BENTHIC BIODIVERSITY OF THE INDIAN OCEAN

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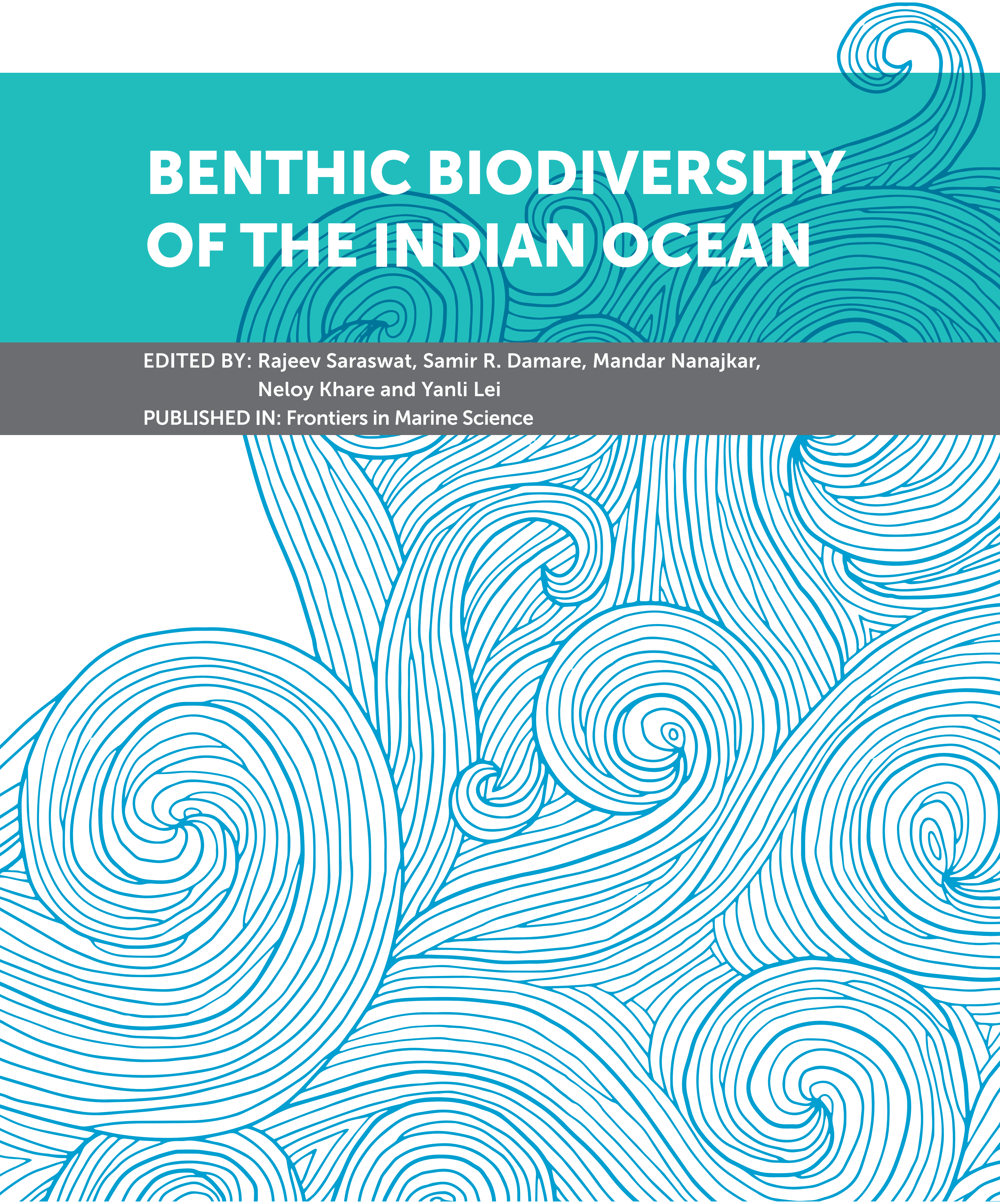

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BENTHIC BIODIVERSITY OF THE INDIAN OCEAN

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Table of Contents

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Editorial: Benthic Biodiversity of the Indian Ocean

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Editorial on the Research Topic

Benthic Biodiversity of the Indian Ocean

INTRODUCTION

Benthic organisms are an important component of the marine biodiversity. Although the benthic organisms constitute only a fraction of the total marine biomass (Bar-On and Milo, 2019), their contribution to the remineralization and biogeochemical cycling of different elements in the ocean is immense (Bourgeois et al., 2017; Aller and Cochran, 2019). Benthic biomass varies from as low as ∼1.5 mg C/m^2 in the deep abyssal regions to as high as ∼4.0 mg C/m^2 in the highly productive marginal marine regions (Wei et al., 2010). The biomass estimates are highly uncertain due to the limited information about the distribution of marine organisms in the deeper oceans (Ichino et al., 2015). A large number of studies on marine benthic biodiversity are restricted to the marginal marine regions including the continental shelves and slopes (Wei et al., 2010). The regions deeper than 3,000 m, comprising ∼75% of the total oceanic area contribute ∼50% of the total marine benthic biomass (Wei et al., 2010). Marine benthic organisms survive on the organic matter flux from the ocean surface and thus are highly vulnerable to the changes in the surface primary productivity (Yool et al., 2017). Therefore, it is important to document the benthic biodiversity of oceans and also to understand their contribution to the elemental cycling.

The Indian Ocean, the only ocean with its northern landlocked boundary in the tropics is unique in several aspects. The northern Indian Ocean has one of the world's most intense oxygen-deficient zone at the intermediate depth. The waters on its margins turn hypoxic seasonally (Naqvi, 2021). These oxygen-deficient zones support a unique biota (Sivadas et al., 2020; Suokhrie et al., 2020), with the capability to denitrify (Sokoll et al., 2012). The chemosynthetic community is abundant in the hydrothermal vents on the mid-oceanic ridges (Perez et al., 2021), as well as the submarine volcanoes in the Andaman-Nicobar region. The vast gas hydrate reserves along the margins of several Indian Ocean rim countries also house unique biodiversity (Mazumdar et al., 2019). Therefore, it is imperative to understand not only the host-substrate relationship of benthic biota inhabiting these diverse environments in the Indian Ocean, but also their unique adaptations as well as the contribution to the elemental cycling in this region. This Research Topic was proposed to include the contributions on benthic biodiversity of the Indian Ocean and its influence on the biogeochemical cycling.

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CURRENT STATUS OF THE INDIAN OCEAN BENTHIC BIODIVERSITY STUDIES

The benthic diversity of the Indian Ocean has been explored for the meiobenthic, macro-benthic, and mega-benthic organisms and the best-explored habitats are the coastal and intertidal ecotones while the sampling effort decreases as we go deeper offshore (Wafar et al., 2011). Although sparse and sporadic, the slopes have sizable benthic diversity records, primarily from the marginal regions of India, South Africa and a few gulf countries. Among the coastal habitats, rocky shores, sand flats, and the mudflats (including mangroves) have been well-studied for mostly macro-benthic community. There are several autecological studies as part of the doctoral thesis for a few important benthic organisms such as horseshoe crabs, large gastropods, polychaetes, bivalves, as well as numerous studies on toxicological experiments using benthic species as model organisms. Although the Indian Ocean harbors rich reef habitats, most of the earlier studies extensively focused on documenting the species. However, with the advent of climate induced coral bleaching and the subsequent eradication of reef habitats, the major focus has shifted to understanding the responsible factors and their varied effects on the reef community. The mega-benthic communities of the shelf region are well-inventoried as a part of the benthic fishery documentation while it also enabled the description of many new species as part of the by-catch investigation. The shallow subtidal areas and the shelf macro-faunal community have been well-investigated in the past two decades, with a large emphasis on polychaete fauna especially due to their use as "indicator species" of anthropogenic perturbation. There were several programs that aided the exploration of deep sea benthic biodiversity which were initiated with the onset of the Indian Ocean Expedition in the 60's/80's followed by the poly-metallic nodule and ridge programme for the exploration of deep-sea resources. The studies from the deep Indian Ocean are, however, limited. There are multiple constraints that govern these limiting factors such as funding, logistics, expertise, and long-term programmes.

SYNTHESIS OF SPECIAL ISSUE PUBLICATIONS

The papers published in this Research Topic include diverse groups of marine benthic organisms including, corals, sponges, foraminifera, nematode, gastropod, bivalve, fungi, bacteria, and barnacles. This Research Topic highlights the work from the Indian Ocean, which is beyond just the community structure but includes aspects of seasonality, functioning and their comprehensive distribution with respect to regions.

The 2,360 km long coast of North West India, is a heavily industrialized and urbanized zone. This coast with unique biogeographical and climatic features with two notified marine protected areas also supports rich biodiversity. Therefore, it is imperative to collate and review the base line data of marine macrobenthos of North West India mainly because the tropical ecosystems sustain higher biodiversity and face faster species extinction. Sukumaran et al., have aptly provided an overview of these macrobenthos. In order to understand the status of studies from the deeper regions, Barnes et al. have provided a detailed review of the bacterial and fungal diversity in the abyssal regions of the Indian Ocean. The authors note that as compared to other oceans, bacterial and especially fungal diversity studies are limited from the deeper Indian Ocean. The work on the meiofaunal community by Ghosh and Mandal from the Sundarbans, the largest mangrove forest on earth, located on the east coast of India, showed a marked seasonality. The study documents 11 meiobenthic taxa dominated by nematodes. The functions derived from morphological traits reveal that most of the species are opportunistic and feed on organic matter. Sautya et al. studied the distribution pattern of the benthic meiofaunal community from the western Indian continental margin, including the oxygen-deficient zones and the abyssal plain. A total of 22 taxa (groups) were found, with nematodes dominating the population. The article by Gajera et al. is an elaborate work on the coastal gastropod's radular morphology. Radula is an important anatomical feature, specific to a species as well as affecting the feeding ecology of the gastropods. They provide useful insights in to the differences within taxa and similarities in closely related clades, which were also assessed *via* the construction of a phylogenetic tree of the species. The other two articles focus on the distribution of barnacles and the influence of environmental settings on their habitat preference from the coastal habitats of the Indian subcontinent. The article by Trivedi et al. gives a comprehensive inventory of barnacles' distribution in different eco-regions of India with the validation of species occurrence. The other study by Buasakaew et al. emphasizes the role of salinity and temperature, as it deters the recruitment of barnacles in the rock pools, while the submergence time also plays a significant role in the recruitment success.

Marine sponges are sessile filter feeders. Sponges maintain a continuous water flow to obtain food and oxygen. Their structural components are species specific, affecting sponge morphology and pumping capacity. Dahihande and Thakur investigated the influence of different structural components on the pumping capacity of the marine sponges. Mote et al. report an interesting host-symbiont relationship in the corals and sponges. They report a significant difference in the abundance and diversity of Symbiodiniaceae in the encrusting sponge and coral. A highly diverse bivalve population modulated by the multitude of oceanographic parameters, has been found along the eastern margin of India, by Chattopadhyay et al. A decreasing bivalve diversity is found on both the northern and southern side of 14°N latitude, which is different from the widely accepted latitudinal biodiversity gradient.

The presence of hard parts in several marine microorganisms, like the foraminifera and diatoms, helps in the long-term preservation of the ecological signatures. Minhat et al. have studied the influence of ambient conditions, including the depth and organic matter, on the distribution of foraminifera in the Strait of Malacca. Similarly, Suokhrie et al. reported depth specific benthic foraminifera assemblages from the Bay of Bengal. A strong influence of the riverine influx, coupled with the organic matter and dissolved oxygen, is reported on benthic foraminifera distribution and diversity. The remains of such skeleton bearing organisms are an excellent tool to reconstruct the past climate and oceanographic conditions. Verma et al. have used the temporal changes in the benthic foraminiferal assemblage to reconstruct millennial-scale changes in the monsoon induced productivity, the subsequent organic matter flux to the ocean bottom and the development of the oxygen deficient zones, in the western Bay of Bengal during the last 45 kyr. A large shift in the dissolved oxygen concentration is observed during the last glacial interval as compared to the Holocene.

THE WAY FORWARD

The contributions in this Research Topic are miniscule as compared to the expected biodiversity of the Indian Ocean. We recommend to make global efforts to explore the benthic biodiversity of the Indian Ocean. The future research efforts should be directed toward understanding the factors modulating the diversity of benthic macro-, meio- and microfauna, fungi, bacteria, and viruses, especially from the specialized habitats and deeper regions of the Indian Ocean.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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ORIGINAL RESEARCH
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The Occurrence and Distribution of Benthic Foraminifera in Tropical Waters Along the Strait of Malacca

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Foraminifera are shelled single-celled protists that are found in all marine environments. Benthic foraminifera either live in sediments or attach to surfaces on the seafloor. Understanding the distribution and ecological response of benthic foraminifera is crucial, as they can indicate past and current ocean conditions. However, the benthic foraminifera distribution along the busy Strait of Malacca, which connects the Indian Ocean (north) to the Java Sea (south), is undersampled. In this study, we collected 24 surface samples from the northern Strait of Malacca to understand the distribution of foraminifera assemblages in shallow tropical waters. A total of 49 species of benthic foraminifera were identified. Calcareous hyaline species dominated the assemblages, with an extremely low occurrence of calcareous porcelaneous species. The common calcareous hyaline taxa were *Asterorotalia pulchella*, *Pseudorotalia schroeteriana*, *Discorbinella bertheloti*, *Ammonia tepida*, and *Heterolepa praecincta*. Cluster analysis categorised the foraminiferal assemblages into three major groups. The first cluster (Group A) consisted of a more diverse assemblage of hyaline and agglutinated species that inhabited a mean water depth of 45 m. The second cluster represented a population that inhabited deeper water environments (average water depth of 59 m). Finally, the third cluster (Group C) consisted of a foraminifera assemblage that inhabited shallow coastal environments (average depth of 22 m) with higher organic matter enrichment. The multivariate canonical correspondence analysis (CCA) showed that the foraminiferal assemblages reflected the shallow to deep water transition in the Malacca Strait. Water depth, which defines the depositional environment, had a greater influence on foraminifera distribution here than organic matter and salinity.

Keywords: *Asterorotalia*, organic matter, monitoring, water depth, LIMA scientific expedition

INTRODUCTION

The Strait of Malacca is a shallow water passage between peninsular Malaysia and Sumatra that connects the Indian and Pacific Oceans. It is also a global shipping marine route, with more than 120,000 ships passing through the straits annually. The narrow Strait of Malacca was a savannah corridor during the Last Glacial Maximum when the sea level was much lower than the present day. Today, the shallow strait receives freshwater runoff from both peninsular Malaysia and Sumatra, resulting in more hyposaline environments closer to the coastline. These characteristics have endowed the region with abundant non-renewable and renewable resources, including profitable coastal ecosystems, aquaculture, coastal tourism, extensive capture fisheries, valuable natural gas reserves, and mining (Evers and Gerke, 2006). However, the region is also repeatedly threatened by the overexploitation of living resources and the introduction of harmful domestic and industrial waste (Chua et al., 2000). With growing maritime and coastal activities, key stakeholders are under increasing pressure to minimise the future impact on environmental services along the Malacca Strait.

Foraminifera can help monitor the environmental status of both sandy and soft-bottom marine ecosystems (Hallock et al., 2003; Sreenivasulu et al., 2019; Sousa et al., 2020). Due to their widespread distribution, modern benthic foraminifera have been used to assess the ecological health of lagoon environments (Culver et al., 2012; Bouchet et al., 2018), estuaries (Nagendra and Reddy, 2019; Sreenivasulu et al., 2019), coral reefs (Nurruhwati et al., 2020; Prazeres et al., 2020), and modern harbours (Dijkstra et al., 2017). Moreover, foraminiferal assemblages are influenced by their immediate environment and have often served as modern and past analogues to characterise paleoenvironments (Rao et al., 2013; Benito et al., 2016; Minhat et al., 2016; Kemp et al., 2018). Therefore, documenting and understanding the regional distribution of foraminifera are essential. This study documented the distribution of benthic foraminifera species in the Malacca Strait. We also assessed the dominant environmental factors influencing benthic foraminifera distribution in one of the world's busiest shipping lanes.

STUDY AREA

The northern region of the Strait connects with the deeper Andaman Sea and is more saline (>34 PSU) than the middle and southern sectors of the strait (Amiruddin et al., 2011). Major rivers from Sumatra and peninsular Malaysia discharge approximately 19 × 10^{10} m^3 of freshwater annually to both sites of the strait, creating hyposaline conditions along most parts of the strait (Hii et al., 2006; Amiruddin et al., 2011). Numerous ecosystems have been reported along the strait, including mangroves, coral reefs, seagrass, and extended mudflats (Yasin et al., 2019). Two tropical monsoon seasons influence the weather along the Strait of Malacca. These monsoon winds create wetter conditions during the northeast monsoon period and drier conditions during the southwest monsoon period (Hii et al., 2006; Amiruddin et al., 2011).

SAMPLE COLLECTION

A total of 24 surface sediment samples were collected using a Smith McIntyre grab onboard the UMT RV Discovery (15 × 5 m) during the UMT Scientific Expedition Voyage LIMA'19 from 13 to 23 March, 2019. These samples were collected along the northern regions of the Malacca Strait within Malaysian waters (**Figure 1**). We collected sub-samples from the bulk sediments for both sediment (~40 g) and foraminifera analyses (10 cm^3; 10 cm^2 × 1 cm; Scott and Medioli, 1980; Minhat et al., 2020). Ethanol solution (>70%) was used to preserve the foraminifera samples. We recorded the coordinates of each station, and water depth and bottom water salinity were measured using a Conductivity, Temperature,

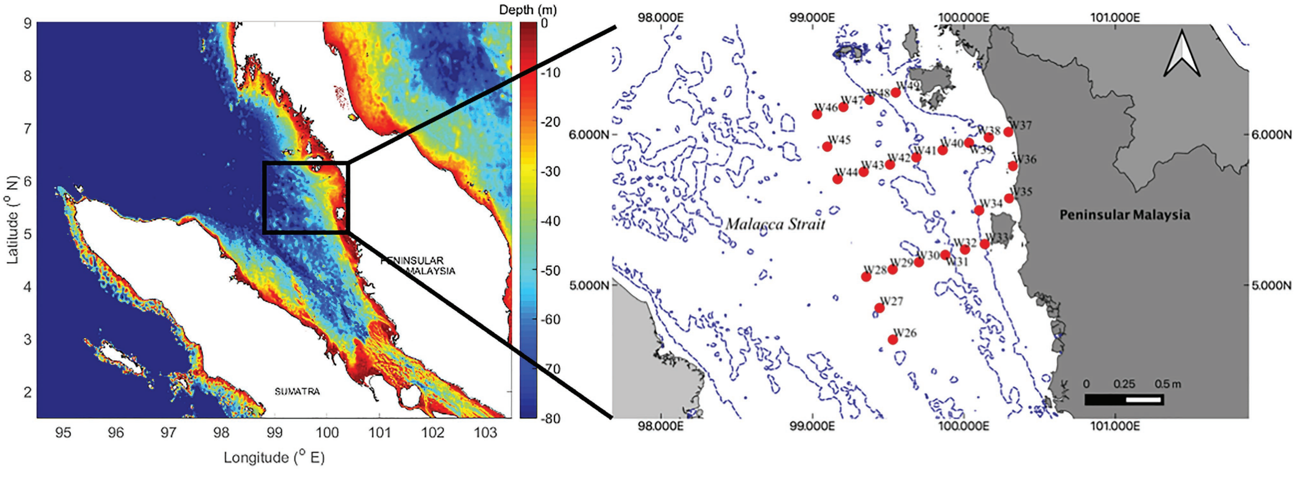

FIGURE 1 | Twenty-four sampling stations located in the northern sector of the Malacca Strait. All samples were collected within Malaysian waters.

Depth (CTD) castaway profiler. We obtained salinity records for all stations except W35, as the depth was too shallow for CTD deployment.

LABORATORY ANALYSIS

Foraminifera Analyses

Sediment samples were passed through 63 μm sieves under running tap water (Schönfeld et al., 2012). The residues on the sieve were decanted into labelled boats and left to dry overnight in an oven at 50°C. The dried foraminifera samples were then transferred and stored in plastic bags until analysed.

Prior to sorting, the samples were equally divided into aliquots using a microsplitter. A total of 300 foraminifera specimens were randomly picked from a gridded picking tray using a fine artist brush and then sorted on micropalaeontology slides. During the picking process, foraminiferal tests that were discoloured, broken, or poorly preserved (Yordanova and Hohenegger, 2002) were excluded. The sorted specimens were identified at the species level based on Loeblich and Tappan (1988, 1994) and regional taxonomic references (Szarek, 2001; Martin et al., 2018; Minhat et al., 2020).

Sediment and Organic Matter Analyses

The sediment grain size was determined *via* the dry sieving method (Folk, 1980), and the organic matter composition was determined *via* the loss-on-ignition method (Heiri et al., 2001).

Computation of Diversity Indices and Statistical Analyses

To compare our results with previous work by Minhat et al. (2020), Fisher's alpha diversity and Pielou's evenness indices (Pielou, 1969) were calculated using PRIMER v.6 software (Clarke and Gorley, 2006). To avoid using reworked specimens, only foraminiferal taxa with a relative abundance of >2% in atleast one sample were used to determine the foraminiferal zonation and fauna-environment relationship. The Q-mode hierarchical cluster analysis based on the Euclidean distance similarity measure was used to understand the biozonation of foraminiferal assemblages (Mello and Buzas, 1968; Culver et al., 2012; Azmi et al., 2020). Multivariate canonical correspondence analysis (CCA) was calculated using XLSTAT software to determine the influence of environmental variables, water depth, and sediment characteristics on foraminiferal assemblages. The CCA was performed on all 49 foraminifera species with >2% relative abundance.

RESULTS

Environmental Conditions Along the Northern Sector of the Malacca Strait

The water depth of the study area ranged from 9 to 86 m, with recorded salinities of 32–34 PSU (**Table 1**; **Figure 2A**). The average proportion of organic matter in this study was 7.1%, with the highest organic matter content recorded at station W36 (17%; **Figure 2B**). Most stations were predominantly sandy, with a sand composition of 97% at W30. Moreover, stations with deeper water depths (>60 m) had relatively high mud compositions (mud >60%; **Figures 2C**,**D**).

TABLE 1 | List of 24 stations within the Malacca Straits with station coordinates, water depth, salinity, organic matter, and sand and mud compositions.

Stations	Longitude	Latitude	Water depth (m)	Salinity (PSU)	Organic matter (%)	Sand (%)	Mud (%)
W26	99.53160	4.63997	60.0	34.0	7.0	72.0	27.0
W27	99.44375	4.84896	68.0	34.1	8.0	48.0	51.0
W28	99.35590	5.05796	68.0	34.1	10.0	48.0	51.0
W29	99.52960	5.10588	71.0	34.1	7.0	87.0	13.0
W30	99.70329	5.15380	63.0	34.0	5.0	97.0	3.0
W31	99.87698	5.20172	55.0	33.2	5.0	82.0	17.0
W32	100.00724	5.23766	46.0	33.0	6.0	76.0	25.0
W33	100.13751	5.27361	24.0	31.7	14.0	68.0	30.0
W34	100.10020	5.49654	25.0	32.0	13.0	76.0	23.0
W35	100.29854	5.57636	9.2	n/a	10.0	74.0	26.0
W36	100.32448	5.79165	10.3	32.0	17.0	71.0	27.0
W37	100.29401	6.01648	10.0	32.1	16.0	77.0	22.0
W38	100.16374	5.98053	21.0	31.9	1.2	37.4	62.6
W39	100.03348	5.94459	27.0	31.9	1.5	13.8	86.2
W40	99.85979	5.89667	38.0	32.3	8.2	53.3	46.7
W41	99.68610	5.84875	52.0	31.6	8.3	85.3	14.7
W42	99.51240	5.80083	57.0	33.8	3.6	27.9	72.1
W43	99.33871	5.75291	71.0	34.1	3.0	55.4	44.6
W44	99.16502	5.70499	62.0	33.9	1.9	20.1	79.9
W45	99.09714	5.91949	86.0	34.2	3.6	22.2	77.8
W46	99.02926	6.13399	68.0	34.1	2.4	44.2	55.8
W47	99.20295	6.18191	63.0	34.0	1.5	85.6	14.4
W48	99.37664	6.22984	57.0	33.6	12.4	56.4	43.6
W49	99.55034	6.27776	46.0	32.5	3.6	51.0	49.0

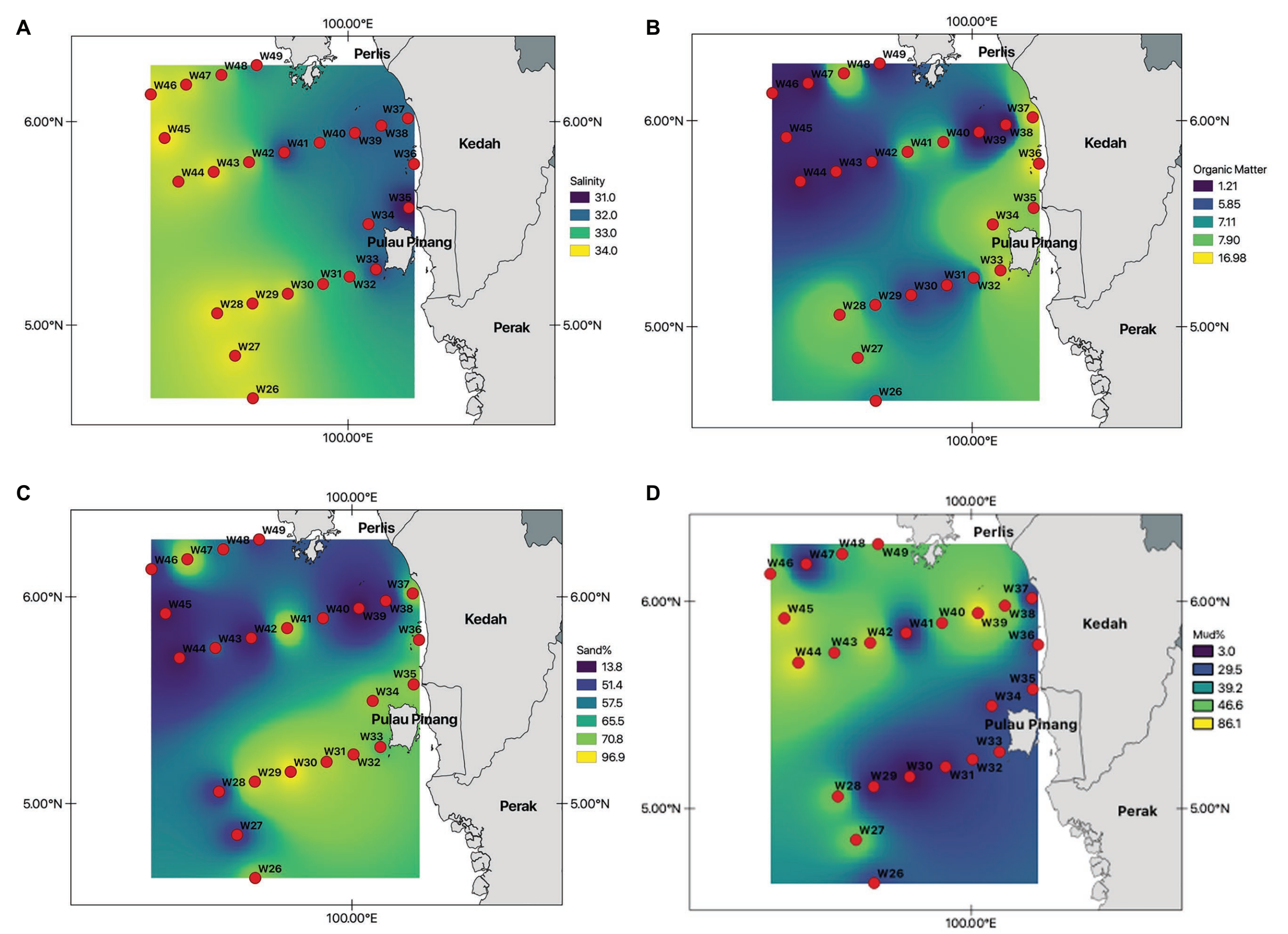

FIGURE 2 | Selected environmental variables recorded at all 24 stations within the northern sector of Malacca Straits. **(A)** – Salinity (PSU); **(B)** – Organic matter (%); **(C)** – Sand (%); and **(D)** – Mud (%).

