and their ecosystem functioning has been monitored using a traditional taxonomy-based approach in most of the Indian estuaries. Nevertheless, in recent years BTA (Biological Traits Analysis) approach is getting considerable attention. BTA can be applied to a series of characters like life history, feeding habit, body size, a pattern of mobility, type of development (Bremner et al., 2003) to delineate ecosystem functioning (Dolédec et al., 2006). The selected biological characteristics might be shared by different representatives of macrobenthic assemblages with different taxonomic identities; therefore this approach can portray large geographical ranges with gradients in species composition and diverse taxonomic entities. Moreover, it is a valuable approach to measure ecosystem structure independently of its biogeography (Doledec et al., 1999). BTA advocates the theory of environmental filters that recognize a subset of total species assemblages with distinct traits or phenotypes representing a particular environmental condition. According to this theory, more tolerant species can sustain in adverse condition by replacing sensitive species (Keddy, 1992). With recent methodological advances, another multivariate ordination method (RLQ) has been used in combination with fourth-corner analysis (Doledec et al., 1996; Dray and Legendre, 2008; Legendre et al., 1997) in our study. This approach is contemporary to macrobenthic studies (Hu et al., 2019; Piló et al., 2016; Wouters et al., 2018) and robust in estimating functional diversity and the impact of disturbances on benthic animals. The RLQ has gained its importance in recent years due to its potential to identify the relationship among traits and environmental parameters.

Sundarbans Estuarine System (SES) is the largest monsoonal micro-tidal deltaic front comprising hundred-odd estuaries located alongside the Indian coast. It has been declared as a world heritage site by UNESCO in 1997 and recently as a Ramsar site in 2019 (http://wiienvis.nic.in/Database/ramsar_wetland_sites_8224.aspx). The geographic location has made the SES vulnerable to tidal surges and cyclones. Its mangrove inhabitants absorb and reduce the impact of cyclonic storms coming from the Bay of Bengal (Chatterjee et al., 2013). Besides, climate change induced eustatic sea-level rise has altered the tropical deltas and SES is not an exception.

In the last couple of decades, a handful of studies have been conducted from the viewpoint of biogeochemistry, water quality analysis, phytoplankton, zooplankton and meiobenthos from the Indian sector of Sundarbans (Dey et al., 2012; Ghosh et al., 2018; Ghosh and Mandal, 2019; Manna et al., 2010; Mukhopadhyay et al., 2006; Nandy et al., 2018a, 2018b). Due to its strategic location inside the biosphere reserve, most of the areas are inaccessible to researchers. Though the meagre amount of studies on macrobenthos has been reported from the western part, howbeit a dearth of information is available from the central sector of Indian Sundarbans. Furthermore, only analysis of species composition is not enough to unriddle their seasonal succession pattern from such a complex ever-changing habitat like SES which needs to be supplemented by BTA approach.

Against this backdrop, the present study is a maiden endeavour to unravel the following questions: (I) how does macrobenthic community structure along with trait modalities alter spatiotemporally at the Matla River? (II)

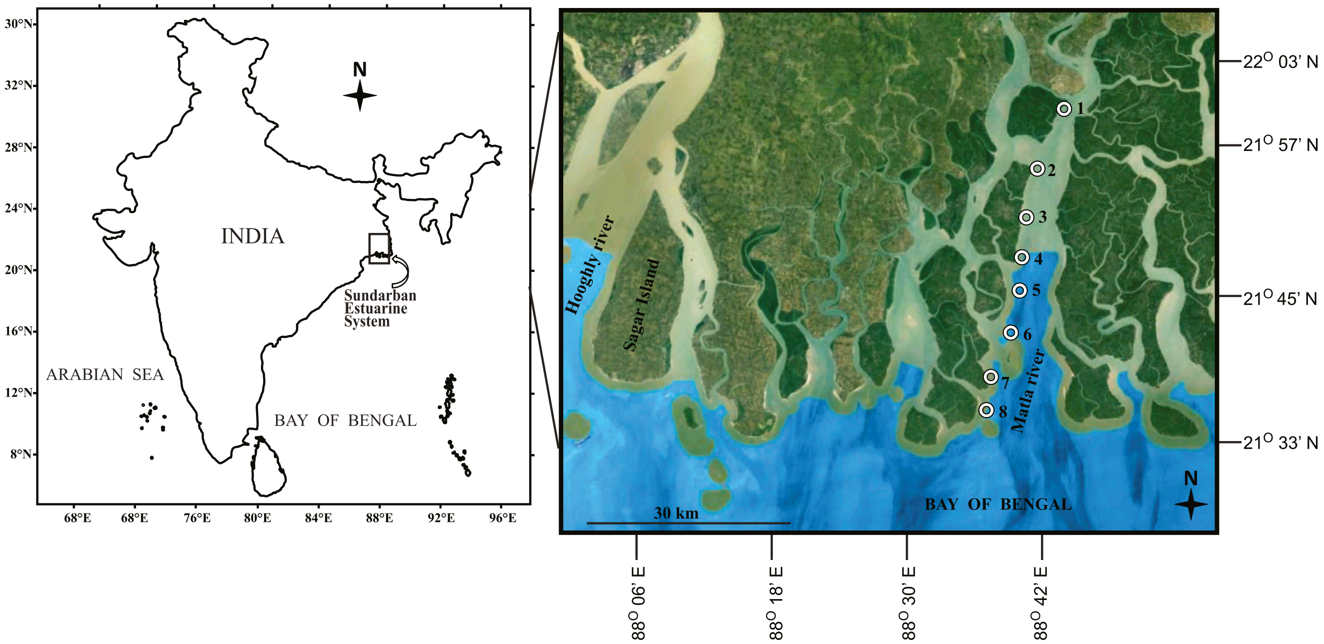

Figure 1 The geographic location of the stations sampled in the Sundarbans estuarine system (SES). All sampling stations spread on the Matla River are marked with station number.

how do environmental alterations govern the community structure of macrobenthic assemblages?

2. Material and methods

2.1. Study area

The present investigation was carried out as a part of Ministry of Earth Sciences (MoES) funded project in Sundarbans Estuarine System (SES) during May 2017 (Summer), August 2017 (Monsoon), November 2017 (Winter) and March 2018 (Spring). The sampling period was chosen based on the IMD (Indian Meteorological Department) report. Seasons can be categorized as a dry summer with frequent storm and cyclonic events, huge precipitation during the southwest monsoon, cool and dry winter, and spring with phytoplankton bloom. However, seasonal demarcation is gradually becoming lost due to unpredictable downpour induced by low-pressure cyclonic events in recent years (Fukushima et al., 2019; Rastogi et al., 2018). The samples were collected along the estuarine gradient from north to south selecting eight stations at the Matla River. The details of the study stations have been furnished in Figure 1.

The Matla River is considered to be the largest estuary in SES. Being the longest and widest (L: 125 km, W: 26 km) river, it experiences high meandering courses with a sharp bend (Chatterjee et al., 2013). In recent times, due to high siltation, the central sector of this river has been disconnected from freshwater supply and discharge led the river primarily fed by the oceanic tide and characterized by variable sediment texture, salinity, conductivity and other environmental parameters. The estuarine condition of the Matla River is maintained by monsoonal runoff alone (Trivedi et al., 2016) which has been reflected in the biodiversity associated with it (Rudra, 2018).

2.2. Sample collection and analysis

Macrobenthic samples were collected in triplicate using a Van Veen grab (0.04 m^2) from each of the eight stations. The collected samples were in situ washed through a 0.5 mm mesh sieve, transferred to plastic bags and immediately fixed in 4% buffered formalin in seawater, and stained with rose Bengal aqueous solution. In the laboratory, animals were sorted, identified to the lowest practical taxonomic level following standard literature (Day, 1967; Dey, 2006; Fauvel, 1953; Misra, 1995; Southern, 1921), and counted. Numerical data was extrapolated into ind. m^{-2}. Water and sediment samples were collected along with macrobenthic sampling for analysis of major environmental parameters. Sediment samples were taken separately for the analysis of organic content by wet oxidation method using chromic acid digestion followed by titration with 0.2 N ferrous ammonium sulfate solutions (El Wakeel and Riley, 1957). Soil texture was determined following pipette analysis (Buchanan, 1984). The temperature was measured in situ using a mercury thermometer. Microphytobenthos was estimated as chlorophyll *a* (Chl *a*) concentration. The top one cm of sediment was cut, placed in a 15 ml polyethylene bottle and preserved in liquid nitrogen onboard. Chl *a* concentration was measured with 90% acetone extraction of pigments and same for phaeopigment subsequent acidification with diluted hydrochloric acid, in the laboratory, following a standard protocol (Strickland and Parsons, 1972).

Bottom water samples were collected by Niskin water sampler (5 L) for analysis of water quality parameters including dissolved nutrients. Water temperature and pH were recorded in situ with the help of mercury-in-glass Celsius thermometers and digital pH meters (Orion star A211), respectively. Furthermore, Secchi disc was also used to determine the transparency of water at each station. Water samples for analysis of salinity and nutrients were collected in pre-cleaned 500 ml plastic bottles and transported to the laboratory stored in iceboxes. Dissolved oxygen (DO) and salinity were analyzed following a standard protocol (Strickland and Parsons, 1972). Water samples for nutrient analysis were filtered through GF/F (mesh size 0.7 μm) filter papers using Millipore filtering unit and were analyzed for nitrite (NO_2-N), nitrate (NO_3-N), ammonium (NH_4-N), inorganic phosphate (PO_4-P) and silicate (SiO_4-Si) following the standard protocol (Grasshoff et al., 1999). Suspended particulate matter (SPM) analysis was performed according to the method of Grasshoff et al. (1999). Monthly average rainfall data for the study period were collected from the Customized Rainfall Information System (CRIS), Hydromet Division, India Meteorological Department, Ministry of Earth Sciences, New Delhi IMD (http://hydro.imd.gov.in/hydrometweb/(S(gkp1rg45430qze45lwildiil))/DistrictRaifall.aspx).

