

Distribution, Diversity and Abundance of Macrobenthic Fauna Along the South-Eastern Coast of Bangladesh: Seasonal Patterns and Environmental Drivers

Omite Ashraf

Shahjalal University of Science and Technology

Md. Sharif Hossain

Shahjalal University of Science and Technology

Md. Bayzid

Shahjalal University of Science and Technology

Mohammad Nahidul Islam Sakib

Shahjalal University of Science and Technology

Saidul Afnan

University of Chittagong

Mohammad Forkanul Hamid

University of Chittagong

Abu Bokkar Siddique

Shahjalal University of Science and Technology

Faisal Sobhan

Shahjalal University of Science and Technology

Subrata Sarker

Shahjalal University of Science and Technology

Md. Alamgir Kabir

Shahjalal University of Science and Technology

Md. Azizul Fazal

mafazal-ocg@sust.edu

Shahjalal University of Science and Technology

Research Article

Keywords: Benthic invertebrates, Polychaeta, Coastal habitats, Bay of Bengal, Bioindicators

Posted Date: September 29th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10678516/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.
[Read Full License](#)

Additional Declarations: No competing interests reported.

Distribution, Diversity and Abundance of Macrobenthic Fauna Along the South-Eastern Coast of Bangladesh: Seasonal Patterns and Environmental Drivers

Omite Ashraf¹, Md. Sharif Hossain¹, Md. Bayzid¹, Mohammad Nahidul Islam Sakib¹, Saidul Afnan², Mohammad Forkanul Hamid³, Abu Bokkar Siddique¹, Faisal Sobhan¹, Subrata Sarker¹, Md. Alamgir Kabir⁴, Md. Azizul Fazal¹

¹Department of Oceanography, Shahjalal University of Science and Technology, Sylhet-3114, Bangladesh

²Institute of Marine Sciences, University of Chittagong, Chittagong-4331, Bangladesh

³Department of Fisheries, University of Chittagong, Chittagong-4331, Bangladesh

⁴Department of Mathematics, Shahjalal University of Science and Technology, Sylhet-3114, Bangladesh

*Corresponding Author

Name: Md. Azizul Fazal

Email: mafazal-ocg@sust.edu

ORCID: 0000-0001-7861-1002

Email of Co-Author:

Omite Ashraf: 2024156001@student.sust.edu

Md. Sharif Hossain: sharifsust20@gmail.com

Md. Bayzid: bayzid.ocean@gmail.com

Mohammad Nahidul Islam Sakib: shakib40142017@gmail.com

Saidul Afnan: afnansaidulma@gmail.com

Mohammad Forkanul Hamid: fhamid.imsf.cu@gmail.com

Abu Bokkar Siddique: absiddique-ocg@sust.edu

Faisal Sobhan: f.sobhan-ocg@sust.edu

Subrata Sarker: subratasrk-ocg@sust.edu

Md. Alamgir Kabir: akabir-mat@sust.edu

Submission Date: 12-08-2026

Abstract

The macrobenthic community is a key driver of ecosystem functioning, yet a research gap persists on how habitat heterogeneity, seasonality, and environmental drivers influence their structure. This study investigated the seasonal distribution, diversity, and abundance of the macrobenthic community across ecologically distinct habitats (mudflat, saltmarsh, and mangrove) at three sites over three seasons along the south-eastern coast of Bangladesh. Examining 1592 individuals throughout 81 sediment samples, 64 macrobenthic taxa belonging to 11 classes and 38 families were identified. Polychaetes were the dominant group (62.12%), followed by Gastropoda (8.79%) and Malacostraca (5.90%). The highest abundance (4027.78 ind/m²) was recorded at the Sonadia mudflat during post-monsoon, whereas the lowest (740.7 ind/m²) was recorded at the Bakkhali mangrove during the pre-monsoon. Shannon diversity ($H' = 3.03$) and Margalef richness ($D = 6.41$) peaked at Sonadia during post-monsoon and were lowest at Bakkhali during monsoon. nMDS ordination, PERMANOVA ($R^2 = 0.49$, $P = 0.001$) showcased distinct seasonal and spatial structuring of macrobenthic assemblages. SIMPER analysis revealed *Glycera sheikhmujibi* and *Capitella capitata oculata* as the key taxa driving the inter-seasonal variability. Spearman's rank correlation and canonical correspondence analysis (CCA) explained 68.2% of the variance and revealed dissolved oxygen, water salinity, organic carbon, and silt content as the environmental drivers shaping the macrobenthic diversity and distribution. These findings contribute to the global understanding of how environmental gradients influence macrobenthic communities in a multi-habitat, seasonally dynamic coastal system and provide baseline data for biomonitoring and conservation management along the south-eastern coast of Bangladesh.

Keywords: Benthic invertebrates, Coastal habitats, Bay of Bengal, Seasonal variation

Introduction

Macrobenthos, a bottom-dwelling component of benthic ecosystems that facilitates ecosystem functioning by promoting mineralization, aeration, and bioturbation (Belley et al., 2016). Larger than 1 mm in size, macrobenthos are primarily composed of Mollusca, Polychaeta, Echinodermata, and Crustacea (Chowdhury et al., 2024). Macrobenthos in marine sediments regulate sediment-water interactions, nutrient cycling, secondary production, and contaminant dispersion, thereby maintaining overall ecosystem stability (Washburn et al., 2017). As a major dietary preference for juvenile and adult fish, macrobenthic communities drive nutrient and energy transfer across food webs, ensuring ecosystem recovery and restoration (Sheaves et al., 2017). The distribution of macrobenthic organisms is largely governed by core physical and sedimentary features, particularly water depth, sediment composition, current velocity, and organic material concentration in the habitat (Hanz et al., 2019; Saad & Wade, 2017). Additional environmental variables, including temperature, salinity, pH, dissolved oxygen (DO), pressure, silt accumulation, and sedimentation patterns, drive macrobenthic distribution and community response (Jayachandran et al., 2019; Mely et al., 2023). Their sensitivity to environmental dynamics and ecosystem changes has established macrobenthic bio-indicators as a straightforward and effective approach for bio-monitoring (Tampo et al., 2021). Their comparatively long lifespans, sessile nature, and bioaccumulation of pollutants in tissues create a historical record of habitat quality, while their abundance patterns help evaluate the

degree and type of environmental stress (Adesakin et al., 2023; Nayak et al., 2022). As a subtropical country, Bangladesh possesses an extensive coastline of about 710 kilometers that supports an exceptionally diverse ecosystem, and the region experiences pronounced monsoonal seasonality, leading to strong seasonal variability in rainfall, air temperature, and moisture (Sarker et al., 2018). The southeastern coastal zone, shaped by complex estuarine systems (Karnaphuly, Bakkhali, Matamuhuri, and the Naf River) and tropical climate, comprises highly productive habitats like mangrove, saltmarsh, seagrass, coral reef, and non-vegetated mudflat (Miah et al., 2023). Being exposed to natural pressures (sea level rise, saltwater intrusion, erosion, tidal surge), coupled with anthropogenic stressors including shipping operations, fish harbors, aquaculture expansion, dredging and shoreline infrastructures, the south-eastern coastal zone has experienced ecological shifts and demands continuous monitoring (Sultana et al., 2023). Several studies have employed macrobenthos to assess environmental conditions and investigate their responses to variations in physicochemical factors and habitat conditions worldwide (Izegaegbe et al., 2020; Mohamamad & Jalal, 2018; Nephin et al., 2014; Van Colen et al., 2014). In Bangladesh, research on macrobenthos communities has been conducted across several coastal and estuarine habitats (Islam et al., 2025; Khatun et al., 2023; Mely et al., 2023), yet these studies remain relatively few and largely fragmented. Specifically, along the south-eastern coast, existing studies rarely compare multiple seasons and do not compare macrobenthic communities across ecologically distinct substrates such as mudflats, saltmarshes, and mangroves within the same geographic setting. The coarse systematic identification of live specimens to the lowest taxonomic level often limits ecological interpretability. Published literature also offers limited analysis of macrobenthic associations with environmental parameters, leaving important aspects of community dynamics unexplored (Barua et al., 2019; Islam et al., 2025). This situation underscores the need for site-to-site and habitat-to-habitat evaluations along the southeastern coast. The present study addresses this knowledge gap with three specific objectives: (1) to identify macrobenthic taxa to the lowest taxonomic resolution across ecologically distinct habitats; (2) to assess spatial and seasonal patterns in macrobenthic abundance, species richness, diversity, and community structure; and (3) to analyze macrobenthic community responses to key abiotic and biotic drivers through multivariate approaches.

Materials and methods

2.1 Study area and sample collection

The present study was conducted across three sites in the south-eastern coastal zone of Bangladesh, which possesses three distinct coastal habitats (mudflat, saltmarsh, and mangrove) (**Fig. 1**). Sampling sites were located at Bakkhali River (21°28'39.6"N, 91°58'17.6"E), Nuniarchara (21°27'05.5" N, 91°58'07.5" E) and Sonadia Island (21°30'19.5" N, 91°53'45.3" E). Sampling followed a complete cross-design, covering each of the three habitats at every three sites in each of the three seasons. In this study, seasonal field samples were carried out at three sites on three occasions: pre-monsoon, monsoon, and post-monsoon, from May 2023 to June 2024. Seasonally, three replicate sediment samples were collected at low tide from each of the three habitats, yielding a total of 9 samples per site. Therefore, a total of 81 sediment samples were collected during this study. Environmental variables, including water temperature, salinity, pH, Dissolved Oxygen (DO), and turbidity, were recorded during sediment

sampling. Sediment samples were collected using a hand-held mud corer with an opening of 0.01m² and a penetration depth of 15 cm. Upon collection, 100g of sediment from each replicate was retained for analysis of sediment parameters (organic carbon, soil salinity, soil pH, sand, silt, and clay percentages). The remaining sediment samples were mixed with water and sieved through a 19.5-cm-diameter steel sieve with a 0.5-mm mesh to isolate benthic macrofauna (Jayachandran et al., 2019). The retained live specimens were immediately separated into Eppendorf and Falcon tubes to avoid the body damage that typically occurs when a specimen is kept in a sample jar with other specimens.



Fig. 1 Geographical locations of the sampling stations surveyed for macrobenthic study along the south-eastern coast of Bangladesh.

Following separation, the live specimens were transferred to labeled glass dishes with a black background and subjected to live imaging and identification under a microscope. Taxonomic identification was carried out using a trinocular stereomicroscope (Eakins 7X-50X; OMAX A35180U3) coupled with a calibrated ocular micrometer and a light microscope (OPTIKA B-192 Binocular microscope, 1000X). Taxonomic identification was validated against the standard taxonomic database, WoRMS (<https://www.marinespecies.org>). After completion of the

imagery and identification process, the specimens were preserved in labeled Falcon tubes using 7% formalin prepared with habitat water (Joydas & Damodaran, 2009).

2.2 Environmental variable analysis

Sediment parameters, including organic carbon (OC), soil salinity, soil pH, and grain size (sand, silt, and clay), were recorded. In addition, five water parameters (i.e., temperature, salinity, pH, Dissolved Oxygen (DO), and turbidity) were also analyzed. Sediment texture was determined following the hydrometer method (Bouyoucos, 1962). Soil organic carbon (OC; %) was determined following the modified Walkley–Black wet oxidation method (Black, 1965). Soil salinity was measured in a 1:5 soil-to-water suspension using a portable conductivity meter (Model HI99301, Hanna Instruments). Soil pH was measured by preparing a 1:2.5 sediment-water suspension using a digital pH meter (Model: Hanna HI98128), as suggested by Jackson (1962). Surface water temperature (°C) and conductivity (mS/cm) were recorded with a mini CTD. Salinity (ppt) was calculated from conductivity values using the Fofonoff and Millard (1983) conversion equation. The water pH and DO concentration (ppm) were assessed using a calibrated multiparameter probe (Lutron WA-2015, Taiwan). Water turbidity was recorded using a turbidity meter (Lutron TU-2016, Taiwan).