Foraminiferal Assemblages

A total of 90 foraminifera species were identified from the 24 stations in the northern region of the Strait of Malacca. However, only 49 species had >2% relative abundance, and 20 species had >10% relative abundance in atleast one station (**Supplementary Table S1**). On average, the calcareous hyaline (86%) group dominated the total foraminifera assemblages in the study area. In comparison, the agglutinated group and porcelaneous group accounted for 13 and <1% of the total assemblages, respectively (**Table 2**). The common calcareous hyaline species identified were *Asterorotalia pulchella*, *Pseudorotalia schroeteriana*, *Discorbinella bertheloti*, *Ammonia tepida*, and *Heterolepa praecincta* (**Figure 3**). Of these, *A. pulchella* was recorded at all sampling stations and was therefore the most common species in the study area (**Table 2**). Moreover, four other species (*P. schroeteriana*, *D. bertheloti*, *A. tepida*, and *H. praecincta*) were recorded at more than 15 stations.

The assemblage diversity, measured by Fisher's alpha (α), ranged between 1.11 (W37) and 7.56 (W30 and W31), and the number of species present at each station was between $S = 5$ and $S = 20$ (**Table 2**). The species distribution was the most evenly distributed [Pielou evenness (J') = 0.82] at W29 and the least evenly distributed (J' = 0.25) at W34. The latter site was dominated by *A. pulchella* (76%).

Cluster Analysis

The Q-mode hierarchical cluster analysis based on the 24 stations produced three distinct groups (**Figure 4**). The first cluster (Group A) included samples from eight stations with an average water depth of 45 m. The foraminiferal assemblage within this group was dominated by *A. pulchella* (19%), followed by *D. bertheloti* (8%), and *Elphidium advenum* (7%). Agglutinated taxa, such as *Agglutinella agglutinans* (3%) and *Textularia* spp. (1–4%), were also relatively higher in Group A than in the other groups. The second cluster (Group B) contained half of the sampling stations that were generally located at deeper water depths (average water depth = 59 m). This group was co-dominated by *A. pulchella* (16%) and *Bolivina glutinata* (15%). Moreover, the porcelaneous species *Quinqueloculina*

TABLE 2 | Distribution of hyaline, agglutinated, and porcelaneous foraminifera groups within the Malacca Straits. The computed diversity indices and Fisher alpha (α) are also included.

Site	Hyaline (5%)	Agglutinated (%)	Porcelaneous (%)	No. of species	Fisher alpha (α)	Evenness (J')
W26	58	42	0	17	5.94	0.74
W27	85	15	0	18	6.41	0.64
W28	69	31	0	18	6.47	0.72
W29	46	54	0	19	6.95	0.82
W30	51	49	0	20	7.56	0.80
W31	65	35	0	20	7.56	0.75
W32	53	47	0	18	6.41	0.74
W33	100	0	0	10	2.77	0.34
W34	99	1	0	12	3.56	0.25
W35	83	17	0	12	3.56	0.67
W36	100	0	0	6	1.40	0.56
W37	97	3	0	5	1.11	0.55
W38	100	0	0	9	2.40	0.54
W39	95	5	0	11	3.17	0.58
W40	96	3	1	17	5.94	0.57
W41	98	2	0	19	7.03	0.63
W42	99	1	0	13	3.99	0.56
W43	97	0	0	14	4.51	0.60
W44	100	0	0	13	4.02	0.66
W45	92	4	4	15	4.94	0.77
W46	99	1	0	16	5.38	0.59
W47	100	0	0	12	3.56	0.65
W48	99	0	1	14	4.47	0.74
W49	100	0	0	20	7.48	0.69

crassicarinata was only recorded in Group B. Finally, the third cluster (Group C) consisted of a foraminiferal assemblage from shallow coastal waters (average water depth = 23 m) and was dominated by three species: *A. pulchella* (27%), *Ammonia convexa* (26%), and *A. tepida* (21%). Agglutinated species were absent in Group C, except for *Trochaminna* sp. 1, which had very low abundance (1%).

Species-Environment Relationship

The total variance calculated by CCA between species and the environmental parameters was 70.1% for both axis-1 (eigenvalue: 0.61) and axis-2 (eigenvalue: 0.33; **Figure 5**). The results of the Monte Carlo permutation test ($p < 0.0001$; 500 permutation reduced model) suggest that these variables (i.e., water depth, salinity, organic matter content, and percentage of sand and mud) significantly influenced the foraminiferal distribution in the Malacca Strait. CCA axis-1 showed that water depth and organic matter content were the two most significant variables influencing foraminiferal distribution. This axis also reflects the shallow to deep water transition in the Malacca Strait.

DISCUSSION

Species Composition

The most common species recorded at all stations was *A. pulchella*, with a relative abundance of 1–76%. This species, which was identified as *Asterorotalia trispinosa* by Panchang and Nigam (2012) along the Myanmar shelf, prefers low salinity and fine-grained sediment. In this study, the relative abundance of *A. pulchella* was >10% in stations with a salinity of 32 PSU or less. In addition, the relatively higher abundance of *A. pulchella* (>40%) in the Malacca Strait was associated with a water depth of 21–25 m. *Pseudorotalia schroeteriana* was also common in the Malacca Strait (present in 20 out of the 24 stations) but in low relative abundances (<10%). Moreover, the distribution of *D. bertheloti* was observed at 50–60 m water depth at relative abundances of >15%. A similar finding was reported by Azmi et al. (2020) in the southern region of the South China Sea, where *D. bertheloti* represented 20% of the foraminiferal assemblages at ~56 m depth. We, therefore, confirm that this species represents depths of 50–60 m in sandy tropical waters. *Heterolepa praecincta* is another common species that contributed >10% to the foraminiferal assemblages in deep-water environments (57–71 m water depth). Both *D. bertheloti* and *H. praecincta* were absent in samples from stations W36 and W37, where *A. tepida* (37–40%) appears to dominate. The higher organic matter composition (>15%) allowed stress tolerance taxa, such as *A. tepida*, to flourish.

Foraminifera Species-Environment Relationship

The CCA results suggest that the distribution of benthic foraminifera within the Malacca Strait varies with water depth (**Figure 5**). The cluster analysis produced three groups of foraminifera assemblages (**Figure 4**), which represented the transition from shallow to deep water environments (**Figure 5**). The Group A assemblage represented samples obtained from locations with varying magnitudes of environmental gradients; agglutinated foraminifera were also present in these samples.

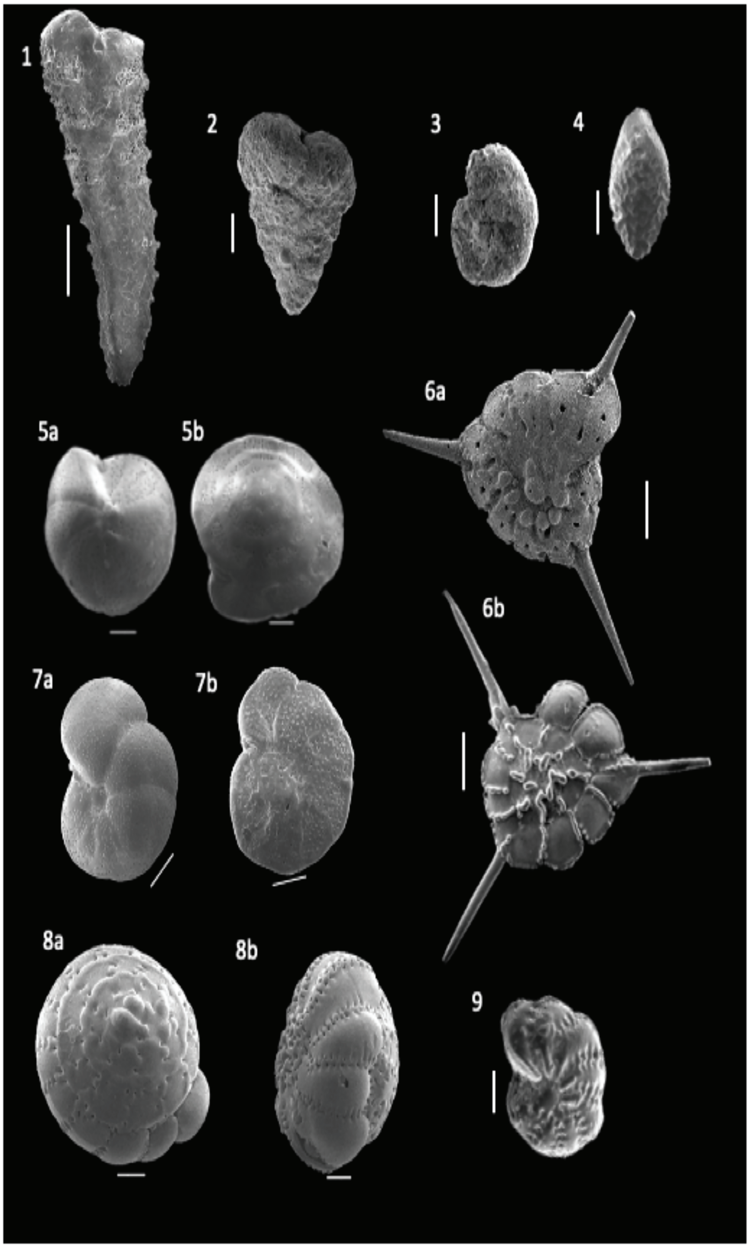

FIGURE 3 | Scanning Electron Microscope images of among the benthic foraminifera identified from Malacca Straits. **(1)** *Textularia fistula* (magnification- x70; scale bar = 200 μm). **(2)** *Textularia fistula* (magnification- x150; scale bar = 100 μm). **(3)** *Trochammina* sp. 1 (magnification- x150; scale bar = 100 μm). **(4)** *Bolivina glutinata* (magnification- x250; scale bar = 100 μm). **(5a)** *Heterolepa praecincta* (magnification- x150; scale bar = 100 μm). **(5b)** *Heterolepa praecincta* (magnification- x140; scale bar = 100 μm). **(6a)** *Asterorotalia pulchella* (magnification- x70; scale bar = 200 μm). **(6b)** *Asterorotalia pulchella* (magnification- x85; scale bar = 200 μm). **(7a)** *Discorbinella berteloti* (magnification- x100; scale bar = 100 μm). **(7b)** *Discorbinella berteloti* (magnification- x180; scale bar = 100 μm). **(8a)** *Pseudorotalia indopacifica* (magnification- x60; scale bar = 200 μm). **(8b)** *Pseudorotalia indopacifica* (magnification- x55; scale bar = 200 μm). **(9)** *Elphidium advenum* (magnification- x200; scale bar = 100 μm).

This group can be further divided into subgroups A1 and A2. The foraminifera assemblages of A1, which correlated with deeper water and sandy substrates, showed a more diverse species distribution (average Fisher's alpha = 6.43; **Table 2**). The abundance of agglutinated foraminifera was also higher in A1 than in other groups. For example, *Textularia* spp. (13–24%) and *A. agglutinans* (4–9%) showed relatively higher abundances at water depths of 55–71 m (stations W29–31). In contrast, the relative abundance of agglutinated foraminifera was lower in Group A2 and was correlated with higher percentages of mud. Within Group A2 assemblages, *A. pulchella* and *E. advenum* were more abundant in the

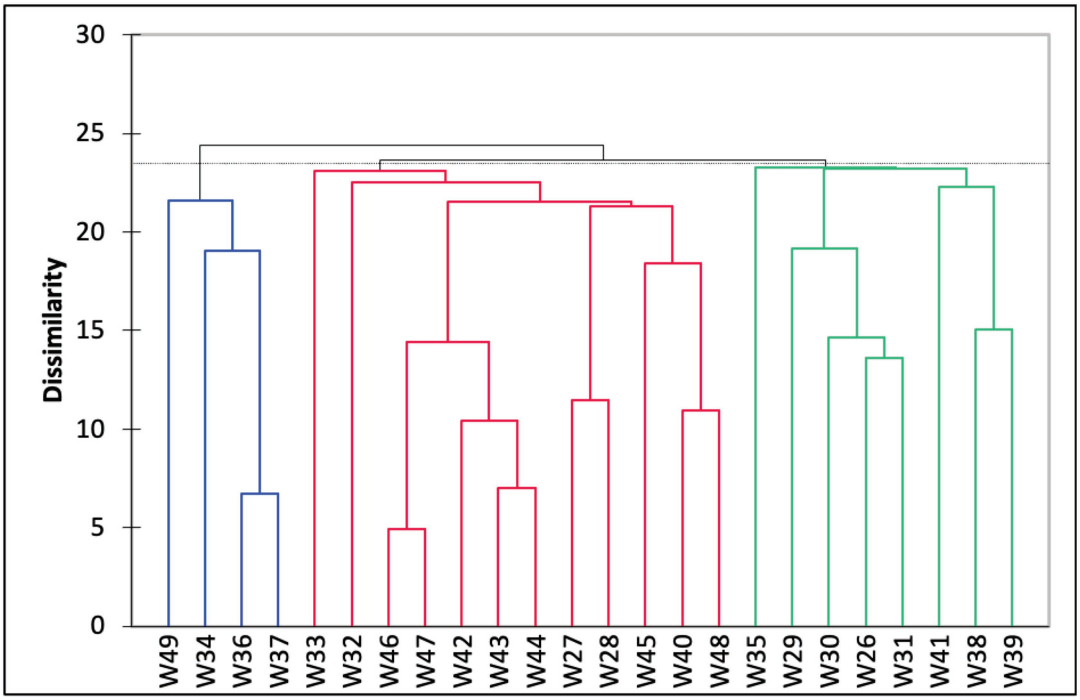

FIGURE 4 | Dendrogram based on hierarchical cluster analysis on all 24 samples collected in the study area, Malacca Straits. The clusters were defined into three major clusters (i.e., Groups A–C) based on the dissimilarity between cluster groups.

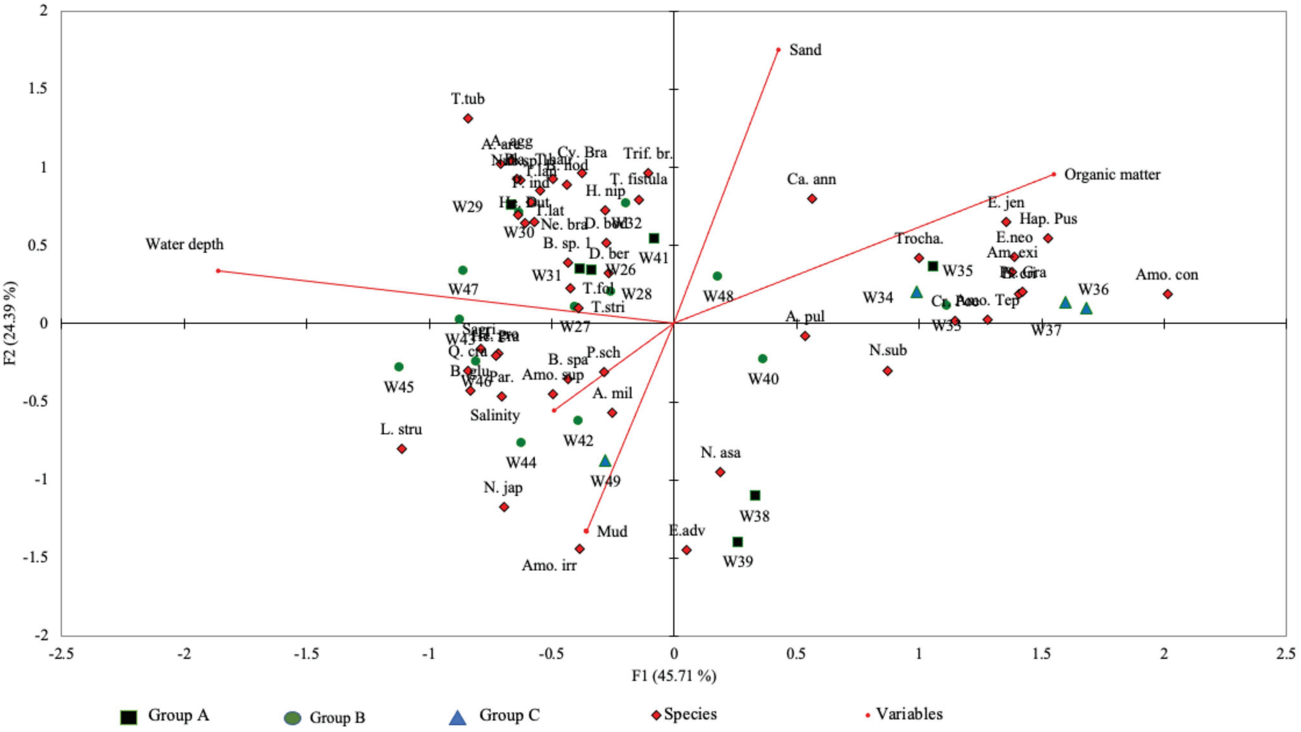

FIGURE 5 | Canonical correspondence analysis (CCA) triplot based on species-environmental relationship along the Malacca Straits. The total variances of both axes were 70.1%.

muddy substrate. In addition, *E. advenum* only showed >15% relative abundance at stations W38 and W39, which belong to the Group A2 assemblages. Similar species have been reported in the muddy substrates of the Andaman Sea at water depths of 4–20 m (Gandhi et al., 2016). This explains the maximum abundance of this species at similar water depths within the Malacca Strait.

Group B was characterised by open marine foraminiferal assemblages. Most of the stations belonged to this group and had water depths of >40 m. Although *A. pulchella* was the dominant species in Group B, its relative abundance was much lower than that of the other cluster groups. Instead, *Bolivina* spp. had a higher relative abundance in Group B assemblages, and the maximum abundance of *B. glutinata* (38%) was observed at station W42. *Bolivina* spp. is opportunistic taxa that may tolerate low oxygen conditions and prefer substrates with higher organic matter content (Murray, 2006; Eichler et al., 2012). The Group B assemblages were associated with muddy substrates, with an average sediment organic matter content of 6%. Group C represented foraminifera assemblages from shallow water, with a much higher sediment organic matter (average 11.5%) content than other cluster assemblages. Similar to previous reports in organic-rich sediments, *Ammonia* spp. had higher relative abundances in Group C (Melis and Violanti, 2006; Minhat et al., 2014, 2020; Martins et al., 2015). In this study, *A. tepida* and *A. convexa* together represented >80% of the total foraminiferal assemblage at stations W36 and W37, which had organic matter contents of >15%. In addition, the much higher organic matter content in Group C may be the reason for the absence of agglutinated species, except for *Textularia* spp. *Ammobaculites exiguus*, and *Trochammina* sp. 1.

This study documented the distribution and ecological preferences of foraminifera species along the busy Malacca Strait. Based on our findings, species such as *A. pulchella* were found to be useful for paleo-salinity interpretations. Moreover, understanding the distribution of *H. praecincta* and *D. bertheloti* and their correlation with water depth can help to determine past depositional environments. The Malacca Strait is one of the busiest shipping regions in the world, as it connects several major shipping ports in East and West Asia (Cheng et al., 2019). As a result, it is affected by land-based pollution from littoral states and marine-based pollution from maritime activities (Yasin et al., 2019). Malaysia is a dominant littoral state in the Malacca Strait and therefore plays a major role in monitoring and governing marine health in the region. The benthic foraminifera data reported in this study are thus highly useful for monitoring the marine conditions in the region. Despite the high volume of terrestrial discharge from various rivers to the Malacca Strait, this study reported predominantly sandy substrates in most stations, similar to those reported by Keller and Richards (1967). In addition, we found that stations located closer to the coastlines experienced hyposaline conditions and organic matter enrichment. Similar to other shallow water environments around peninsular Malaysia (Minhat et al., 2016; Martin et al., 2018; Suriadi et al., 2019), the foraminifera assemblages in the Malacca Strait are dominated by calcareous hyaline groups. The extremely low relative abundance or absence of porcelaneous groups could be attributed to the low concentration of calcium carbonate along the strait (Keller and Richards, 1967).

CONCLUSION

The benthic foraminifera along the Malacca Strait were dominated by calcareous hyaline species with extremely low numbers of porcelaneous species. *Asterorotalia pulchella* was the most common and dominant species in this study because of the relatively low salinity along the strait. According to the CCA and cluster analysis, foraminifera assemblages correspond to the transition from shallow coastal water to deeper marine environments. Depth was, therefore, the major factor influencing foraminifera species along the Malacca Strait.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

FM has proposed this study, funded the laboratory analysis, and contributed in major revision of the manuscript including statistical interpretation and writing the discussion. SG has contributed in critical revision of the manuscript with input on language and the flow of the manuscript. NA, NH, OM, and SS have involved in field samples collection, laboratory analysis of sediment foraminifera and organic matter content. LL, MAk, and MAb have contributed in the revision of the manuscript and research funding for field works. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.647531/full#supplementary-material

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Multiple Ecological Parameters Affect Living Benthic Foraminifera in the River-Influenced West-Central Bay of Bengal

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The huge riverine influx and associated processes decrease the ambient salinity, stratify the water column, modulate the oxygen-deficient zone, and are also responsible for the recent acidification in the Bay of Bengal. Here, we have studied the effect of these riverine influx-dominated ecological parameters on living benthic foraminifera in the west-central Bay of Bengal. We report that the pH below 7.6 in front of the Krishna river, reduces the diversity and the richness of living benthic foraminifera on the adjacent shelf and the slope. A similar decreased diversity and richness is also observed in front of the Godavari River. We delineate three prominent assemblages, representing different depth zones with associated distinct physico-chemical conditions. The shallow water assemblage (∼27–100 m) is represented by *Nonionella labradorica*, *Hanzawaia nipponica*, *Brizalina dilatata*, *Ammonia tepida,* and *Nonionella limbato-striata*. These species are adapted to relatively warmer temperatures and more oxygenated waters. The deepwater assemblage (∼1,940–2,494 m) includes *Bulimina* cf. *delreyensis, Bulimina marginata*, *Hormosinella guttifera*, *Cassidulina laevigata,* and *Gyroidinoides subzelandica* and can tolerate a relatively colder temperature. The intermediate-depth assemblage (∼145–1,500 m) dominated by *Eubuliminella exilis, Bolivinellina earlandi*, *Fursenkoina spinosa*, *Bolivinellina lucidopunctata*, *Globobulimina globosa, Fursenkoina spinosa, Eubuliminella cassandrae, Uvigerina peregrina, Rotaliatinopsis semiinvoluta,* and *Cassidulina laevigata*, represents oxygen-deficient and organic carbon-rich environment. Besides the pH, temperature, dissolved oxygen and organic matter, we also report a strong influence of bathymetry, coarse fraction (CF) and the type of organic matter on a few living benthic foraminifera. The ecological preferences of 40 such dominant living benthic foraminifera, each representing a specific environment, have also been reported for site-specific proxy. We conclude that although the huge riverine influx affects living benthic foraminifera on the shelf, the dissolved oxygen and organic carbon mostly control benthic foraminiferal distribution in the deeper west-central Bay of Bengal.

Keywords: foraminifera, ecology, organic matter, pH, Bay of Bengal, riverine influx

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INTRODUCTION

The huge riverine influx creates a unique environment in the Bay of Bengal. A few of the world's largest snow and rainfall-fed rivers (Irrawaddy, Ganga, Brahmaputra, Mahanadi, Krishna, and Godavari) drain freshwater and sediments into the Bay of Bengal, creating a specific environment with associated physical and chemical parameters. The riverine influx reduces the salinity, warms the seawater and creates strong stratification (Sengupta et al., 2006). The associated sediment influx contributes enormous nutrients, sustaining the primary productivity (Prasanna Kumar et al., 2002). In addition to the riverine influx, the anthropogenic input (sulfate and nitrogen aerosols) to the Bay of Bengal significantly affects its biogeochemistry (Sarma et al., 2016). Therefore, the riverine influx primarily modulates the ambient physico-chemical conditions in the northern Bay of Bengal. Additionally, the dissolved oxygen, a critical requirement of a large fraction of marine biota, is also perennially low at the Bay of Bengal's intermediate depths (Sarma et al., 2013). As suggested by the acidification and a possibility of the bay turning into the foremost nitrogen contributor soon (Bristow et al., 2017), the increasing stress implies that it is essential to understand the effect of these critical ecological parameters on the marine biota.

Benthic foraminifera are the dominant marine biota in the continental margin sediments and are the primary component of the global carbon cycling. The large abundance, combined with the sensitivity to the ambient conditions and long-term preservation in sediments, makes benthic foraminifera a widely used proxy to reconstruct paleoceanographic changes (Saraswat, 2015; Saraswat et al., 2017). The precise knowledge of the influence of ambient environmental parameters on abundance and distribution, is a prerequisite to use benthic foraminiferal characteristics for paleoceanographic and paleoclimatic interpretation (Murray, 2001; Gooday, 2003; Jorissen et al., 2007; Gooday and Jorissen, 2012; Saraswat and Nigam, 2013). Various environmental parameters, including food, oxygen concentration, salinity, pH, temperature, substrate, water depth and others, influence the diversity and abundance of benthic foraminifera (Lutze and Coulbourn, 1984; Kaminski et al., 1988; Altenbach, 1992; Mackensen et al., 1995; Gooday and Rathburn, 1999; Van der Zwaan et al., 1999; Ernst et al., 2002; Altenbach et al., 2003; Lei et al., 2017, 2019). The relative influence of various factors on faunal distribution, however, varies from region to region. The salinity and temperature are the major factors in riverine influx dominated continental shelves (Manasa et al., 2016). However, the deeper depth continental slope assemblages are mainly controlled by the availability of food and dissolved oxygen concentration (Gooday, 1986; Corliss and Chen, 1988; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Barmawidjaja et al., 1992; Jorissen et al., 1992; Rosoff and Corliss, 1992; Rathburn and Corliss, 1994; Nisha and Singh, 2012; Singh et al., 2015a, 2018; Verma et al., 2018). Benthic foraminiferal abundance, diversity, species richness and evenness also depend on ambient conditions (Gibson and Buzas, 1973; Buzas and Culver, 1991; Murray, 2006; Singh et al., 2015a,b). The overall benthic foraminiferal abundance and diversity decreases, whereas the abundance of abnormal or stress-tolerant specimen increases, under both naturally and anthropogenically stressed environment (Alve, 1995; Saraswat et al., 2004; Nigam et al., 2007). As the extent of stress varies regionally, the benthic foraminiferal response has to be assessed from different regions.