2.3. Data analysis

Univariate and multivariate analyses of data were performed using PRIMER v 6 software (Clarke and Gorley, 2006; Clarke et al., 2008) with PERMANOVA add-on package (Anderson et al., 2008). Non-multidimensional scaling (NMDS) and Bray—Curtis similarity index were constructed based on macrofaunal density after square root transformation. A similarity profile (SIMPROF) test was conducted to detect the significantly different station groups using the default of 1000 permutations for the mean similarity profile and 999 permutations for the simulated profile with a significance level of 0.05. Similarity percentage (SIMPER) was then used to identify the species contributing to intra-group similarity and those species responsible for the dissimilarity between groups. A global BEST permutation test (999 permutations) was performed on log (x+1) transformed and normalized environmental data, and square root transformed biological data using Spearman rank correlation between environmental variables and benthic patterns (Clarke et al., 2008). The following indices were also determined based on macrobenthic density: Shannon diversity H' ($\log_e$), Margalef's species richness d, Pielou's evenness J' and Simpson index $1-\lambda'$. To investigate the spatiotemporal effect on total macrofaunal density, trait categories and environmental parameters were analyzed through two way Permutational Multivariate Analysis of Variance (PERMANOVA) with a station as the first factor (8 stations) and a season as the second factor (4 seasons). All PERMANOVA tests were done on Bray-Curtis similarity matrices using permutation of residuals under a reduced model, with 999 permutations. The BIOta ENVironmental matching (BIO-ENV) analysis was performed on the similarity matrix based on density data to relate macrofaunal assemblages to environmental parameters (Clarke and Warwick, 2001). To evaluate the relationship between the polychaete community and environmental variables, Canonical Correspondence Analysis (CCA) was applied using the Multivariate Statistical Package (MVSP) v3.1 (Kovach, 1998).

The selection of trait categories and their analysis followed the method described in Bremner et al. (2003, 2006), Hu et al. (2019), Pacheco et al. (2011), Piló et al. (2016). The biological traits database of total macrobenthos identified in the study was developed by extracting information from various sources like published literature (Bremner et al., 2003, 2006; Egres et al., 2019), books (Dey, 2006; Fauchald and Jumars, 1979; Giese and Pierse, 1977; Jumars et al., 2015), websites (Polytraits) (Faulwetter et al., 2014) and Biological Traits Information Catalogue (BIOTIC, MarLIN, 2006). For certain cases, traits for individual genera or species were not available, data from other species in the same family were used (Supplementary Table S1). Among three matrices, first and second were made with trait categories and density data for individual species on each study stations in four seasons. The third matrix was constructed by multiplying the trait categories with respective density value. Taxa were scored for each trait using fuzzy coding principle (Chevene, 1994) and then converted to proportions of one for each trait. In this study, the coding followed a scale ranging from 0 (no affinity) to 3 (total affinity). For any obligate trait, it has been scored as 3 and rest of the other traits as 0. The final matrix was transformed square root and analyzed with PCA for each trait separately.

2.4. RLQ and fourth-corner analysis

Another multivariate technique RLQ (Dolédec et al., 1996) in combination with the fourth-corner method (Dray et al., 2014; Legendre et al., 1997) was conducted to estimate the relationship between environmental factors and species trait modalities in relation to RLQ axis. Before analyzing, three separate tables L (species distribution across samples: sites in the row and species in the column), R (environmental parameters of samples: sites in rows and environmental variables in columns) and Q (species traits: species in rows and traits in the columns) were constructed. In order to perform the RLQ, each of the tables needs to be analyzed separately. Correspondence analysis (CA) and principal component analysis (PCA) were applied to table L and Q respectively (Dray et al., 2014) whereas, for table R, Hill-Smith analysis (Dray, 2013) was employed. RLQ analysis alone can give insights on the global visual summary of the relationship among these three metrics however, in combination with fourth-corner analysis; it can portray the significance of these bivariate associations. Additionally, the Monte-Carlo test was run with 49999 random permutations of model 2 (to test the null hypothesis: taxon densities with fixed traits are unrelated to environmental parameters) and model 4 (taxon densities with fixed environmental factors are not influenced by species traits), then adjusted the p-value accordingly (Benjamini and Hochberg, 1995; Dray, 2013). The RLQ/fourth-corner combined analysis was performed using "ade4" package (Dray and Dufour, 2007) available in R software (version 4.0.1).

Table 1 Seasonal mean ± SD of water quality parameters.

	Summer	Monsoon	Winter	Spring
Temperature (°C)	31.95 ± 1	30.10 ± 0.69	24.73 ± 0.88	28.14 ± 1.10
Salinity (psu)	29.26 ± 5.14	17.00 ± 0.65	14.80 ± 1.59	27.21 ± 1.84
DO (mg L^{-1})	4.77 ± 0.12	5.15 ± 0.56	7.46 ± 0.39	6.54 ± 0.32
pH	8.12 ± 0.03	7.83 ± 0.18	8.12 ± 0.04	8.11 ± 0.03
Chlorophyll *a* (μg L^{-1})	4.10 ± 0.55	2.45 ± 0.65	1.13 ± 0.68	3.74 ± 2.15
Phaeopigment (μg L^{-1})	0.44 ± 0.20	0.21 ± 0.12	0.17 ± 0.07	0.53 ± 0.44
Nitrate (μM)	13.55 ± 1.20	13.11 ± 3.89	16.41 ± 2.76	6.46 ± 0.97
Nitrite (μM)	0.57 ± 0.16	0.39 ± 0.20	0.73 ± 0.14	1.31 ± 0.18
Phosphate (μM)	1.37 ± 0.08	1.36 ± 0.22	1.03 ± 0.13	0.83 ± 0.17
Silicate (μM)	28.80 ± 2.83	15.17 ± 2.22	32.89 ± 4.67	14.51 ± 0.88
Ammonium (μM)	2.64 ± 0.57	0.45 ± 0.13	0.18 ± 0.02	0.19 ± 0.03

3. Results

3.1. Environmental parameters

Environmental parameters were characterized by a strong temporal but meagre spatial variation. PERMANOVA result depicted all the parameters were significant ($p \leq 0.05$) with seasons only, whereas dissolved silicate and nitrate had significant value at both scales. Bottom water salinity ranged from 35.04—12.13 in summer (Stn. 4) and winter (Stn. 1) respectively whereas, level of dissolved oxygen showed an increasing trend towards monsoon and post-monsoon seasons (Table 1). The essential micronutrients concentrations varied both spatially and temporally in the present study. The average nitrate concentration varied between (6.46 ± 0.97 μM) to (16.41 ± 2.76 μM) during spring and winter respectively (Table 1). However, average nitrite concentration varied from (0.39 ± 0.20 μM) to (1.31 ± 0.18 μM) during monsoon and spring correspondingly (Table 1). Dissolved inorganic nutrients like ammonium or phosphate were recorded in negligible amount except in upper stretch stations where anthropogenic activities are evident (Table 1). The sediment contained the highest amount of Chl *a* in winter compared to other seasons (Table 2). Organic enrichment was moderate, being lowest during winter (Table 2). The sediment texture was mostly silty with a variable amount of clay and sand (Figure 2). Silt percentage ranged from 59.35 to 66.92 in spring and summer respectively. Likewise, the clay percentage also showed a similar seasonal trend. Overall, the BIOENV revealed a weak correlation ($p = 0.498$) between environmental parameters and benthic data. Among all, organic matter, chlorophyll *a*, nitrite and phosphate showed the best correlation.

3.2. Taxonomic composition of macrobenthic community

Total macrobenthic density revealed a significant differences (PERMANOVA) among seasons ($F = 7.7355$, $p = 0.001$) and stations ($F = 4.6651$, $p = 0.001$). The macrofaunal community of 95 taxa, belonging to 6 phyla was recorded during the faunistic surveillance. Among these, 56 species belong to Annelida, 1 to Sipuncula, 24 to Mollusca, 11 to Arthropoda, 2 from Cnidaria and 1 from Echinodermata. Overall, Annelida were numerically dominant (76.25% of the total macrobenthos), followed by Mollusca (10.5%), Arthropoda (9.2%), Cnidaria (2%), Sipuncula (1.6%) and Echinodermata (0.3%). The maximum species count (11675 ± 11883.31 ind. m^{-2}) was observed during spring that declines considerably (5875 ± 6224.08 ind. m^{-2}) during monsoon. Effects of environmental perturbation on macrobenthic density varied accordingly in spatial scale throughout the study period. Among all, the macrobenthic density at station 1 in summer was mostly affected during monsoon and drastically reduced from 3758 ± 3916 ind. m^{-2} to 233 ± 270 ind. m^{-2} (Figure 3a). Density in stations 1, 4, 6 and 7 comparatively declined in spring compared to the previous season (Figure 3a).