2.3 Data analysis

Macrofaunal abundance was measured and expressed as individuals per square meter (ind./m²) prior to statistical analyses. The mean abundance of each species was calculated by dividing the total number of individuals recorded at each station by the total number of sampling stations. A suite of univariate ecological indices was applied. These included total macrobenthic abundance (N), species richness (S), the Shannon–Wiener diversity index (H'), Pielou's evenness index (J'), Margalef's richness index (D), and Simpson's diversity index (λ). Data normality was tested using the Shapiro-Wilk test and homogeneity of variance using Levene's test. In some cases, some variables accepted normality, while others rejected it. For normality assumptions, one-way ANOVA was employed, followed by Tukey's HSD. In other cases, the non-parametric Kruskal–Wallis test was applied, followed by Dunn's post hoc test. Spearman's rank correlation (ρ) was used to assess the strength and direction of relationships between environmental parameters and macrobenthic community attributes (e.g., abundance and diversity). A Bray–Curtis similarity matrix was constructed from square-root-transformed macrobenthic abundance data, and a non-metric multidimensional scaling (nMDS) ordination plot was generated to visualize patterns and differences in macrobenthic community structure. Permutational multivariate analysis of variance (PERMANOVA) was performed at both the global (999 permutations) and pairwise (9999 permutations) levels, along with similarity percentage analysis (SIMPER; 999 permutations) to identify species that contribute to variability at different scales. Additionally, Canonical Correspondence Analysis (CCA) was applied as a unimodal ordination method to examine relationships between macrobenthic community composition and environmental variables. The CCA incorporated macrobenthic density data and selected environmental variables, including water temperature, water salinity, water pH, DO, turbidity, and sediment characteristics (OC, pH, salinity, and grain size). Multicollinearity was assessed using variance inflation factors (VIFs), and variables with VIF > 10 were removed. All statistical analyses were performed using R (version 4.6.0) and Python (version 3.12).

Results

3.1 Composition and distribution of macrobenthic taxa across habitats

A total of 1592 individuals was recorded, corresponding to a summed mean abundance of 36851.85 ind/m², representing a diverse assemblage of 64 macrobenthic taxa across 11 classes and 38 families (Table 1).

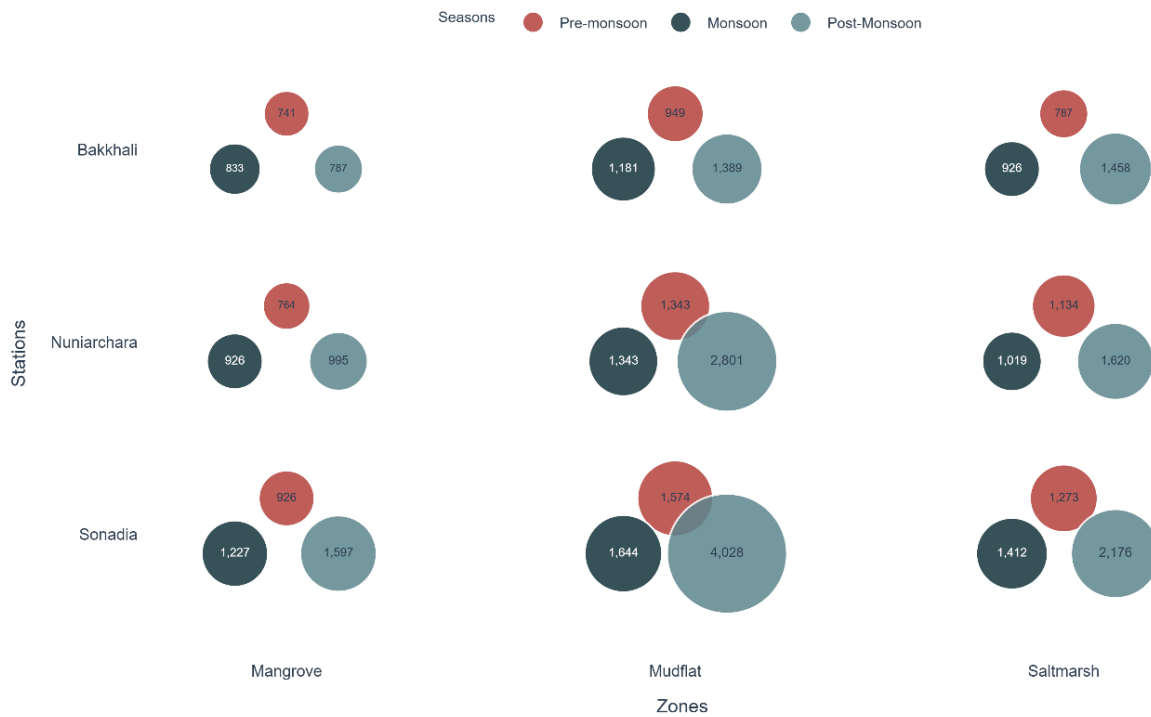


Fig. 2 Mean macrobenthic abundance of macrobenthos (ind. /m², n = 3 replicate cores) in different stations, seasons, and habitats along the south-eastern coast of Bangladesh

Polychaeta was the dominant group (62.12% of total density), comprising 25 families, followed by Gastropoda (8.79%), Malacostraca (5.90%), Clitellata (4.96%), and Palaeonemertea (4.33%). Other contributing groups included Holothuriidae (3.39%), Hexacorallia (2.95%), Demospongiae (2.26%), Sipunculidae (1.88%), Hoplonemertea (1.76%), and Pilidiophora (1.63%).

Table 1 Taxonomic classification of macrobenthos collected from the South-eastern coast of Bangladesh

Class Name	Family Name	Taxa code & Species Name	%	Class Name	Family Name	Taxa code & Species Name	%
Polychaeta	Nereididae	1. <i>Neanthes glandicincta</i>	3.52	Polychaeta	Phyllodocidae	33. <i>Mysta ornata</i>	0.57
		2. <i>Platynereis calodonta</i>	2.64		Spionidae	34. <i>Prionospio krusadensis</i>	0.38
		3. <i>Neanthes indica</i>	3.77		Terebellidae	35. <i>Eupolymnia nebulosa</i>	1.07
		4. <i>Namalycastis indica</i>	1.7		Opheliidae	36. <i>Ophelina grandis</i>	0.75
		5. <i>Neanthes chilkaensis</i>	1.63		Maldanidae	37. <i>Axiothella australis</i>	0.5
		6. <i>Neanthes chingrighattensis</i>	2.51		Pectinariidae	38. <i>Pectinaria</i> sp.	0.69
		7. <i>Namalycastis fauveli</i>	1.44		Orbiniidae	39. <i>Scoloplos marsupialis</i>	1.01

	8. <i>Nereis coutieri</i>	1.95			40. <i>Leitoscoloplos papillatus</i>	0.63
	9. <i>Nereis persica</i>	1.82			41. <i>Scoloplos armiger</i>	0.57
	10. <i>Notomastus aberans</i>	2.01		Serpulidae	42. <i>Hydroides albiceps</i>	0.5
	11. <i>Notomastus latericeus</i>	1.26		Sabellidae	43. <i>Sabella fusca</i>	0.25
Capitellidae	12. <i>Capitella capitata</i>	1.19		Dorvilleidae	44. <i>Protodorvillea</i> sp.	0.69
	13. <i>Notomastus fauvelii</i>	1.26		Sternaspidae	45. <i>Sternaspis</i> sp.	1.07
	14. <i>Capitella ambonensis</i>	1.44		Sigalionidae	46. <i>Pisionidens indica</i>	0.63
	15. <i>Capitella capitata oculata</i>	2.07		Syllidae	47. <i>Trypanedenta gigantea</i>	0.57
Paraonidae	16. <i>Aricidea (Acmira) simplex</i>	0.94		Lumbrineridae	48. <i>Lumbrineris simplex</i>	0.44
Hesionidae	17. <i>Oxydromus angustifrons</i>	1.7		Onuphidae	49. <i>Diopatra neapolitana</i>	1.44
	18. <i>Nephtys polybranchia</i>	1.13		Oeonidae	50. <i>Drilonereis</i> sp.	0.82
	19. <i>Aglaophamus dibranchis</i>	1.19	Clitellata	Naididae	51. <i>Monopylephorus parvus</i>	2.64
Nephtyidae	20. <i>Nephtys gravieri</i>	1.88			52. <i>Tubifex tubifex</i>	2.32
	21. <i>Nephtys bangladeshi</i>	0.88	Gastropoda	Turritellidae	53. <i>Turritella attenuata</i>	4.96
	22. <i>Micronephtys oligobranchia</i>	1.7		Potamididae	54. <i>Pirenella cingulata</i>	3.83
	23. <i>Glycera sheikhmujibi</i>	1.57	Malacostraca	Corophiidae	55. <i>Americorophium triaenonyx</i>	2.83
Glyceridae	24. <i>Glycera tessellata</i>	1.07		Photidae	56. <i>Gammaropsis esturinus</i>	3.08
	25. <i>Glycera alba</i>	1.19	Palaeonemertea	Cephalotrichidae	57. <i>Cephalothrix</i> sp.	2.01
Eunicidae	26. <i>Lysidice collaris</i>	0.75		Tubulanidae	58. <i>Tubulanus</i> sp.	2.32
Goniadidae	27. <i>Glycinde kameruniana</i>	0.82	Hexacorallia	Actiniidae	59. <i>Actiniaria</i> sp.	2.95
Arenicolidae	28. <i>Arenicola cristata</i>	0.75	Holothuriidae	Holothuriidae	60. <i>Holothuria</i> sp.	3.39
	29. <i>Phyllodoce</i> sp.	1.13	Demospongiae	Tetillidae	61. <i>Tetilla dactyloidea</i>	2.26
Phyllodocidae	30. <i>Eumida sanguinea</i>	1.13	Sipunculidae	Golfingiidae	62. <i>Golfingia</i> sp.	1.88
	31. <i>Nereiphylla castanea</i>	0.69	Hoploneurtea	Amphiporidae	63. <i>Amphiporus</i> sp.	1.76
	32. <i>Eumida albopicta</i>	0.82	Pilidiophora	Valenciinidae	64. <i>Baseodiscus hemprichii</i>	1.63

169

170 The assemblage comprised 50 polychaete taxa and two taxa each of Clitellata, Gastropoda, Malacostraca, and

171 Palaeonemertea, while Hexacorallia, Holothuriidae, Demospongiae, Hoplonemertea, Pilidiophora, and Sipunculidae

172 were each represented by a single species. Total macrobenthic abundance varied markedly among stations, seasons,

173 and habitats (**Fig. 2**). The highest abundance (4027.78 ind./m²) was recorded at Sonadia during the post-monsoon

174 season in the mudflat habitat, whereas the lowest abundance (740.74 ind/m²) was recorded at Bakkhali during the pre-

175 monsoon season in the mangrove habitat. Comprising 50 species of 25 families, polychaeta constituted 78.12% of the

176 total species number and 62.12% of the total macrobenthic abundance. The dominant polychaeta families included

177 Nereididae (9 sp.), Capitellidae (6 sp.), Nephtyidae (5 sp.), Phyllodocidae (5 sp.), Glyceridae (3 sp.), and Orbiniidae

178 (3 sp.). The most abundant polychaeta species were *Neanthes indica* (3.77%), *Neanthes glandicincta* (3.52%),

179 *Platynereis calodonta* (2.64%), and *Neanthes chingrighattensis* (2.51%). The major Gastropod representatives were

180 *Turritella attenuata* (4.96%) and *Pirenella cingulata* (3.83%). Malacostracans were represented by the *Gammaropsis*

181 *esturinus* (3.08%) and *Americorophium triaenonyx* (2.83%), whereas Clitellata were represented by *Monopylephorus*

182 *parvus* (2.64%) and *Tubifex tubifex* (2.32%). Hexacorallia was represented by *Actiniaria* sp., while Holothurians by

183 the *Holothuria* sp. Demospongiae were represented by *Tetilla dactyloidea*, Hoplonemerteans by *Amphiporus* sp.,