The fossil benthic foraminiferal assemblage is often biased by the biological and taphonomical processes, including transport, test disintegration or dissolution (Murray, 1991; Jorissen and Wittling, 1999; Berkeley et al., 2014). Therefore, living benthic foraminifera (rose-Bengal stained) provide a comparatively more reliable response to the ecological conditions. The previous studies on the distribution and ecology of living benthic foraminifera (rose-Bengal stained) from the northern Bay of Bengal are rare (Boltovskoy, 1978). The few studies documenting living benthic foraminifera from the Bay of Bengal cover a limited spatial extent, concentrating only on nearshore-beaches and estuaries (maximum 19 m water depth) (Gandhi et al., 2007; Gandhi and Solai, 2010). The influence of deep water ecological conditions on benthic foraminifera from the Bay of Bengal is rarely documented. Recently, Suokhrie et al. (2020), compared the living benthic foraminifera of the western Bay of Bengal's oxygen-deficient zone with that from a similar region in the Arabian Sea. A distinctly different benthic foraminiferal assemblage was reported from the Bay of Bengal oxygen deficient waters. However, the effect of other stressors, including salinity, temperature, pH, riverine influx on benthic foraminifera, both above and below the oxygen-deficient zone of the western Bay of Bengal, was not addressed. Therefore, we study the combined effect of multiple ambient parameters on the living (stained) benthic foraminiferal assemblage from the shallow inner shelf to the slope and further deeper region of the west-central Bay of Bengal. The main objective of this study is to establish representative living (rose-Bengal stained) benthic foraminifera assemblages characterizing a particular set of ecological niches on the shallow continental shelf to the abyssal depth in the west-central Bay of Bengal, where the freshwater influx and associated processes primarily influence the physico-chemical parameters. The baseline information will be beneficial to understand the foraminiferal response to climatic changes in the future. The precise information about benthic foraminifera's ecological preferences, will also be useful for a better reconstruction of the past environmental conditions.

OCEANOGRAPHIC SETTING

The west-central Bay of Bengal is strongly influenced by the riverine influx. Some of the world's largest rivers drain into the western Bay of Bengal, with an average runoff being Ganga-11,892 m^3s^{-1}, Brahmaputra-16,186 m^3s^{-1}, Godavari-3,180 m^3s^{-1}, Krishna-1,730 m^3s^{-1}, Pennar-95 m^3s^{-1}, and Cauveri-664 m^3s^{-1} (Rao, 1975; Subramanian, 1979; Dai and Trenberth, 2002). The lithogenic components' contribution is ∼39% in the northern bay and ∼12.6% in the southern bay (Unger et al., 2003). The riverine influx is most intense during the summer monsoon and is also responsible for the salinity-controlled stratification (Gomes et al., 2000; Unger et al., 2003; Sarma et al., 2016) and surface circulation in the Bay of Bengal. The southwestern Bay of Bengal receives significant precipitation during the winter monsoon. The surface circulation (East India Coastal Current) reverses seasonally along the bay's western boundary, flowing southward during the winter season and northward during the summer season (Vinayachandran et al., 1999; Shankar et al., 2002). The precipitation resulting from the seasonal reversal of winds in the Bay of Bengal is maximum during the summer monsoon (318 mm/month) as compared to the winter monsoon (88 mm/month) (Ramesh Kumar and Prasad, 1997). The summer precipitation causes substantial spatial variation in the salinity and temperature in the bay. The sea surface salinity varies from 29.1 psu closer to the continental margin on the inner shelf to 33.7 psu toward the open ocean. The warmer water input from the rivers is evident by the relatively higher sea surface temperature (29–30°C) in the river mouths' vicinity (Durand et al., 2011; Locarnini et al., 2013). The dissolved oxygen is low at intermediate depths (∼100–1,000 m), with concentration being as low as 5 μM (Wyrtki, 1971; Rao et al., 1994; Sardessai et al., 2007; Bristow et al., 2017). The shallower inner shelf water in the vicinity of the river has a higher dissolved oxygen. The chlorophyll-a concentration varies from ∼0.3 mg/m^3 to 2.0 mg/m^3 in the western Bay of Bengal, with higher concentration closer to the river mouth (NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group, 2014). A strong wind-induced upwelling spread over ∼40 km wide band, all along the eastern margin of India, is observed in the western Bay of Bengal, during the summer season (Shetye et al., 1991). As a consequence of this upwelling, salinity increases coastward (Shetye et al., 1991). The modern-day lysocline depth is at 2,000–2,600 m, shallowing from south to north in the Bay of Bengal (Cullen and Prell, 1984).

MATERIALS AND METHODS

Field Sampling

A total of 46 surface sediment samples (35 multi-core and 11 spade-core) were collected in 2014 and 2012, during the 308th cruise of ORV *Sagar Kanya* (SK 308) and RV *Sindhu Sankalp* (SSK 35) from the west-central Bay of Bengal, respectively (**Figure 1** and **Supplementary Table 1**). The samples were collected along the coast perpendicular transects at regular depth intervals, starting from the continental shelf to the slope (27–2,494 m), during the pre-summer monsoon season of 2012 and 2014 (more details in Suokhrie et al., 2020). After retrieval, the top 10 cm (0–10 cm) of the sediment collected by using *Ocean Science Industries Limited (OSIL) – Maxi multi-corer* was sub-sampled at 1 cm interval. Half of the sediment from each section was immediately preserved in ethanol rose-Bengal solution (2 g rose-Bengal per liter of ethanol), to stain living benthic foraminifera. The top two sections (0–2 cm) were analyzed, as they contain the majority of the living benthic foraminifera in the northern Indian Ocean (Singh et al., 2018). The use of rose-Bengal stained living benthic foraminifera has been widely discussed since its introduction by Walton (1952). A study by Walker et al. (1974) compared rose-Bengal and Sudan Black B stains and reported that rose-Bengal stain identified 70% of the specimens containing protoplasm. The concern also remains in differentiating the protoplasm living at the time of sample collection with the recently dead protoplasm (Bernhard, 1988). However, a majority of the tests lying in the sediments are usually devoid of protoplasm because of reproduction, predation, or growth stages (Murray and Bowser, 2000). Also, the living protoplasm (those living at the time of staining) tend to acquire deeper and denser stain up to one additional chamber. So, if the pattern of staining can be understood thoroughly, the error of over-estimating the stained living fauna can be reduced (Linshy, 2010).

The overlying bottom water in the multi-cores was collected at each station, and its salinity, pH and temperature were measured onboard by using a hand-held multimeter (S47-K/"SevenMulti") (**Supplementary Table 2**). The bottom water sample was not retrieved at a few multi-core stations. For these stations, salinity, temperature, dissolved oxygen, and also all the environmental data for the 11 spade core stations were downloaded from the World Ocean Atlas 2013 (Garcia et al., 2013; Locarnini et al., 2013; Zweng et al., 2013) by using the Ocean Data View software (Schlitzer, 2016, Ocean Data View)[1] (**Figure 2**).

Laboratory Analysis

The stained sediments were stored in cold-storage (4°C) for a minimum of 2 weeks and were then processed following the standard procedure (Manasa et al., 2016; Singh et al., 2018; Suokhrie et al., 2020). The excess ethanol rose-Bengal was removed, and the sediments were freeze-dried. The dried samples were then weighed, and ∼2 g of the sediment was finely powdered for total carbon, nitrogen and inorganic carbon analysis. The rest of the sample was wet sieved by using a 63 μm sieve. The >63 μm material coarse fraction (CF) was dried, weighed and then transferred into plastic vials. A representative aliquot of the CF was weighed to pick a minimum of 300 living benthic foraminifera, wherever possible. All available living benthic foraminifera were picked from a fixed 0.1 g CF, in samples where a limited number of specimens were found. The picked specimens were mounted on the micropaleontological slides for counting and identification. Only those specimens with precise pink coloration with more than one chamber completely stained were picked and counted for living benthic foraminifera. All specimens were identified by using the previously published literature. The foraminiferal treatise (Loeblich and Tappan, 1988) was followed for genus confirmation, and for species confirmation, we have referred to the foraminiferal catalog (Ellis and Messina, 1940–2015). The genus of a few species have been shifted, as per the taxonomic shifts. *Bolivinellina* has been shifted from *Bolivina* following Saidova (1975). One species (*Eubuliminella cassandrae*) was also shifted from genus *Bulimina* to *Eubuliminella* following Revets (1993). Only those references mentioned in the main text of the paper have been added to the reference list. All other species identification references are mentioned in **Supplementary Table 4** for further reading.

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[1] http://odv.awi.de

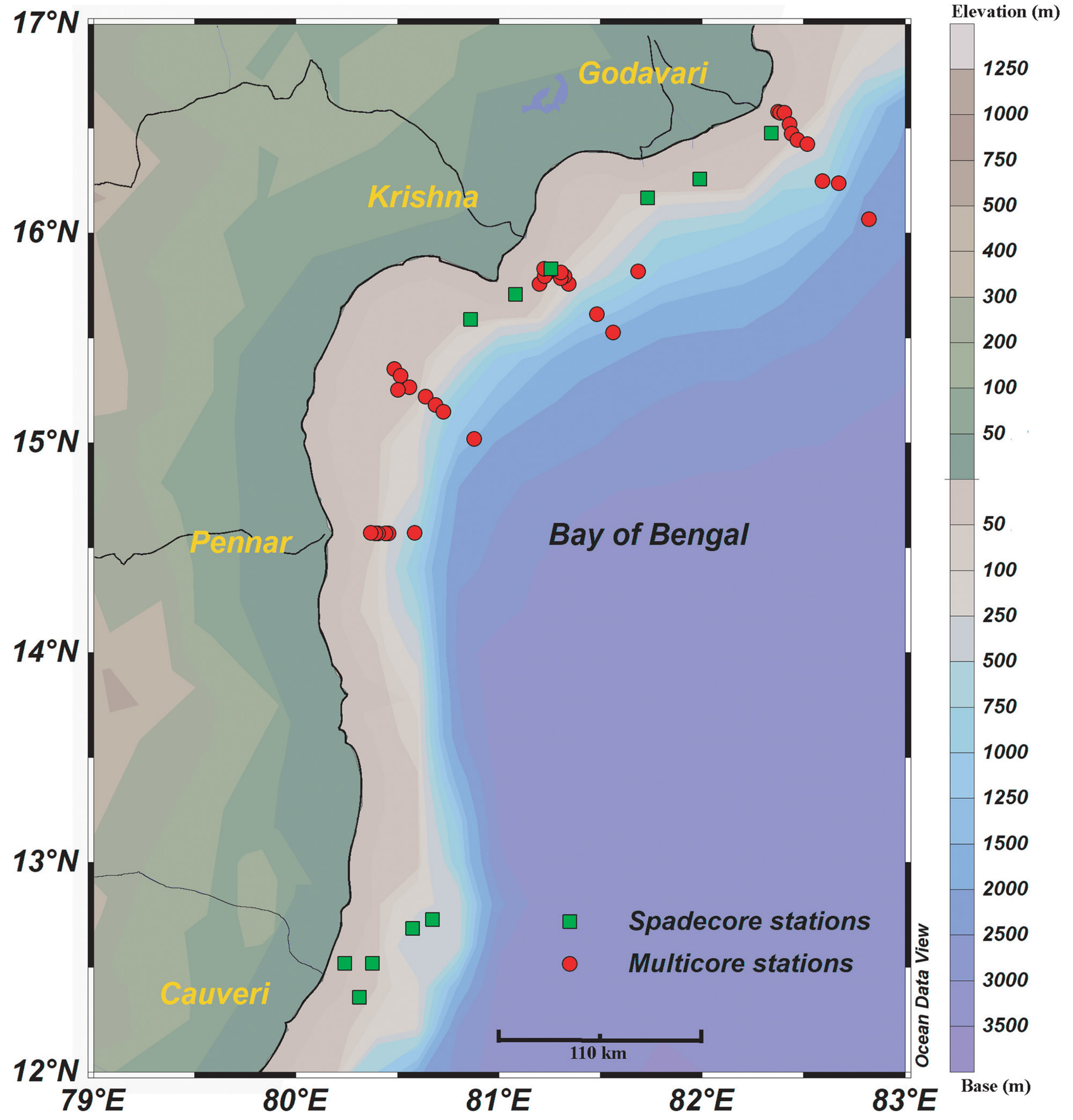


FIGURE 1 | The location of surface sediment samples in the west-central Bay of Bengal. Multicore stations are marked with red circles and green squares represent spade core stations. The major rivers draining in the area are marked by thin black lines. The bathymetry is marked by colored contours.

The sedimentary characteristics, namely total inorganic carbon (IC), total nitrogen (TN), and total carbon (TC), were analyzed by using dried and finely powdered sediment (∼10 mg weight). TIC was analyzed by using UIC CM 5015 CO_2 Coulometer and TC, TN by CNS elemental analyzer (Thermo Fisher Scientific). Calcium carbonate ($CaCO_3$) was calculated from IC and organic carbon (C_{org}) was estimated by subtracting TIC from TC.

Statistical Analysis

To draw meaningful inferences from the large dataset of the relative abundance of all benthic foraminifera species identified from the western Bay of Bengal, 54 dominant species (≥3%

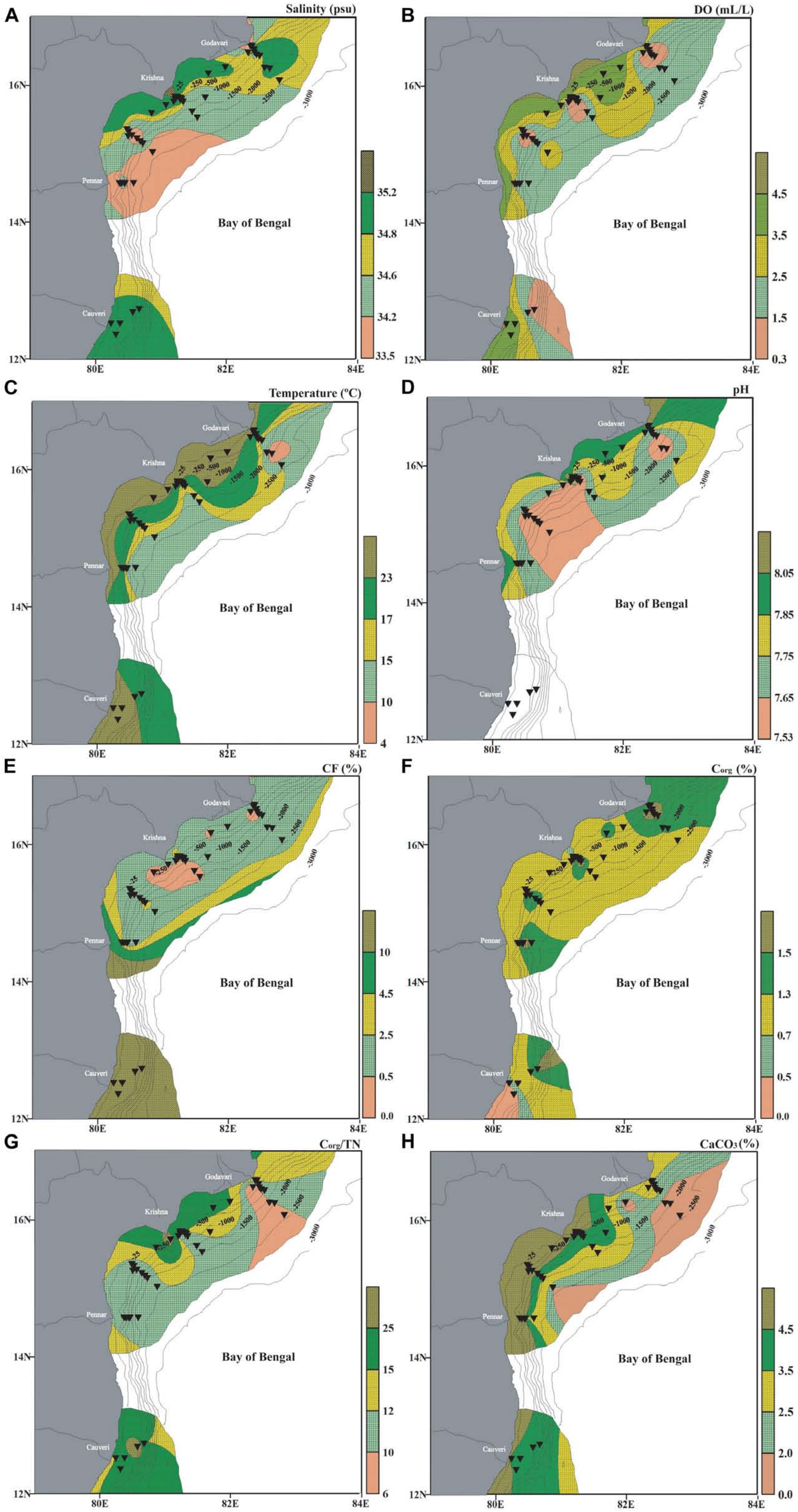


FIGURE 2 | Bottom water environmental parameters measured onboard from the water collected in multicores along with data downloaded from the World Ocean Atlas (Garcia et al., 2013; Locarnini et al., 2013; Zweng et al., 2013), and analyzed sediment characteristics in the western Bay of Bengal. **(A)** Salinity (psu), **(B)** dissolved oxygen (ml/l), **(C)** temperature (°C), **(D)** pH (The pH data in the southern part of the region is not available as we could not collect samples from the sediment-water interface), **(E)** coarse fraction (CF%), **(F)** organic carbon (%C_{org}), **(G)** organic carbon/total nitrogen (C_{org}/TN) and **(H)** calcium carbonate ($CaCO_3$%). The stations are marked by black inverted triangles. The thin black lines mark the bathymetric contours.

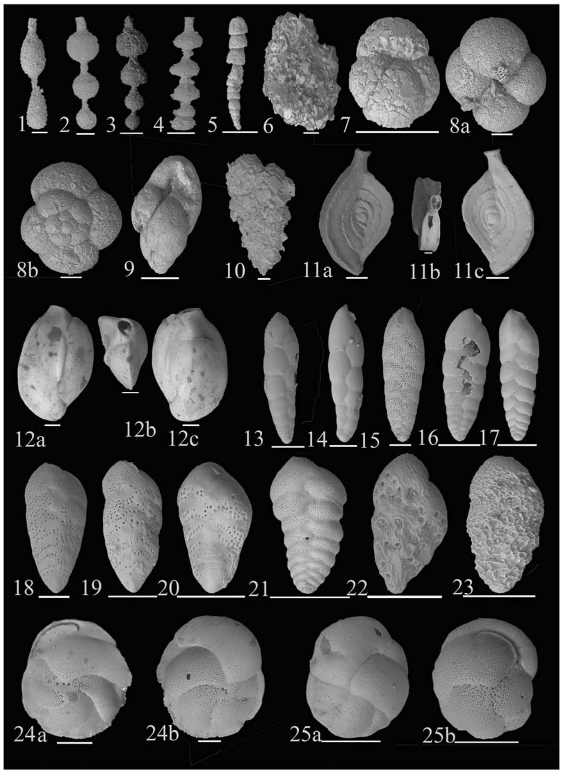


FIGURE 3 | The dominant living benthic foraminifera (relative abundance ≥ 3% at atleast three stations) in the west-central Bay of Bengal (1) *Hormosinella distans* (Brady, 1881); (2–4) *Hormosinella guttifera* (Brady, 1881); (5) Reophax *scottii* (Chaster, 1892); (6) *Ammobaculites agglutinans* (d'Orbigny 1846); (7) *Ammoglobigerina globigeriniformis* (Parker and Jones, 1865); (8) *Trochamminopsis quadriloba* (Hoglund, 1947); (a) Ventral view (b) Dorsal view; (9) *Eggerella propinqua* (Brady, 1884); (10) *Textularia oceanica* Cushman, 1932; (11) *Spiroloculina convexa* Said, 1949, (a–c); (12) *Quinqueloculina bicarinata* (d'Orbigny, 1878); (a) 4-chambered view (b) Apertural view (c) 3-chambered view; (13, 14) *Bolivinellina earlandi* (Parr, 1950); (15) *Bolivinellina lucidopunctata* (Conato, 1964); (16) *Bolivinellina pacifica* (Cushman and McCulloch, 1942); (17) *Bolivinellina translucens* (Phleger and Parker, 1951); (18, 19) *Brizalina dilatata* (Reuss, 1850); (20) *Bolivina mekranensis* (Haque, 1970); (21) *Brizalina spathulata* (Williamson, 1858); (22) *Latibolivina lepida*; (23) *Latibolivina persiensis* (Lutze, 1974); (24) *Cassidulina carinata* Silvestri, 1896; (a) Ventral view showing aperture (b) Dorsal view; (25) *Cassidulina laevigata* (d'Orbigny, 1826), (a) Dorsal view, (b) Ventral view showing aperture. Scale bar is 100 µm.

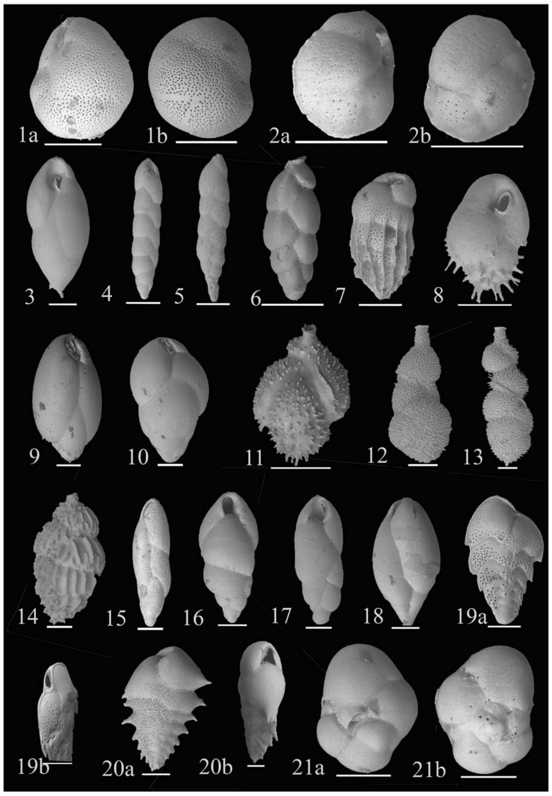


FIGURE 4 | (1) *Globocassidulina oblonga* (Reuss, 1850); (a) Ventral view (b) Dorsal view; (2, 3) *Islandiella cushmani* (Stewart and Stewart, 1930); (a,b) Side views (c) Apertural view; (3) *Eubuliminella cassandrae* (Revets, 1993); (4, 5) *Eubuliminella exilis* (Brady, 1884); (6) *Hopkinsinella glabra* (Millett, 1903); (7) *Bulimina* cf. *delreyensis* (Cushman and Galliher, 1934); (8) *Bulimina marginata* (d'Orbigny, 1826); (9) *Globobulimina globosa* (Leroy, 1944) (10); *Protoglobobulimina pupoides* (d'Orbigny 1846); (11) *Uvigerina globulosa* (Egger, 1895); (12, 13) *Neouvigerina ampullacea* (Brady, 1884); (14) *Uvigerina peregrina* (Cushman, 1923); (15) *Fursenkoina pauciloculata* (Brady, 1884); (16) *Fursenkoina spinosa* (Heron-Allen and Earland, 1932); (17) *Fursenkoina schreibersiana* (Czjzek, 1848); (18) *Rutherfordoides rotundiformis* (McCulloch, 1977); (19) *Suggrunda alata* (Seguenza 1862); (a) Side view (b) Lateral view showing aperture; (20) *Suggrunda semiclara* (McCulloch 1977); (a) Side view (b) Lateral view showing aperture; (21) *Baggina irregularis* (McCulloch, 1977); (a) Ventral view (b) Dorsal view. Scale bar is 100 µm.

abundance at a minimum of two stations) (**Figures 3–6**), were used for the Cluster analysis. Bray Curtis similarity index was applied through Q-mode cluster analysis by using Primer 6.1.10 software. The major clusters were identified with similar species having a particular percentage contribution in each cluster. The dominant assemblage representing a cluster and the relative contribution of each species to the respective cluster was identified by using the Simple Percentage (SIMPER) program at 100%. The canonical correspondence analysis (CCA) was done to understand the influence of multiple parameters on the dominant species. The multivariate statistical package version 3.1 (Kovach, 1998) was used for CCA. The CCA provides a better insight into the cumulative effect of a set of ambient environmental parameters on the abundance of species.

RESULTS

Bottom Water Parameters (Salinity, Temperature, Dissolved Oxygen, and pH)

The salinity at the sediment-water interface was higher in the shallow regions than at the deeper regions. The salinity ranged from ∼32.15 psu to 35.2 psu (**Figure 2A**). The dissolved oxygen varies from ∼0.3 ml/l to a maximum of ∼4.9 ml/l. The dissolved oxygen is low within the depth range of ∼100–1,000 m (**Figure 2B**). The previous reports suggest excessively

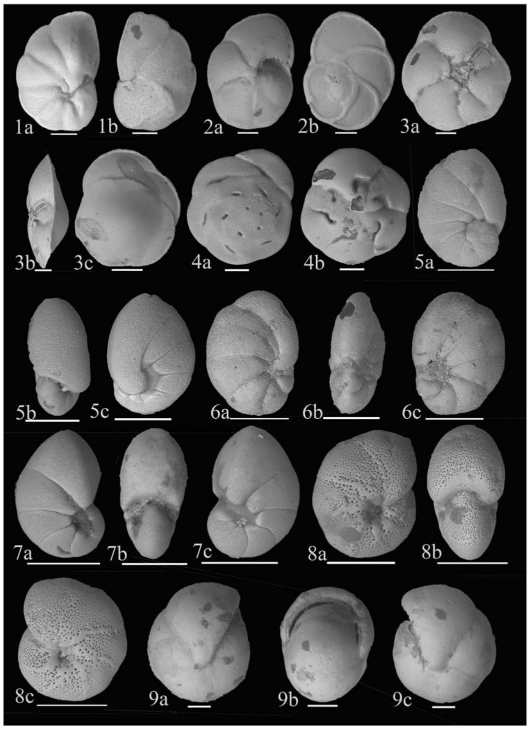


FIGURE 5 | (1) *Cancris oblongus* (Williamson, 1858); (a) Ventral view (b) Dorsal view; (2) *Eponides cribrorepandus* (Asano and Uchio, 1951); (a) Ventral view (b) Dorsal view; (3) *Gavelinopsis mira* (Cushman, 1922); (a) Ventral view (b) Lateral view (c) Dorsal view; (4) *Pseudoeponides japonicum* (Uchio, 1950); (a) Dorsal view (b) Ventral view; (5) *Nonionella auris* (d'Orbigny, 1839); (a) Side view (b) Apertural view (c) Side view showing the last chamber flap covering the umbilicus; (6) *Nonionella limbato-striata* (Cushman 1931); (7) *Nonionellina labradorica* (Dawson, 1860); (a,c) Side views (b) Apertural view; (8) *Melonis* (?) *chathamensis* (McCulloch, 1977); (a,c) Side views (b) Apertural view; (9) *Pullenia bulloides* (d'Orbigny, 1846); (a,b) Side views (c) Apertural view. Scale bar is 100 μm.