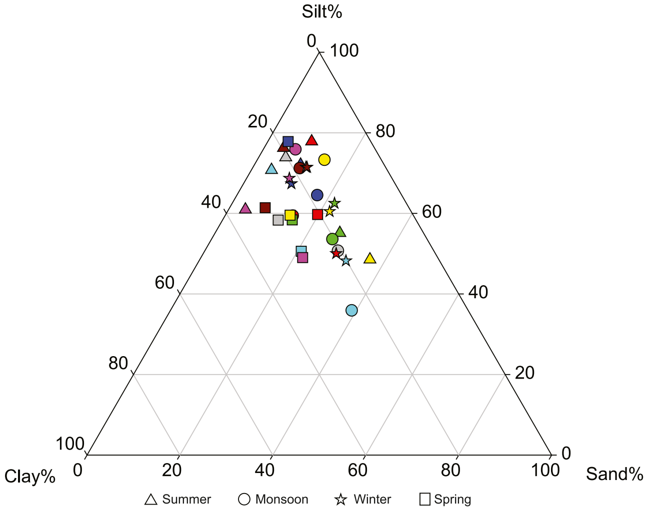

Figure 2 Ternary plot showing the sediment texture pattern of eight stations in four distinct seasons. Red: stn. 1, Dark blue: stn. 2, Green: stn. 3, Yellow: stn. 4, Grey: stn. 5, Brown: stn. 6, Light blue: stn. 7, Purple: stn. 8

Polychaete density was found to be highest (8117 ± 5235.67 ind. m^{-2}) in winter and lowest (4300 ± 3716.99 ind. m^{-2}) in monsoon (Figure 3b). A total of 56 species from 26 families have constructed the entire polychaete community during the study period (Table 3). Few species like *Cossura coasta, Dendronereis aestuarina*,

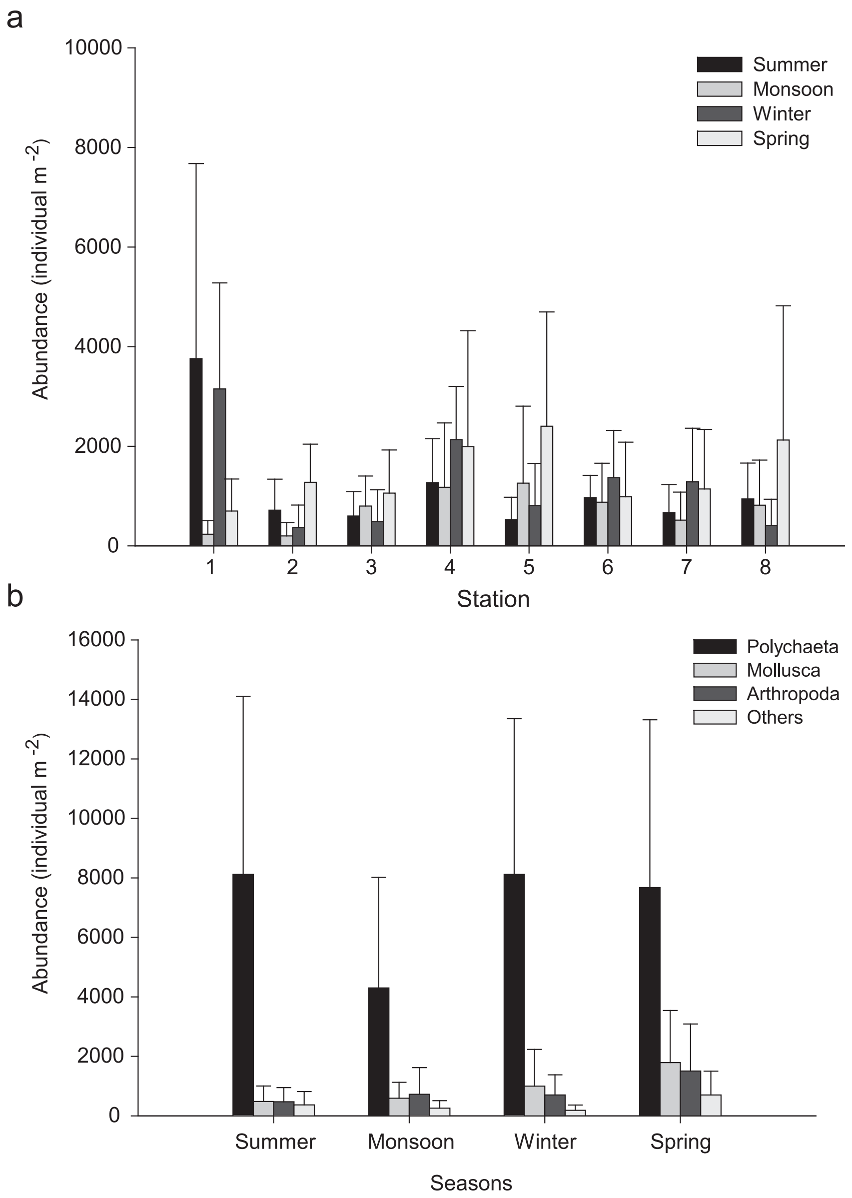

Figure 3 a) Spatiotemporal variation of macrobenthic density during the study period, b) seasonal variation of macrofaunal groups during the study period.

Heteromastus similis, Magelona cincta, Micronephthys oligobranchia, Prionospio cirrifera and *Sternaspis scutata* prevailed the estuary throughout the study period. *Paraprionospio pinnata, H. similis* and *M. cincta* dominated during summer and monsoon albeit in winter *H. similis* was replaced by another cognate capitellid (*Parheteromastus tenuis*) (Supplementary Table S2). However, in spring the composition was completely different, represented by species from Spionidae (*Prionospio cirrifera*) and Nereididae families (*Neanthes meggitti*) which recorded highest densities among four seasons. Individuals of genus *Prionospio* showed a marked variation in appearance as well in density. In summer and winter, *P. pinnata* dominated the estuary, mostly towards down stretch stations, howbeit in winter they were abundant in innermost station. Moreover, *P. pinnata* and *P. cirrifera* showed interspecific replacement in spring (Supplementary Table S2). Overall, capitellids and spionids prevailed the estuary throughout seasons. The innermost stations were mostly composed of opportunistic species due to organic enrichment and anthropogenic input. The average molluscan density varied from 1792 ± 1751.04 ind. m^{-2} to 483 ± 518.60 ind. m^{-2} in spring and summer respectively. Molluscs were composed of 8 species (5 families) of bivalve and 16 species (15 families) of gastropod. Among bivalves, *Donax incarnatus* and *Meretrix meretrix* were most dominant, whereas on the other hand, *Pirenella cingulata* and *Acteocina estriata* were dominant among gastropods. Molluscs were abundant mostly in middle stretch (stations 4 and 5) of the estuary.

3.3. Statistical analysis

Bray—Curtis similarity based on the macrofaunal density categorized the estuarine zone into several groups with

Table 2 Spatio-temporal variation in sediment parameters.

Stations	Temperature (°C)				Chlorophyll *a* (μg g^{-1})				Phaeopigment (μg g^{-1})				Organic carbon %				Organic matter %			
	Summer	Monsoon	Winter	Spring	Summer	Monsoon	Winter	Spring	Summer	Monsoon	Winter	Spring	Summer	Monsoon	Winter	Spring	Summer	Monsoon	Winter	Spring
1	32.50	29.50	25.50	30.00	2.37	3.76	1.53	0.71	0.33	0.35	0.27	0.21	1.15	1.14	0.53	1.95	1.99	1.96	0.91	3.37
2	31.50	30.00	25.50	29.00	1.48	1.02	0.51	0.97	0.23	0.14	0.09	0.18	0.89	0.81	0.02	0.88	1.53	1.39	0.03	1.52
3	31.00	30.50	24.75	30.00	0.64	0.51	2.85	0.97	0.12	0.00	0.29	0.27	0.76	0.96	0.06	0.83	1.31	1.66	0.10	1.44
4	31.00	31.00	25.50	30.00	0.33	2.06	0.36	0.45	0.06	0.20	0.06	0.51	0.75	0.70	0.73	1.03	1.28	1.21	1.26	1.77
5	31.50	31.50	26.50	31.00	1.45	1.04	3.08	1.68	0.23	0.14	0.46	0.30	0.86	0.96	0.15	0.82	1.48	1.66	0.26	1.41
6	32.00	30.50	26.00	26.00	0.95	0.51	0.69	1.07	0.15	0.14	0.21	0.18	0.96	1.14	0.23	0.81	1.65	1.96	0.39	1.39
7	31.50	31.50	25.50	28.00	0.97	1.35	1.53	0.45	0.18	0.29	0.32	0.33	0.90	0.28	0.24	0.49	1.55	0.48	0.42	0.85
8	32.00	30.50	26.00	29.50	1.66	0.84	1.35	0.10	0.27	0.15	0.24	0.27	1.20	0.78	0.11	0.63	2.06	1.34	0.19	1.08

Table 3 CCA code and RLQ code for the list of taxa are tabulated.