184 Sipunculidae by *Golfingia* sp., and Pilidiophora by *Baseodiscus hemprichii*.

3.2 Seasonal variation in macrobenthic abundance, diversity, and community structure

In this study, summed mean abundances of 9,490.74, 10,509.26, and 16,851.85 ind./m² were recorded during the pre-monsoon, monsoon, and post-monsoon seasons, respectively (corresponding to 410, 454, and 728 individuals). The macrobenthic community exhibited significant seasonal, spatial, and habitat variation ($p < 0.05$). The highest mean abundance of macrobenthos was observed during the post-monsoon season (1872.42 ± 1005.70 ind./m²), followed by the monsoon (1167.69 ± 267.23 ind./m²), and the lowest in the pre-monsoon season (1054.52 ± 293.51 ind./m²). The number of species was substantially higher during the post-monsoon (64 species) than the pre-monsoon (41 species) and monsoon (31 species). Across the seasons, Sonadia showed the highest mean abundance (1761.86 ± 917.09 ind./m²) with a range of 1257.72 ± 324.35 to 2600.3 ± 1269.64 ind./m², while Bakkhali showed the lowest mean abundance (1005.66 ± 270.97 ind./m²) with a range of 825.62 ± 109.39 to 1211.42 ± 367.16 ind./m². Among the macrobenthic classes, Polychaeta were dominant at all seasons and stations (**Table 2**). Considering the secondary taxa, Palaeonemertea (8.54%) and Hexacorallia (6.10%) were the second and third most abundant groups during the pre-monsoon. Clitellata (7.93%) and Palaeonemertea (5.51%) held the ranks during the monsoon season, whereas Gastropoda (14.42%) and Malacostraca (10.44%) were the abundant groups in the post-monsoon. Similar patterns of spatial shift in secondary taxa were observed: Gastropoda were dominant in Sonadia, contributing 16.06% of total density, while Malacostraca (8.72%) and Holothuriidae (6.39%) were dominant in Nuniarchara and Bakkhali, respectively. Sonadia showed the highest species number (64) with reported numerical dominance by *Turritella attenuata*, *Pirenella cingulata*, and *Diopatra neapolitana*, whereas Bakkhali showed the lowest species number (53) with reported numerical dominance by *Holothuria* sp. and *Neanthes glandicineta*. Nuniarchara reported 58 species occurrences and substantial numerical dominance by *Americorophium triaenonyx*, *Actiniaria* sp., and *Cephalothrix* sp. The taxa contributing most to the observed inter-seasonal variability are presented in **Table 3**. The Mudflat habitat recorded the highest abundance (1805.56 ± 983.32 ind./m²), followed by the Saltmarsh (1311.73 ± 420.83 ind./m²), and lastly the Mangrove habitat (977.37 ± 276.27 ind./m²). This pattern revealed strong variability ($p=0.01183$) and a spatial gradient in macrobenthic abundance, with a clear decline from non-vegetated mudflats to more vegetated mangrove habitats. The number of macrobenthic species was highest in the Mudflat and Saltmarsh habitats, each supporting 61 of the 64 recorded species. The numerically dominant species inhabiting the mudflat habitat include *Turritella attenuata*, *Diopatra neapolitana*, *Americorophium triaenonyx*, and *Neanthes glandicineta*. Numerically dominant species of saltmarsh habitat in this study were *Actiniaria* sp., *Gammaropsis esturinus*, *Oxydromus angustifrons*, and *Neanthes glandicineta*. Mangrove habitat exhibited a relatively lower species occurrence (54 species) and reported *Platynereis calodonta*, *Neanthes indica*, and *Pirenella cingulata* as the numerically dominant species. Spatio-temporal variation of diversity indices is presented in **Fig. 3**. Shannon diversity showed a significant variability among habitats ($p=0.0154$), while Margalef's richness showed a significant variability both by habitat ($p=0.0301$) and seasons ($p=0.0116$). Higher mean diversity (3.03) was recorded in Sonadia mudflat during post-monsoon, compared to the minimum (2.25) in Bakkhali mangrove during monsoon. Mean Margalef richness ranged from 3.06 in the Bakkhali mangrove during the monsoon to 6.41 in the Sonadia mudflat during the post-monsoon season. Pielou's evenness index showed a significant seasonal variation ($p=0.0228$), with a maximum (0.96) during the monsoon and a minimum (0.85) during the post-monsoon, both in Sonadia. The mean Simpson diversity index

showed a peak (0.93) at Sonadia mudflat during the monsoon and a minimum (0.89) at Bakkhali mangrove during the pre-monsoon, driven by significant habitat variability ($p = 0.0070$).

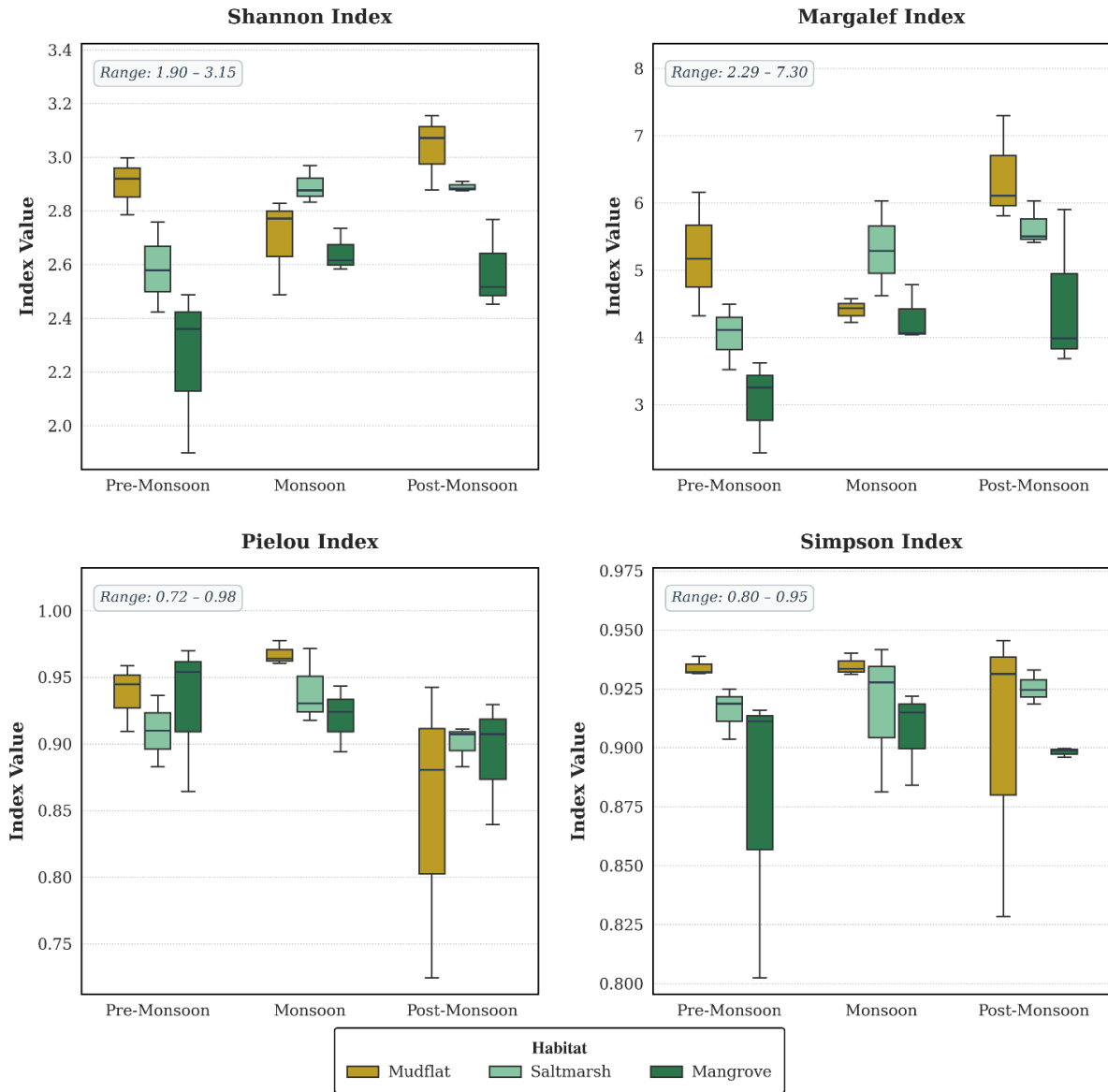


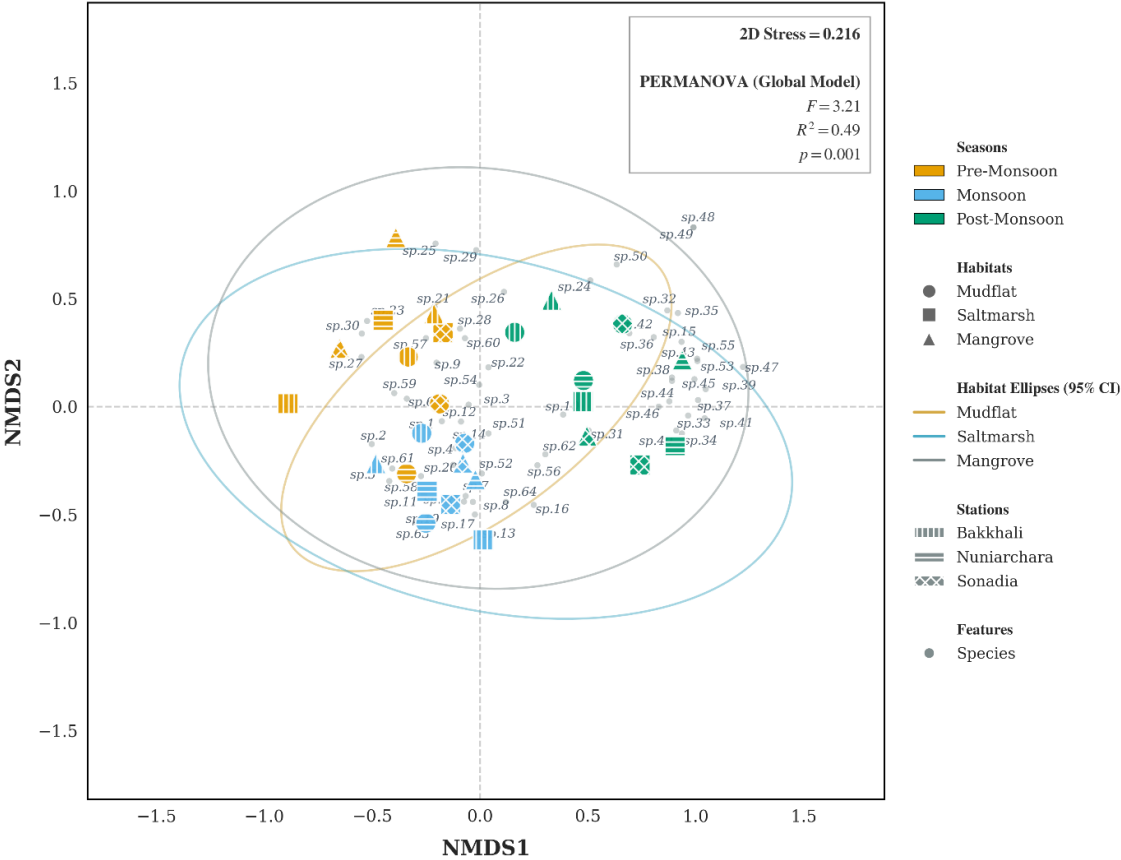
Fig. 3 Seasonal and spatial variation of diversity indices at different habitats along the south-eastern coast of Bangladesh. (Range: replicate level)

Table 2 Mean macrobenthic abundance (Ind m^{-2}) and percent composition of Taxonomic groups across seasons and stations along the south-eastern coast of Bangladesh.