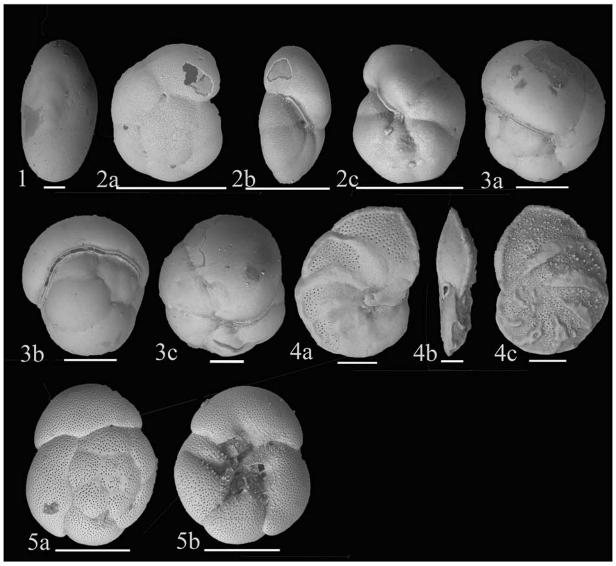


FIGURE 6 | (1) *Chilostomella oolina* Schwager 1878; (2) *Gyroidinoides subzelandica* Hornibrook, 1961; (a) Dorsal view (b) Apertural view (c) Ventral view; (3) *Rotaliatinopsis semiinvoluta* (Germeraad, 1946); (a,c) Side views (b) Apertural view; (4) *Hanzawaia nipponica* Asano, 1944; (a) Ventral view (b) Apertural view (c) Dorsal view; (5) *Ammonia tepida* (Cushman, 1926); (a) Dorsal view (b) Ventral view. Scale bar is 100 μm.

low oxygen concentration (as low as 18 nM) at ∼150–450 m (Bristow et al., 2017). The temperature at the sediment-water interface was relatively warmer (>23°C) in the shallow coastal zone as compared to the deeper region (<17°C) (**Figure 2C**). The seawater pH at the spade core stations was not available, and hence the data from the multicore stations only are plotted. The measured pH at the sediment-water interface in the study area ranges from 7.5 to 8.1. The region off Godavari and Pennar rivers has higher pH than off the Krishna river (**Figure 2D**).

Sediment Characteristics

The fraction retained on the sieve (>63 μm) is considered as the CF and comprises both biogenic remains (shells and tests), and terrigenous material (quartz, mica, feldspars, and others). A relatively more CF is observed in the southern segment and at the shallower and deeper stations (**Figure 2E**). Overall, the upper slope stations (∼250–1,000 m) have a comparatively higher finer fraction. CF varied from ∼0.5% to an enormously high percentage upto ∼90% at the southern stations. The influence of riverine influx on CF, by contributing terrigenous material, is evident from the increase in CF in front of the river mouths, especially in the southern part of the study area (SC42, SC43, and SC44). Interestingly, the increased CF is also observed in the deeper region and is attributed to increased contribution from biogenic remains, including foraminiferal tests (**Figure 2E**).

The organic carbon varied from 0.3 to 1.8% in the west-central Bay of Bengal (**Supplementary Table 2**). The maximum %C_{org} was at the deeper depths. The influence of riverine discharge by contributing terrigenous organic matter and the fine fraction is also evident (**Figure 2F**). The organic carbon comes both from the terrigenous influx as well as marine productivity. These two sources' relative contribution is delineated by the organic carbon to nitrogen ratio of the organic matter (C_{org}/TN). Generally, C_{org}/TN > 6.0 is considered to be of terrestrial input, as vascular plants have nitrogen depleted organic matter (Müller and Mathesius, 1999; Ramaswamy et al., 2008), and values < 6.0 are used to infer marine input. A majority of the C_{org}/TN values are >6.0 and hence suggests that the organic matter is mainly contributed by terrestrial sources rather than by marine productivity. Expectedly, the maximum C_{org}/TN is infront of the Godavari, Krishna, and Cauvery rivers (SC37, SC38, MC30, MC31, SC40, SC39, MC27, and MC28) (**Figure 2G**).

The biogenic skeletal remains mainly contribute $CaCO_3$ to the sediments. $CaCO_3$ concentration in the west-central Bay of Bengal ranged from 1.3 to 87.2%. $CaCO_3$ concentration increases toward the southern part of the west-central Bay of Bengal. Additionally, $CaCO_3$ is low at a few stations on the lower slope (depth >1000 m), likely due to a reduction in the total foraminiferal abundance, which mainly contributes to the $CaCO_3$ in the sediments at these depths (**Figure 2H**).

Cluster Analysis

A total of 263 living benthic foraminifera have been identified (**Supplementary Tables 3, 4**). The cluster analysis groups similar objects together to draw meaningful inferences from a large dataset like the number of species and their relative abundance in the western Bay of Bengal (Kaufman and Rousseeuw, 2009; Khare et al., 2017). Based on the distribution at different stations, 54 dominant species were selected for the cluster analysis. We delineate four major clusters at 20% similarity index, other than a few insignificant ones (**Figure 7**). The clusters were named as Cluster I, II, III, and IV. The dominant assemblage representing a cluster and each species' relative contribution to the respective cluster is described below.

Cluster I

This cluster is represented by six stations, namely SC45, MC36, MC32, SC36, MC24, and MC09. The stations in this cluster are from a shallow depth (107–274 m) except for one station MC36 (1,511 m). The similarity percentage (SIMPER) analysis shows that this cluster has an average similarity of 20.59% consisting of 12 species. The dominant species are *Eubuliminella exilis* (24.88%), *Bolivinellina earlandi* (19.89%), *Fursenkoina spinosa* (12.54%), *Bolivinellina lucidopunctata* (8.76%), and *Globobulimina globosa* (6.48%).

Cluster II

Fursenkoina spinosa (15.64%), *Eubuliminella cassandrae* (11.41%), *Rotaliatinopsis semiinvoluta* (11.07%), *Uvigerina peregrina* (10.4%), and *Cassidulina laevigata* (8.26%) are the dominant species in this cluster having an average similarity of 51.31%. This cluster represents a depth range of 500–1,518 m.

Cluster III

This cluster is represented by five stations (MC15, MC2, MC37, MC18, and MC38) representing a depth range of ~1,940–2,494 m with a similarity of 47.62%. Twelve species comprise of this cluster and the five most dominant ones are *Bulimina* cf. *delreyensis* (18.59%), *Bulimina marginata* (18.14%), *Hormosinella guttifera* (9.05%), *Cassidulina laevigata* (8.02%), and *Gyroidinoides subzelandica* (6.18%).

Cluster IV

The SIMPER analysis shows that the average similarity of this cluster is 34.53%. The representative benthic foraminiferal assemblage of this cluster includes nine species of which the five most dominant ones are listed here, *Nonionellina labradorica* (37.85%), *Hanzawaia nipponica* (17.58%), *Brizalina dilatata* (17.31%), *Ammonia tepida* (4.71%), and *Nonionella limbato-striata* (4.08%).

From the spatial distribution of various clusters, it is clear that Cluster I, Cluster II and Cluster III, and Cluster IV follow a depth zonation (**Figure 8**). Cluster IV is confined to the shallow water depth. Cluster I represents a shallow to intermediate depth zone covering the upper slope region. Cluster II mainly comprising of angular asymmetrical foraminifera, represents a wide range of intermediate water depth to deep water depth locations. The assemblages in this cluster consist of species that are indicative of an oxygen-deficient region. The species in Cluster III represent the deep-water species.

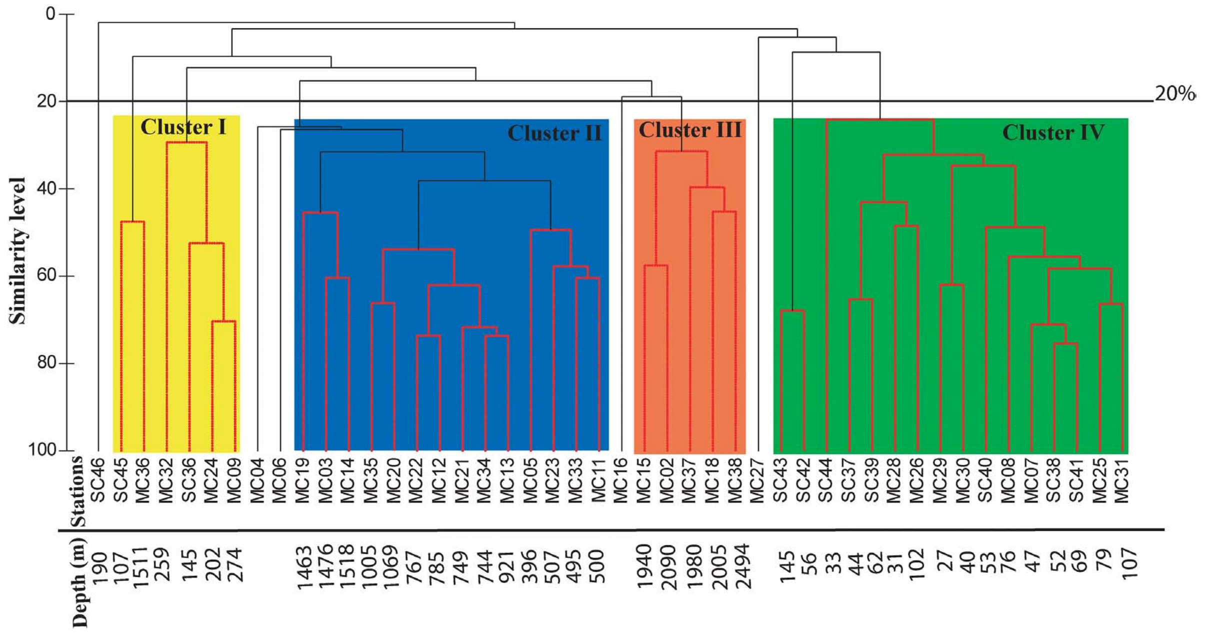


FIGURE 7 | Cluster analysis using Bray-Curtis similarity at 20% similarity level. The four identified clusters have been shaded in different colors as Cluster I, II, III, and IV.

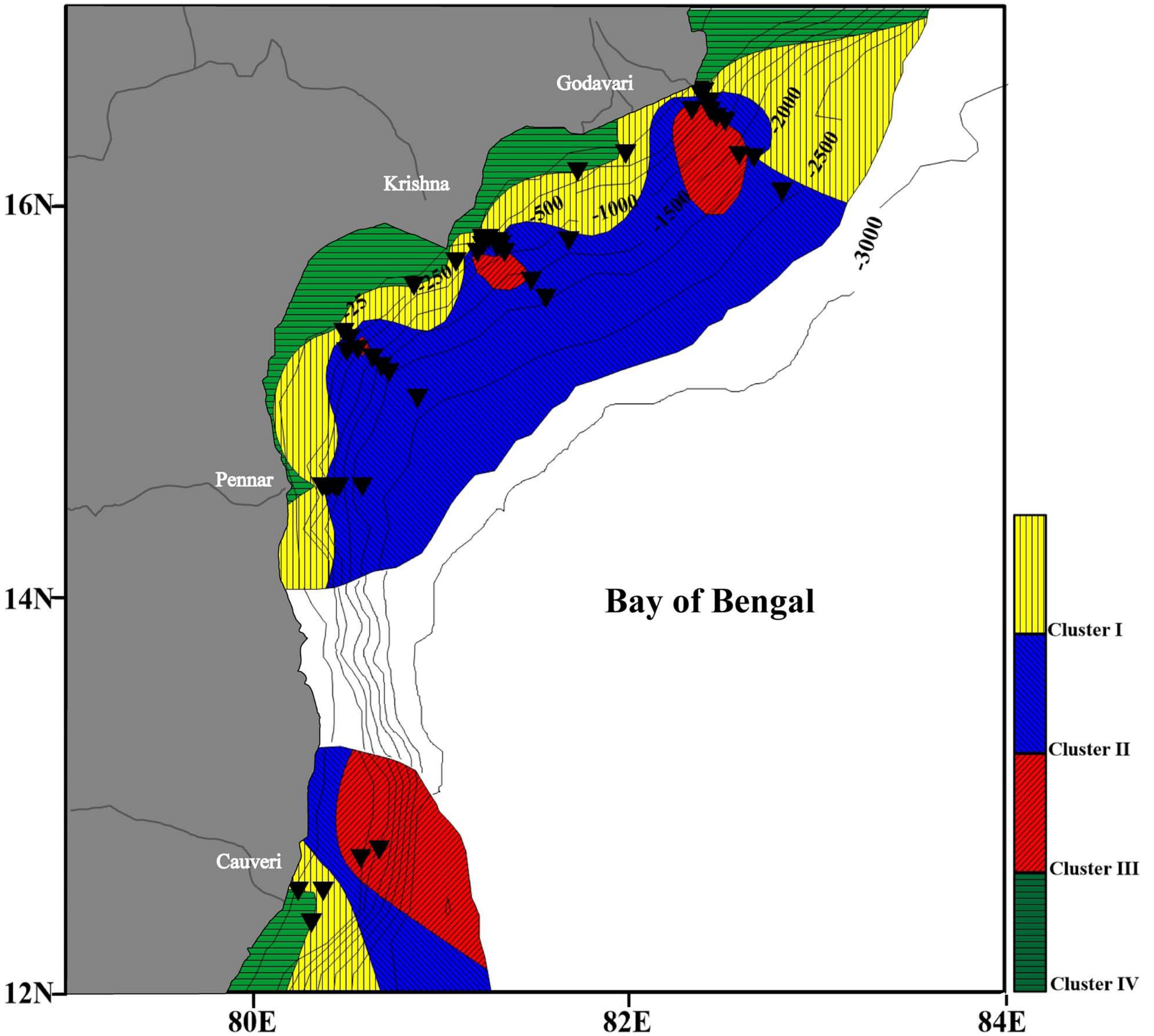


FIGURE 8 | Distribution of the four clusters in the western Bay of Bengal. A clear depth preference of the clusters is evident. Cluster I and II, intermediate water; Cluster III, deep water; and Cluster IV, shallow water. The black triangles represent the sampling stations.

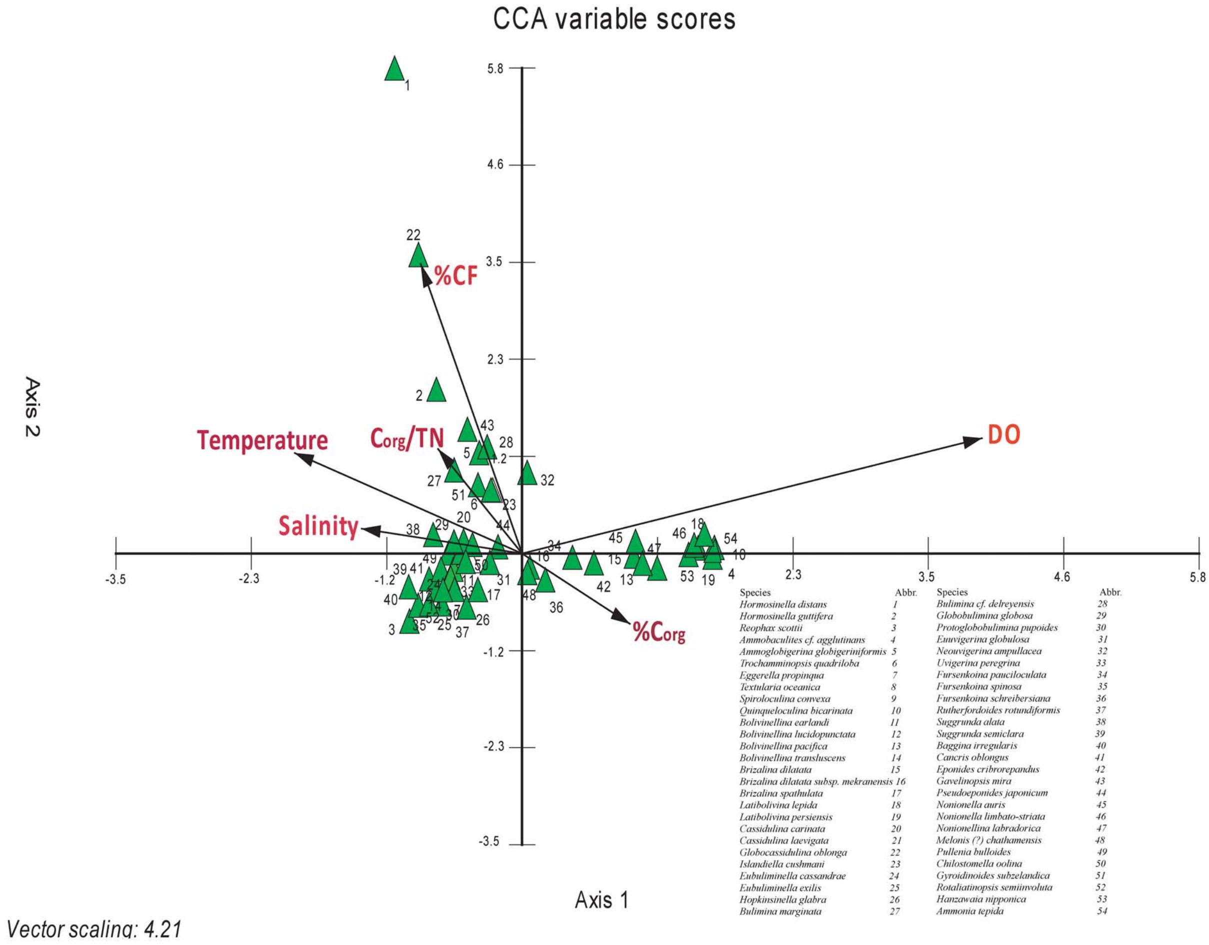
Canonical Correspondence Analysis

The dominant effect of one or a combination of several parameters, out of a set of multiple parameters in the field, on living benthic foraminiferal species, can be identified from CCA. Out of the 54 dominant species, only 40 species showed a significant relationship with atleast one of the ambient environmental parameters (**Figure 9**). The rest of the species do not show a significant relationship with any particular parameter, as evident from the close proximity of these species to the centroid in the CCA biplot (Ter Braak, 1986). From CCA, it is evident that the dissolved oxygen, CF, and temperature, are the most significant parameters controlling the living benthic foraminifera species distribution in the west-central Bay of Bengal. Besides these dominant factors, C_{org}, salinity, and C_{org}/TN also influence the distribution of living benthic foraminifera.

Species Representing Specific Set of Parameter

Species Preferring Oxic, Colder Water With Organic Matter Rich Sediments

Ammobaculites cf. *agglutinans*, *Quinqueloculina bicarinata*, *Bolivinellina pacifica, Brizalina dilatata*, *Latibolivina lepida*, *Latibolivina persiensis*, *Fursenkoina pauciloculata*, *Eponides cribrorepandus*, *Nonionella auris*, *Nonionella limbato-striata*, *Nonionellina labradorica*, *Hanzawaia nipponica,* and *Ammonia tepida* were positively correlated with dissolved oxygen and organic carbon, whereas negatively correlated with temperature



Species	Abbr.	Species	Abbr.
Hormosinella distans	1	*Bulimina cf. delreyensis*	28
Hormosinella guttifera	2	*Globobulimina globosa*	29
Reophax scottii	3	*Protoglobobulimina pupoides*	30
Ammobaculites cf. agglutinans	4	*Euuvigerina globulosa*	31
Ammoglobigerina globigeriniformis	5	*Neouvigerina ampullacea*	32
Trochamminopsis quadriloba	6	*Uvigerina peregrina*	33
Eggerella propinqua	7	*Fursenkoina pauciloculata*	34
Textularia oceanica	8	*Fursenkoina spinosa*	35
Spiroloculina convexa	9	*Fursenkoina schreibersiana*	36
Quinqueloculina bicarinata	10	*Rutherfordoides rotundiformis*	37
Bolivinellina earlandi	11	*Suggrunda alata*	38
Bolivinellina lucidopunctata	12	*Suggrunda semiclara*	39
Bolivinellina pacifica	13	*Baggina irregularis*	40
Bolivinellina transluscens	14	*Cancris oblongus*	41
Brizalina dilatata	15	*Eponides cribrorepandus*	42
Brizalina dilatata subsp. mekranensis	16	*Gavelinopsis mira*	43
Brizalina spathulata	17	*Pseudoeponides japonicum*	44
Latibolivina lepida	18	*Nonionella auris*	45
Latibolivina persiensis	19	*Nonionella limbato-striata*	46
Cassidulina carinata	20	*Nonionellina labradorica*	47
Cassidulina laevigata	21	*Melonis (?) chathamensis*	48
Globocassidulina oblonga	22	*Pullenia bulloides*	49
Islandiella cushmani	23	*Chilostomella oolina*	50
Eubuliminella cassandrae	24	*Gyroidinoides subzelandica*	51
Eubuliminella exilis	25	*Rotaliatinopsis semiinvoluta*	52
Hopkinsinella glabra	26	*Hanzawaia nipponica*	53
Bulimina marginata	27	*Ammonia tepida*	54

FIGURE 9 | Canonical correspondence analysis (CCA) between species abundance and environmental parameters. The arrows represent environmental parameters-C_{org}, organic carbon; C_{org}/TN, organic carbon/total nitrogen; CF, coarse fraction; DO, dissolved oxygen; T, temperature; S, salinity; D, depth. The triangles represent the species (modified from Suokhrie et al., 2020).

(**Figure 9**). *Ammobaculites* cf. *agglutinans*, an agglutinated benthic foraminifer, was present only at four stations, all shallower than ~60 m. *Quinqueloculina bicarinata* was present at three stations, all shallower than 56 m. Even *Bolivinellina pacifica* was present only upto 76 m. *Brizalina dilatata* was found at stations mostly within depths of ~300 m, beyond which <1% abundance was observed at two stations. *Latibolivina lepida* was found only at two stations with abundance varying from 4.2% (53 m) to 6.2% (52 m). Likewise, *Latibolivina persiensis* was also present at shallow depths between 40 and 76 m, beyond which it was absent. *Fursenkoina pauciloculata* was abundant over a wider depth range (~30–1,000 m) but the highest abundance was at the shallower depths. *Eponides cribrorepandus* was present only at three stations with relative abundance varying from 0.15% (500 m water depth) to 25% (107 m water depth). It was totally absent at stations deeper than ~500 m. *Nonionella auris* was present at most of the stations and abundant between ~200 m and ~1,000 m. *Nonionellina labradorica* was present upto a depth of ~750 m. *Hanzawaia nipponica, Ammonia tepida* and *Nonionella limbato-striata* were abundant at stations shallower than ~150 m.

Species Preferring Oxygen Deficient, Warmer, and Hypersaline Water

The species having a negative correlation with dissolved oxygen and a positive correlation with temperature and salinity were *Reophax scottii*, *Eggerella propinqua*, *B. earlandii, B. lucidopunctata*, *Bolivinellina translucens, Brizalina spathulata, Eubuliminella cassandrae, E. exilis, Hopkinsinella glabra, Protoglobobulimina pupoides, Uvigerina globulosa, Uvigerina peregrina, Fursenkoina spinosa, Rutherfordoides rotundiformis, Suggrunda semiclara, Baggina irregularis, Cancris oblongus, Pullenia bulloides, Chilostomella oolina,* and *Rotaliatinopsis semiinvoluta* (**Figure 9**).

Agglutinated benthic foraminifera, *Reophax scottii* was abundant only at four stations with abundance ranging from 0.14% (1,069 m) to 40.96% (259 m). Other agglutinated foraminifer, *Eggerella propinqua* was abundant at depths varying from ~200 m to ~700 m except for two shallow stations at 27 m and 31 m. The species of genus *Bolivinellina* reported in the west-central Bay of Bengal include *B. translucens*, *B. earlandi,* and *B. lucidopunctata*. The abundance of these three species was influenced by bathymetry, with *B. translucens* and *B. lucidopunctata* being the most abundant between 76 m and ∼500 m, while *B. earlandi* was abundant from 76 m upto ∼2,000 m. *Brizalina spathulata* was the most abundant between ∼100 m and 270 m. *Eubuliminella cassandrae* was abundant at depths >∼150 up to ∼1,000 m, whereas *E. exilis* was present only upto a depth of 274 m. *Hopkinsinella glabra* was present only at 11 stations, with most of the stations being within ∼200–900 m. *Protoglobobulimina pupoides* was present only at depth >∼250 m. *Uvigerina globulosa* was present at depths >∼750 m except at one shallow station (55 m). *Uvigerina peregrina* was also dominant at deeper than 190 m with a maximum abundance of 21%. *Fursenkoina spinosa* was also abundant at stations >200 m deep, with a relative abundance ranging from 0 to a maximum of 36%. *Rutherfordoides rotundiformis* was present at stations deeper than ∼100 m, except for one station at ∼40 m. *Suggrunda semiclara* was present at seven stations, of which four stations were on the upper slope, within a depth range of ∼390–500 m. *Baggina irregularis*, *Pullenia bulloides* and *Rotaliatinopsis semiinvoluta* were abundant at stations deeper than 500 m. *Cancris oblongus* was present only at nine stations with the highest abundance of 4.3% at 500 m depth. Similarly, *Chilostomella oolina* with a maximum relative abundance of 6.2% was present at stations deeper than ∼200 m. Interestingly the maximum abundance of all the species listed above was within the oxygen deficient zone (∼100–1,000 m).

Species Preferring Coarse Sediments With High C_{org}/TN

Ammoglobigerina globigeriniformis, Trochammina quadriloba, Islandiella cushmani, Bulimina marginata, Bulimina delreyensis, Gavelinopsis mira, and *Gyroidinoides subzelandica* were positively correlated with CF and Corg/TN (**Figure 9**). *Ammoglobigerina globigeriniformis*, an agglutinated foraminifer was present at almost all the stations with the highest abundance (∼19%) at ∼1,980 m. *Trochammina quadriloba*, another agglutinated foraminifer, was abundant at stations deeper than ∼250 m, except for three shallower stations with abundance ≤2%. *Islandiella cushmani* was present at most of the stations in the study area but mostly abundant at stations deeper than ∼200 m. *Bulimina marginata*, *Bulimina delreyensis, Gavelinopsis mira,* and *Gyroidinoides subzelandica* were abundant at the deeper stations (>∼250 m) in the west-central Bay of Bengal. Although the CCA biplot shows influence of both CF as well as Corg/TN on these species, the influence of CF was more significant. Interestingly, *Hormosina guttifera* shows a positive correlation only with CF.

DISCUSSION

Differential Foraminiferal Abundance on the Shelf and Slope

Interestingly, the abundance of living (stained) benthic foraminifera between ∼200 m and ∼1,000 m was higher (∼1,300 specimen/g sediment), as compared to the continental shelf (∼300 specimen/g sediment upto ∼200 m) as well as at depths deeper than ∼1,500 m (∼46 specimen/g sediment) (Suokhrie et al., 2020). We suggest that the lower dissolved oxygen concentration with an average of ∼0.5 ml/l within the depth range of ∼100–1,000 m and corresponding high organic matter content, dominantly control the living benthic foraminiferal population at these depths in the western Bay of Bengal. The high %C_{org} concentration between ∼250 m and 1,500 m water depth is attributed to the relatively finer sediments at these depths. The finer sediments can preserve more C_{org} (Mayer, 1994). Additionally, there is an enormous influx of both freshwater and sediments in the northern Bay of Bengal. The riverine influx is also a source of organic carbon. The immense terrestrial organic carbon contribution is further confirmed by a clear pattern of very high C_{org}/TN (∼20.0) close to the river mouth as compared to low C_{org}/TN, indicating marine organic carbon, away from the river mouth (>6.0).

The foraminiferal abundance is low at stations shallower than ∼100 m water depth with sediments dominated by terrestrially sourced organic matter. This low abundance is attributed to the taphonomic processes, including more disturbance or turbulence from the riverine influx leading to less proliferation and diversification of benthic foraminifera (Berkeley et al., 2014). Besides, the %C_{org} at the shallow depths is also lower than the intermediate water depth, except in front of the Godavari river mouth. The enormous freshwater runoff in the bay results in ocean surface stratification and an oligotrophic condition and thus the low organic matter on the shelf. This is also a factor for the low living benthic foraminiferal abundance at the shallow depth stations as the organic carbon is the food for benthic foraminifera. The lack or low organic carbon content in sediments is detrimental to benthic foraminifera (Duffield et al., 2014). The coarser sediments close to the river mouth are one reason for the lower %C_{org} despite the high primary productivity at these depths, as evident from the chlorophyll-a content (NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group, 2014). The intermediate depths within ∼100–1,000 m have abundant organic matter, which leads to reduced bottom water DO, and hence the abundance of total living abundance is a positive response to the organic matter supply. The increased foraminiferal abundance at these depths is also due to the significantly reduced predatory pressure as the macrofauna are comparatively more susceptible to oxygen-deficient environments. These depths are dominated by opportunistic species that thrive well in low DO concentrations. With a decrease in organic matter, the DO concentration increases beyond ∼1,000 m water depth. A drastic decrease in foraminiferal abundance is seen below ∼1,000 m water depth in the study area, and is attributed to the increase in predatory pressure. Additionally, the environment is more food limiting than oxygen and leads to a significant reduction in the total living fauna.