Species name	CCA code	RLQ code
Annelida		
Ancistrosyllis matlaensis	1	Anma
Ancistrosyllis sp.	2	AnS
Aphelochaeta multifilis	3	Apmu
Aricidea sp.	4	ArS
Axiothella obockensis	5	Axob
Barantolla sculpta	6	Basc
Capitella capitata	7	Caca
Chloeia parva	8	Chpa
Cossura coasta	9	Coco
Dendronereis aestuarina	10	Deae
Diopatra cuprea	11	Dicu
Dipolydora normalis	12	Dino
Mysta ornata	13	Myor
Euclymene annandalei	14	Euan
Gattyana fauveli	15	Gafa
Glycera alba	16	Glal
Glycera longipinnis	17	Gllo
Glycera tesselata	18	Glte
Glycinde oligodon	19	Glol
Goniada emerita	20	Goem
Hermundura annandalei	21	Hean
Hesione splendida	22	Hesp
Heteromastus similis	23	Hesi
Kuwaita heteropoda	24	Kuhe
Levinsenia sp.	25	LeS
Lumbrineris latreilli	26	Lula
Lumbrineris polydesma	27	Lupo
Lumbrineris sp.	28	LuS
Magelona cincta	29	Maci
Micronephthys oligobranchia	30	Miol
Namalycastis fauveli	31	Nafa
Namalycastis indica	32	Nain
Neanthes glandicincta	33	Negl
Neanthes meggitti	34	Neme
Nephtys polybranchia	35	Nepo
Notomastus giganteus	36	Nogi
Owenia fusiformis	37	Owfu
Paraprionospio pinnata	38	Papi
Parheteromastus tenuis	39	Pate
Perinereis cultrifera	40	Pecu
Perinereis nigropunctata	41	Peni
Polydora ciliata	42	Poci
Polydora sp.	43	PoS
Potamilla leptochaeta	44	Pole
Prionospio cirrifera	45	Prci
Prionospio saldanha	46	Prsa
Sabellaria pectinata	47	Sape
Scoloplos sagarensis	48	Scsa
Scyphoproctus armatus	49	Scar
Sigambra constricta	50	Sicn
Sigatargis commensalis	51	Sico
Spio bengalensis	52	Spbe
Sternaspis scutata	53	Stsc

(*continued on next page*)

Table 3 *(continued)*

Species name	CCA code	RLQ code
Syllis cornuta	54	Syco
Terebellides stroemii	55	Test
Anelassorhynchus microrhynchus	56	Anmi
Sipuncula		
Phascolosoma (Phascolosoma) arcuatum		Phar
Mollusca		
Donax incarnatus		Doin
Macoma sp.		MaS
Meretrix meretrix		Meme
Modiolus sp.		MoS
Protapes sp.		PrS
Solen vagina		Sova
Strigilla splendida		Stsp
Tegillarca granosa		Tegr
Acrilla acuminata		Acac
Acteocina estriata		Aces
Austropilula beddomeana		Aube
Ellobium gangeticum		Elga
Haloa crocata		Hacr
Littorina obtusata		Liob
Nassarius foveolatus		Nafo
Notocochlis sp.		NoS
Phalium sp.		PhS
Pirenella alata		Pial
Pirenella cingulata		Pici
Stenothyra deltae		Stde
Telescopium telescopium		Tete
Thais sp.		ThaS
Thiara sp.		ThiS
Turritella sp.		TuS
Arthropoda		
Ampelisca pusilla		Ampu
Balanus sp.		BaS
Gammarus sp.1		GaS1
Gammarus sp.2		GaS2
Harpacticoid Copepod		Hac
Ingolfiella sp.		InS
Paradiastylis sp.		PaS
Penaeus monodon		Pemo
Metaplax intermedia		Mein
Scylla serrata		Scse
Sphaeroma annandalei annandalei		Span
Cnidaria		
Actiniaria sp.1		AcS I
Actiniaria sp.2		AcS II
Echinodermata		
Amphioplus (Lymanella) depressus		Amde

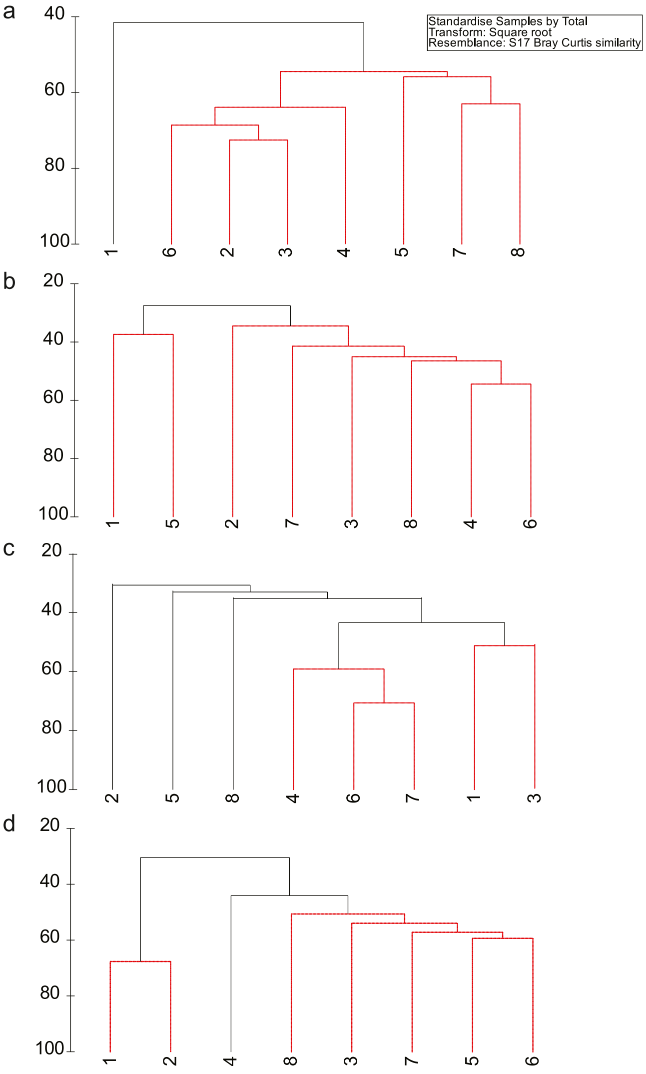

Figure 4 Cluster plot based on Bray—Curtis similarity coefficient of macrobenthic species in four distinct seasons; a) summer, b) monsoon, c) winter, d) spring.

marked variation between the sampling seasons and stations. It has delineated two groups and one separate station (SIMPROF test $p<0.05$) during summer (Figure 4a). According to SIMPER analysis, *Heteromastus similis* contributed 15.91% and 21.63% in group 1 (66.91% similarity) and group 2 (58.22%) formation respectively (Supplementary Table S3). Moreover, station 1 has been separated from these two groups due to its different species composition like *Magelona cincta*, *Micronephthys oligobranchia* and *Perinereis nigropunctata*. In monsoon, two major groups have been identified, mirrored by *H. similis* a major contributor (23.88%) behind the formation of group 2 (41.40% similarity) and separation of group 1 and 2 (Figure 4b). *Terebellides stroemii* played an overriding role in shaping the station 8 distinguished from the rest of the stations in winter that has made station 8 completely separated from rest of the other stations might be due to the location of this particular station was at the mouth of the estuary (Figure 4c). In spring, upstream and downstream stations have diverged into two prominent groups except station 4 having unique species composition like *Acteocina estriata*, *Stenothyra deltae* and *Meretrix meretrix* (Figure 4d).

Ordination resulting from CCA biplot for 56 polychaete community showed five axes representing 82.42% cumulative constrain percentage where axis 1 and 2 showed 0.93% and 0.86% species environmental correlation, respectively. A total of ten variables significantly explained in the biplot (Figure 5a). Axis 1 was influenced by clay percentage, sand