Class	Pre-monsoon		Monsoon		Post-monsoon		Bakkhali		Nuniarchara		Sonadia	
	Ind m^{-2}	%	Ind m^{-2}	(%)	Ind m^{-2}	%	Ind m^{-2}	(%)	Ind m^{-2}	(%)	Ind m^{-2}	%
Polychaeta	6226.85	65.61	6064.82	57.71	10601.85	62.91	5995.37	66.24	7523.15	62.98	9375.00	59.12
Gastropoda	532.41	5.61	277.78	2.64	2430.56	14.42	555.56	6.14	138.89	1.16	2546.30	16.06

Malacostraca	23.15	0.24	393.52	3.74	1759.26	10.44	439.81	4.86	1041.67	8.72	694.44	4.38
Clitellata	439.81	4.63	833.33	7.93	555.56	3.30	347.22	3.84	740.74	6.20	740.74	4.67
Palaeonemertea	810.19	8.54	578.70	5.51	208.33	1.24	416.67	4.60	717.59	6.01	462.96	2.92
Holothuriidae	324.07	3.41	300.93	2.86	625.00	3.71	578.70	6.39	162.04	1.36	509.26	3.21
Hexacorallia	578.70	6.10	462.96	4.41	46.30	0.27	138.89	1.53	509.26	4.26	439.81	2.77
Demospongiae	300.93	3.17	509.26	4.85	23.15	0.14	416.67	4.60	92.59	0.78	324.07	2.04
Sipunculidae	115.74	1.22	254.63	2.42	324.07	1.92	46.30	0.51	393.52	3.29	254.63	1.61
Hoplonemertea	92.59	0.98	532.41	5.07	23.15	0.14	69.44	0.77	370.37	3.10	208.33	1.31
Pilidiophora	46.30	0.49	300.93	2.86	254.63	1.51	46.30	0.51	254.63	2.13	300.93	1.90
Summed abundance	9490.74	100.00	10509.26	100.00	16851.85	100.00	9050.93	100.00	11944.44	100.00	15856.47	100.00

230



231

232

233

234

235

236

237

238

Fig. 4 Non-metric multidimensional scaling (NMDS) ordination of macrobenthic community using Bray-Curtis similarities based on square-root-transformed data (Taxa code and Species name in Table 1). 2-D stress = 0.216

Providing a stress value of 0.216, the non-metric multidimensional scaling (NMDS) ordination plot revealed clear season-driven partitioning of macrobenthic structure (**Fig. 4**). However, as a 2D stress value above 0.20 suggests a potentially suspect ordination, this plot should be interpreted with caution (Clarke, 1993).

Table 3 Results of SIMPER analysis for macrobenthic community assemblages along the South-eastern coast of Bangladesh.

Comparison	Species Name	Average Contribution (%)	Cumulative (%)	p-value
Pre-monsoon Vs Monsoon	<i>Glycera sheikhmujibi</i>	3.99	3.99	0.001
	<i>Amphiporus</i> sp.	3.26	7.25	0.001
	<i>Eumida sanguinea</i>	3.2	10.45	0.001
	<i>Gammaropsis esturinus</i>	3.12	13.57	0.007
	<i>Tubulanus</i> sp.	3.09	16.66	0.008
Pre-monsoon Vs Post-monsoon	<i>Capitella capitata oculata</i>	3.14	3.14	0.001
	<i>Glycera sheikhmujibi</i>	2.79	5.93	0.003
	<i>Gammaropsis esturinus</i>	2.59	8.51	0.017
	<i>Pirenella cingulata</i>	2.36	10.87	0.374
	<i>Sternaspis</i> sp.	2.36	13.23	0.001
Monsoon Vs Post-monsoon	<i>Capitella capitata oculata</i>	3.1	3.1	0.001
	<i>Platynereis calodonta</i>	2.86	5.95	0.007
	<i>Amphiporus</i> sp.	2.53	8.48	0.007
	<i>Sternaspis</i> sp.	2.32	10.81	0.001
	<i>Eupolymnia nebulosa</i>	2.3	13.11	0.001

Values in bold indicate statistical significance

PERMANOVA confirmed that the macrobenthic community structure exhibits significant multivariate differences across the combined factor levels of season, station, and habitat, with the full model explaining 49.1% of multivariate variation ($F = 3.21$, $R^2 = 0.491$, $p = 0.001$; **Fig. 4**). The Bonferroni-corrected pairwise comparison in PERMANOVA also revealed significant differences ($p = 0.0001$) across all seasonal pairs: monsoon vs. post-monsoon ($R^2 = 0.326$), pre-monsoon vs. post-monsoon ($R^2 = 0.278$), and pre-monsoon vs. monsoon ($R^2 = 0.236$). Among the study sites, Sonadia and Bakkhali exhibited significant variability ($p = 0.0037$), and among habitats, Mudflat and mangrove exhibited significant variability ($p = 0.0118$). SIMPER analysis identified key taxa driving seasonal dissimilarities among macrobenthic assemblages (Table 3). The five highest-contributing taxa across the seasonal comparison accounted for only 13.1–16.7% of the variability in community composition. SIMPER analysis revealed that *Tubulanus* sp. was the contributing taxa to the site-specific community variability between Sonadia and Bakkhali, whereas *Tubulanus* sp., *Nereis persica*, *Amphiporus* sp., and *Nephtys gravieri* were the contributing taxa to the community variability between mudflat and mangrove habitats.

3.3 Association between macrobenthic community structure and environmental variables

The overall mean values for water temperature, salinity, pH, dissolved oxygen (DO), and turbidity were recorded as 28.70 ± 4.25 °C, 16.11 ± 6.14 ppt, 8.09 ± 0.53 , 4.53 ± 0.70 ppm, and 41.42 ± 55.42 NTU, respectively. Due to strong right skewness (median 16.08 NTU, range 2.35–165.00 NTU), the standard deviation exceeds the mean of turbidity. The

mean values for sediment parameters were recorded as follows: OC ($1.42 \pm 0.55\%$), soil salinity ($0.59 \pm 0.21\%$), soil pH (5.72 ± 0.91), sand (31.81 ± 11.57), silt (41.92 ± 7.34), and clay (26.26 ± 7.34). The highest water temperature was recorded in Bakkhali (33.3 ± 0.2 °C) during the monsoon, while the lowest was recorded in Sonadia (22.63 ± 0.20 °C) during the post-monsoon. Water salinity reached its maximum in Sonadia during post-monsoon (20.75 ± 0.16 ppt) and reached its minimum in Bakkhali during monsoon (6.07 ± 0.08 ppt). The highest water pH was observed in Sonadia during pre-monsoon (8.87 ± 0.04), while the lowest was also observed in Sonadia during post-monsoon (7.44 ± 0.07). Water DO was highest in Nuniarchara (5.91 ± 0.02 ppm) during the post-monsoon and lowest in Bakkhali (3.68 ± 0.20 ppm) during the pre-monsoon. Turbidity fluctuated drastically, with a peak in Sonadia (165.00 ± 0.00 NTU) during the monsoon and a minimum in Sonadia (2.35 ± 0.00 NTU) during the post-monsoon. The recorded turbidity values were spatially homogeneous within habitats at each site during each season, though they varied drastically among sites across seasons ($SD = 0$). Soil OC was highest in Bakkhali ($2.27 \pm 0.75\%$) during the pre-monsoon and lowest in Nuniarchara ($0.52 \pm 0.08\%$) during the post-monsoon. High soil salinity was recorded in Nuniarchara (0.92 ± 0.14) during the pre-monsoon, whereas a lower value was recorded in Sonadia (0.38 ± 0.07) during the monsoon. Soil pH varied from a maximum in Nuniarchara (7.07 ± 0.60) during the pre-monsoon to a minimum in Bakkhali (4.42 ± 0.35) during the monsoon. The sand fraction ranged from $22 \pm 1.61\%$ in Nuniarchara to $55.65 \pm 3.15\%$ in Bakkhali during the pre-monsoon. The silt was $30.06 \pm 1.59\%$ in Bakkhali during the pre-monsoon and $52.42 \pm 7.12\%$ in Bakkhali during the post-monsoon. Clay content ranged from $14.29 \pm 2.10\%$ in Bakkhali to $36.59 \pm 2.96\%$ in Nuniarchara during the pre-monsoon. One-way ANOVA and the Kruskal–Wallis test applied to the water and soil parameters showed significant seasonal variation (Table 4), except for soil sand and clay content, which showed significant spatial variation (Table 4). The Spearman’s rank correlation analysis revealed significant correlations between abiotic factors and biotic community indices (Table 5). Sedimentary organic carbon (OC) showed significant negative correlations with abundance but positive correlations with Pielou’s evenness. Water salinity and DO both exhibited significant positive correlations with Margalef richness and abundance, while showing significant negative correlations with Pielou’s evenness.

Table 4 Environmental variables (mean $\pm$ SD) and ANOVA / Kruskal–Wallis results, south-eastern coast of Bangladesh.

Parameter	Pre-monsoon			Monsoon			Post-Monsoon			Source	p value
	Bak ¹	Nun ¹	Son ¹	Bak ¹	Nun ¹	Son ¹	Bak ¹	Nun ¹	Son ¹		
Water Temperature ³ (°C)	30.33 $\pm$ 0.25	29.53 $\pm$ 0.25	30.3 $\pm$ 0.1	33.3 $\pm$ 0.2	32.43 $\pm$ 0.25	32.43 $\pm$ 0.25	22.67 $\pm$ 0.11	24.67 $\pm$ 0.23	22.63 $\pm$ 0.20	Station	0.89666
										Season	0.000009
										Habitat	0.98814
Water Salinity ³ (ppt)	19.74 $\pm$ 0.33	19.63 $\pm$ 0.749	19.87 $\pm$ 0.27	6.07 $\pm$ 0.08	7.27 $\pm$ 0.20	10.99 $\pm$ 0.14	19.98 $\pm$ 0.10	20.65 $\pm$ 0.14	20.75 $\pm$ 0.16	Station	0.38047
										Season	0.000035
										Habitat	0.784948
Water pH ³	8.62 $\pm$ 0.13	8.60 $\pm$ 0.18	8.87 $\pm$ 0.04	7.83 $\pm$ 0.04	8.14 $\pm$ 0.04	7.60 $\pm$ 0.03	8.18 $\pm$ 0.08	7.50 $\pm$ 0.08	7.44 $\pm$ 0.07	Station	0.564371
										Season	0.00011
										Habitat	0.996917
Water DO ³ (ppm)	3.68 $\pm$ 0.20	4.54 $\pm$ 0.08	4.16 $\pm$ 0.05	4.16 $\pm$ 0.04	4.09 $\pm$ 0.02	4.23 $\pm$ 0.06	4.63 $\pm$ 0.12	5.91 $\pm$ 0.02	5.35 $\pm$ 0.10	Station	0.23144
										Season	0.00025
										Habitat	0.98641

^aWater Turbidity³ (NTU)	11.67±0.00	16.92±0.00	16.08±0.00	60±0.00	92±0.00	165±0.00	4.74±0.00	4.01±0.00	2.35±0.00	Station	0.86550
										Season	0.000008
										Habitat	1
Organic Carbon² (%)	2.27 ± 0.75	1.63 ± 0.17	1.13 ± 0.26	1.40 ± 0.24	2.12 ± 0.21	1.53 ± 0.51	1.18 ± 0.18	0.52 ± 0.08	1.00 ± 0.56	Station	0.4183
										Season	0.0041
										Habitat	0.328
Soil Salinity² (%)	0.87 ± 0.19	0.92 ± 0.14	0.75 ± 0.15	0.39 ± 0.12	0.49 ± 0.21	0.38 ± 0.07	0.42 ± 0.08	0.62 ± 0.05	0.48 ± 0.14	Station	0.4095
										Season	0.000002
										Habitat	0.185
Soil pH²	6.40 ± 0.35	7.07 ± 0.60	6.67 ± 0.54	4.42 ± 0.35	4.57 ± 0.29	5.13 ± 0.10	5.50 ± 0.21	5.81 ± 0.44	5.90 ± 0.30	Station	0.5543
										Season	0.0000000
										Habitat	0.531
Sand³ (%)	55.65±3.15	22±1.61	24.29±3.32	46.76±3.23	26.79±3.13	23.83±2.26	30.38±3.29	25.96±10.40	30.66±3.56	Station	0.00086
										Season	0.943
										Habitat	0.196
Silt² (%)	30.06±1.59	41.40±1.88	42.91±3.25	30.47±5.71	45.58±5.58	43.47±2.74	52.42±7.12	47.19±6.73	43.82±1.14	Station	0.1362
										Season	0.0166
										Habitat	0.231
Clay² (%)	14.29±2.10	36.59±2.96	32.79±3.55	22.77±6.81	27.63±7.31	32.70±2.97	17.2±7.68	26.85±4.94	25.53±2.86	Station	0.00016
										Season	0.4033
										Habitat	0.0729