Drivers of Benthic Foraminiferal Diversity and Richness

The low diversity and species richness in front of the major rivers suggests a strong riverine influx. Both the diversity and species richness are low in the southern part, suggesting a restricted environment facilitating a select few species to survive (Suokhrie et al., 2020). Incidentally, the seawater pH is very low in front of the major river mouths. Although benthic foraminifera can tolerate a wide range of pH, comparatively less alkaline pH is detrimental to calcareous tests (Saraswat et al., 2015). Therefore, the low diversity in low pH regions is attributed to the thin-walled benthic foraminifera's inability to survive in adverse conditions. In contrast, more diverse microenvironments in the northern part are inferred from the high diversity and richness. From our earlier work based on CCA between benthic foraminiferal abundance and ambient parameters in the oxygen-deficient zone of this region, we inferred that the increased abundance of a few angular benthic foraminifera thriving as opportunistic species (*F. spinosa, E. cassandrae, U. peregrina, R. semiinvoluta, S. semiclara, E. propinqua,* and *B. irregularis*) contributes to the overall more population of living benthic foraminifera in the oxygen-deficient zones on the slope. The dominance of a few opportunistic species is supported by low diversity and richness at these depths (Suokhrie et al., 2020). The present study's cluster analysis groupings also indicate the abundance of angular forms at the depths where dissolved oxygen is low. Such a decrease in diversity of living benthic foraminifera in a low dissolved oxygen environment has also been reported from the oxygen minimum zone (Jannink et al., 1998; Gooday et al., 2000; Schumacher et al., 2007; Suokhrie et al., 2020).

Living Benthic Foraminiferal Assemblages

From cluster analysis, we delineate three faunal assemblages based on significant correlation of the assemblages to a similar set of environmental parameters in the study area. Incidentally, the assemblages dominate different depth zones as well. The details of the representative assemblages are discussed below.

Assemblage I (27–107 m)

This assemblage comprises of Cluster IV. The dominant species are *N. labradorica*, *H. nipponica*, *B. dilatata*, *A. tepida,* and *N. limbato-striata* with minor contributions from *F. pauciloculata*, *B. pacifica*, *L. persiensis,* and *N. auris* (**Figure 10**). These species are abundant on the continental shelf (<∼100 m water depth). The Assemblage I includes only calcareous benthic foraminifera. *Nonionellina labradorica* is a dominant species in this assemblage and has also been reported from the C_{org} rich fjords in the Arctic (Shetye et al., 2011). This species has been referred to as Arctic-boreo species (Seidenkrantz, 1993). Its high abundance is also reported from the oxygen-depleted environments where it sequesters chloroplast as it enables it to survive even in the anoxic conditions (Cedhagen, 1991; Bernhard and Bowser, 1999). In our study area, however, the abundant presence of *N. labradorica* is associated with the shallow inner shelf warm well-oxygenated waters with low organic carbon. We report another species belonging to the Assemblage I, namely *H. nipponica*, with its preference for shallow, well-oxygenated waters. From the Bay of Bengal, this species has been reported as a 'turbidity sensitive species' (Jayaraju et al., 2010).

Similarly, *B. dilatata* is also abundant on the shallow shelf, with a rare presence at a few stations upto ∼700 m. Its abundance in shallow to intermediate water depth is also reported by Gooday (1993) and Bernhard and Gupta (1999). *Brizalina dilatata* is also commonly reported from low oxygenated and high organic carbon-rich environments (Gupta and Machain-Castillo, 1993; Rouchy et al., 1998; Kuhnt et al., 2007). In the present study, this species correlates well with the shallow and warmer waters. The characteristic shallow-water species *A. tepida* is also abundant on the shelf of the present study. *Ammonia tepida* is widely distributed over estuaries, shelf and salt marshes (Murray, 1991; Nisha and Singh, 2012). Most workers have reported *A. tepida* as a pollution-sensitive species (Bergin et al., 2006; Burone et al., 2007; Frontalini and Coccioni, 2008; Elshanawany, 2011; Debenay et al., 2015; Schintu et al., 2016; Saalim et al., 2017). *Ammonia tepida* is also reported as a dominant species in the modern intertidal and estuarine areas (Nigam, 1984; Adarsh and Rajeshwara Rao, 2010). We also report *A. tepida* being abundant in shallow and warm water with a moderate organic matter supply in the study area. *Nonionella limbato-striata* is another dominant species in this assemblage, preferring the shallow and well-oxygenated waters.

Fursenkoina pauciloculata is a minor species in this assemblage. *Bolivinellina pacifica*, another dominant species of this assemblage, was earlier reported from the shallow water depths (Saidova, 2010), same as that in this study area. *Latibolivina persiensis* is reported from shallow depth (Sliter, 1969, 1970; Panchang and Nigam, 2014). It has been found to prefer oligotrophic and well-oxygenated water (Abu-Zied, 2013), similar to its distribution in this study, where this species is present only in shallow, well-oxygenated water (upto 76 m). Another minor species is *N. auris* in this assemblage.

The species belonging to Assemblage I representing the shallow locations indicate that they are positively correlated with dissolved oxygen, temperature and C_{org}. The dissolved oxygen concentration is high (>3.0 ml/l) and the organic matter content is low (∼0.9%) with warmer temperature on the shelf. Thus, Assemblage I represents a shallow, well-oxygenated, warm environment with relatively high organic matter in the sediments.

Assemblage II (∼145–1,500 m)

The dominant species in this assemblage are *E. exilis, B. earlandi*, *F. spinosa*, *B. lucidopunctata*, *G. globosa* from Cluster I and *F. spinosa, E. cassandrae, U. peregrina, R. semiinvoluta, C. laevigata* from Cluster II (**Figure 11**).

Eubuliminella exilis has been reported as deep infaunal taxa (Jorissen, 1999) and an indicator of low oxygenated environments and unchanged supply of organic matter (Caralp, 1989; Jannink et al., 1998; Schumacher et al., 2007*)*. Amongst the dominant species belonging to Assemblage II, *F. spinosa* is a shallow infaunal species inhabiting waters upto a depth of ∼120 m (Phleger, 1963). In the present study, *F. spinosa* is abundant at depths deeper than ∼200 m, indicating less depth dependence and a large influence of dissolved oxygen. The relative abundance of infaunal foraminifera is controlled by the availability of both the metabolizable organic matter and dissolved oxygen. The infaunal foraminifera are abundant in organic matter rich but oxygen-deficient environments (Jorissen et al., 1995; Van der Zwaan et al., 1999). The higher relative

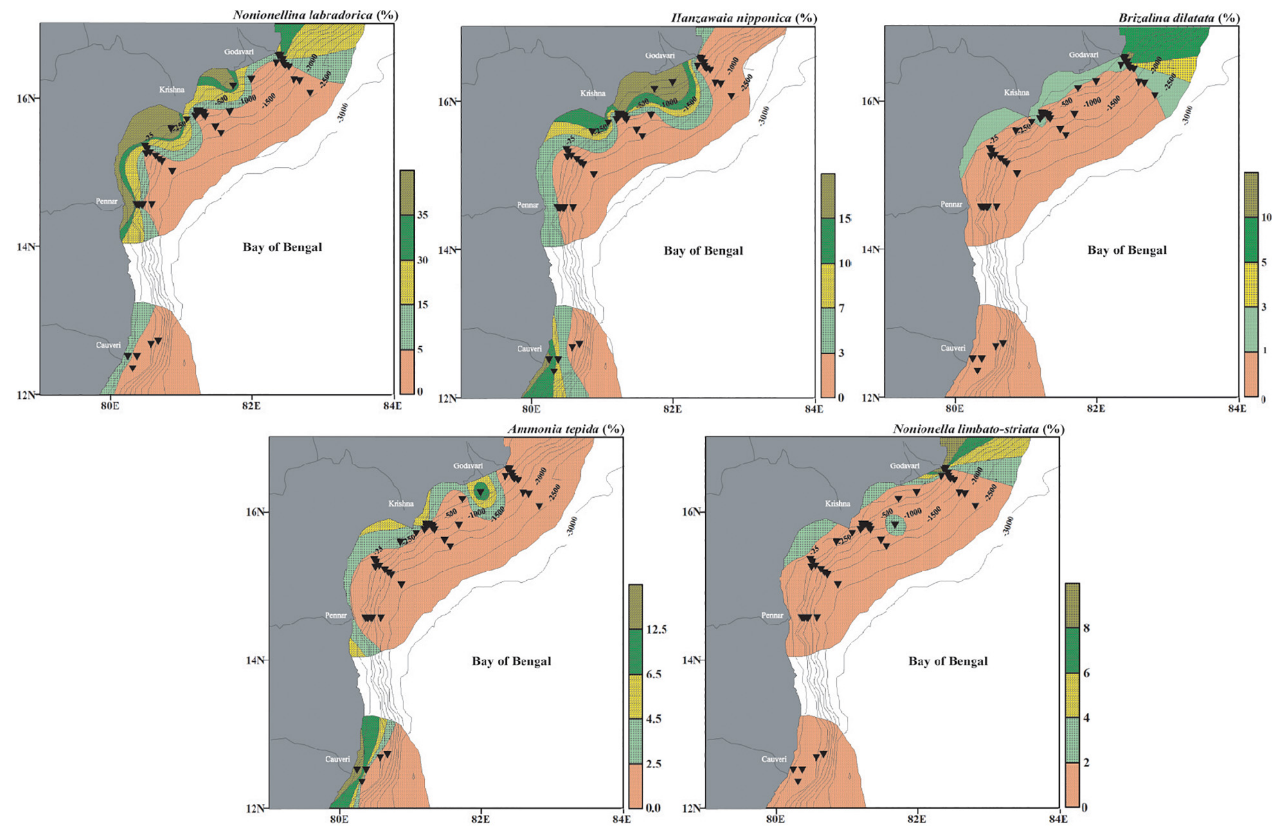


FIGURE 10 | Surface distribution (relative abundance) of dominant living benthic foraminifera from Cluster IV representing Assemblage I and having a significant positive correlation with dissolved oxygen and temperature. *Nonionella labradorica*, *Hanzawaia nipponica, Brizalina dilatata*, *Ammonia tepida,* and *Nonionella limbato-striata.* The stations are marked by black inverted triangles. The thin black lines mark the bathymetric contours.

abundance of *F. spinosa* at depths >200 m within the low DO concentration in the western Bay of Bengal, is more in line with its infaunal nature. The species belonging to *Bolivinellina* have been reported from shallow regions (Nigam and Chaturvedi, 2006; Nagendra et al., 2011; Panchang and Nigam, 2014; Gandhi et al., 2016). Both *B. earlandi* and *B. lucidopunctata* have been recorded from the upper slope region in the study area. *G. globosa* is another dominant species in this assemblage. Generally, rectilinear foraminifera comprising of genera like *Bolivina, Brizalina*, *Bulimina*, *Fursenkoina*, and *Uvigerina* have previously been reported as a common indicator of low oxygenated environments by several workers (Gupta and Machain-Castillo, 1993; Kaiho, 1994; Murray, 2006; Nigam et al., 2009; Mazumder and Nigam, 2014; Das et al., 2017; Verma et al., 2018). In the study area, these species are abundant at the stations falling within a depth range of ∼ >100 to ∼1,500 m where DO concentration is minimum (0.5 ml/l). All the major species of this assemblage are significantly negatively correlated with the dissolved oxygen, suggesting that they are well adapted to low dissolved oxygen (Suokhrie et al., 2020). The type species of *E. cassandrae* is *E. exilis* (Revets, 1993). The ecology of *E. cassandrae* has been rarely described. However, like its type species, *E. cassandrae* is also abundant at the intermediate depth locations with the low oxygenated environment. *Uvigerina peregrina* is also reported from this assemblage, suggesting its preference to low dissolved oxygen at these depths, which is in line with its reported dominance within OMZ (Hermelin and Shimmield, 1990). It has also been described as a shallow dysoxic-infaunal species (Das et al., 2017). *Rotaliatinopsis semiinvoluta* has been well documented as a low oxygen tolerant species reported from the Arabian Sea OMZ at intermediate water depths (den Dulk et al., 1998; Jannink et al., 1998; Caulle et al., 2015), and a similar preference to low dissolved oxygen is also found in our study. *Cassidulina laevigata* is another intermediate to deep-water fauna and is a dominant species in this assemblage. Amongst the other minor species of this assemblage, *R. scottii* is predominantly infaunal (Kaminski et al., 1988) and a characteristic fauna of muddy substrate, sometimes present in low oxygenated fjords (Murray, 1970; Filipsson and Nordberg, 2004). The substrate seems to be a less influential factor for this species in the west-central Bay of Bengal. Here, *R. scottii* is more indicative of low oxygenated conditions as its abundance increases at the stations with low DO values. *Bolivina spathulata* has been described as a deep infaunal and dysoxic species occurring in high organic flux environments (Bernhard and Gupta, 1999; Das et al., 2017). Furthermore, *B. spathulata* has been associated with a more saline environment (Eris et al., 2011), as is also seen in the study area. *Brizalina spathulata* is often the last

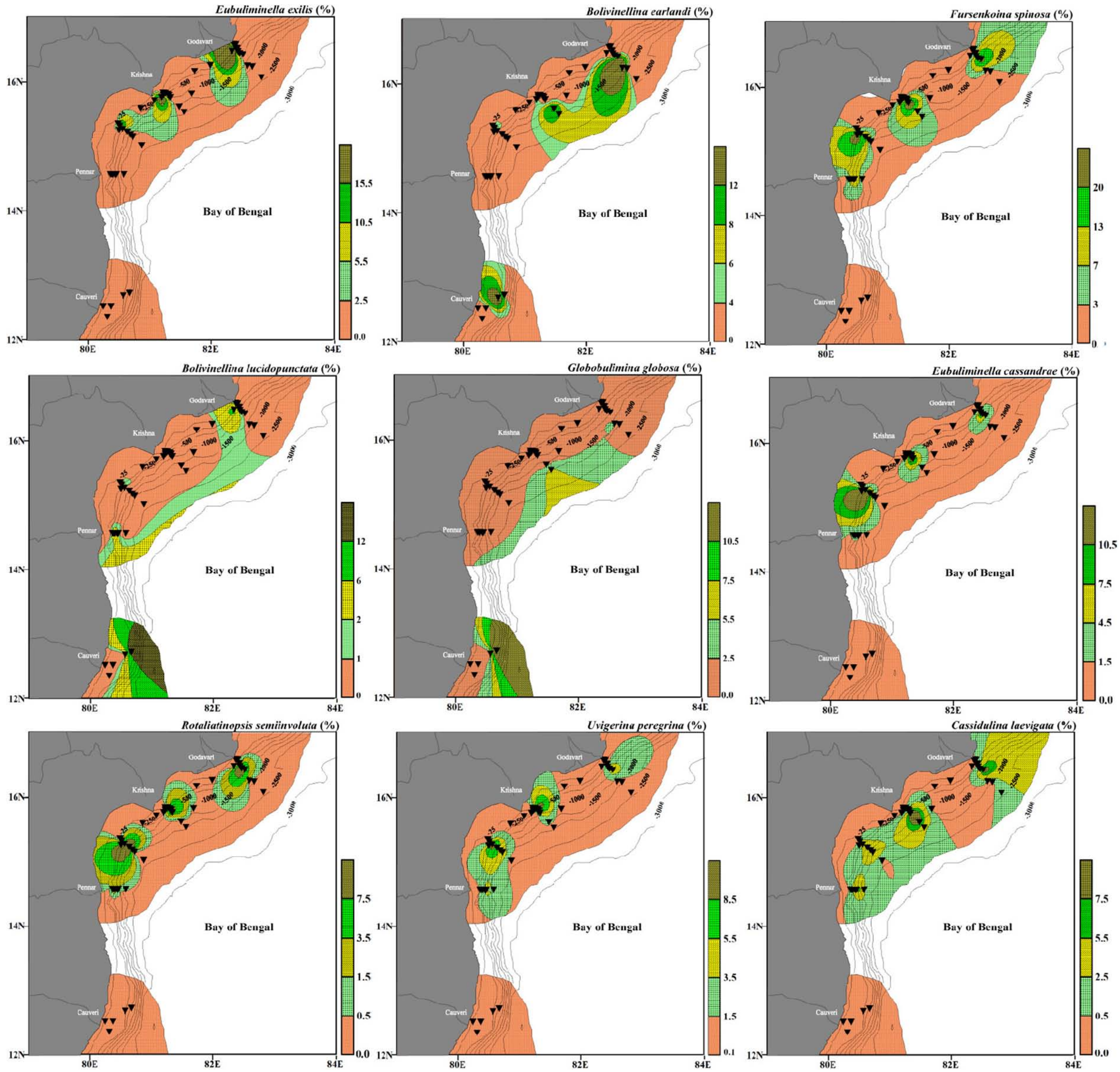

Eubuliminella exilis (%)
Bolivinellina earlandi (%)
Fursenkoina spinosa (%)
Bolivinellina lucidopunctata (%)
Globobulimina globosa (%)
Eubuliminella cassandrae (%)
Rotaliatinopsis semiinvoluta (%)
Uvigerina peregrina (%)
Cassidulina laevigata (%)

FIGURE 11 | Relative abundance of species representing intermediate depth assemblage (Assemblage II), having significant negative correlation with dissolved oxygen and positive correlation with organic carbon. *Eubuliminella exilis, Bolivinellina earlandi*, *Fursenkoina spinosa*, *Bolivinellina lucidopunctata*, *Globobulimina globosa, Fursenkoina spinosa, Eubuliminella cassandrae, Uvigerina peregrina, Rotaliatinopsis semiinvoluta, and Cassidulina laevigata.* The stations are marked by black inverted triangles. The thin black lines mark the bathymetric contours.

species to disappear before oxygen deficiency starts to inhibit any benthic life (Jonkers, 1984). In the west-central Bay of Bengal, *B. spathulata* is most common at stations between ∼120 m and ∼250 m. A significant drop in DO is observed at these depths. *Uvigerina peregrina* and *E. cassandrae* are minor species in this assemblage. *Trochamminopsis quadriloba* is more abundant at ∼2,000 m. Alve et al. (2011) reported the abundant presence of *T. quadriloba* at ∼100 m. However, the depth does not seem to significantly control its abundance (Buzas et al., 1993).

The ecology of *S. semiclara* is rarely described. Here, its abundance in the intermediate waters suggests its preference for low oxygen and relatively more saline environment. *Pullenia bulloides* was earlier reported as a part of the assemblage representing the Antarctic Bottom Water (AABW) (Corliss, 1979). In the present study, *P. bulloides* prefers lower levels of oxygen, high food supply and deeper depth, as also reported by other workers [north Atlantic-Schnitker, 1979; southwestern Indian Ocean- Corliss, 1983; Gooday, 1994; south Atlantic-Mackensen et al., 1995; Off Pakistan (Arabian Sea)-Schumacher et al., 2007; southeastern Indian Ocean-Verma et al., 2013; Arabian Sea-Caulle et al., 2015]. Although the type and preservation status of the organic matter also matters (Nomaki et al., 2005; Duffield et al., 2014), the organic carbon (C_{org}) is a good indicator of the food availability for foraminifera.

Some foraminifera prefer the "easily metabolizable food particles" while the infaunal forms mainly tolerate more refractory organic matter (Gooday, 1993; Jorissen et al., 1995). *Rutherfordoides rotundiformis* was found in extremely low oxygen conditions and in sapropelic sequences (Rohling et al., 1997; Mercone et al., 2001; Abu-Zied et al., 2008). *Rutherfordoides rotundiformis* is the most abundant at the stations with minimum DO concentration in the present study. *Chilostomella oolina* is a deep infaunal species abundant in low oxygenated environments similar to its generic preferences (Corliss, 1991; Gooday and Rathburn, 1999; Jorissen, 1999; Schmiedl et al., 2003; Schumacher et al., 2007; Kuhnt et al., 2013). The survival and abundance of *C. oolina* in low oxygenated environment is attributed to its nitrate respiration strategy (Kuhnt et al., 2013). *Cassidulina carinata* and *G. globosa* are also part of this intermediate assemblage. *Cassidulina carinata* is part of the assemblage preferring high food supply (Gupta and Thomas, 1999), while *G. globosa* is often described as an abyssal species (Takata et al., 2013). *Bolivina earlandi* have been described as a deep infaunal and dysoxic species occurring in high organic flux environments (Bernhard and Gupta, 1999; Das et al., 2017). Genus *Chilostomella* with the characteristic unornamented and thin-walled tests was an abundant genus among organic carbon-rich and less oxygenated sediments (Kaiho and Nishimura, 1992). *Trochamminopsis quadriloba* is another minor species in this assemblage as well as the previous assemblage. Other minor species also include *F. pauciloculata* abundant in the low oxygenated regions of the Indian waters (Mazumder and Nigam, 2014) and *N. auris* is an indicator of high organic carbon rich environments (Wefer et al., 1994; Bhaumik and Gupta, 2007). In the west-central Bay of Bengal, *B. marginata* is a deep infaunal species (Jorissen, 1999). Both *B. marginata* and *B.* cf. *delreyensis*, are abundant at depths deeper than ∼2,000 m, on the slope. Although *B. marginata* is often used as oxygen-deficient water proxy, we report a strong negative influence of temperature on the abundance of both *B. marginata* and *B.* cf. *delreyensis*, in the study area. *Baggina irregularis* is also part of the same assemblage that prefers less oxygenated waters. This species' ecology is not well known, although they are reported from the Bay of Bengal (Panchang and Nigam, 2014). In short, all the species described above are abundant in more saline, organic matter rich and poorly oxygenated environment.

Assemblage III (∼1,940–2,494 m)

A set of 12 species from Cluster III (*B.* cf. *delreyensis, B. marginata, H. guttifera, C. laevigata, G. subzelandica, C. carinata, G. mira, N. ampullacea, P. bulloides, U. peregrina, A. globigeriniformis,* and *T. quadriloba*) has been clubbed together in Assemblage III. The dominant species of this assemblage are *B.* cf. *delreyensis, B. marginata*, *H. guttifera*, *C. laevigata,* and *G. subzelandica* (**Figure 12**). *Bulimina marginata* is a deep

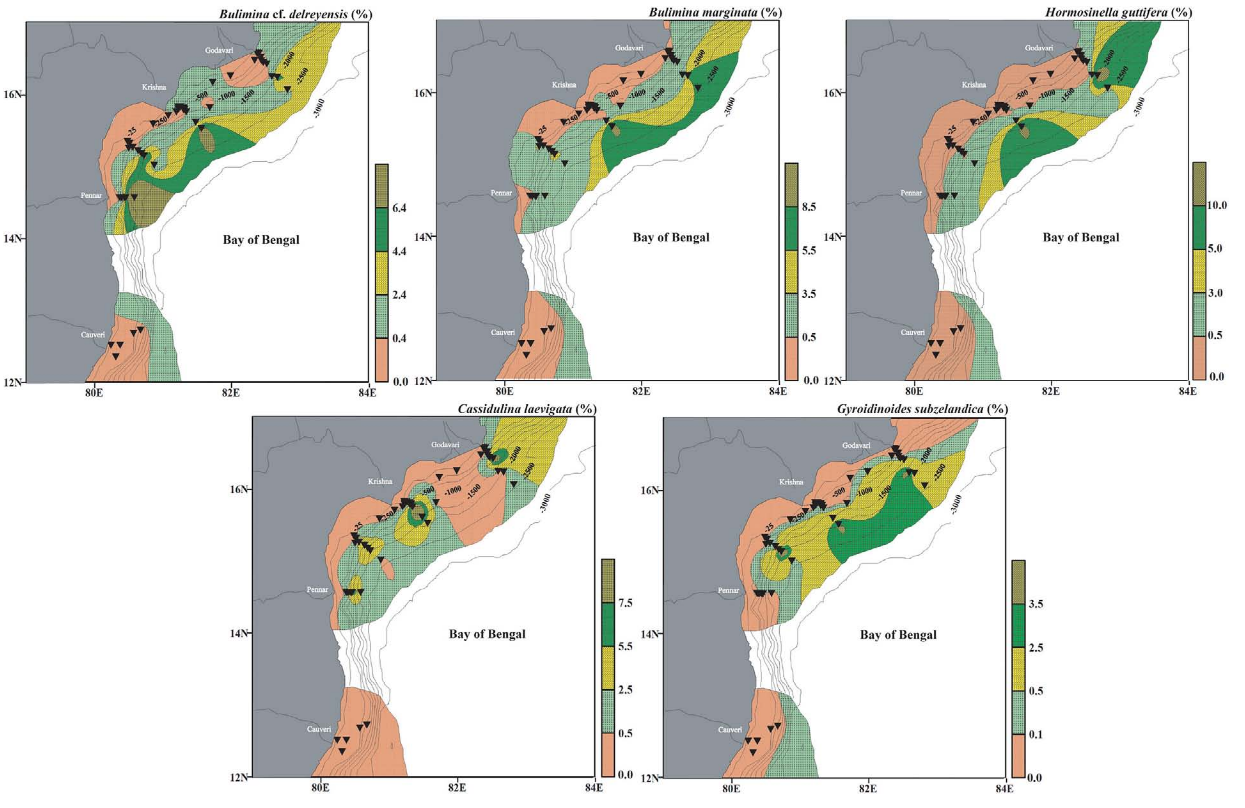


FIGURE 12 | Surface distribution (relative abundance) of dominant living benthic foraminifera representing deep water assemblage (Assemblage III), having a significant negative correlation with CF and C_{org}/TN, in the west-central Bay of Bengal. *Bulimina* cf. *delreyensis, Bulimina marginata*, *Hormosinella guttifera*, *Cassidulina laevigata,* and *Gyroidinoides subzelandica.* The stations are marked by black inverted triangles. The thin black lines mark the bathymetric contours.

infaunal species (Jorissen, 1999). Both *B. marginata* and *B.* cf. *delreyensis*, are abundant at depths deeper than ~2,000 m, on the slope. Although, *B. marginata* is often used as oxygen deficient water proxy, the abundance of these two species at deeper colder waters (>1,500 m) is suggestive of a strong negative influence of temperature on the abundance of both *B. marginata* and *B.* cf. *delreyensis*. The dominant agglutinating species in this assemblage is *H. guttifera*, which represents deep-water assemblages (Bernhard et al., 2009; Enge et al., 2012). *C. laevigata* is a shallow to deep infaunal species (Singh et al., 2012). *Gyroidinoides subzelandica* is a part of the same assemblage. All these species are significantly negatively correlated with the ambient temperature as the deeper waters have colder temperature. Additionally, the species in Assemblage III are also influenced by the type of organic matter (marine origin) and sediment texture, evidenced from the relatively lower C_{org} content in the samples at these depths.

The other minor species in this assemblage like *C. carinata*, *U. peregrina* and *P. bulloides* also represent Assemblage III indicating that these species have a wide range of abundance from the intermediate to the deep waters in the study area. *U. peregrina* is a dominant species in Assemblage III which suggests its preference for the environmental conditions prevalent at the intermediate waters rather than the deep waters. *Gavelinopsis mira, N. ampullacea* in Assemblage III, also have a significant preference for colder water with lower CF abundance and marine organic matter.