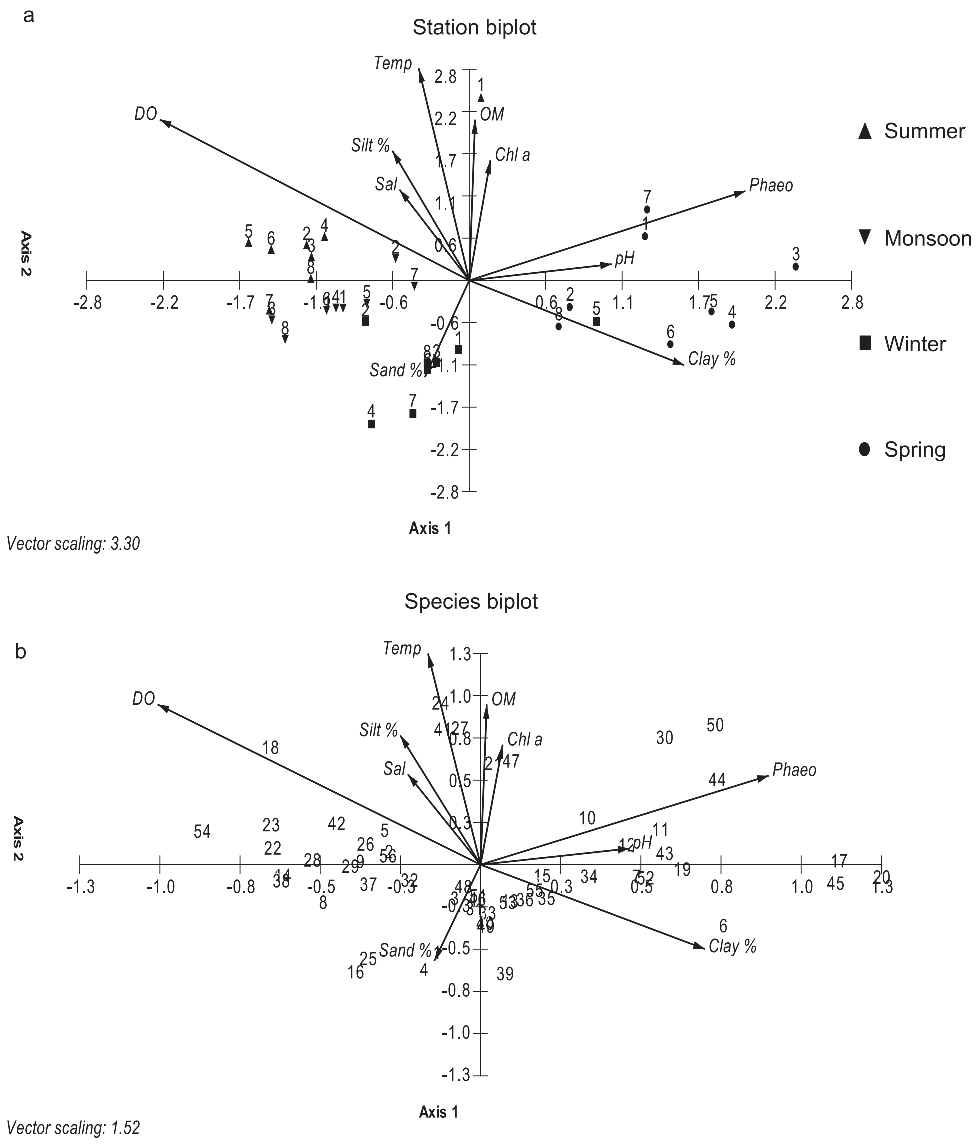

Figure 5 Canonical correspondence analysis (CCA) ordination for polychaete species and environmental variables. The environmental variables (temperature, salinity, pH, Dissolved Oxygen, sand %, silt %, clay %, chlorophyll *a*, phaeopigment, Organic Matter) are indicated by arrows. Station codes and species codes are given in Figure 1 and Table 3 respectively.

percentage whereas; axis 2 was driven by remaining parameters. Being influenced by DO vector, most of the stations in summer occupied the upper left quadrant but station 1 was exceptionally profited by organic content. Most of the stations in monsoon and winter clustered together in lower left quadrant and majority were favoured by sand % vector. During winter, all the stations were positioned towards sand percentage vector except station 5 which showed affinity towards clay percentage. In spring, all the stations were positioned in the right quadrant profiting mostly by clay percentage. In species biplot (Figure 5b), *Ancistrosyllis matlaensis, Namalycastis fauveli, Prionospio saldanha, Scoloplos sagarensis, Sigatargis commensalis, Levinsenia* sp. have shown a positive correlation with sand % whereas, *Nephtys polybranchia, Notomastus giganteus, Sternaspis scutata, Terebellides stroemii* showed affinity to the percentage of clay present in the sediment.

3.4. Biotic indices

All the diversity indices showed significant (PERMANOVA, $p \leq 0.05$) variation with seasons. Shanon diversity H'($\log_e$) followed a seasonal trend of winter > spring > monsoon > summer, where the maximum and minimum values were recorded at station 1 in winter (3.55) and station 2 in monsoon (2.02), respectively. The similar seasonal pattern was also observed in case of total population density (N) and Simpson index ($1-\lambda$). Margalef's species richness recorded highest (10.27) during winter at station 1 and lowest (2.13) during monsoon at station 2 (Table 4).

3.5. Biological Trait Analysis

In the present study, BTA on total macrobenthos has depicted a distinct variation influenced by seasonal

Table 4 Seasonal variation in macrobenthic community indices for all stations. S = Total number of species, N = Total population density, d = Species richness (Margalef's), J' = Pielou's evenness, H'(log$_e$) = Shannon index, $1-\lambda$ = Simpson index.

Stations	S	N	d	J'	H'(log$_e$)	$1-\lambda$
Summer						
1	24	43	6.13	0.95	3.03	0.97
2	15	34	3.97	0.95	2.57	0.94
3	16	37	4.17	0.97	2.68	0.95
4	18	37	4.70	0.95	2.75	0.95
5	11	27	3.04	0.91	2.19	0.89
6	13	29	3.55	0.92	2.36	0.92
7	10	27	2.73	0.92	2.13	0.90
8	18	36	4.73	0.95	2.74	0.95
Monsoon						
1	12	33	3.15	0.98	2.44	0.94
2	8	27	2.13	0.97	2.02	0.89
3	13	31	3.49	0.94	2.41	0.93
4	28	49	6.92	0.98	3.26	0.98
5	23	41	5.91	0.95	2.99	0.96
6	23	44	5.82	0.97	3.04	0.97
7	15	35	3.92	0.97	2.62	0.95
8	22	42	5.62	0.96	2.98	0.97
Winter						
1	42	54	10.27	0.95	3.55	0.98
2	16	38	4.13	0.98	2.71	0.96
3	19	41	4.83	0.98	2.89	0.97
4	27	42	6.96	0.93	3.08	0.97
5	23	40	5.95	0.95	2.98	0.96
6	23	41	5.91	0.95	2.97	0.97
7	22	43	5.58	0.97	3.00	0.97
8	15	35	3.94	0.96	2.61	0.95
Spring						
1	17	38	4.41	0.97	2.74	0.96
2	13	27	3.66	0.89	2.27	0.89
3	22	37	5.80	0.93	2.87	0.95
4	28	46	7.04	0.96	3.18	0.97
5	33	48	8.26	0.95	3.31	0.98
6	22	42	5.62	0.96	2.97	0.97
7	22	41	5.66	0.95	2.95	0.96
8	32	47	8.06	0.94	3.27	0.98

Table 5 List of biological traits, abbreviations and categories used to describe macrobenthic assemblages.

Trait (Abbreviations)	Categories
Body size (BS)	1. Small (SM) (<3 cm) 2. Medium (ME) (3—6 cm) 3. Large (LA) (>6 cm)
Motility (M)	1. Motile (MO) 2. Discretely motile (DM) 3. Sessile (SE)
Living habitat (LH)	1. Tube dweller (TU) 2. Burrower (BU) 3. Free swimmer (FS) 4. Crawler (CR) 5. Attached (AT)
Feeding strategy (F)	1. Sub surface deposit feeder (SSDF) 2. Surface deposit feeder (SDF) 3. Suspension feeder (SF) 4. Carnivore (CAR) 5. Herbivore (HER)
Reproductive strategy (RS)	1. Asexual (A) 2. Sexual — Brooder (SB) 3. Sexual — Spawner (SS)

perturbation. Among 19 trait categories (Table 5), 17 were most prominent at both the spatiotemporal scale. Trait categories like motile, burrower and surface deposit feeder dominated the estuary whereas, discretely motile, tube dweller, carnivores or scavengers and sexual reproduction (brooder and spawner) were also widespread (Figure 6). In case of body size trait, large animals were found in upper stretch being maximum at station 2 during spring (Figure 6a). Motile species showed significant variation among seasons ($p < 0.05$). Maximum contribution (61.33%) of discretely motile species was gradually replaced by motile species in the following seasons. Sessile animals could not significantly persist in this entire estuarine stretch (Figure 6b). Burrowers were most prevalent in all four seasons. Moreover, the contribution of other categories of this trait showed a significant difference in the temporal scale (Figure 6c). Deposit feeding was the most dominant feeding strategy in this estuary, though a gradual appearance of suspension-feeding groups in spring has also been noticed. Sub-surface deposit feeders (SSDF) contributed maximum in summer which declined in spring (Figure 6d). In most of the stations, spawners were the dominant trait modality, howbeit in few stations like 1, 2 (spring), a gradual succession of brooders has been noticed compared to previous seasons (Figure 6e).

In the PCA, four seasons have distinctly clustered where monsoon and winter were clustered alongside. For body size trait, PC1 and PC2 showed 79.9% and 98.9% cumulative variation where the small size (SM) was positively correlated with PC 2 (0.509) and negatively with PC 1 (−0.666) (Figure 7a). For mobility trait, MO was negative towards PC1 (−0.667) howbeit, DM was positive towards that axis (0.737) (Figure 7b). Burrowers were positively aligned to both PC1 and PC2 where stations 6 in summer and spring were positioned (Figure 7c). In Figure 7d, among feeding strategy trait categories, PC1 and PC 2 explained 56.8% and 77.3% cumulative variation where, SDF and SF both were negatively explained by PC2 (−0.306 and −0.749, respectively), CAR and HER were negative towards PC1 (−0.659 and −0.140 respectively); conversely, SSDF was positive towards both the axes. Except stations 1 and 2, the rest of the stations showed the maximum percentage of SF during spring (Figure 6d) as illustrated in the PCA plot (Figure 7d). In Figure 7e, SB positively explained PC2 (0.011), whereas SS was positive towards PC1 (0.534).