Mean±SD¹, ANOVA², Kruskal–Wallis test³, **Bak**=Bakkhali, **Nun**=Nuniarchara, **Son**=Sonadia, **DO**= Dissolved

Oxygen. ^aSD = 0.00 indicates homogeneity in turbidity among habitats within a site during the corresponding season

Water temperature exhibited a significant positive correlation with Pielou’s evenness and a negative correlation with Margalef richness. Water pH exhibited significant negative correlations with abundance, while water turbidity showed significant positive correlations with Pielou’s evenness. Silt fractions exhibited significant positive correlations with Shannon diversity, Margalef richness, Simpson diversity and Abundance. Canonical Correspondence Analysis (CCA) was applied to assess the influence of environmental variables on the seasonal distribution of macrobenthic assemblages. The permutation test (9,999 permutations) confirmed that the overall CCA model was statistically significant (Total Inertia = 2.259, Constrained Inertia = 0.886, Pseudo-F = 1.750, $p < 0.01$). Sequential axis testing demonstrated that the first two axes were statistically significant: CCA Axis 1 (Pseudo-F = 5.807, $p = 0.0001$) and CCA Axis 2 (Pseudo-F = 2.667, $p = 0.0033$). The first (47.4 %) and second (20.8 %) CCA axes jointly explained 68.2% of the constrained variation in species composition (**Fig. 5**).

Table 5 Spearman’s rank correlations between macrobenthic community and environmental variables along the south-eastern coast of Bangladesh.

Environmental Parameters	Shannon	Margalef	Pielou	Simpson	Abundance
Organic Carbon (%)	-0.23939	-0.30901	0.38107*	-0.02473	-0.56326**
Soil Salinity (%)	-0.09009	-0.21255	0.18873	-0.00763	-0.16797
Soil pH	0.06383	0.12399	-0.26233	-0.01405	0.07657
Water salinity (ppt)	0.28148	0.5013**	-0.421*	0.0406	0.47502*
Water Temperature (°C)	-0.14052	-0.41424*	0.50802**	0.10997	-0.3556
Water pH	-0.20241	-0.29492	0.19844	-0.03908	-0.51092*

Water DO (ppm)	0.21591	0.39273*	-0.46847*	-0.06932	0.558**
Water Turbidity (NTU)	-0.04788	-0.35175	0.57459**	0.22836	-0.29033
Clay	-0.1786	-0.26744	0.08854	-0.11998	-0.10237
Silt	0.51504**	0.51534**	-0.0116	0.40757*	0.55279**
Sand	-0.07052	-0.0006	-0.02809	-0.03816	-0.13873

Values in bold indicate statistical significance, *($p < 0.05$), **($p < 0.01$)

Axis 1 showed a positive association with water DO ($r = 0.909$), water salinity ($r = 0.641$), silt content ($r = 0.402$), and soil pH ($r = 0.113$), whereas a negative association with organic carbon ($r = -0.698$), water turbidity ($r = -0.603$), and sand content ($r = -0.376$). Axis 2 further demonstrated positive affinity with soil pH ($r = 0.815$), water salinity ($r = 0.710$), sand ($r = 0.492$) and organic carbon ($r = 0.104$), whereas negative affinity with water turbidity ($r = -0.665$), silt content ($r = -0.298$), and water DO ($r = -0.163$). Post-monsoon condition supported *Turritella attenuata*, *Gammaropsis esturinus*, *Americorophium triaonyx*, *Eumida albopicta*, *Notomastus aberans*, *Hydroides albiceps* and was positively associated with high water salinity, elevated DO, and increased silt content. Pre-monsoon conditions supported *Glycera sheikhmujibi*, *Glycinde kameruniana*, *Eumida sanguinea*, *Cephalothrix* sp., *Actiniaria* sp., *Arenicola cristata*, and were positively associated with OC, sand content, and soil pH. Monsoon conditions supported *Nephtys polybranchia*, *Aglaophamus dibranchis*, and *Amphiporus* sp. in association with high turbidity. Along Axis 1, *Capitella capitata oculata* was ordinated on the positive side together with *Notomastus aberans*, in the direction of the DO and water salinity. *Namalycastis indica* and *Nereis coutieri* were positioned close to the ordination centroid.

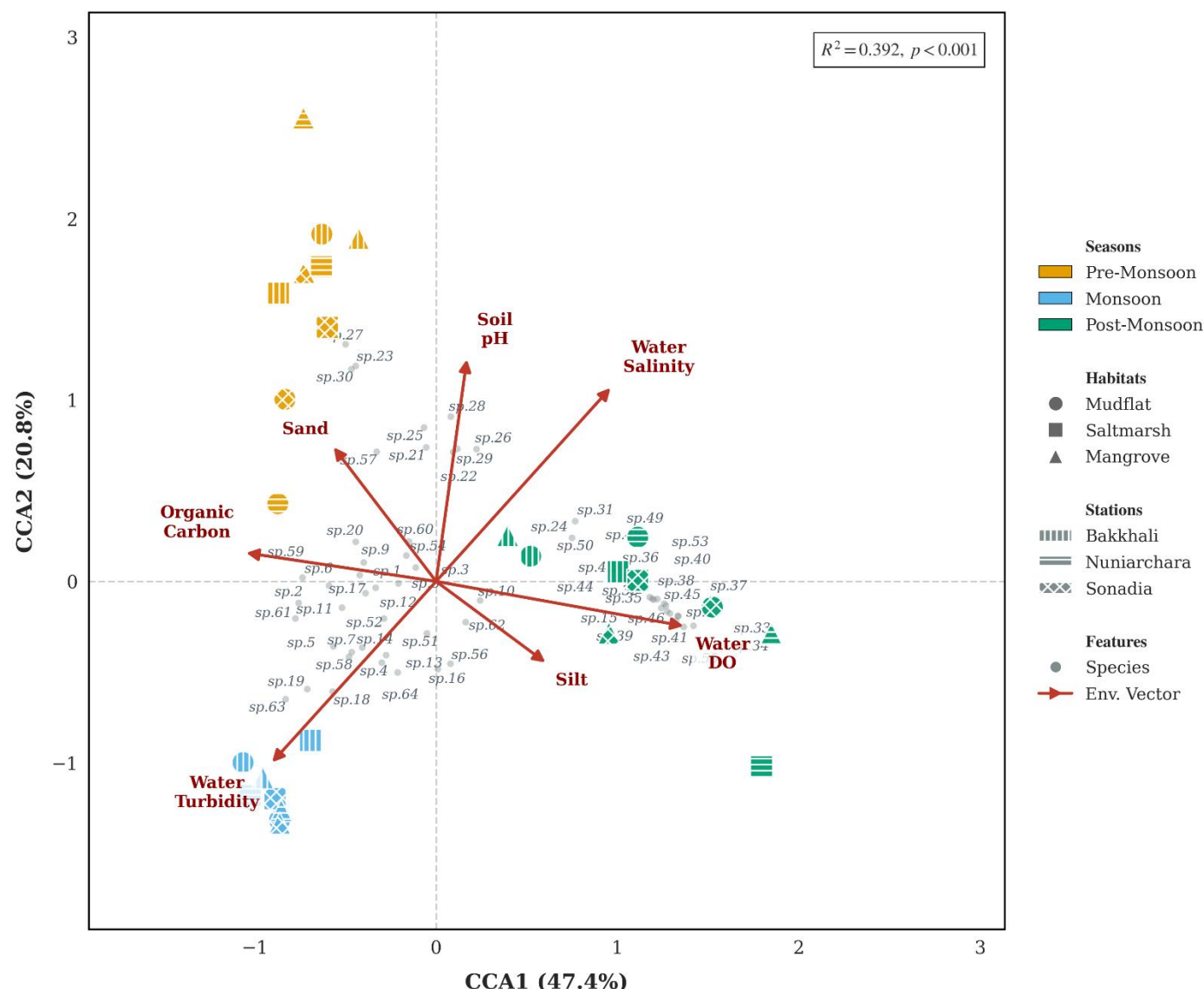


Fig. 5 CCA ordination of macrobenthic species abundance data and environmental parameters in the south-eastern coast, Bangladesh (Taxa code and Species name in Table 1).

Discussion

4.1 Habitat-driven variability in macrobenthic taxonomic composition

In the present study, a total of 1592 individuals were examined (total abundance 36,851.85 ind./m²), with records of 64 macrobenthic taxa distributed across 11 classes and 38 families. These results closely aligned with those of Musale & Desai (2011), who recorded 63 macrobenthic taxa with polychaete dominance along the South Indian coast. Noman et al. (2019) identified 47 taxa across nine groups and seven distinct feeding categories in the Naf River estuary. Comparatively higher diversity was reported by Begum (2017), who identified 82 species in the Rupsha-Pasur River

system. Polychaeta was the dominant group and constituted the majority (62.12%), reflecting their ecological predominance. These findings are consistent with the conclusion of polychaeta dominance in previous studies (Barua et al., 2019; Noman et al., 2019). In the present study, the abundance of benthic organisms followed the sequence: Polychaeta > Gastropoda > Malacostraca > Clitellata > Palaeonemertea > Holothuriidae > Hexacorallia > Demospongiae > Sipunculidae > Hoplonemertea > Pilidiophora. The present study documented Polychaeta dominance, underscoring their ecological adaptability, tolerance, and widespread distribution in soft-sediment intertidal habitats. Among polychaetes, the dominant families in the present study were Nereididae and Capitellidae, followed by Nephtyidae, Phyllodoceidae, Glyceridae, and Orbiniidae. Similarly, Khatun et al. (2023) recorded Nereididae, Capitellidae, Nephtyidae, Lumbrineridae, Cossuridae, and Glyceridae in the Sundarban estuarine region. The polychaete families in this study were represented by multiple species (*Neanthes indica*, *Neanthes glandicincta*, *Platynereis calodonta*, *Capitella capitata oculata*, *Notomastus aberans*, *Glycera sheikhmujibi*, *Nephtys gravieri*, *Micronephtys oligobranchia*, *Phyllodoce* sp., highlighting their ecological plasticity and widespread distribution. Aligned with the present study, Mely et al. (2023) recorded *Nereis* sp., *Lumbrineris* sp., *Sigambra* sp., *Nemanereis* sp., *Nephtys* sp., *Capitella* sp., *Melinna* sp., *Paraprionospio* sp., and *Glycera* sp. along the Noakhali coast, Bangladesh. The representation of Capitellidae (*Capitella capitata oculata*, *Notomastus aberans*, *Notomastus latericeus*) was subjected to organic enrichment, supported by Musale & Desai (2011). Species such as *Glycera sheikhmujibi*, *Glycera alba*, *Nephtys gravieri*, *Micronephtys oligobranchia*, and *Drilonereis* sp. are influenced by silt-clay content (Jayachandran et al., 2019). The study also reported *Diopatra neapolitana*, an omnivorous, tube-forming species (Dağlı et al., 2005) that functions as an ecosystem engineer (Arias et al., 2023). Individually, the most dominant species recorded were *Turritella attenuata* (4.96%) and *Pirenella cingulata* (3.83%), which may be attributed to their tolerance of high salinity and low organic stress. Malacostracan opportunistic species such as *Gammaropsis esturinus* and *Americorophium triaenyonx* have been reported and may be well suited to environments with high salinity and siltation (Jayachandran et al., 2019). Other dominant non-polychaete species recorded were *Holothuria* sp., *Actiniaria* sp., *Tetilla dactyloidea*, *Monopylephorus parvus*, *Tubifex tubifex*, *Cephalothrix* sp., and *Tubulanus* sp. The single-species representative classes, such as Hexacorallia, Holothuriidae, Demospongiae, Hoplonemertea, Pilidiophora, and Sipunculidae, likely reflect habitat-specific occurrence attributed to stable environmental variables and sediment chemistry. Previous studies also reported the presence of non-polychaeta groups, including Bivalvia, Malacostraca, Gastropoda, Clitellata, and Insecta (Mely et al., 2023; Rahman et al., 2022).