CONCLUSION

The spatial distribution of living benthic foraminifera and its comparison with the ambient parameters in the riverine influx dominated west-central Bay of Bengal, suggests a strong influence of multiple ecological parameters, mainly the dissolved oxygen, CF, and temperature to some extent. The organic carbon content is high (~1.4% on average) at intermediate depths (~100–1,000 m) where bottom water dissolved oxygen is at its lowest (~0.5 ml/l on average). The maximum living benthic foraminiferal abundance at these depths with limited diversity indicates high abundance of a few opportunistic species. The high C_{org}/TN suggests that C_{org}% is mostly of terrestrial origin, especially closer to the river mouths. Three significant faunal assemblages delineated from the statistical analysis give more insight on the ecological preferences of foraminifera in the west-central Bay of Bengal. The shallow water (~27–100 m) assemblage comprising of *N. labradorica*, *H. nipponica*, *B. dilatata*, *A. tepida,* and *N. limbato-striata* represents well oxygenated warmer waters with low C_{org}% and coarser sediment. The intermediate water (~145–1,500 m) assemblage comprising of *E. exilis, B. earlandi*, *F. spinosa*, *B. lucidopunctata*, *G. globosa, F. spinosa, E. cassandrae, U. peregrina, R. semiinvoluta,* and *C. laevigata* assemblage represents poorly oxygenated, colder waters with high C_{org}%. The deep water (~1,940–2,494 m water depth) assemblage comprising of *B.* cf. *delreyensis, B. marginata*, *H. guttifera*, *C. laevigata,* and *G. subzelandica* represents high C_{org}% but relatively higher bottom water dissolved oxygen than the intermediate water depth. We also report the specific preference of 40 dominant species each influenced by a set of environmental parameters. The ecological preferences of foraminiferal species and foraminiferal assemblages delineated from this study can be utilized as proxies in sub-surface samples to understand paleo-ecology and paleoclimatic changes from the west-central Bay of Bengal.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

TS curated the data and wrote the first draft of the manuscript. RS conceptualized and investigated the research work. RN helped in the funding acquisition needed to carry out the work. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.656757/full#supplementary-material

Supplementary Table 1 | The details of the sampling locations for multicore as well as spadecore.

Supplementary Table 2 | The details of stations and ambient physico-chemical parameters at each station. Also given are the measured sedimentary characteristics (CF, C_{org}, C_{org}/TN, and $CaCO_3$). The salinity and pH at the sediment water interface were measured from the water retrieved in multi-core tops. The DO and other data for the spade core station were retrieved from the World Ocean Atlas 2013 (Garcia et al., 2013; Locarnini et al., 2013; Zweng et al., 2013).

Supplementary Table 3 | The relative abundance of the dominant species having atleast >3% abundance at a minimum of two stations.

Supplementary Table 4 | Check-list of living benthic foraminiferal species found in the surface sediments of the western Bay of Bengal. The maximum relative abundance of the species and the depth of the respective station is also provided.

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Disentangling the Effect of Seasonal Dynamics on Meiobenthic Community Structure From River Matla of Sundarbans Estuarine System, India

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In estuarine sediment, meiobenthos serve as an excellent candidate to perform a range of ecosystem services. However, even though the taxonomic sufficiency of meiobenthos in detecting spatiotemporal gradients is well recognized, very little is known about their functional attributes in response to environmental descriptors. To bridge this knowledge gap, the taxonomic structure and trait-based functional diversity patterns of meiobenthic assemblage, focusing on nematode species composition, were assessed for the first time from the unexplored central sector of Sundarbans Estuarine System (SES). Sediment samples were collected seasonally (monsoon, winter, spring, and summer) selecting a total of eight stations across River Matla (the widest and longest river of SES). Distinct seasonal successional patterns had been observed in meiobenthic abundance modulated by seasonal alteration in the sedimentary environment (PERMANOVA, $p < 0.05$). Our study revealed a strong preponderance of meiobenthic density in spring (2978 ± 689.98 ind. 10 cm^{-2}) and lowest during monsoon (405 ± 51.22 ind. 10 cm^{-2}). A total of 11 meiobenthic taxa were identified with the dominance of nematodes. Altogether, 79 species of nematode belonging to 22 families had been identified across the entire study area and nematode assemblage was dominated by *Sabatieria praedatrix*, *Sphaerolaimus balticus*, *Desmodora communis*, *Dorylaimopsis punctata*, and *Daptonema hirsutum*. Principal component analysis depicted a distinct separation of seasons with reference to environmental variables. Distance-based redundancy analysis delineated that meiobenthic communities were mainly structured by organic matter, salinity, and dissolved oxygen concentration. Biological trait analyses of nematode assemblages were applied to gather the ecological information based on morphological and ecological characteristics. The most common morphotypes were slender body shape, clavate tail shape, striated cuticle pattern, and non-selective deposit feeders with colonizing abilities of 2–3 (c–p score in a scale from 1 to 5). Results from BIO-ENV showed that sediment organic matter and dissolved oxygen played overriding roles in shaping the functional compositions of nematodes. Thus,

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the characterization of meiobenthos and nematode assemblages in the context of taxonomic as well as functional attributes represents a first step toward building of baseline data which could help to evaluate the ecological status of SES and direct future research priorities concurrently.

Keywords: meiobenthos, free-living nematodes, functional diversity, biological trait analysis, taxonomic sufficiency, Sundarbans

INTRODUCTION

Meiobenthos represents a highly diverse biocenosis that is made up of microscopically small-sized aquatic invertebrates (Giere, 2009; Curini-Galletti et al., 2012). In aquatic habitats, they serve as excellent candidates to perform a range of ecosystem services. They play a pivotal role in biomineralization of detrital matter and enhance the nutrient regeneration by breaking down detritus (Coull, 1999; Nascimento et al., 2012). Furthermore, they act as key components of energy provision to higher trophic levels (macrobenthos, juvenile demersal fishes, and bottom-feeding shore birds, etc.), thereby constituting an integral part in the benthic food web (Schmid-Araya et al., 2016; Schratzberger and Ingels, 2018). Notably, they can be used as a promising auxiliary to monitor environmental changes due to their small sizes, ubiquitous distribution, higher abundance and taxonomic diversity, fast generation cycles, direct benthic development, and limited mobility (Pusceddu et al., 2007; Vanaverbeke et al., 2011; Semprucci and Balsamo, 2012; Zeppilli et al., 2015). Therefore, a long-term monitoring program using meiobenthic animals could explicitly provide better and accurate information about their surrounding environment.

Within the meiobenthic network of organisms, free-living nematodes are a numerically dominant and species-rich group, constituting more than 90% of the fauna (Lambshead and Boucher, 2003). Their density and diversity vary with the availability of sediment pore water oxygen, organic matter deposition, sediment texture, and other interacting environmental variables (Heip et al., 1985). Recently, attention has been paid to investigate marine ecosystem functioning by analyzing nematode communities. Ecosystem functioning can be summarized as biological, physical, and geochemical processes that operate within an ecosystem, performing by individual ecosystem components or in combination (Jax, 2005; Edwards et al., 2014). It is now well known that higher functional biodiversity contributes to a stable and resilient ecosystem. Thus, species identification and their functional patterns appear to be essential for the maintenance of a healthy ecosystem (Radwell and Brown, 2008). In general, the functional structure or diversity of a community is defined as a combination of species distribution and their abundances in the functional space (Mouillot et al., 2013) and biological traits are those characteristics that define species in the context of their ecological roles (Diaz and Cabido, 2001). Biological trait analysis (BTA) is used to assess the functional diversity of any assemblages based on multiple traits or characteristics (Bremner et al., 2003, 2006). The traditional taxon-based descriptors of nematode community structure analyses from species abundance data, however, may not account their autecological information. Species in functional groups that share morphological or ecological traits are thought to improve our mechanistic understanding of different habitat conditions along with environmental gradients (Chalcraft and Resetarits, 2003; Ristau et al., 2015). Species-level identification may not provide comprehensive knowledge regarding ecosystem functions as closely related species may differ in their functional roles (Maurer, 2000). Nematode assemblages represent numerous morphological characteristics which are considered to play important ecological roles: buccal morphology (a proxy to assess trophic relationships, Wieser, 1953), tail shape (crucial for locomotion, reproduction, and sediment retention, Thistle and Sherman, 1985; Thistle et al., 1995), body shape (important adaptive feature to different sedimentary environments, Soetaert et al., 2002; Vanaverbeke et al., 2003, 2004), and cuticle morphology (a protective covering of the body to avoid intoxication of organisms through diffusion, Soetaert et al., 2002). Moreover, ecological traits such as life history strategy (Bongers, 1990) can also be informative of the habitat condition. The assemblage patterns of marine nematode functional diversity and their spatiotemporal variations in response to environmental settings remain still poorly resolved. Thus, owing to such immense importance of BTA in ecosystem functioning, their studies need to be approached in a proper systematic manner that has never been attempted from any estuaries belonging to the eastern coast of India.

Estuaries are the most hydrodynamically active and pervasive transitional zones, where crucial biogeochemical processes take place (Costanza et al., 1997). They are considered as vital conduits for the transport of nutrients, organic materials, and sediments from rivers to oceans, making them an essential carbon sink. The amenities estuaries offer render them as the most precious national treasures, which may impinge on the health and vibrancy of human society and economy. Due to their irreplaceable ecological functions, such as high productivity, nutrient enrichment, and ephemeral habitats for reproduction, feeding, and nurseries for a variety of animals (Beck et al., 2001; Gili, 2002), estuaries are consequently subjected to fishing, harbor, and dredging activities. It is now widely acknowledged that these naturally stressed ecosystems are characterized by the continuum gradient of environmental factors, which might play an overriding role in shaping the heterogeneous distribution of meiobenthic communities (Adão et al., 2009; Alves et al., 2009, 2013, 2014; Sroczyńska et al., 2020).

From Indian estuaries, meiobenthic organisms have garnered extensive attention in the field of taxonomy and diversity accompanying their environmental descriptors. Along the eastern coastal belt of India, majority of the studies were carried out from the Tamil Nadu (Chinnadurai and Fernando, 2007; Ansari et al., 2014), Kerala (Chinnadurai and Fernando, 2006), and Odisha coasts (Baliarsingh et al., 2015). As yet, monitoring of the status of estuarine meiobenthic components and their key ecosystem functions from Sundarbans Estuarine System (SES) still remains discrete and limited to selected sites, which are not sufficient to exhaustively ensuring ecological goals of sustainability. Meager amount of studies are available on meiofauna inhabiting the western (Rao and Misra, 1983; Dey et al., 2012; Ghosh et al., 2018) and eastern parts (Sen et al., 2016) of Indian Sundarbans, howbeit there is a dearth of information about their composition along the central sector of SES. At the central tract of SES, River Matla divides Indian Sundarbans into Reserved Forest on the west and Sundarban Tiger Reserve on the east and large portions of it are quite inaccessible to human intervention. Therefore, our primary goal was to define the current state of scientific knowledge regarding meiobenthic fauna in a systematic manner to fill the knowledge gap and to provide useful information for future researchers and environmental policymakers. To fulfill that aim, the following questions were addressed: (i) how does meiobenthic community structure, especially nematode species composition, in concert with trait modalities change throughout the year along the same spatial axis and (ii) how do seasonally governed environmental factors influence their distribution pattern?

MATERIALS AND METHODS

Study Area

Sundarbans, the largest contiguous deltaic mangrove ecosystem of the world, is situated on the delta created by the Ganges, Meghna, and Brahmaputra rivers covering the coastal belt of India and Bangladesh (Papa et al., 2010). This coastal mangrove ecosystem is interconnected by hundreds of islands and numerous creeks, inlets, and canals. For the present investigation, we selected the estuary of Matla River, the widest (26 km) and longest (125 km) (Chatterjee et al., 2013) river of SES, situated at the central part of Indian Sundarbans (**Figure 1**). This river originates at the confluence of Bidyadhari, Khuratya, and Rampur Khal close to the town of Canning in South 24 Parganas and flows to the Bay of Bengal. This tidally fed river has lost its original freshwater connections with the Ganges due to continuous neotectonic shifts of the Bengal Basin and heavy siltation, resulting in significant changes in the hydrology, sedimentation pattern, and salinity dynamics of the central tract of SES as compared to the western sector (Banerjee, 2013; Ghosh et al., 2015). Our study area includes a total of eight stations (designated as Matla or M1 to M8) along a salinity gradient at the north–south direction starting from Herobhanga Reserve Forest toward Bulchery Island situated near the mouth of the estuary. The detailed GPS locations of the sampling stations are shown in **Table 1**. The funnel-shaped estuary lies adjacent to the Sundarban Tiger Reserve; howbeit, the northern part of the estuary is notably affected by urbanization and other anthropogenic activities along its river bank. On the other hand, the downstream stretch of this estuary is pristine with luxuriant growth of dense mangrove patches. The study period extended from September 2016 to May 2017, including four different seasons: monsoon (September), winter (December), spring (February), and summer (May).

Sample Collection

The observation of all concerned parameters was carried out during the aforementioned four seasons selecting eight stations from Matla River. Triplicate sediment samples were taken for meiobenthos analyses by a van Veen grab (0.04 m^2) from each study site, and from each grab sample two subsamples were collected using a hand corer (5.6-cm internal diameter). One core of the subsample was preserved immediately in 4% buffered Rose Bengal (0.5 g L^{-1}) formalin (Danovaro et al., 2004) and subsequently returned to the laboratory for further analyses. Another core was stored for environmental parameter analyses.

Environmental Parameter Analyses

Sediment temperature was measured by a handheld mercury thermometer *in situ*. The Niskin water sampler (5 L) was used to collect bottom water for analyses of pH, dissolved oxygen (DO), and salinity according to standard protocols of Strickland and Parsons (1972). The microphytobenthos or chlorophyll *a* (Chl *a*) concentration of sediment was estimated by 90% acetone extraction method (Strickland and Parsons, 1972). Organic matter and sediment granulometry were analyzed using the chromic acid oxidation method followed by titration with 0.2 N ammonium ferrous sulfate (El Wakeel and Riley, 1957) and following the sieve and pipette method (Folk, 1968) correspondingly. Suspended particulate matter (SPM) was determined by subsequent literature of Harrison et al. (1997).

Meiofaunal Analyses

Sediment subsamples were washed through a set of sieves (500 and 63 μm) to segregate macro- and meiobenthic organisms, respectively (Pfannkuche and Thiel, 1988). The sediment retained in the 63-μm sieve was then decanted to extract meiofauna following the method of Armenteros et al. (2008). Collected organisms were sorted and enumerated under a stereo zoom microscope (Nikon SMZ745T). The abundance was expressed in individuals 10 cm^{-2} ± SD.

Nematofaunal Analyses

A total of 2283 nematode specimens were picked and mounted with the help of anhydrous glycerin (Seinhorst, 1959) onto glass slides for identification up to species level under a compound microscope fitted with a camera (Nikon ECLIPSE Ci) based on standard pictorial keys (Platt and Warwick, 1983, 1988; Warwick et al., 1998) and online identification key: NeMys (Bezerra et al., 2021).

For BTA, five traits were selected: four morphological (buccal cavity structure, adult body shape, tail shape, and cuticle morphology) and one ecological (life-history strategy) (**Table 2**). On the basis of buccal morphology, feeding guilds of each nematode species were assigned according to Wieser's (1953) classification: 1A—selective deposit feeders, 1B—non-selective deposit feeders, 2A—epistrate feeders, and 2B—carnivorous/omnivorous. Three groups of adult body shapes of

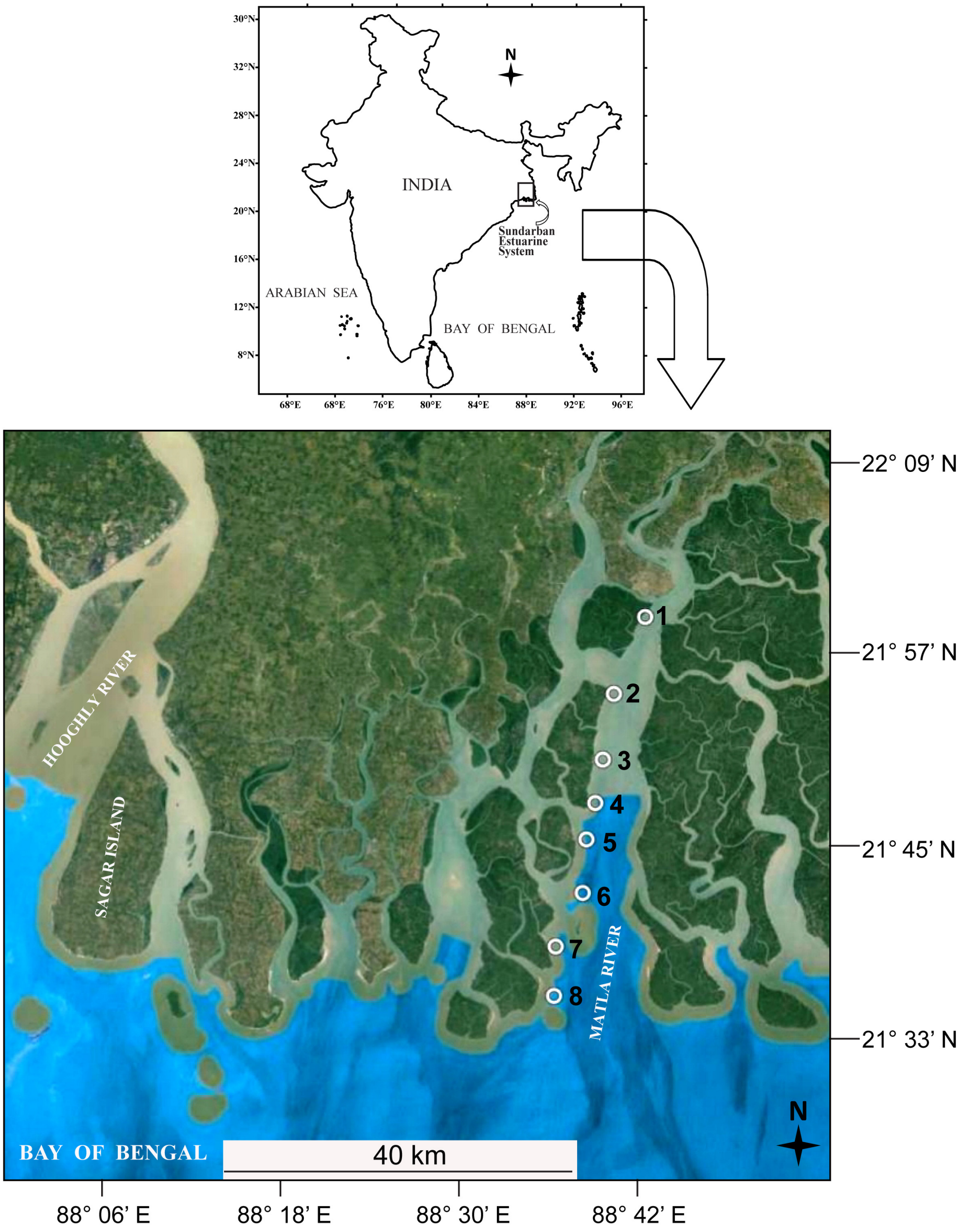

FIGURE 1 | Map showing the sampling locations at SES.

nematodes were obtained from the literature of Soetaert et al. (2002)—stout, slender, and long/thin. Individual nematodes were categorized into four tail shapes following the classification of Thistle et al. (1995)—short/round, elongated/filiform, conical, and clavate. Based on cuticle morphology, nematode species were categorized into four groups: smooth, striated, covered with dots, and ornamented (Soetaert et al., 2002). According to Bongers et al. (1991, 1995), each nematode specimen was classified one of the five c–p (colonizer–persister) categories: 1—colonizers (opportunistic species; *r*-strategists); 2—tolerant to stress; 3—intermediate; 4—highly sensitive to stress; and 5—persisters (*k*-strategists).

Statistical Analyses

Principal component analysis (PCA) was performed to identify essential environmental variables that characterize the study

TABLE 1 | GPS locations of sampling stations at River Matla.

Stations	Longitude	Latitude
M1	88°42′23.50″E	21°59′11.30″N
M2	88°40′16.50″E	21°54′23.00″N
M3	88°39′31.70″E	21°50′16.90″N
M4	88°39′1.02″E	21°47′34.37″N
M5	88°38′25.20″E	21°45′18.20″N
M6	88°38′10.08″E	21°41′58.00″N
M7	88°36′21.07″E	21°38′37.60″N
M8	88°36′14.48″E	21°35′32.80″N

TABLE 2 | List of biological traits and categories used to describe nematode assemblages.

Biological traits	Categories
(A) Body shape	(i) Stout
	(ii) Slender
	(iii) Long/thin
(B) Tail shape	(i) Short/round
	(ii) Elongate/filiform
	(iii) Conical
	(iv) Clavate
(C) Cuticle morphology	(i) Smooth
	(ii) Striated
	(iii) Covered with dots
	(iv) Ornamented
(D) Life-history strategy (c-p score)	(i) c-p 1-Extreme colonizer
	(ii) c-p 2-Colonizer
	(iii) c-p 3-Intermediary
	(iv) c-p 4-Persister
	(v) c-p 5-Extreme persister
(E) Feeding guild	(i) 1A-Selective deposit feeders
	(ii) 1B-Non-selective deposit feeders
	(iii) 2A-Epistrate feeders
	(iv) 2B-Predators

area. A two-way permutational multivariate analysis of variance (PERMANOVA) was also applied to examine the role of seasonal effects on meiobenthos across Matla River. This analysis was performed using two fixed factors "seasons" and "stations" with four seasons (monsoon, winter, spring, and summer) and eight stations [M1 to M8], respectively. The relationship between meiobenthic communities and environmental parameters was investigated using distance-based linear modeling (DistLM) and visualized using distance-based redundancy analysis (dbRDA) to derive an ordination plot (Anderson et al., 2008). A stepwise selection procedure was used in DistLM with the AICc model selection criteria to permit the fitting of best explanatory environmental factors and to model the meiobenthic community data (Bray Curtis resemblance matrix) against the normalized environmental variables. From Bray–Curtis similarity matrices, the cluster plot and NMDS ordination plot were derived following nematode species abundance in each season and biological traits of nematode species, respectively, after Log $(X + 1)$ transformation. A SIMPROF (similarity profile) test was done to detect the significantly different stations in each season 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. Furthermore, similarity of percentage (SIMPER) analysis was conducted to identify the% contribution of major nematode species responsible for the total dissimilarity between groups. The following biotic indices were also analyzed based on nematode species composition: Shannon–Wiener diversity (H' $\log_e$), Margalef's species richness (d), Pielou's evenness (J') and Simpson index $(1 - \lambda')$. The relationships of nematode functional traits with environmental parameters were explored by means of BIOta ENVironmental matching (BIO-ENV) analysis (Clarke and Ainsworth, 1993). All statistical and biological trait analyses were performed using PRIMER (version 6) software (Clarke and Gorley, 2006; Clarke et al., 2008) equipped with add-on package PERMANOVA (Anderson et al., 2008) and SigmaPlot 11.0 correspondingly. Canonical correspondence analysis (CCA) (ter Braak, 1986) was performed in order to visualize the trend of nematode species composition with different environmental variables using the MVSP program (version 3.1) (Kovach, 1998).

RESULTS

Environmental Factors

A suit of environmental factors such as temperature, pH, DO, salinity, Chl *a*, SPM, organic matter, and sediment texture were measured during each sampling occasion (**Table 3**). Sediment temperature showed seasonal variability indicating highest in summer [varied between 31 (M3 and M4) and 32.5°C (M1)] and lowest in winter [varied between 21.5 (M5 and M6) and 23.5°C (M8)]. pH was slightly alkaline and relatively constant all over the study period (7.38–8.16). A moderate DO concentration was observed during the course of the sample collection, being highest in monsoon (8.24 mg L^{-1}) and lowest in spring (4.21 mg L^{-1}). A typical estuarine gradient of salinity of bottom water from low to high toward the mouth of the estuary was observed (**Table 3**). The highest salinity values were recorded in summer [minimum 21.06 (M6) and maximum 35.04 PSU (M4)] and lowest in monsoon [minimum 6.41 (M5) and maximum 16.68 PSU (M3)]. The maximum SPM concentration was detected in summer (433.8 mg L^{-1}), minimum in spring (17 mg L^{-1}). Microphytobenthos biomass (Chl *a*) was evidenced with seasonal disparity being highest in spring [minimum 2.24 (M2) and maximum 7.61 $\mu g\ g^{-1}$ (M5)] and lowest in winter [minimum 0.18 (M1) and maximum 5.63 $\mu g\ g^{-1}$ (M4)]. Organic matter concentrations were ranged from 0.08 (M7) to 5.28% (M1) in monsoon, 1.29 (M1) to 5.61% (M8) in winter, 1.30 (M4) to 1.91% (M8) in spring, and 1.28 (M4) to 2.06% (M8) in summer. A classic gradient of estuarine sediment was observed as silt and clay fractions increased from upstream toward downstream with some exception. Overall, the sediment samples were characterized by a predominance of clayey silt with a few variations (**Table 3**).

TABLE 3 | Minimum (Min), maximum (Max), mean and standard deviation (SD) of biotic and abiotic parameters of eight stations of Matla River sampled during four seasons.

Parameters	Monsoon				Winter				Spring				Summer			
	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD
Temperature (°C)	28.5	31.5	30.03	1.00	21.5	23.5	22.19	0.64	24.5	27	25.41	0.93	31	32.5	31.63	0.52
Salinity (PSU)	6.41	16.68	11.93	3.96	11.70	19.36	17.03	2.63	30.44	33.86	32.50	1.14	21.06	35.04	29.27	5.15
Dissolved oxygen (mg L^{-1})	5.83	8.24	6.56	0.80	4.92	6.14	5.73	0.40	4.21	5.83	5.03	0.57	4.61	4.91	4.77	0.13
pH	7.38	7.98	7.83	0.19	7.97	8.09	8.03	0.05	7.99	8.14	8.07	0.05	8.04	8.16	8.13	0.04
SPM (mg L^{-1})	18.21	159.4	54.90	48.06	34.61	339.34	162.44	95.98	17.00	40.00	27.38	9.16	116.6	433.8	261.18	96.68
Chl *a* ($\mu g\ g^{-1}$)	0.34	2.66	1.35	0.95	0.18	5.63	1.66	1.77	2.24	7.61	4.25	1.93	0.33	2.37	1.23	0.64
Phaeopigment ($\mu g\ g^{-1}$)	0.05	0.31	0.17	0.07	0.02	0.59	0.14	0.19	0.02	0.34	0.13	0.11	0.06	0.33	0.20	0.09
Organic Matter (%)	0.08	5.28	1.44	1.62	1.29	5.61	3.46	1.46	1.30	1.91	1.63	0.17	1.28	2.06	1.61	0.29
Sand (%)	0.98	51.45	20.87	16.07	3.80	54.57	18.21	17.28	3.74	26.20	11.72	7.13	3.62	36.62	12.60	12.32
Silt (%)	21.95	79.00	55.77	17.60	18.47	91.92	68.70	24.78	51.31	71.99	59.95	8.40	48.54	77.85	66.92	10.75
Clay (%)	16.48	30.60	23.36	5.37	4.28	34.40	13.09	11.21	20.96	38.28	28.33	6.14	12.72	35.44	20.48	7.06

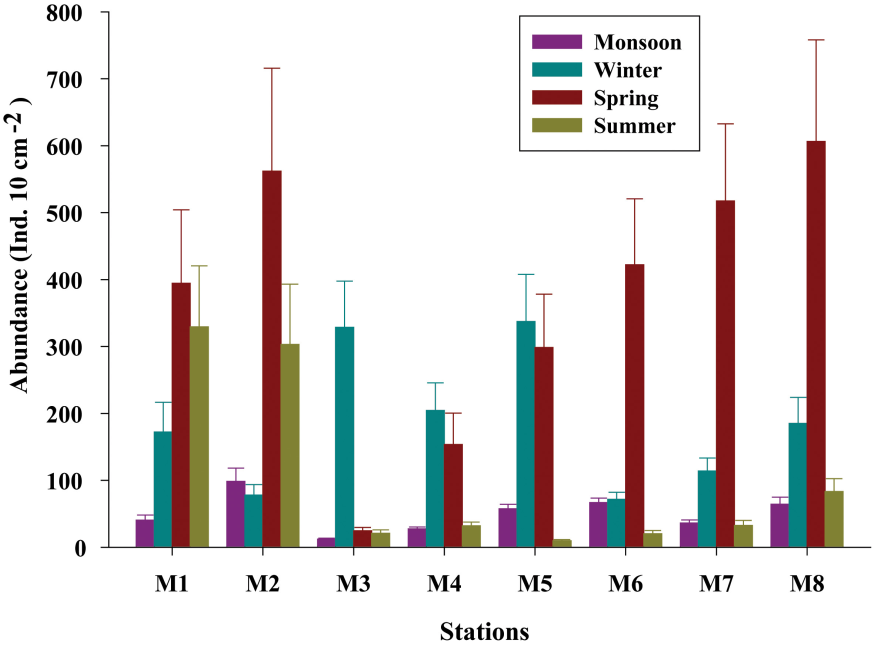

FIGURE 2 | Seasonal variations of the meiobenthic population across eight stations (M1 to M8) of Matla (M) River.