The RLQ analysis has depicted some correlation between the metrics (Table 6). Subsequently, forth corner analysis was performed, among the 323 possible associations at a significance level of ($\alpha = 0.05$), only 11 significant associations (3 negative and 8 positive) were found following Dray and

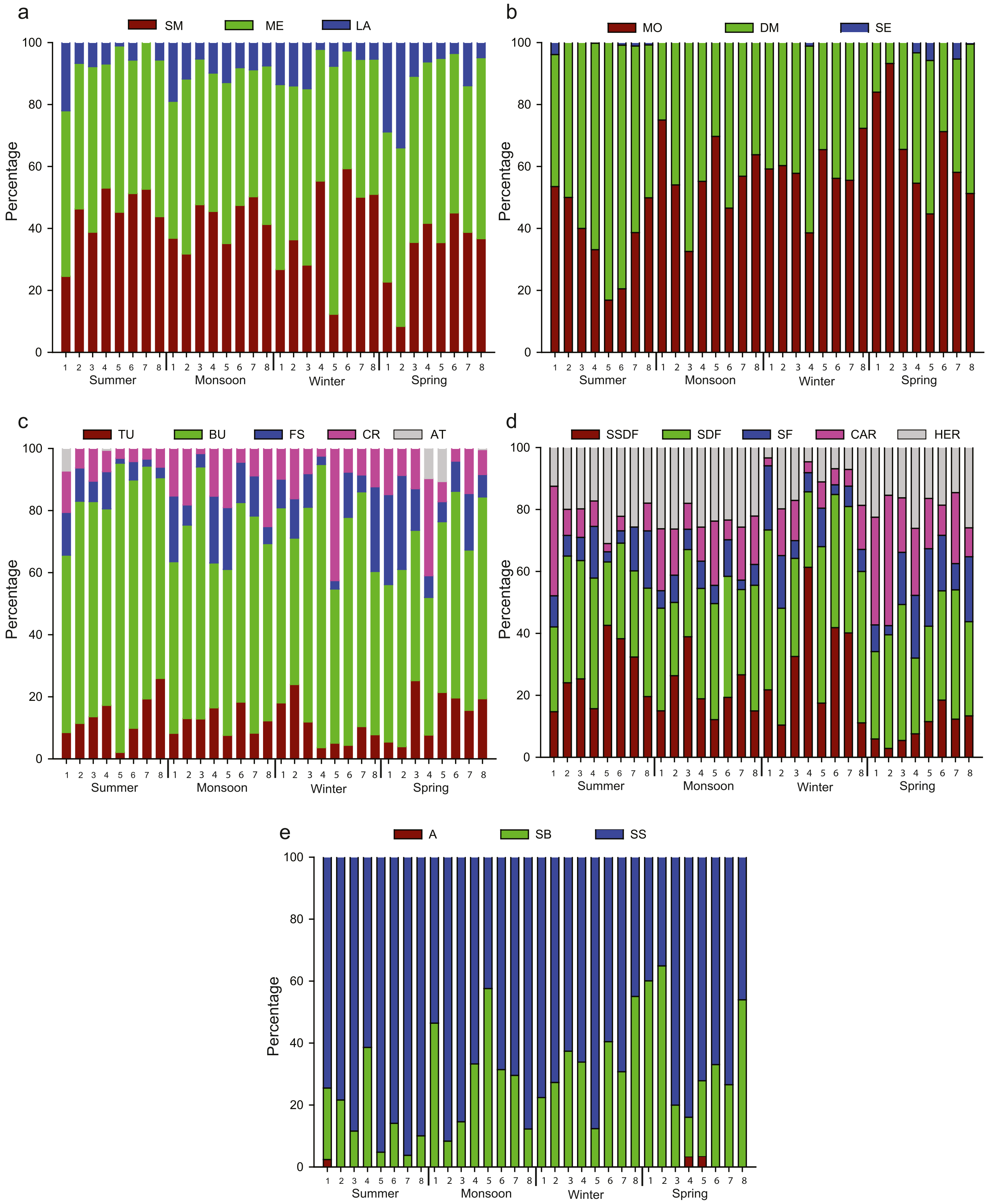

Figure 6 Percentage of trait categories for macrobenthic assemblages at eight different stations for four different seasons. a) Body size, b) mobility, c) living habitat, d) feeding strategy, e) reproductive strategy. The abbreviations are available in Table 5.

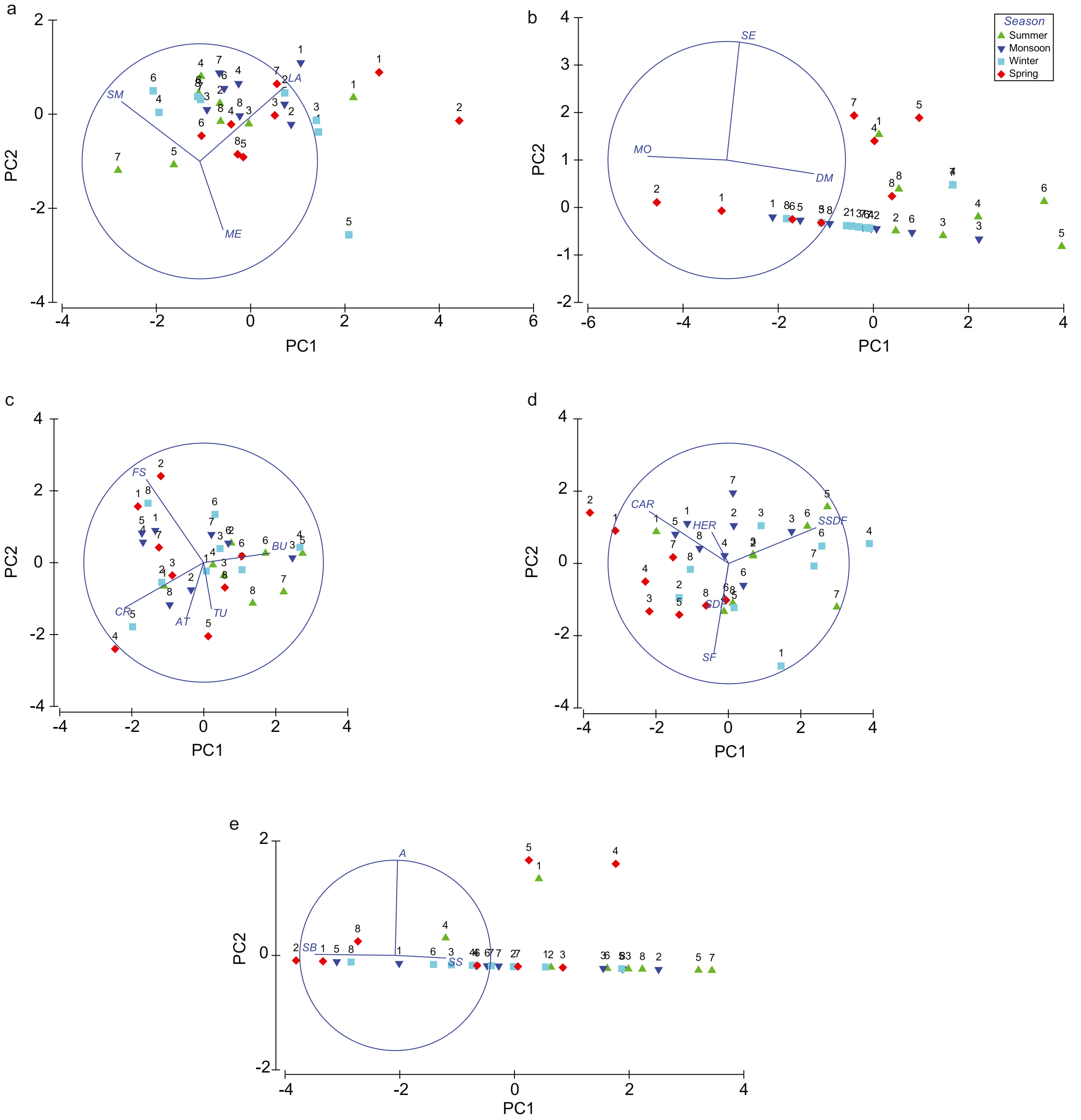

Figure 7 PCA ordinations depicting the variability in assemblage trait composition across stations and seasons. a) Body size, b) mobility, c) living habitat, d) feeding strategy, e) reproductive strategy. The abbreviations are available in Table 5.

Legendre (2008) approach. When p values were adjusted for multiple testing, there was no significant association. Subsequently, combining both RLQ and the fourth corner analysis, the global test did not reveal any significant relationships between species distribution and environmental parameters (model 2, p value = 0.08100) as well as between species distribution and species traits (model 4, p value = 0.40174). The first RLQ axis represents the 58.09% of the total variation while the second RLQ axis represents 23.97% (Table 6), encompassing the most important associations between traits, environment parameters and responsible species composition (Supplementary Table S4a,b). The positive part of axis 1 and negative part of axis 2 have revealed that suspension feeders and free swimmers are negatively associated with the level of suspended particulate matter (SPM) in water (Figure 8a,b). The negative part of axis 1 and positive part of axis 2 clearly highlight the presence of small-sized burrowers represented by polychaete genus *Ancistrosyllis* and *Sigambra* (Fig. 8b). Traits like carnivores and large or medium body size are mostly occupied at the positive part of axis 1 and the negative part of axis 2 (Figure 8b). Discretely motile animals such as glycerids are