4.2 Seasonal dynamics of macrobenthic assemblages and their environmental controls

The present study demonstrated significant seasonal and spatial variation in macrobenthic abundance along the south-eastern coast of Bangladesh. Post-monsoon exhibited marked differences from the monsoon ($p = 0.0001$) and pre-monsoon ($p = 0.0001$), and showed pronounced variability between Sonadia and Bakkhali ($p = 0.0037$). Our results revealed a higher abundance (1872.42 ± 1005.70 ind./m²) in post-monsoon than in monsoon and pre-monsoon. PERMANOVA further confirmed marked seasonal variability (32.6%) between the monsoon and post-monsoon communities, and comparatively lower variability (23.6%) between the pre-monsoon and monsoon communities. SIMPER analysis revealed that the variability trend was associated with the contributions of Polychaetes: *Glycera sheikhmujibi*, *Capitella capitata oculata*, *Eumida sanguinea*, *Platynereis calodonta*, *Sternaspis* sp., *Eupolyornia*

nebulosa, Hoplonemertea: *Amphiporus* sp., and Malacostraca: *Gammaropsis esturinus*. Though the contributing taxa explain the trend in variability, the seasonal restructuring must be read as a broad shift across the assemblage rather than turnover in a few species. The nMDS plot revealed distinct grouping patterns, sharply separating post-monsoon assemblages from the monsoon and pre-monsoon. The highest abundance was observed in the post-monsoon season in previous studies (Kumar & Khan, 2013; Mely et al., 2023; Khatun et al., 2023; Rehitha et al., 2019). In contrast, few studies reported high macrobenthic abundance during the monsoon (Begum, 2017) and the pre-monsoon (Noman et al., 2019). Notably, the high density in the post-monsoon may be attributed to stable environmental conditions with optimal salinity and DO, while the decline observed during the pre-monsoon coincided with the highest organic carbon in sediments and the lowest DO record, attributed to anthropogenic pressures. Species number (64 sp.) was higher during the post-monsoon period, whereas the lowest reported (31 sp.) was during the monsoon season, which was consistent with the findings of Mulik et al. (2020) and Islam et al. (2022). This variability could be attributed to lower temperature and turbidity, coupled with more stable environmental conditions during the post-monsoon season and heavy monsoonal stress coupled with salinity fluctuations during the monsoon. The study identified Sonadia as a macrobenthic faunal hotspot, with the highest mean abundance (1761.86 ± 917.09 ind./m²) and species number (64 sp.), consistent with Islam et al. (2022). The abundance and richness of Sonadia exceed those reported for several regions, including Nijhum Dwip (Rahman et al., 2021), the Pondicherry coast in India (Kumar & Khan, 2013), and the northern Arabian Sea (Joydas & Damodaran, 2009). However, abundance was recorded as lower than in high-energy estuarine environments such as the Meghna and Naf River Estuaries (Rahman et al., 2022; Noman et al., 2019). Nuniarchara exhibited moderate abundance (1327.16 ± 610.25 ind./m²), while Bakkhali displayed the lowest abundance (1005.66 ± 270.97 ind./m²) and species number (53 species). The study revealed a much higher abundance in Bakkhali than the 301.04 ind./m² reported by Haque et al. (2021) and a lower abundance than the 9000 ind./m² reported by Abu Hena et al. (2012). These fluctuations may result from different mesh sizes and sampling gear used in those studies, as well as genuine temporal variability and anthropogenic pressures in the Bakkhali River, whereas Sonadia exhibited lower organic stress and smaller sediment particle sizes. The dissimilarity between Sonadia and Bakkhali was driven largely by *Tubulanus* sp. The present study revealed the dominance of polychaetes across all seasons, with a mean abundance of 7631.17 ± 2573.96 ind./m², consistent with Noman et al. (2019). The observed seasonal and spatial patterns of polychaete predominance are consistent with regional studies across several coastal and estuarine environments (Rahman et al., 2021; Mulik et al., 2020). In contrast, studies in other regions reported crustacean dominance (Mely et al., 2023) and gastropod dominance (Das et al., 2022) over seasonal dynamics. In the present study, the seaward mudflat demonstrated the highest abundance (1805.56 ± 983.32 ind./m²) and, together with the saltmarsh, the highest species number (61 species each), compared to the saltmarsh (1311.73 ± 420.83 ind./m²) and mangrove (977.37 ± 276.27 ind./m²; 54 sp) habitats. The result of high macrobenthic abundance at the mudflat was supported by Lowe et al. (2022). The non-vegetated mudflat and vegetated mangrove habitats showed strong dissimilarity ($p=0.01183$), driven by *Tubulanus* sp, *Nereis persica*, *Amphiporus* sp., and *Nephtys gravieri*. However, the habitat variability may be attributed to organic carbon, sediment particle size, and monsoonal flooding. The mudflat habitat exclusively supported a few polychaete taxa (*Lumbrineris simplex*, *Diopatra neapolitana*, and *Drilonereis* sp.), indicating its ecological distinctiveness. A distinct set of taxa was exclusively recorded at Sonadia,

including *Ophelina grandis*, *Tetilla dactyloidea*, *Turritella attenuata*, and several specialized polychaetes such as *Diopatra neapolitana*, *Eumida albopicta*, and *Leitoscoloplos papillatus*. These findings are consistent with reports from previous research (Mely et al., 2023; Rahman et al., 2021; Shen et al., 2006). The present study also showed distinct seasonal and spatial shifts in secondary-dominant macrobenthic groups. Such variations reflect seasonal restructuring in response to environmental gradients and hydrological changes. These patterns of taxa shifts align with the findings of Barua et al. (2019) and Mely et al. (2023). In the present study, the highest species diversity and richness were recorded in Sonadia during the post-monsoon and the lowest in Bakkhali during the monsoon, consistent with the findings of Khatun et al. (2023) and Molla et al. (2015). However, higher evenness and Simpson's diversity index were reported during the monsoon, which was in line with Sharif et al. (2017). These scenarios may be attributed to habitat types and other environmental parameters such as organic carbon, water temperature, salinity, turbidity, and DO, which control the species distribution.

4.3 Environmental drivers shaping macrofaunal community structure

Water temperature and turbidity were higher during the monsoon season, while water PH, soil salinity, and soil pH were higher during the pre-monsoon season. Organic carbon (OC) was reported comparatively higher in both the pre-monsoon (mean 1.68%) and monsoon (mean 1.68%) seasons and markedly lower during the post-monsoon (mean 0.90%), though the single highest OC value was recorded in Bakkhali during the pre-monsoon. Sand and clay content were recorded as highest during the pre-monsoon, although their differences were statistically significant only at the spatial scale (Table 4). The remaining parameters, such as water salinity, water DO, and soil silt content, were higher during the post-monsoon season. The remaining parameters, such as water salinity, water DO, and soil silt content, were higher during the post-monsoon season. In the present study, the highest water temperature was recorded during the monsoon and the lowest during the post-monsoon season. This may be due to higher air temperature combined with high humidity and cloud cover during the monsoon suppress evaporative and net long-wave heat loss, while declining air temperature under clearer and drier conditions drives cooling during the post-monsoon (Caissie, 2006). The observed monsoon maximum and post-monsoon minimum in water temperature were identical to those reported by Mely et al. (2023) and Sharif et al. (2017). The record of post-monsoon salinity peak (20.75 ppt) and monsoon salinity minimum (6.07 ppt) may be attributed to lower freshwater discharge and higher evaporation in post-monsoon, and to freshwater input from seasonal rainfall and flood current influence during monsoon, as supported by Mulik et al. (2020) and Lowe et al. (2022). The water pH fluctuations between 7.44 and 8.87 in Sonadia indicate an alkaline, favorable aquatic environment, as supported by previous reports (Boyd, 2000; Mulik et al., 2020). Seawater dilution from freshwater sources, organic decomposition, and continuous CO₂ removal may lead to higher pH in Sonadia during the pre-monsoon. The highest water DO (5.91±0.02 ppm) was recorded in Nuniarchara during the post-monsoon, while the lowest was recorded in the Bakkhali River during the pre-monsoon. This may be attributed to lower post-monsoon temperatures, which increase oxygen solubility, and to the presence of oxygen-demanding waste in the Bakkhali River, consistent with previous research (Barua et al., 2019; Khatun et al., 2023). Water turbidity demonstrated a monsoon maximum (165 ± 0.00 NTU) and post-monsoon minimum (2.35 ± 0.00 NTU) in Sonadia, which supports the findings of Lamptey & Armah (2008). The absence of within-site variation across habitats indicates

that the three habitats were flooded by the same water mass with a uniform suspended-sediment concentration at the study sites. However, the marked site and season-specific variability were driven by freshwater discharge, rainfall, tides, and local sediment sources. This drastic variability record in Sonadia may be attributed to the monsoonal cycle, erosion from adjacent hills, and anthropogenic practices such as shrimp-salt farming, deforestation, and unplanned infrastructure (Hossain et al., 2023). The highest OC level was reported in Bakkhali during the pre-monsoon, and the lowest in Nuniarchara during the post-monsoon. This pre-monsoon peak followed by a post-monsoon decline is also consistent with previous research (Hasrizal et al., 2009; Kathiresan et al., 2014; Real et al., 2018). Soil salinity and soil pH were highest during the pre-monsoon and lowest during the monsoon, consistent with Molla et al. (2015). The study reported silt dominance over sand and clay in most sampling sites. The exception of sand dominance was reported from Bakkhali during the pre-monsoon and monsoon seasons. Seasonal increases in sand and clay content were evident during the monsoon and pre-monsoon, whereas silt dominance was most pronounced during the post-monsoon, consistent with previous research (Khatun et al., 2023; Jayachandran et al., 2019). A distinct association between environmental variables and macrobenthic community is evident in estuarine ecosystems (Khatun et al., 2023; Islam et al., 2025; Ysebaert & Herman, 2002; Zhang et al., 2012). Macrobenthic communities are influenced by multiple environmental factors rather than a single factor that could alone drive their ecology (Gray & Elliott, 2009). Negative affinity of Soil organic carbon (OC) with abundance and positive affinity with evenness may indicate reduced numerical dominance within a depleted assemblage at elevated OC rather than a more favorable community condition. Comparable negative impacts of elevated organic content have also been reported in previous studies (Musale & Desai, 2011). Water salinity and water DO were positively associated with richness and abundance but negatively associated with evenness, consistent with previous studies (Joydas & Damodaran, 2009; Mely et al., 2023). A strong positive association between silt content and diversity, richness, and abundance indicates that finer-grained sediment beds are suitable habitats for diverse macrobenthic assemblages, as noted by Mathers et al. (2024) and Khatun et al. (2023). Water temperature showed a negative correlation with species richness, while a positive association with evenness reflects the same pattern of dominance reduction within a species-poor assemblage, in agreement with Mely et al. (2023). Consistent with these results, Molla et al. (2015) recorded high richness at lower temperatures. The observed negative influence of pH on macrobenthic abundance was contrary to the findings of Haque et al. (2021) and Khatun et al. (2023). Water turbidity showed a significant positive correlation with evenness, mainly driven by monsoonal influence. Peak turbidity coincided with maximum evenness ($J' = 0.96$) and the lowest richness (31 spp.), indicating reduced numerical dominance within a species-poor assemblage under environmental stress rather than improved community condition (Svensson et al., 2012; Sharif et al., 2017). The CCA ordination explained the compound influence of environmental parameters on the macrobenthic community. The first two CCA axes jointly explained 68.2% of the constrained variation, and the constrained axes combinedly accounted for 39.2% of total inertia ($R^2 = 0.392$; permutation test, $p < 0.01$). In comparison, Mely et al. (2023) reported 49.54% explained variance along the Noakhali Coast, while Jayachandran et al. (2019) reported 52% of CCA explained variance along the southwest coast of India. The CCA results further confirmed that elevated water salinity, DO, and silt percentage are imperative to increased macrobenthic abundance and diversity (Mely et al., 2023; Khatun et al., 2023), whereas increased OC, water turbidity, and sand percentage lead to reduced macrobenthic abundance, diversity, and richness.