Meiobenthic Structure

Total meiofaunal abundance differed significantly among seasons (PERMANOVA, $p < 0.05$) with the highest number (±SD) in spring (2978 ± 689.98 ind. 10 cm^{-2}) followed by 1493 ± 301.39 ind. 10 cm^{-2} (winter) and 832 ± 203.64 ind. 10 cm^{-2} (summer) and lowest in monsoon (405 ± 51.22 ind. 10 cm^{-2}) (**Figure 2**). The taxonomic composition of meiofauna was constituted by 11 taxa throughout the eight stations of Matla during sampling periods with the dominance of free-living nematodes representing 74% of total assemblages. The densities of nematodes were higher in spring and winter than those of summer and monsoon. Harpacticoid copepods contributed 15% to the total fauna, and their densities remained constant in all four seasons. The other abundant groups were kinorhyncha (4%), polychaete juveniles (2%), and benthic foraminifera (1%), while the occurrence of halacarid mites, ostracods, turbellaria, oligochaetes, bivalve settlers, and gastropod juveniles were present in low densities. Turbellaria and gastropod juveniles were found only in monsoon and winter. In order to visualize the impact of crucial abiotic variables, PCA was performed with 11 environmental factors, which depicted a distinct separation of seasons with reference to environmental variables (**Figure 3**). Stations from monsoon and winter were associated with higher DO, organic matter, and silt and clay fractions of sediment, while higher values of salinity and temperature characterized spring and summer stations. In turn, spatial discrepancy was not evident, although the seasonal gradient appeared distinct. DistLM analysis allowed identifying those abiotic variables that

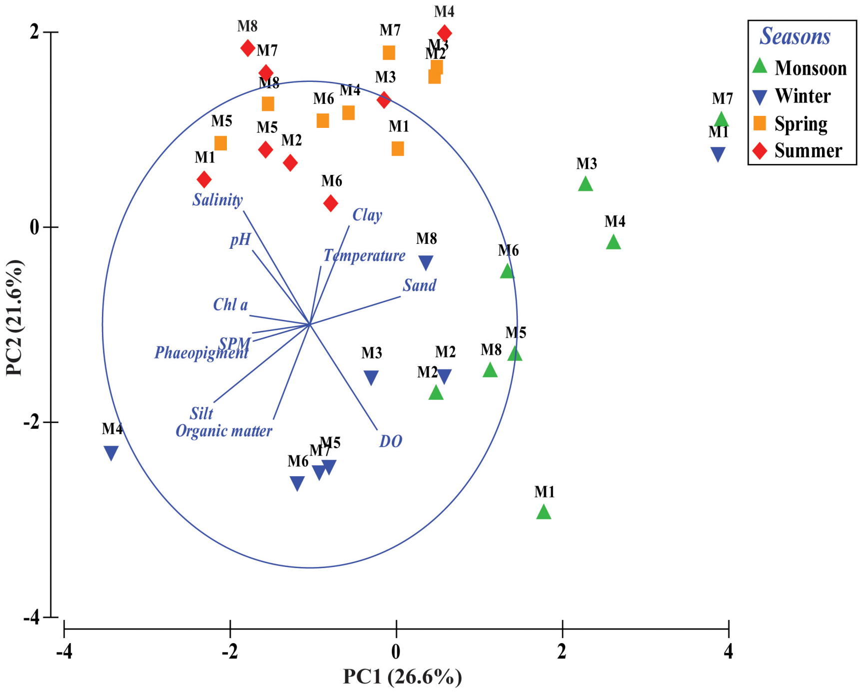

FIGURE 3 | Principal component analysis (PCA) based on abiotic variables of four different seasons across eight stations (M1 to M8) from Matla (M) River.

were best correlated with the seasonal distribution patterns of the meiobenthic community. DistLM indicated that the 11 abiotic variables related to the variation in meiofaunal community structure, even though not all variables were significant. Variables such as DO, temperature, and salinity showed the highest correlations ($p < 0.05$) with meiofaunal assemblages. In the dbRDA ordination diagram, the best explanatory model included DO and temperature in monsoon, whereas salinity, microphytobenthos, and organic matter characterized summer and winter, respectively (**Figure 4**).

Nematode Assemblages

Altogether, 79 species of free-living nematodes belonging to 22 families were identified for the first time from Matla River (**Table 4**). There was a strong dominance with 19 species contributing individually to greater than 1% to total density. The most spatially widespread species were *Sabatieria praedatrix* (8%), *Sphaerolaimus balticus* (6%), *Desmodora communis* (6%), *Dorylaimopsis punctata* (5%), *Daptonema hirsutum* and *D. procerum* (5% each), *Monoposthia costata* (5%), and *Terschellingia longicaudata* (4%). Several species appeared to be characteristic of particular seasons: *Camacolaimus barbatus*, *Eleutherolaimus minutus*, *Comesa* sp., *Nemanema* sp., and *Parasphaerolaimus* sp. (winter); *Sabatieria alata*, *Viscosia cobbi*, and *Pontonema* sp. (spring); and *Eurystomina* sp., *Longicyatholaimus* sp., and *Trissonchulus* sp. (summer). In addition, certain species showed a strong patchy distribution, i.e., appeared only in one station and one season, for instance *Sabatieria alata* (station M6 in spring) and *Trissonchulus* sp. (station M4 in summer). Biotic indices based on nematode communities are shown in **Table 5**. A typical seasonal pattern was observed in Shannon–Wiener index (H′ loge), with the highest value (3.24 bit·ind^{-1}) in winter (station M6) and lowest (1.01 bit·ind^{-1}) in monsoon. Margalef's species richness (d) was high during winter (7.17) and low during monsoon (1.12), while Pielou's evenness index (J′) was extended from 0.83 (monsoon) to 0.97 (summer).

Cluster analyses of the Bray–Curtis similarity matrix based on free-living nematode species delineated two groups and two separate stations (SIMPROF test $p < 0.05$) during monsoon (**Figure 5A**). Stations 3 and 7 were segregated due to the presence of some exclusive species: *Tricoma* sp. in station 3 and *Quadricoma* sp. at station 7. According to SIMPER analysis, *S. balticus* and *Sabatieria* sp. contributed 13.93% and 31.88% in group 1 (56.34% average similarity) and group 2 (60.27% average similarity) formation, respectively (**Table 6**). In winter, two major groups have been identified: *D. procerum* (12.84%) and *S. praedatrix* (10.19%) as major contributors behind the formation of group 1 (52.50% average similarity) and group 2 (56.37% average similarity), correspondingly (**Figure 5B**). Moreover, stations 1, 4, and 8 were separated from these two groups due to unique species compositions like *Aponema torosa* in M1, *Pselionema longiseta* in M4, and *Chromaspirina inglisi* in M8. Only one group was observed during the spring and summer seasons (**Figures 5C,D**). Upstream stations, for example, M1, M2, and M3 in spring and M1, M3, and M4 in summer, completely diverged from their downstream counterparts. *D. hirsutum* in spring and *S. praedatrix* in summer contributed 9.84% and 10.65%, respectively, in the construction of the groups (SIMPER analysis, **Table 6**).

TABLE 4 | List of free-living marine nematode species identified from Matla River along with their CCA codes and biological traits. "+" and "**-**" indicate present and absent, respectively.

Species	CCA code	Seasons				Body shape			Tail shape				Cuticle morphology				Life-history strategy (c-p score)					Feeding guild			
		Monsoon	Winter	Spring	Summer	Stout	Slender	Long/ thin	Short/ round	Elongate/ filiform	Conical	Clavate	Smooth	Striated	Covered with dots	Ornamented	c-p 1	c-p 2	c-p 3	c-p 4	c-p 5	1A	1B	2A	2B
Anticoma sp.	1	-	-	-	+	-	+	-	-	-	-	+	+	-	-	-	-	+	-	-	-	+	-	-	-
Antomicron elegans	2	-	-	+	-	-	+	-	-	-	-	+	-	+	-	-	-	-	+	-	-	+	-	-	-
Aponema sp.	3	-	+	+	-	-	+	-	-	-	-	+	-	+	-	-	-	-	+	-	-	-	-	+	-
Aponema torosa	4	-	+	+	-	-	+	-	-	-	-	+	-	+	-	-	-	-	+	-	-	-	-	+	-
Axonolaimus paraspinosus	5	+	+	-	-	-	+	-	-	-	-	+	-	+	-	-	-	+	-	-	-	-	+	-	-
Axonolaimus sp.	6	-	+	+	-	-	+	-	-	-	-	+	-	+	-	-	-	+	-	-	-	-	+	-	-
Camacolaimus barbatus	7	-	+	-	-	+	-	-	-	-	+	-	-	+	-	-	-	-	+	-	-	-	+	-	-
Chromadora sp.	8	+	-	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-	-	+	-
Chromaspirina inglisi	9	-	+	-	+	+	-	-	-	-	+	-	-	+	-	-	-	-	-	+	-	-	-	+	-
Comesa sp.	10	-	+	-	-	+	-	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-	-	+	-
Comesoma sp.	11	+	+	-	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	+	-	-
Daptonema biggi	12	+	+	-	-	-	+	-	-	-	-	+	-	+	-	-	-	+	-	-	-	-	+	-	-
Daptonema hirsutum	13	+	+	+	-	-	+	-	-	-	-	+	-	+	-	-	-	+	-	-	-	-	+	-	-
Daptonema oxycerca	14	-	+	+	-	-	+	-	-	-	-	+	-	+	-	-	-	+	-	-	-	-	+	-	-
Daptonema procerum	15	-	+	+	+	-	+	-	-	-	-	+	-	+	-	-	-	+	-	-	-	-	+	-	-
Daptonema sp.	16	+	+	+	-	-	+	-	-	-	-	+	-	+	-	-	-	+	-	-	-	-		-	-
Daptonema tenuispiculum	17	-	+	-	-	-	+	-	-	-	-	+	-	+	-	-	-	+	-	-	-	-	+	-	-
Desmodora communis	18	+	+	+	+	+	-	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	-	+	-
Desmodora pontica	19	-	-	+	-	+	-	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	-	+	-
Desmodora scaldensis	20	-	+	+	+	+	-	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	-	+	-
Desmodora sp.	21	+	-	+	+	+	-	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	-	+	-
Desmodora sphaerica	22	-	+	-	-	+	-	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	-	+	-
Desmoscolex sp.	23	-	-	-	+	+	-	-	-	-	+	-	-	-	-	+	-	-	-	+	-	+	-	-	-
Dichromadora sp.	24	-	-	+	+	-	+	-	-	-	+	-	-	-	+	-	-	+	-	-	-	-	+	-	-
Dorylaimopsis punctata	25	+	+	+	+	-	+	-	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	+	-
Dorylaimopsis sp.	26	+	+	+	+	-	+	-	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	+	-

(Continued)

TABLE 4 | Continued

Species	CCA code	Seasons				Body shape			Tail shape				Cuticle morphology				Life-history strategy (c-p score)					Feeding guild			
		Monsoon	Winter	Spring	Summer	Stout	Slender	Long/ thin	Short/ round	Elongate/ filiform	Conical	Clavate	Smooth	Striated	Covered with dots	Ornamented	c-p 1	c-p 2	c-p 3	c-p 4	c-p 5	1A	1B	2A	2B
Eleutherolaimus minutus	27	-	+	-	-	-	+	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	+	-	-
Eleutherolaimus stenosoma	28	-	+	-	+	-	+	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	+	-	-
Eurystomina sp.	29	-	-	-	+	-	+	-	-	+	-	-	+	-	-	-	-	-	-	+	-	-	-	+	-
Halalaimus gracilis	30	-	+	+	-	-	-	+	-	+	-	-	+	-	-	-	-	-	-	+	-	+	-	-	-
Halalaimus longicaudatus	31	-	+	-	+	-	-	+	-	+	-	-	+	-	-	-	-	-	-	+	-	+	-	-	-
Hopperia sp.	32	-	-	+	+	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	-	+	-
Leptolaimoides sp.	33	-	-	-	+	-	+	-	-	+	-	-	-	+	-	-	-	-	+	-	-	+	-	-	-
Longicyatholaimus sp.	34	-	-	-	+	-	+	-	-	+	-	-	-	+	-	-	-	-	+	-	-	-	+	-	-
Marylynnia complexa	35	-	+	+	-	-	+	-	-	+	-	-	-	-	+	-	-	-	+	-	-	-	-	+	-
Mesacanthion sp.	36	-	-	-	+	-	+	-	-		+	-	+	-	-	-	-	-	+	-	-	-	-	+	-
Metachromadora vivipara	37	-	+	-	+	+	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-	-	-	+	-
Metalinhomoeus sp.	38	-	-	-	+	-	+	-	-	+	-	-	-	+	-	-	-	+	-	-	-	-	+	-	-
Microlaimus sp.	39	+	+	-	-	-	+	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	-	+	-
Monhystera sp.	40	-	-	+	-	-	+	-	-	-	+	-	+	-	-	-	+	-	-	-	-	+	-	-	-
Monoposthia costata	41	-	+	+	+	-	+	-	-	-	+	-	-	+	-	-	-	-	+	-	-	-	-	+	-
Nemanema sp.	42	-	+	-	-	-	+	-	+	-	-	-	+	-	-	-	-	-	-	+	-	+	-	-	-
Neochromadora sp.	43	-	-	+	-	+	-	-	-	+	-	-	-	-	-	+	-	+	-	-	-	-	+	-	-
Oncholaimellus sp.	44	-	+	+	-	-	+	-	-	-	-	+	+	-	-	-	-	-	+	-	-	-	-	+	-
Oxystomina asetosa	45	-	+	+	+	-	-	+	-	-	-	+	+	-	-	-	-	-	-	+	-	+	-	-	-
Oxystomina elongata	46	-	+	+	-	-	-	+	-	-	-	+	+	-	-	-	-	-	-	+	-	+	-	-	-
Oxystomina sp.	47	-	+	-	-	-	-	+	-	-	-	+	+	-	-	-	-	-	-	+	-	+	-	-	-
Paracomesoma dubium	48	-	+	+	+	-	+	-	-	-	-	+	+	-	-	-	-	-	+	-	-	-	-	+	-
Parasphaerolaimus sp.	49	-	+	-	-	-	+	-	-	-	-	+	-	+	-	-	-	-	+	-	-	-	-	-	+
Parodontophora sp.	50	-	+	+	-	-	+	-	-	-	-	+	-	+	-	-	+	-	-	-	-	-	-	+	-

(Continued)

TABLE 4 | Continued

Species	CCA code	Seasons				Body shape			Tail shape				Cuticle morphology				Life-history strategy (c-p score)					Feeding guild			
		Monsoon	Winter	Spring	Summer	Stout	Slender	Long/ thin	Short/ round	Elongate/ filiform	Conical	Clavate	Smooth	Striated	Covered with dots	Ornamented	c-p 1	c-p 2	c-p 3	c-p 4	c-p 5	1A	1B	2A	2B
Polygastrophora sp.	51	-	+	+	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	+	-	+	-	-	-
Pontonema sp.	52	-	-	+	-	-	+	-	+	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	+
Pselionema longiseta	53	-	+	+	+	-	+	-	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	-
Quadricoma scanica	54	-	+	+	-	+	-	-	-	-	+	-	-	-	-	+	-	-	-	+	-	+	-	-	-
Quadricoma sp.	55	+	+	+	+	+	-	-	-	-	+	-	-	-	-	+	-	-	-	+	-	+	-	-	-
Sabatieria alata	56	-	-	+	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	+	-	-
Sabatieria elongata	57	-	+	-	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	+	-	-
Sabatieria ornata	58	-	+	-	+	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	+	-	-
Sabatieria praedatrix	59	+	+	+	+	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	+	-	-
Sabatieria pulchra	60	+	+	-	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	+	-	-
Sabatieria punctata	61	-	+	-	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	+	-	-
Sabatieria sp.	62	+	+	+	-	-	+	-	-	-	-	+	-	-	+	-	-	+	-	-	-	-	+	-	-
Sphaerolaimus balticus	63	+	+	+	+	-	+	-	-	-	-	+	-	+	-	-	-	-	+	-	-	-	-	-	+
Sphaerolaimus gracilis	64	-	+	+	-	-	+	-	-	-	-	+	-	+	-	-	-	-	+	-	-	-	-	-	+
Sphaerolaimus islandicus	65	-	+	+	-	-	+	-	-	-	-	+	-	+	-	-	-	-	+	-	-	-	-	-	+
Sphaerolaimus sp.	66	-	+	+	-	-	+	-	-	-	-	+	-	+	-	-	-	-	+	-	-	-	-	-	+
Spirinia parasitifera	67	-	+	-	-	-	+	-	-	-	+	-	-	+	-	-	-	-	+	-	-	-	+	-	-
Terschellingia communis	68	-	+	+	+	-	+	-	-	+	-	-	-	+	-	-	-	-	+	-	-	+	-	-	-
Terschellingia longicaudata	69	+	+	+	+	-	+	-	-	+	-	-	-	+	-	-	-	-	+	-	-	+	-	-	-
Terschellingia sp.	70	-	+	-	-	-	+	-	-	+	-	-	-	+	-	-	-	-	+	-	-	+	-	-	-
Theristus acer	71	+	+	-	-	-	+	-	-	-	+	-	-	+	-	-	-	+	-	-	-	+	-	-	-
Tricoma sp.	72	+	+	-	+	+	-	-	-	-	+	-	-	-	-	+	-	-	-	+	-	+	-	-	-
Trissonchulus sp.	73	-	-	-	+	-	+	-	+	-	-	-	+	-	-	-	-	-	+	-	-	-	+	-	-
Vasostoma sp.	74	+	+	-	-	-	+	-	-	-	-	+	-	-	+	-	-	-	-	+	-	-	+	-	-
Viscosia abyssorum	75	-	+	+	+	-	+	-	-	-	-	+	+	-	-	-	-	-	+	-	-	-	-	-	+
Viscosia cobbi	76	-	-	+	-	-	+	-	-	-	-	+	+	-	-	-	-	-	+	-	-	-	-	-	+
Viscosia glabra	77	-	+	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-	+	-	-	-	-	-	+
Viscosia sp.	78	-	-	-	+	-	+	-	-	-	-	+	+	-	-	-	-	-	+	-	-	-	-	-	+
Viscosia viscosa	79	-	+	+	+	-	+	-	-	-	-	+	+	-	-	-	-	-	+	-	-	-	-	-	+

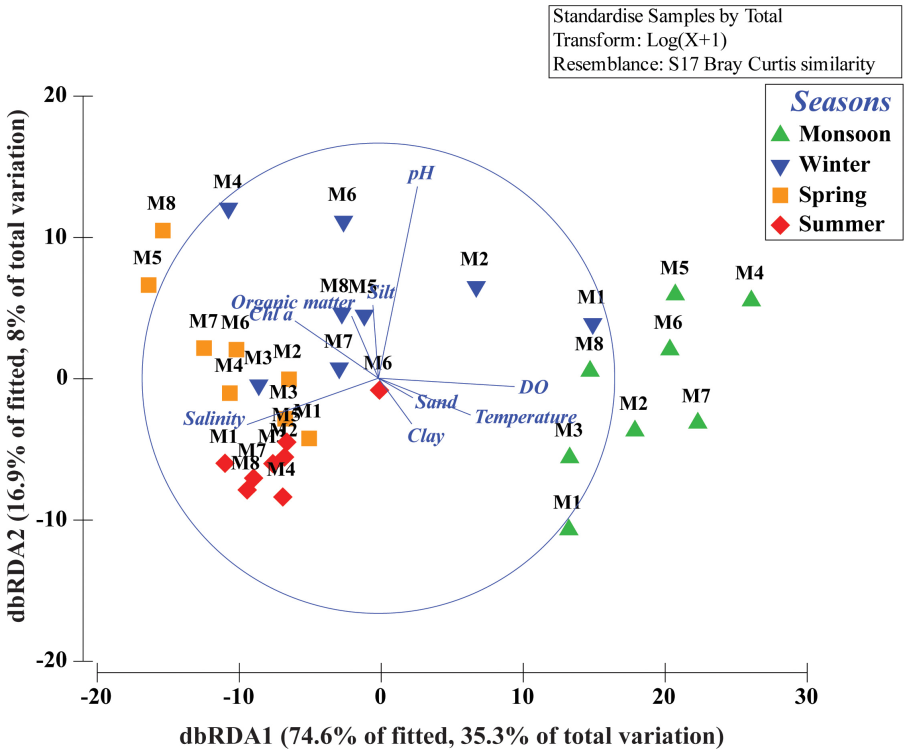

FIGURE 4 | Distance-based redundancy analysis (dbRDA) ordination plot of fitted best environmental variables illustrating meiobenthic community patterns.

Ordination resulting from the CCA biplot for 79 nematode species showed five axes representing 75.42% cumulative constrain percentage. Sediment texture, organic matter, and Chl *a* were the most important controlling environmental factors in shaping the nematode species composition during four seasons (**Figure 6A**). In the species biplot, *Daptonema biggi*, *D. oxycerca*, *Desmodora sphaerica*, *Sabatieria praedatrix*, and *Terschellingia* sp. have shown a positive correlation with organic matter. *Dorylaimopsis punctata*, *Sphaerolaimus islandicus*, and *Chromaspirina inglisi* were connected with the silty substratum of sediment, whereas *Monoposthia costata*, *Daptonema procerum*, and *Sabatieria alata* associated with clayey sediment texture. *Viscosia viscosa*, *Marylynnia complexa*, *Oxystomina elongata*, and *Sphaerolaimus gracilis* profited by microphytobenthos (Chl *a*). Being influenced by the temperature vector, most of the stations in summer occupied the upper left quadrant, except station 4. Maximum stations from spring were favored by Chl *a* and clay % vectors. During winter, all the stations were positioned toward the organic matter percentage vector except station 8 which showed affinity toward silt percentage. On the other hand, all the stations from the monsoon were not influenced by any other any other environmental factors (**Figure 6B**).

With regard to the functional diversity, different traits were strongly linked to seasonally fluctuating environmental gradients (**Figure 7**). A strong predominance of slender body shape was observed among nematode communities across the study periods, whereas proportions of stout and long/thin were comparatively low. Surprisingly, in monsoon, there was absence of long/thin-bodied nematodes (**Figure 7A**). From the four tail shapes analyzed, clavate tails were the most prevalent at all the seasons and stations and conical and elongate ranked in second and third position, respectively. Stout tail-shaped nematodes were found occasionally. Remarkably, stout accompanied by elongated tails were completely absent in monsoon (**Figure 7B**). Overall, nematode assemblages were dominated by non-selective deposit feeders (1B), followed by epistrate feeders (2A), selective deposit feeders (1A), and carnivorous/omnivorous (2B) (**Figure 7C**). Most nematodes attained a colonizer–persister score of 2 followed by 3; at the same time, a score of 1 was rare (**Figure 7D**). Another trait for cuticle morphology showed differences in the contribution to nematode assemblage structure, which were mainly characterized by striated cuticle. On the other hand, cuticles covered with dots, smooth, and ornamented ranked second, third, and fourth, respectively (**Figure 7E**). The seasonal separation of sampling stations was less pronounced in the ordinations derived from functional attributes of nematode communities; albeit the spring and summer seasons were clustered into groups, winter and monsoon stations were randomly distributed (**Figure 8**). Results of BIO-ENV analyses revealed several notable relationships of biological traits with environmental variables. For example, nematode body shapes had the best correlation with DO and organic matter. Tail shapes and cuticle patterns were well correlated with temperature and organic matter, whereas c–p scores and feeding types were significantly associated with organic matter (**Table 7**).

TABLE 5 | Seasonal variation in biotic indices for nematode community structure across all stations.

	S	N	d	J′	H′(log e)	1−λ′
Monsoon						
M1	14	30	3.82	0.96	2.53	0.94
M2	16	68	3.55	0.93	2.59	0.93
M3	4	7	1.54	0.83	1.15	0.71
M4	9	14	3.03	0.96	2.11	0.93
M5	7	24	1.89	0.92	1.80	0.85
M6	6	18	1.73	0.85	1.52	0.77
M7	3	6	1.12	0.92	1.01	0.73
M8	14	36	3.63	0.96	2.53	0.94
Winter						
M1	29	100	6.08	0.95	3.20	0.96
M2	20	100	4.13	0.94	2.81	0.94
M3	26	100	5.43	0.95	3.10	0.96
M4	27	100	5.65	0.93	3.07	0.95
M5	26	100	5.43	0.95	3.10	0.96
M6	34	100	7.17	0.92	3.24	0.96
M7	24	100	4.99	0.92	2.91	0.94
M8	19	100	3.91	0.94	2.78	0.94
Spring						
M1	20	100	4.13	0.96	2.88	0.95
M2	25	100	5.21	0.94	3.01	0.95
M3	19	100	3.91	0.90	2.66	0.92
M4	27	100	5.65	0.92	3.05	0.95
M5	28	100	5.86	0.93	3.09	0.96
M6	19	100	3.91	0.91	2.67	0.93
M7	23	100	4.78	0.92	2.89	0.94
M8	23	100	4.78	0.90	2.83	0.94
Summer						
M1	12	100	2.39	0.91	2.27	0.89
M2	16	100	3.26	0.95	2.65	0.93
M3	15	50	3.58	0.96	2.60	0.94
M4	15	50	3.58	0.93	2.52	0.92
M5	13	30	3.53	0.97	2.50	0.94
M6	16	50	3.83	0.93	2.57	0.93
M7	16	50	3.83	0.95	2.64	0.94
M8	17	50	4.09	0.92	2.60	0.93

S, total number of species; N, total population density; d, Margalef's species richness; J′, Pielou's evenness; H′ (log$_e$), Shannon–Wiener index; 1-λ′, Simpson index.