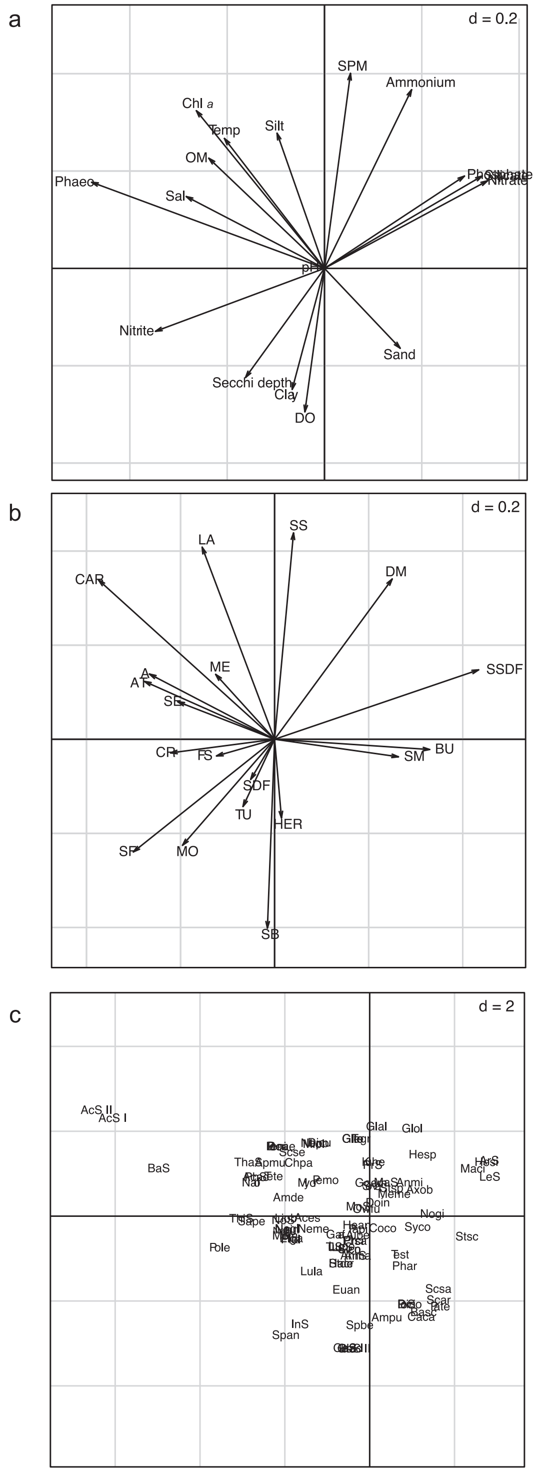

Figure 8 a) RLQ diagram as defined by the 1st and 2nd axes with the projection of environmental variables (SPM — suspended particulate matter, DO — dissolved oxygen, Sal — salinity, OM — organic matter, Chl *a* — Chlorophyll *a*, Temp — sediment temperature, b) RLQ diagram as defined by the 1st and 2nd axes with the projection of trait categories (see Table 5 for the abbreviations of trait categories), c) RLQ diagram as defined by the 1st and 2nd axes with the projection of species (see Table 3 for respective RLQ codes of species). The d value in the upper right corner is the scale of the graph given by a grid.

Table 6 RLQ results. Individual R-L-Q separate analysis and RLQ analysis.

Separated analysis	**Axis 1 eigenvalue (Variance %)**	**Axis2 eigenvalue (Variance %)**
R/Hill-Smith	5.78 (40.06)	3.91 (27.12)
L/CA	0.58 (28.66)	0.43 (21.41)
Q/PCA	4.37 (32.16)	3.22 (23.71)
RLQ Analysis	**Axis 1**	**Axis 2**
Eigenvalues	1.22	0.50
Variance %	58.09	23.97
R/RLQ		
Variance	1.80	2.21
Variance %	28.75	43.27
Q/RLQ		
Variance	1.81	1.47
Variance %	28.88	28.72
L/RLQ		
Variance	0.34	0.22
Variance %	5.37	4.28

positioned at the positive part of both the axis (Figure 8b,c).

4. Discussion

4.1. Environmental parameters

As estuaries are expressions of communication among land, river and ocean processes, therefore climate change mediated any environmental perturbation has a potential to affect estuarine ecosystem (Rybczyk and Day, 2013). In the present study, most of the environmental parameters were significantly influenced by seasons. Bottom water salinity showed a marked seasonal variation but spatially it was almost homogeneous throughout the entire estuarine stretch. Seasonal dynamics of Sundarbans delta is mostly controlled by monsoon induced hydrological changes. Unusual rainfall and a monsoon break are common phenomena in this system. SES experienced an unusual downpour (in October) at the beginning of the post-monsoon season (Supplementary Figure S1) and that might have exerted effects on hydrological parameters as reflected in our study. Bottom water salinity showed a marked seasonal variation being lowest during winter. A similar observation was recorded from the northern part of Bay of Bengal (Pant et al., 2015) as well as from Sundarbans (Saha et al., 2001), where authors explained that apart from rainfall mediated freshwater flux, high horizontal advection and lower tidal amplitude are crucial factors of anomalous salinity during winter. However, homogeneity in salinity can be explained as the Matla River has lost its freshwater connection due to high siltation and neotectonic activity mediated tilting of Eastern Bengal basin in recent years (Manna et al., 2010; Raha et al., 2012; Stanley and Hait, 2000). This phenomenon has been also reported from different estuaries around the globe, as in Kromme estuary (Wortmann et al., 1998) and Nile River (Aleem, 1972). As the central sector of Sundarbans has been isolated from the western part, and no freshwater connection of this part exists, so estuarine nature of the Matla River is exclusively maintained by monsoonal runoff and tidal action. According to Raha et al. (2012), the salinity of this central part (in the year 2001—2002) ranged from 5—6, but in recent years it has gradually increased up to 35.4 as reflected in our study. Besides that, the lowest DO value was recorded during summer which can be attributed to increased water temperature during this period (Vega et al., 1998). However, rests of the other seasons have higher values of DO, showing no sign of hypoxia in the bottom water. Generally, seasonal pattern in mangrove litterfall and decomposition influences the temporal dynamics of dissolved inorganic nutrients in mangrove dominated estuaries (Lara and Dittmar, 1999) was also emulated in our study. Sundarbans estuarine system is comparatively a pristine zone and there is no record of sewage discharge or groundwater seepage, hence litterfall and excretory and/or decomposition product of aquatic organisms might be the only source of ammonia throughout the estuarine stretch. Except few upper stretch stations, rest of our study stations fall under the Sundarbans biosphere reserve and have restricted anthropogenic activities. From the viewpoint of granulometry, the area is mostly silty with a variable amount of finer and coarser sediment particles. The slow tectonic activity of the entire Bengal basin has a profound effect on the sedimentation pattern of Sundarbans delta. In contrast to the western part, islands of the central region (study site) are expanding owing to accretion (Raha et al., 2012). Due to this continuous sediment reworking process, the granulometry of our study sites has not followed any pattern. Besides this, monsoonal runoff has a substantial influence on the sediment granulometry. Furthermore, monsoonal rainfall leads to sediment agitation that scours the finer particles and therefore, coarser element like sand predominate the sediment texture (Ghosh et al., 2018). Conclusively, change in the grain size was influenced by high sedimentation as well as rainfall during the study period.

4.2. Macrobenthic assemblages

Estuarine macrobenthos are always under the influence of disharmonic environment with fluctuating salinity and variable sediment composition (Elliott and Whitfield, 2011). Generally, they have higher physiological capabilities to tolerate fluctuating saltwater incursion mediated ionic imbalance, which is common phenomenon in estuaries (Little et al., 2017). Likewise, a natural or abrupt change in salinity is among the major constraints that estuarine fauna must challenge. Moreover, these anomalities in salinity can affect their recruitment pattern and acts as the migrational cue that ultimately module their population dynamics (Wilson and Fleeger, 2013). Nonetheless, the rate and scale of salinity change is important as it can diminish the diversity of a biota (Attrill, 2002). The total macrobenthic density was highest at station 1 during summer, mostly composed of some opportunistic species from families like Capitellidae, Glyceridae, Nephtyidae, Nereidae. Organic enrichment in sediment tends to decrease the penetration of oxygen, creating an anoxic condition which can be favoured by opportunists. In estuaries, monsoonal runoff causes drastic fall in macrobenthic density which starts to replenish by the colonization of juveniles as well as the reestablishment of adult fauna in post-monsoon and continues afterwards (Gaonkar et al., 2013). Nevertheless, few stations like 1, 4, 6 and 7 showed deviation from that conventional pattern where macrobenthic density in winter starts to decline in the subsequent season. This might be attributed to the post-settlement mortality driven by salinity and bioturbation mediated sediment disturbances (Hunt and Scheibling, 1997).

Polychaetes contributed 74% of macrofaunal density and considered as a numerically dominant class which is the common for intertidal sheltered mudflats. It has been also stated that estuaries and coasts that have a high saline zone, preferably contain polychaetes more often than any other macrobenthic taxa (Alongi, 1989). Few dominating families were Capitellidae, Spionidae, Cossuridae constituted the polychaete assemblages. Being the most dominant family, capitellids receive much attention for their capacity to tolerate the environmental fluctuations as well as, their cosmopolitan distribution (Bissoli and Bernardino, 2018; Fernández-Rodríguez et al., 2019; Rao, 1980). A cycle of high density among capitellides was clearly noticed, alternately dominated by *Heteromastus similis* and *Parheteromastus tenuis* where each species can partially exclude the other in different seasons. This type of interaction can be explained by species succession model where intra-specific competition for resource availability took place between two species of the same guild and one outcompete the other and/or habitat modification by earlier species has encouraged the settlement of the next species (Harkantra and Rodrigues, 2003; Peterson, 1977; Rhoads and Germano, 1982; Thistle, 1981). According to Harkantra and Rodrigues (2003) species succession can be brought about by south western monsoon mediated biotic and abiotic changes. Similar to their study, in the present study also species succession became prominent after a downpour in the monsoon season. According to Medeiros et al. (2016), tropical estuaries those are least affected by anthropogenic activities are governed by constant modification or replacement rather than nestedness which has been clearly depicted in the present study by species succession. This type of succession along the spatiotemporal gradient can cause habitat mosaicness in the estuary (Chen et al., 2015; Thistle, 1981). Besides this, both the families like Capitellidae and Spionidae prevailed in the estuary throughout the study period. This can be explained as persistence in family level accomplished by loosing and gaining of the species (Hylleberg and Natewathana, 1984). Among molluscs, *Donax incarnatus* was the most dominant taxa as they are well adapted to tropical intertidal life (Alongi, 1989) and similarly, in our study a seasonal pattern has been portrayed through their population dynamics. During monsoon, their population drastically reduced to 70% of the density found in summer but they were gradually established by new recruiters with their bimodal reproduction in October—January and April—June (Alongi, 1989; Ansell and Trueman, 1973; Harkantra and Parulekar, 1985).