(Hyland et al., 2005; Islam et al., 2025). The CCA ordinated *Capitella capitata oculata* and *Notomastus aberans* along the positive DO vector of Axis 1 ($r = 0.909$; Fig. 5), consistent with Khatun et al. (2023). As DO exceeded 3.6 ppm and did not extend into hypoxia, the ordination reflects these opportunists' position along a well-oxygenated gradient rather than the organically enriched conditions typically associated with *Capitella* (Checon et al., 2021). Positioned closest to the CCA center, Nereididae species such as *Namalycastis indica* and *Nereis coutieri* exhibit high tolerance, consistent with previous findings (Mely et al., 2023).

Conclusion

The study investigated macrobenthic abundance, diversity, and distribution along the south-eastern coast of Bangladesh under different seasons, habitats, and environmental variables. A total of 64 species were recorded, and the community was dominated by Polychaetes. A high abundance of the macrobenthic community was supported by the mudflat habitat at Sonadia during the post-monsoon season. *Turritella attenuata*, a gastropod, was the most abundant individual among the macrofauna. High Shannon diversity and Margalef richness were recorded in Sonadia during the post-monsoon season, and lowest in Bakkhali during the monsoon. Statistical analysis revealed strong seasonal, spatial, and habitat variation and identified *Glycera sheikhmujibi*, *Capitella capitata oculata*, and *Tubulanus* sp. as the taxa contributing to the grouping patterns. Spearman's rank correlation and canonical correspondence analysis (CCA) revealed that environmental variables, including dissolved oxygen (DO), water salinity, organic carbon (OC), and soil silt content, were the driving factors influencing macrobenthic community assemblages. The present study's outcomes promote understanding of the seasonal and spatial patterns of macrobenthic community structure and their relationship with environmental variables. These will further support improvements in management strategies to maintain the healthy functioning of the benthic ecosystem.

Limitations of the study

The study has several limitations. The seasonal field sampling was based on a single occasion and may not fully capture the inter-annual variability. The three replicate cores across the habitats in each site and season cover a small area ($0.01 \text{ m}^2/\text{core}$). Secondary production and trophic transfer were not examined. Finally, the two-dimensional nMDS stress value (0.216) exceeded the conventional threshold for reliable interpretation. Future research should integrate molecular approaches with biotic indices (e.g., AMBI or M-AMBI) to better characterize macrobenthic community assemblages and the ecological quality status of the sites.

Declarations

All authors have read, understood, and complied as applicable with the statement on “ethical responsibilities of authors” as found in the instructions for authors.

Funding

The authors declare that this research was supported by no external funding, grants, or financial assistance.

Competing Interests

The authors declare no direct and indirect financial and non-financial competing interests regarding this work.

Ethics Approval

Not applicable. This study involved only invertebrate macrobenthic fauna collected using standard field sampling methods. No vertebrate animals, human participants, or protected species were involved; therefore, no formal ethical approval was required. Field sampling at Sonadia Island, a declared Ecologically Critical Area, was conducted under permit.

Consent to Participate

Not applicable. This study did not involve human participants.

Consent for Publication

Not applicable. This study did not involve any individual person's data, images, or identifiable information.

Availability of data and materials

The datasets for this study are not publicly available but can be obtained from the corresponding author upon reasonable request.

Author Contributions

Omite Ashraf: Conceptualization, Methodology, Investigation, Species identification, Data curation, Formal analysis, Writing (original draft), Md. Azizul Fazal: Conceptualization, Methodology, Investigation, Validation, Supervision, Writing (review & editing). Subrata Sarker: Conceptualization, Methodology, Validation, Supervision, Writing (review & editing), Md. Alamgir Kabir: Conceptualization, Methodology, Supervision, Writing (review & editing). Md. Sharif Hossain: Investigation, Data curation, Formal analysis, Writing (original draft). Saidul Afnan: Investigation, Writing (review & editing). Mohammad Forkanul Hamid: Investigation, Writing (review & editing). Md. Bayzid: Investigation, Writing (original draft). Abu Bokkar Siddique: Validation, Supervision, Writing (review & editing). Faisal Sobhan: Validation, Supervision, Writing (review & editing). Mohammad Nahidul Islam Sakib: Data curation, Formal analysis, Writing (review & editing). All authors contributed to the review and editing of the manuscript and have approved the final version for publication.

Acknowledgements

The authors would like to thank Md. Abdul Kayum and Md. Fuad Jamil Mahdi for their assistance with microscopic imagery and species counting.

Reference

- Adesakin, T. A., Erhomosele, E. I., Ogunrinola, O. F., Oloyede, O. O., Adedeji, A. A., Odufuwa, P. T., Aimienoho, A., Aduwo, A. I., & Adewumi, E. A. (2023). Using benthic macroinvertebrates as bioindicators to evaluate the impact of anthropogenic stressors on water quality and sediment properties of a West African lagoon. *Heliyon*, 9(9), e19508. <https://doi.org/10.1016/j.heliyon.2023.e19508>
- Arias, A., Woodin, S. A., & Paxton, H. (2023). An introduction to Diopatra, the amazing ecosystem engineering polychaete. *Biology*, 12(7), 1027. <https://doi.org/10.3390/biology12071027>
- Barua, P., Mohasin Meah, M., & Rahman, S. H. (2019). Abundance of macrobenthos with special reference to some physico-chemical parameters of south-eastern coastal area, Bangladesh. *Asian Journal of Water, Environment and Pollution*, 16(4), 51-60. <https://doi.org/10.3233/AJW190048>
- Begum, S. (2017). Macrobenthic assemblage in the Rupsha–Pasur River system of the Sundarbans ecosystem (Bangladesh) for the sustainable management of coastal wetlands. In C. W. Finkl & C. Makowski (Eds.),

- Coastal wetlands: Alteration and remediation* (Coastal Research Library, Vol. 21, pp. 751–776). Springer.
https://doi.org/10.1007/978-3-319-56179-0_22
- Belley, R., Snelgrove, P. V. R., Archambault, P., & Juniper, S. K. (2016). Environmental drivers of benthic flux variation and ecosystem functioning in Salish Sea and Northeast Pacific sediments. *PLOS ONE*, *11*(3), e0151110. <https://doi.org/10.1371/journal.pone.0151110>
- Black, C. A. (Ed.). (1965). *Methods of soil analysis: Part 2. Chemical and microbiological properties* (Agronomy Series No. 9). American Society of Agronomy. <https://doi.org/10.2134/agronmonogr9.2>
- Bouyoucos, G. J. (1962). Hydrometer method improved for making particle size analysis of soil. *Agronomy Journal*, *54*(5), 464–465. <https://doi.org/10.2134/agronj1962.00021962005400050028x>
- Boyd, C. E. (2000). *Water quality: An introduction*. Kluwer Academic Publishers. <https://doi.org/10.1007/978-1-4615-4485-2>
- Caissie, D. (2006). The thermal regime of rivers: A review. *Freshwater Biology*, *51*(8), 1389–1406. <https://doi.org/10.1111/j.1365-2427.2006.01597.x>
- Checon, H. H., Corte, G. N., Silva, C. F., Bicego, M. C., & Amaral, A. C. Z. (2021). Using the Capitella complex to investigate the effects of sympatric cryptic species distinction on ecological and monitoring studies in coastal areas. *Marine Biodiversity*, *51*(3), 48. <https://doi.org/10.1007/s12526-021-01185-w>
- Chowdhury, A. J. K., John, A., Aqilah, N. S., Abdullah, R., Salihah, N. T., Basir, K. H., & Marsal, C. J. (2024). Macrobenthic community towards sustainable aquatic ecosystem: a systematic review along the coastal waters of Malaysia. *Geology, Ecology, and Landscapes*, *8*(1), 57–70. <https://doi.org/10.1080/24749508.2022.2095088>
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*(1), 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Dağlı, E., Ergen, Z., & Cinar, M. E. (2005). One-year observation on the population structure of *Diopatra neapolitana* Delle Chiaje (Polychaeta: Onuphidae) in Izmir Bay (Aegean Sea, eastern Mediterranean). *Marine Ecology*, *26*(3-4), 265–272. <https://doi.org/10.1111/j.1439-0485.2005.00055.x>
- Das, S. C. S., Jha, D. N., Alam, A., Borah, S., Kumar, V., Srivastava, K., Thakur, V. R., Sahoo, A. K., & Das, B. K. (2022). Assessing assemblage pattern, health status and environmental drivers of macrobenthic invertebrate community structure for sustainable management in a tropical tributary of River Ganga, India. *Sustainable Water Resources Management*, *8*(5), 128. <https://doi.org/10.1007/s40899-022-00722-0>
- Fofonoff, N. P., & Millard, R. C., Jr. (1983). *Algorithms for computation of fundamental properties of seawater* (UNESCO Technical Papers in Marine Science No. 44). UNESCO.
- Gray, J. S., & Elliott, M. (2009). *Ecology of marine sediments: From science to management* (2nd ed.). Oxford University Press. <https://doi.org/10.1093/oso/9780198569015.001.0001>
- Hanz, U., Wienberg, C., Hebbeln, D., Duineveld, G., Lavaleye, M., Juva, K., Dullo, W.-C., Freiwald, A., Tamborrino, L., Reichart, G.-J., Flögel, S., & Mienis, F. (2019). Environmental factors influencing benthic communities in the oxygen minimum zones on the Angolan and Namibian margins. *Biogeosciences*, *16*(22), 4337–4356. <https://doi.org/10.5194/bg-16-4337-2019>
- Haque, M. M., Sharif, A. S. M., Ahmed, M. K., Rani, S., Molla, M. H. R., & Khan, M. I. (2021). Macrobenthic faunal

- abundance, distribution and diversity in the Bakkhali River, east coast of Bangladesh. *The Dhaka University Journal of Earth and Environmental Sciences*, 10(1), 47–55. <https://doi.org/10.3329/dujees.v10i1.56279>
- Hasrizal, S., Kamaruzzaman, B. Y., Sakri, I., Ong, M. C., & Azhar, M. S. N. (2009). Seasonal distribution of organic carbon in the surface sediments of the Terengganu nearshore coastal area. *American Journal of Environmental Sciences*, 5(1), 111–115. <https://doi.org/10.3844/ajessp.2009.111.115>
- Hossain, M. S., Yasir, M., Shahriar, M. S., Jahan, M., Liu, S., & Niang, A. J. (2023). Morphological change assessment of a coastal island in SE Bangladesh reveal high accumulation rates. *Regional Studies in Marine Science*, 62, 102969. <https://doi.org/10.1016/j.rsma.2023.102969>
- Hyland, J., Balthis, L., Karakassis, I., Magni, P., Petrov, A., Shine, J., Vestergaard, O., & Warwick, R. (2005). Organic carbon content of sediments as an indicator of stress in the marine benthos. *Marine Ecology Progress Series*, 295, 91–103. <https://doi.org/10.3354/meps295091>
- Islam, M. S., Pervez, A., Asseri, A. H., Al-Mutair, M., Sumon, M. A. A., Taleb, M. A., Ashik, A.-A., Rahman, M. A., & Molla, M. H. R. (2022). Diversity and seasonal succession of resident and migratory macrobenthic fauna of saltmarsh restoration site at Sonadia Island, Cox’s Bazar, Bangladesh. *Regional Studies in Marine Science*, 53, 102460. <https://doi.org/10.1016/j.rsma.2022.102460>
- Islam, M. S., Zamal, H., Alam, M. S., Bappy, M. M. M., Kamal, A. H. M., Hossain, M. B., & Arai, T. (2025). Biodiversity and seasonal succession of macrobenthos in saltmarsh habitat adjacent to a ship-breaking area. *Diversity*, 17(4), 231. <https://doi.org/10.3390/d17040231>
- Izegaegbe, J., Vivier, L., & Mzimela, H. (2020). Macrobenthic community structure of the Mhlathuze Estuary, a permanently open estuarine embayment in KwaZulu-Natal, South Africa. *African Journal of Aquatic Science*, 45(1–2), 95–107. <https://doi.org/10.2989/16085914.2020.1719818>
- Jackson, M. L. (1962). *Soil chemical analysis*. Prentice-Hall.
- Jayachandran, P. R., Bijoy Nandan, S., Jima, M., Sreedevi, O. K., Philomina, J., & Prabhakaran, M. P. (2019). Bioecology of macrobenthic communities in the microtidal monsoonal Kodungallur–Azhikode Estuary, southwest coast of India. *Lakes & Reservoirs: Science, Policy and Management for Sustainable Use*, 24(4), 372–390. <https://doi.org/10.1111/lre.12292>
- Joydas, T. V., & Damodaran, R. (2009). Infaunal macrobenthos along the shelf waters of the west coast of India, Arabian Sea. *Indian Journal of Marine Sciences*, 38(2), 191–204. <https://nopr.niscair.res.in/handle/123456789/4670>
- Kathiresan, K., Gomathi, V., Anburaj, R., & Saravanakumar, K. (2014). Impact of mangrove vegetation on seasonal carbon burial and other sediment characteristics in the Vellar-Coleroon estuary, India. *Journal of Forestry Research*, 25(4), 787–794. <https://doi.org/10.1007/s11676-014-0526-2>
- Khatun, B., Jewel, M. A. S., Haque, M. A., Akter, S., Hossain, M. B., Albeshr, M. F., & Arai, T. (2023). Seasonal pattern of taxonomic diversity and functional groups of macro-benthos from a sub-tropical mangrove estuary. *Journal of Marine Science and Engineering*, 11(7), 1453. <https://doi.org/10.3390/jmse11071453>
- Kumar, P. S., & Khan, A. B. (2013). The distribution and diversity of benthic macroinvertebrate fauna in Pondicherry mangroves, India. *Aquatic Biosystems*, 9(1), 15. <https://doi.org/10.1186/2046-9063-9-15>

- Lamprey, E., & Armah, A. K. (2008). Factors affecting macrobenthic fauna in a tropical hypersaline coastal lagoon in Ghana, West Africa. *Estuaries and Coasts*, 31(5), 1006–1019. <https://doi.org/10.1007/s12237-008-9079-y>
- Lowe, V., Frid, C. L., Venarsky, M., & Burford, M. A. (2022). Responses of a macrobenthic community to seasonal freshwater flow in a wet-dry tropical estuary. *Estuarine, Coastal and Shelf Science*, 265, 107736. <https://doi.org/10.1016/j.ecss.2021.107736>
- Mathers, K. L., Armitage, P. D., Hill, M., Bickerton, M., Mckenzie, M., Pardo, I., Tickner, D., & Wood, P. J. (2024). Context specific effects of substrate composition on the taxonomic and functional diversity of macroinvertebrate communities in temperate lowland streams. *Ecology and Evolution*, 14(8), e70034. <https://doi.org/10.1002/ece3.70034>
- Mely, S. S., Hossain, M. B., Rahman, M., Albeshr, M. F., & Arai, T. (2023). Changes of macrobenthic diversity and functional groups in saltmarsh habitat under different seasons and climatic variables from a subtropical coast. *Sustainability*, 15(9), 7075. <https://doi.org/10.3390/su15097075>
- Miah, M. G., Islam, M. R., Roy, J., Rahman, M. M., & Abdullah, H. M. (2023). A changing coastal ecosystem: Cox's Bazar in southeastern coastal region of Bangladesh. *Environment, Development and Sustainability*, 25(7), 6141–6165. <https://doi.org/10.1007/s10668-022-02297-4>
- Mohamamad, A., & Jalal, K.-C. A. (2018). Macrobenthic diversity and community composition in the Pahang estuary, Malaysia. *Journal of Coastal Research*, 82(sp1), 206–211. <https://doi.org/10.2112/SI82-030.1>
- Molla, M. H. R., Al-Imran, M., Aktaruzzaman, M., Mandol, S., Sarkar, M. K. I., & Islam, M. S. (2015). Spatio-temporal variations of macrobenthic annelid community of the Karnafuli River Estuary, Chittagong, Bangladesh. *International Journal of Marine Science*, 5(26), 1–11. <https://doi.org/10.5376/ijms.2015.05.0026>
- Mulik, J., Sukumaran, S., & Srinivas, T. (2020). Factors structuring spatio-temporal dynamics of macrobenthic communities of three differently modified tropical estuaries. *Marine Pollution Bulletin*, 150, 110767. <https://doi.org/10.1016/j.marpolbul.2019.110767>
- Musale, A. S., & Desai, D. V. (2011). Distribution and abundance of macrobenthic polychaetes along the South Indian coast. *Environmental Monitoring and Assessment*, 178(1–4), 423–436. <https://doi.org/10.1007/s10661-010-1701-3>
- Nayak, A., Equbal, J., Rout, S. S., Dash, B., Thiruchitrabalam, G., Bhadury, P., Satyanarayana, B., & Raut, D. (2022). Macrobenthic community of an anthropogenically influenced mangrove associated estuary on the East coast of India: An approach for ecological assessment. *Frontiers in Marine Science*, 9, 1008912. <https://doi.org/10.3389/fmars.2022.1008912>
- Nephtin, J., Juniper, S. K., & Archambault, P. (2014). Diversity, abundance and community structure of benthic macro- and megafauna on the Beaufort shelf and slope. *PLOS ONE*, 9(7), e101556. <https://doi.org/10.1371/journal.pone.0101556>
- Noman, M. A., Mamunur, R., Islam, M. S., & Hossain, M. B. (2019). Spatial and seasonal distribution of intertidal macrobenthos with their biomass and functional feeding guilds in the Naf River estuary, Bangladesh. *Journal of Oceanology and Limnology*, 37(3), 1010–1023. <https://doi.org/10.1007/s00343-019-8063-7>
- Rahman, M. H., Hossain, M. B., Habib, A., Noman, M. A., & Mondal, S. (2021). Mangrove associated macrobenthos

- community structure from an estuarine island. *Biodiversitas Journal of Biological Diversity*, 22(1), 247–252. <https://doi.org/10.13057/biodiv/d220130>
- Rahman, M. K., Hossain, M. B., Majumdar, P. R., Mustafa, M. G., Noman, M. A., Albeshr, M. F., Bhat, E. A., & Arai, T. (2022). Macrobenthic assemblages, distribution and functional guilds from a freshwater-dominated tropical estuary. *Diversity*, 14(6), 473. <https://doi.org/10.3390/d14060473>
- Real, M. K. H., Mia, M. Y., Kumar, U., & Khanam, N. (2018). Seasonal and land type based soil chemical and nutrient status in agricultural lands of coastal district, Bagerhat, Bangladesh. *International Journal of Environment*, 7(1), 41–59. <https://doi.org/10.3126/ije.v7i1.21293>
- Rehitha, T. V., Madhu, N. V., Vineetha, G., Vipindas, P. V., Resmi, P., & Revichandran, C. (2019). Spatio-temporal variability in macrobenthic communities and trophic structure of a tropical estuary and its adjacent coastal waters. *Environmental Monitoring and Assessment*, 191(6), 341. <https://doi.org/10.1007/s10661-019-7460-x>
- Saad, S. A., & Wade, C. M. (2017). Seasonal and spatial variations of saltmarsh benthic foraminiferal communities from North Norfolk, England. *Microbial Ecology*, 73(3), 539–555. <https://doi.org/10.1007/s00248-016-0895-5>
- Sarker, S., Bhuyan, M. A. H., Rahman, M. M., Islam, M. A., Hossain, M. S., Basak, S. C., & Islam, M. M. (2018). From science to action: Exploring the potentials of Blue Economy for enhancing economic sustainability in Bangladesh. *Ocean & Coastal Management*, 157, 180–192. <https://doi.org/10.1016/j.ocecoaman.2018.03.001>
- Sharif, A. S. M., Islam, S., & Islam, M. (2017). Occurrence and distribution of macrobenthos in relation to physico-chemical parameters in the lower Meghna River estuary, Bangladesh. *International Journal of Marine Science*, 7(12), 102–113. <https://doi.org/10.5376/ijms.2017.07.0012>
- Sheaves, M., Baker, R., Abrantes, K. G., & Connolly, R. M. (2017). Fish biomass in tropical estuaries: Substantial variation in food web structure, sources of nutrition and ecosystem-supporting processes. *Estuaries and Coasts*, 40(2), 580–593. <https://doi.org/10.1007/s12237-016-0159-0>
- Shen, P.-P., Zhou, H., Lai, H.-Y., & Gu, J.-D. (2006). Benthic infaunal composition and distribution at an intertidal wetland mudflat. *Water, Air, and Soil Pollution: Focus*, 6(5–6), 575–581. <https://doi.org/10.1007/s11267-006-9042-5>
- Sultana, T., Islam, M. T., Rahman, M. S., Siddique, A. B., Huda, A. S., & Sarker, S. (2023). Evaluating the long-term geomorphic process in-relation to hydrodynamics in the central coastal zone of Bangladesh. *Heliyon*, 9(6), e17368. <https://doi.org/10.1016/j.heliyon.2023.e17368>
- Svensson, J. R., Lindegarth, M., Jonsson, P. R., & Pavia, H. (2012). Disturbance–diversity models: What do they really predict and how are they tested? *Proceedings of the Royal Society B: Biological Sciences*, 279(1736), 2163–2170. <https://doi.org/10.1098/rspb.2011.2620>
- Tampo, L., Kaboré, I., Alhassan, E. H., Ouéda, A., Bawa, L. M., & Djaneye-Boundjou, G. (2021). Benthic macroinvertebrates as ecological indicators: Their sensitivity to the water quality and human disturbances in a tropical river. *Frontiers in Water*, 3, 662765. <https://doi.org/10.3389/frwa.2021.662765>
- Van Colen, C., Verbelen, D., Devos, K., Agten, L., Van Tomme, J., Vincx, M., & Degraer, S. (2014). Sediment-benthos relationships as a tool to assist in conservation practices in a coastal lagoon subjected to sediment change. *Biodiversity and Conservation*, 23(4), 877–889. <https://doi.org/10.1007/s10531-014-0638-1>

- 689 Washburn, T. W., Reuscher, M. G., Montagna, P. A., Cooksey, C., & Hyland, J. L. (2017). Macrobenthic community
690 structure in the deep Gulf of Mexico one year after the Deepwater Horizon blowout. *Deep Sea Research Part I:
691 Oceanographic Research Papers*, 127, 21–30. <https://doi.org/10.1016/j.dsr.2017.06.001>
- 692 Ysebaert, T., & Herman, P. M. (2002). Spatial and temporal variation in benthic macrofauna and relationships with
693 environmental variables in an estuarine, intertidal soft-sediment environment. *Marine Ecology Progress
694 Series*, 244, 105-124. <https://doi.org/10.3354/meps244105>
- 695 Zhang, J., Xu, F., & Liu, R. (2012). Community structure changes of macrobenthos in the South Yellow Sea. *Chinese
696 Journal of Oceanology and Limnology*, 30(2), 248–255. <https://doi.org/10.1007/s00343-012-1076-0>