According to SIMPER analysis, upper stretch stations have always been separated from others due to the contribution of *H. similis* in both summer and monsoon. It can be explained as sediment of this area is comparatively rich in organic content due to anthropogenic input or mangrove litter which provides a better habitat for capitellides. However, in winter, the contribution of *T. stroemii* has separated station 8 from other stations. During spring, the environmental parameters made station 4 a favourable habitat for molluscs like *Acteocina estriata, Stenothyra deltae* and *Meretrix meretrix* and thus separated from rest of the stations. In Canonical Correspondence Analysis (CCA), station biplot has shown that stations in summer were influenced by DO which can be attributed to elevated temperature during summer that inversely declined DO (Vega et al., 1998). In monsoon and winter seasons, stations were mostly dominated by sand as heavy rainfall during July as well as in October causing the wash off of uppermost finer particles. Species biplot clearly depicts that environmental parameters like sand %, clay %, sediment phaeopigment, temperature, organic carbon (OC) were the most important factors in structuring the polychaete community. According to the finding of Penry and Jumars (1990), the gut of *S. scutata* has been found to be filled with muds and their preference towards finer particles is in agreement with the present study. *Micronephthys oligobranchia* is a muscular shallow-water burrower and prefer the clayey substratum; as Ronan (1977) has found one of the species from this genus that are mostly found in muddy sediment at Bodega Harbour. Carnivores like pilargids have shown an affinity with sand % (Jumars et al., 2015). Overall, a higher level of biodiversity was indicated by Shanon, Margalef's and Pielou's evenness indices. The substrate heterogeneity of this estuary plays a pivotal role in structuring this ecologically diverse community and allows coexistence of several species with different successional stages.

4.3. Biological Traits Analysis (BTA)

Approaches to BTA from transitional zones like estuaries is often challenging in terms of finding detailed and accurate trait information (Tyler et al., 2012). Biological trait analysis furnishes information on species distribution based on their biological characteristics providing a trait profile of benthic assemblages and complements their bioassessment measures (Munari, 2013). In this study, changes in functional characters are broadly concurrent with the seasonal succession of species assemblages. The most important environmental factor that regulates the body size trait is sediment grain size (Bremner et al., 2006). As depicted in our study, large animals were prevalent in station 2 when the percentage of silt was comparatively higher than any other stations in spring. The small size allows animals to become more specialized in diversified elements of the environmental mosaics (Hutchinson and MacArthur, 1959). Overall, small animals dominated the estuary which imparts an indication of a continuously perturbed environment. Not only body size, but also the rate of mobility is remarkably regulated by the granulometry of the habitat. Mobility is a crucial trait that affects food capture method and also defines the trophic relationship in the benthic community (Sigala et al., 2012). In the present study, the arrival of spring brings the changes in the sedimentology and concurrently all the motile species of the previous season were gradually replaced by discretely motile species. According to Hunt and Scheibling (1997), an increase in macrofaunal predators can hamper the recruitment of sessile organism. In connection with this hypothesis, it can be inferred that the predator effect might have played a crucial role in suppression of sessile animal population throughout the estuary. The same authors have postulated that a gradual increase in motile species over the evolutionary time scale has a strong influence in constructing modern marine benthos by gaining fitness against predation. The living habitat (LH) trait was mostly represented by burrowers who requires soft and penetrable substratum to make successful burrow habitat. As the entire study stretch is mostly silty clay, so the prevalence of burrowers like Paraonidae, Sternaspidae is justified. Burrowers can act as sediment reworker through the suspension of fine particle into overlying water. By acting as a molecular sieve, it allows the increase of the oxygen content at the sediment-water interface (Aller, 1983; Bremner et al., 2006; Constable, 1999). Moreover, burrows provide a microenvironment that leads to nutrient cycling and increased organic matter decomposition. According to RLQ analysis, the prevalence of burrowers is generally correlated with the sand percentage in the sediment. Presence of various feeding type trait indicates diverse food sources available in the estuary and it may also accentuate more diverse pathway of energy recycling (Sigala et al., 2012). Deposit feeders are mostly affected by sediment particle size whereas, suspension feeders are mostly regulated by hydrodynamics and physical processes in the water column and they generally do not prefer to live in areas where fine sediments can disrupt their feeding apparatus (Constable, 1999). In the present study, a gradual appearance of suspension feeders was observed in spring contributed by some spionids like *Paraprionospio pinnata* and *Spio bengalensis* as they have the ability to switch their feeding mode from deposit to suspension feeding in presence of adequate horizontal flux of sediment particles (Jumars et al., 2015). It may also be noticed in bivalves depending on predator pressure and other local environmental factors. The behaviour and the rate of suspension feeders are also regulated by the particulate organic matter content whereas, deposit feeders increase when particles are deposited in the sediment or suspended in the water column (Bock and Miller, 1996; Peterson and Skilleter, 1994). Suspension feeder bivalves are the crucial driver in benthic-pelagic coupling. They capture suspended organic matter and phytoplankton, thus contribute significantly in whole ecosystem productivity (Newell, 2004; Tillin et al., 2006; Rosenberg 2001). Nevertheless, the dominance of deposit feeders was due to their broader range of food materials acceptance (Sigala et al., 2012). Commonly, diet type is highly regulated by grain size of the sediment. As described by Wu and Shin (1997), particle size and organic content are the major drivers that affect colonization of soft-bottom benthos. In carnivory trait category, species like *Micronephthys oligobranchia, Dendronereis aestuarina, Kuwaita heteropoda* contributed the most. Oug et al. (2012) have documented that carnivory is related to coarser and low porosity sediment. The prevalence of carnivores is also an indication of improved sediment quality that allows species with various feeding modes to flourish concurrently (Hu et al., 2019).

In the future climate change scenario, the seasonal dynamics of Sundarbans is going to alter (IPCC, 2013). Furthermore, it has also been conjectured that summers are projected to be dried and warmer with reduced freshwater flow-mediated salinity incursion and Sundarbans is not an exception. This might also be associated with an unusual shift in monsoonal activity with late onset and late withdrawal (IMD, 2010; Little et al., 2017) which would have profound repercussion on benthic biota. According to a time series analysis, the central part of Indian Sundarbans has been predicted to be under the threat of hypersalinisation with an increment of around 13.05 psu/decade, howbeit both western and eastern part have shown a decreasing trend of salinisation (Trivedi et al., 2016). Furthermore, studies have also revealed a gradual disappearance of freshwater preferring mangrove species as well as a compositional shift in phytoplankton community due to rapid salinity incursion in the central sector (Chaudhuri and Choudhury, 1994; Raha et al., 2012). It would be difficult to ascertain the changes in macrobenthic community in comparison with previous studies due to the unavailability of data from this sector of Sundarbans.

Seasonal succession in any community can be better apprehended by tracking trait modalities using BTA. Being dynamic, the estuarine macrobenthos is always facing a continuous seasonal perturbation, where BTA is a new approach to unravel the functionality of every species in a community. However, due to the lack of precise information on traits, sometimes BTA may fail to portray the species level changes on the trait analysis. As depicted in the present study, interspecific replacement between two of the spionid species due to seasonal fluxes cannot be properly pointed out through BTA as these two congener species share almost similar trait modalities. Some of these species have similar traits which may lead to functional redundancy in a community and can be substituted with very little or no effect on ecosystem processes (Rosenfeld, 2002). In Piló 2016, authors have stated that functional redundancy is very much relevant to naturally disturbed estuaries where long term intrinsic adaptations of local species are evident. Furthermore, it is hard to determine the specific environmental factors that are regulating trait categories in a complex estuarine ecosystem like Sundarbans. Hence, the underlined mechanism in gaining evolutionary fitness against climate change mediated habitat modification in the Sundarbans ecosystem would be an interesting area to explore for future researchers.

5. Conclusion

The present study has been the first attempt (1) to document 95 macrobenthic taxa with comprehensive information of their community pattern, distribution and spatiotemporal variation along the Matla River of Sundarbans over four distinct seasons of 2017—2018, (2) to document multiple biological traits of the macrobenthic community for better understanding of their seasonal succession pattern. A prominent succession pattern has been noticed in species of several families like Capitellidae, Spionidae as well as in trait composition like type of a mobility, body size, living habitat and feeding strategy. Trait categories like discretely motile animals gradually replaced by motile animals in monsoon and post-monsoon seasons. The gradual increase in suspension feeder was contributed by certain species like *Paraprionospio pinnata* and *Spio bengalensis* that have the adaptive ability to switch their feeding mode. It has also been explained how environmental perturbations act as a crucial driver for changes in the macrobenthic community structure. Moreover, the changing trend of annual temperature, rainfall pattern and frequencies of tropical cyclones have continually actied as a stressor for the biota which affects the species composition and regular succession pattern as mirrored in our study. Hence, long term monitoring with additional trait categories is needed to understand the benthic ecosystem functioning more precisely and their changes due to perturbed environmental factors from the world's largest deltaic ecosystem.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at https://doi.org/10.1016/j.oceano.2020.10.002.

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