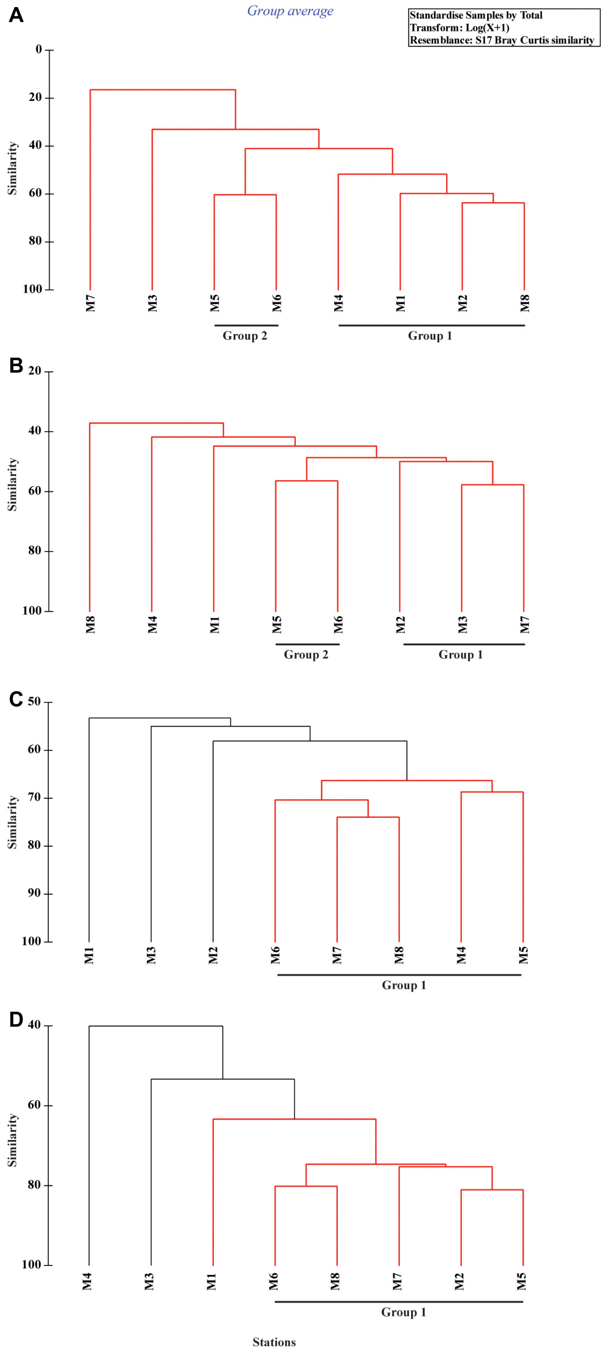

FIGURE 5 | Cluster plot based on Bray–Curtis similarity coefficient of free-living nematode species during four distinct seasons: **(A)** monsoon, **(B)** winter, **(C)** spring, and **(D)** summer.

DISCUSSION

In a transitional ecosystem, unraveling species assembly and the processes that govern their diversity is a major challenge. The estuarine biota is often challenged by different physical, chemical, and biological gradients in this environment. In our study, the environmental descriptors followed a clear pattern of seasonal succession; apart from that, estuarine gradients were also noticed in salinity, microphytobenthos, and sediment texture (**Table 3**). In general, estuaries provide a natural salinity gradient, which is often strongly linked to other physicochemical characteristics and productivity patterns that can change appreciably throughout the year (Newell, 1982). The present observation showed a clear seasonal pattern in bottom water salinity with maximum during the dry summer period and minimum during the monsoonal wet period. However, spatially our study areas attained varying degrees of salinity even in monsoon (6.41–16.68 PSU), which seemed to be a little higher compared to the western sector of SES (Banerjee, 2013). This is because

TABLE 6 | SIMPER analysis of free-living nematode assemblages determined by cluster plot considering each season: average similarity (%) and major species contribution (%).

	Groups	
Monsoon	**1**	**2**
Average similarity (%)	56.34	60.27
Major species contribution (%)	*Sphaerolaimus balticus* (13.93)	*Sabatieria* sp. (31.88)
	Desmodora sp. (11.51)	*Daptonema* sp. (24.41)
	Terschellingia longicaudata (7.97)	*Daptonema hirsutum* (21.86)
	Sabatieria sp. (7.83)	*Sabatieria praedatrix* (21.86)
	Sabatieria pulchra (7.55)	
Winter	**1**	**2**
Average similarity (%)	52.5	56.37
Major species contribution (%)	*Daptonema procerum* (12.84)	*Sabatieria praedatrix* (10.19)
	Sabatieria praedatrix (11.17)	*Desmodora communis* (7.93)
	Daptonema sp. (10.42)	*Sphaerolaimus balticus* (7.93)
	Desmodora communis (9.87)	*Daptonema hirsutum* (6.14)
	Daptonema tenuispiculum (8.47)	*Monoposthia costata* (6.14)
Spring	**1**	
Average similarity (%)	68.09	
Major species contribution (%)	*Daptonema hirsutum* (9.84)	
	Desmodora communis (8.00)	
	Dorylaimopsis punctata (7.70)	
	Monoposthia costata (7.38)	
	Halalaimus gracilis (6.81)	
Summer	**1**	
Average similarity (%)	75.95	
Major species contribution (%)	*Sabatieria praedatrix* (10.65)	
	Sphaerolaimus balticus (9.83)	
	Dorylaimopsis punctata (9.59)	
	Monoposthia costata (9.56)	
	Daptonema procerum (9.21)	

Matla River is mainly driven by tidal actions as the river basin has lost the freshwater flow from Himalayan River systems due to heavy siltation and clogging in recent times (Ghosh et al., 2015; Dhame et al., 2016). Sediment composition together with organic matter and microphytobenthic contents are considered as governing factors to characterize meiobenthic abundance and diversity patterns (Coull, 1985; Steyaert et al., 2003). From upstream areas, silt and clay fractions tend to increase toward the mouth of the estuary and fine sediments with a higher surface area can retain the highest organic matter as well (Parsons et al., 1990). According to our study, sediment textural properties revealed an overall dominance of muddy (clayey silt) substrates across the sampling locations with few exceptions. The dominance of mud suggested low fluvial discharge with an intense estuarine mixing, which could have resulted in settling of finer suspended particles and flocculation (Antizar-Ladislao et al., 2015). The average values of organic matter percentages of four different seasons in our study (**Table 3**) were in agreement with other previously reported studies from the western sector of Indian Sundarbans (Dey et al., 2012; Antizar-Ladislao et al., 2015). A typical seasonal growth pattern of microphytobenthos, as estimated by elevated Chl *a* and pheopigment concentrations, was observed in all stations. Their biomass increased steadily from monsoon through winter up to spring and thereafter dropped sharply and ultimately reached at a minimum value in summer.

The interplay of these crucial factors (salinity dynamics, sediment composition, and organic matter) determining the discrepancy in the distribution of meiobenthic communities is well recognized at several estuarine benthic habitats around the globe (Heip et al., 1985; Soetaert et al., 1995; Moens and Vincx, 2000; Derycke et al., 2007; Ferrero et al., 2008; Adão et al., 2009; Alves et al., 2009, 2013). Along estuaries, their distribution follows a strong heterogeneous and horizontal patchiness as a result of seasonal variation in abiotic conditions (Phillips and Fleeger, 1985). Our investigations revealed a strong preponderance of meiobenthic density in spring, followed by winter, which is likely due to ample amount of food resource availability in the estuarine complex. In tropical estuaries, due to high nutrient load and organic matter input, monsoon is regarded as by high seasonal primary production (Madhu et al., 2007), which slowly settles down to the sea floor, in turn supporting a rich benthic productivity. At the same time, the photosynthetic activity of benthic microalgae can modulate oxygen balance of the overlying sediment–water interface and improve aerobic bacterial degradation of sediment organic matter (Barranguet, 1997; Underwood and Kromkamp, 1999). Additionally, microphytobenthos represent an essential food source for deposit feeding (Montagna et al., 1995; Manini et al., 2000) as well as for suspension feeding meiofauna (Miller et al., 1996). A similar observation was found in a recent study by Ghosh et al. (2018), where intra-monsoonal variability ascribing meiofaunal density was clearly detected. However, this winter–spring peak in food availability was also more pronounced in our study, which subsequently increased faunal abundance in those periods of the year. Moreover, monsoon is generally considered as a breeding period for most of the tropical benthic entities and drop of salinity in monsoon can trigger their gonadal release (Kinne, 1977; Broom, 1982). As a consequence, higher numbers of polychaete juveniles and bivalve settlers were found in spring and winter, respectively. Additionally, as documented

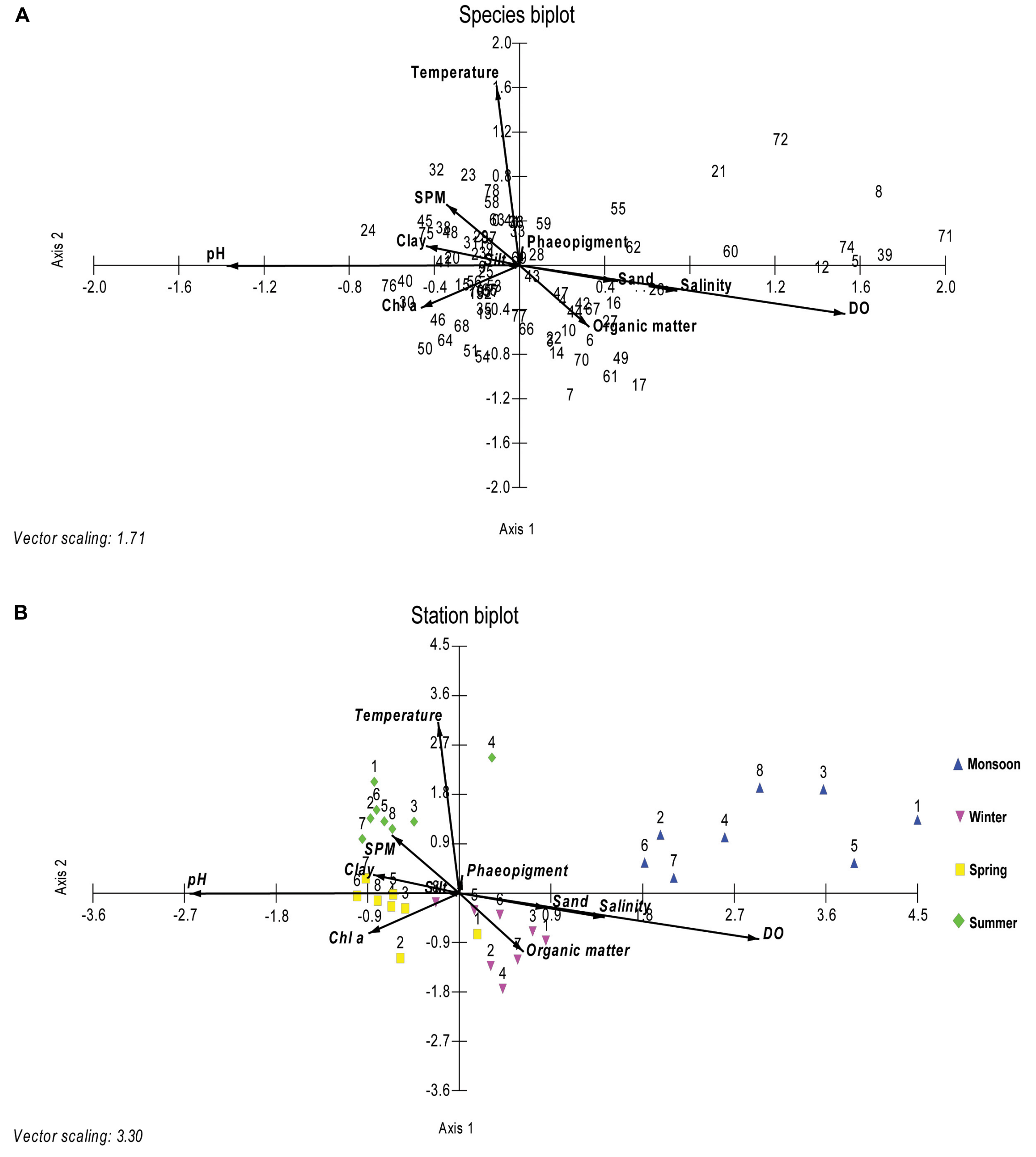

FIGURE 6 | Ordination diagrams for species **(A)** and stations **(B)** based on canonical correspondence analysis (CCA) of the nematode community. The environmental factors (temperature, salinity, pH, DO, SPM, sand %, silt %, clay %, chlorophyll *a* or Chl *a*, pheopigment, and organic matter) are indicated by arrows. Species codes are given in **Table 4**.

by Alongi (1990) and Ghosh et al. (2018), both juvenile and adult populations are more susceptible to monsoonal wash-off owing to lack of any pelagic larval stages in their life cycles. Indeed, the monsoonal density of meiofauna, in the present research, is also a reflection to these scientific evidences. Furthermore, higher temperature, salinity, and low DO concentration might be major limiting factors for the lowest meiofaunal density in summer. Temperature may play a triggering role in regulating reproductive activities of meiobenthos, especially nematodes. In general, higher ambient sedimentary temperature results in a shorter development period, leading to an adult-dominated population (Moens and Vincx, 2000). Our results corroborate these observations, when no bivalve and gastropod juveniles were observed in meiobenthic samples during summer. Therefore, the environmental factors were characteristically variable in each season and were mostly reflected in meiobenthic composition from eight sampling stations.

In marine habitat, nematodes and copepods are generally two of the most abundant groups (Nozais et al., 2005; Moreno et al., 2011). The integration of the present dataset revealed the

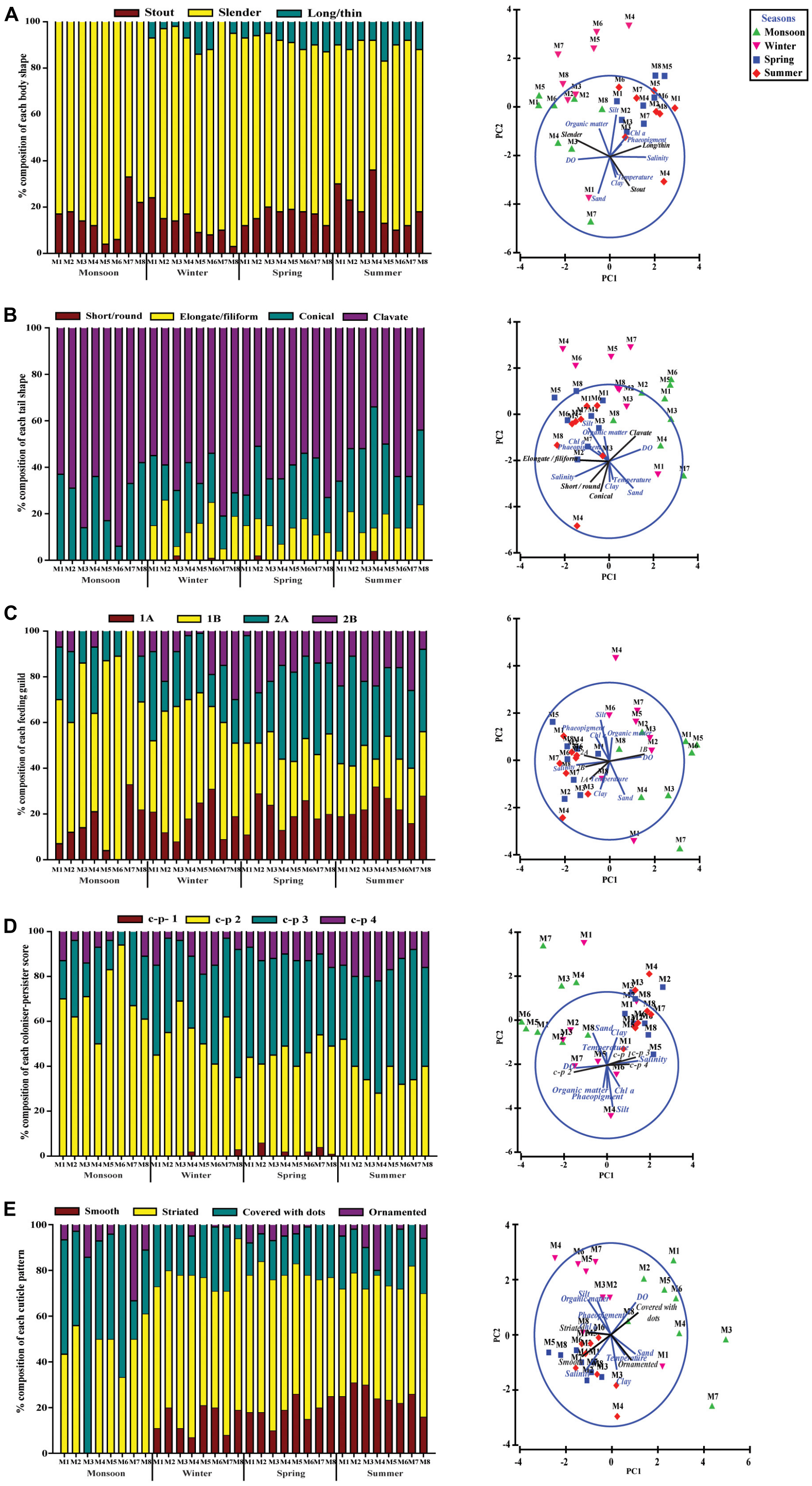

FIGURE 7 | Percentage of trait categories for nematode assemblages and their relationship with environmental factors across eight stations for four seasons. **(A)** Body shape, **(B)** tail shape, **(C)** feeding guild, **(D)** c–p score, and **(E)** cuticle morphology.

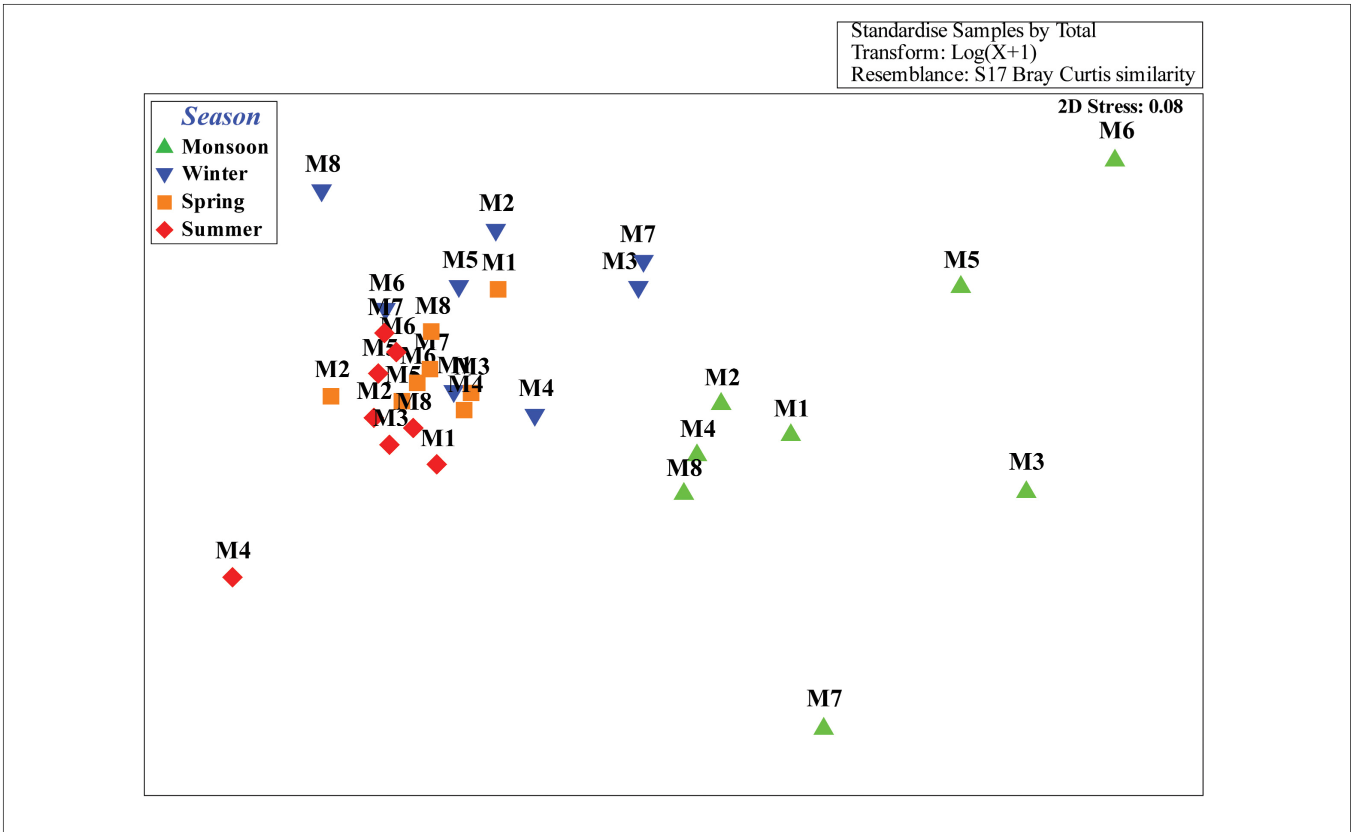

FIGURE 8 | NMDS ordination plot based on nematode species' functional traits according to the Bray–Curtis similarity matrix.

quantitative description of free-living nematode diversity in spatial and temporal (seasonal) scales. Nematode communities were predominantly composed of *Sabatieria*, *Sphaerolaimus*, *Dorylaimopsis*, *Daptonema*, *Desmodora*, *Monoposthia*, and *Terschellingia*, which have been reported the most common genera inhabiting estuarine mudflats worldwide (Soetaert et al., 1995; Wetzel et al., 2002; Rzeznik-Orignac et al., 2003; Schratzberger et al., 2006; Steyaert et al., 2007; Adão et al., 2009; Ghosh and Mandal, 2018, 2019). It is noteworthy that some habitat types such as naturally stressed estuarine muddy bottoms normally host certain tolerant species (Elliott and Quintino, 2007). Several species of *Sabatieria*, *Daptonema*, and *Terschellingia* are considered as "opportunistic" or tolerant to "hypoxia" and simultaneously used as "bioindicators" (Moreno et al., 2008; Alves et al., 2014). They are presumed to successfully thrive in fluctuating oxygen concentrations by decreasing their respiration rate and mobility, which sequentially reduce oxygen demand (Warwick and Price, 1979). The high abundance of these genera might be also associated with seasonal differences in sedimentary phytoplankton and organic matter deposition (Hourston et al., 2009). The correlation between species distribution patterns and sedimentary properties might thus point toward a species-specific response to the nutritional quality of the sediment. Seasonal turnover of fresh phytodetritus input was closely coupled with the abundance of many epistrate-feeding nematode species, e.g., *Desmodora communis*, *D. scaldensis*, *Dorylaimposis punctata*, *Monoposthia costata*, *Paracomesoma dubium*, and *Parodontophora* sp. A considerable number of predator nematodes (*Sphaerolaimus*, *Viscosia*) were also present throughout the annual cycle as they could be able to exploit a wide range of food resources (Moens and Vincx, 1997). Based on CCA station biplot analysis, four seasons were clearly separated from each other with organic matter, sediment chlorophyll, and textural properties contributing most importantly in structuring the nematode community (**Figure 6**). On the whole, the nematode community structure displayed a gradual seasonal transition in abundance, being mostly influenced by the sedimentary properties of the environment as well as the overall productivity of the system.

TABLE 7 | Results of BIOENV analyses based on Spearman's correlation.

Biological traits	Environmenental factors	Global test (Rho)	Significance level of sample statistic (%)
Body shape	DO, organic matter	0.225	5
Tail shape	Temperature, organic matter	0.185	23
Cuticle morphology	Temperature, organic matter, sand	0.178	32
c-p score	Organic matter	0.147	45
Feeding guild	Organic matter	0.17	30

Harpacticoid copepod showed a similar trend as nematodes: the winter–spring peak of copepod nauplii also confirmed food availability, particularly deposition of organic matter after late monsoon.

The functional diversity of nematodes based on five biological traits or characteristics [feeding type, body and tail shape, cuticle morphology and life strategy, or colonizer–persister (c–p) score] was evaluated to understand multiple aspects of ecosystem functioning (**Figure 7**). A significant number of slender body and clavate tail shape nematodes in each season were observed as an adaptation to higher silt and clay fraction of the sediment (Schratzberger et al., 2007). Body shape is associated with available food and sediment biogeochemical condition (Soetaert et al., 2002; Vanaverbeke et al., 2004; Losi et al., 2013). It is well recognized that in changing oxygen concentrations and silty clay sediment, body elongation is an adaptive feature resulting in higher epidermal uptake of oxygen as well as organic matter (Jensen, 1987; Singh and Ingole, 2016). In our case, the PCA biplot revealed a correlation of slender body shape with DO and organic matter of sediment (**Figure 7A**). In contrast, long/thin trait was found during all seasons, except monsoon, which could be hypothesized that a drop in salinity during monsoon prevented the long/thin population to flourish.

Nematode tails play a significant role in locomotion, feeding, and reproduction which are characteristics of a specific environment (Thistle and Sherman, 1985). A strong dominance of clavate tails followed by conical was observed across the sampling stations at each season. These two tail shapes have been suggested by several authors to be typical inhabitants of muddy sediment (Schratzberger et al., 2007; Armenteros et al., 2009). In agreement with their observations, the present study areas are also characterized by silt-rich sediment. The elongated or filiform tail-shaped nematodes, found in low number, are known as partly sessile in nature (Riemann, 1974; Schratzberger et al., 2007). The authors suggested that this type of tail morphology has been a special adaptation enabling them to retract from narrow interstitial sediment systems and forage for food. Most of the nematodes encountered throughout the study were non-selective deposit feeders (1B), which generally prevailed in detritus-rich muddy sediment due to plasticity of their diet (bacteria and organic detritus) (Tietjen, 1969; Heip et al., 1985). Moreover, dissolved oxygen concentration also seemed to be a crucial driver for this functional feeding group (1B) as mirrored by PCA in our study. Thus, dominance of non-selective deposit feeders could be a potential indicator of low oxygen levels related to different types of disturbances. Similar findings were documented by Alves et al. (2014) and Sroczyńska et al. (2020) for nematode communities in the Mondego and Sado estuaries of Portugal, correspondingly. Beside this, a marked increase in the population of epistrate feeders *Desmodora communis*, *D. scaldensis*, *Dorylaimopsis punctata*, *Monoposthia costata*, and *Paracomesoma dubium* after monsoon further reinforces the premise of a microalgal peak in winter and spring (**Figure 7C**). Microalgae, on the one hand, may alter the sedimentary environment by producing exopolymers that modulate sediment cohesiveness, at the same time affecting sediment the geochemistry and distribution pattern of oxygen to which nematodes show differential responses with adaptation in traits (Ritter, 2012; Alves et al., 2014). Some authors have reported a straightforward pattern of seasonal fluctuation of nematode species with selective deposit feeders and epistrate feeders significantly increasing after the spring phytoplankton bloom (Vanaverbeke et al., 2004; Lampadariou and Eleftheriou, 2018). In a similar way, the feeding type analysis in the present study showed that the high concentrations of Chl *a* during the winter–spring period were followed mainly by an increase in the abundance of non-selective deposit and epistrate feeders as they might be effectively benefited from an increased amount of fresh organic matter deposition. Life strategy characterization revealed a dominance of colonizers or opportunistics (c–p 2 followed by c–p 3), suggesting a stressful environmental condition (Bongers et al., 1991). The increase in c–p value along with an increase in grain size might be favored by high abundance of *Quadricoma* and *Tricoma* (c–p 4), which, as noted in our study, are correlated with higher sand content (Semprucci et al., 2018). Likewise, a differential response of individual nematode species has been revealed previously during one annual cycle where food availability and life-history strategy best explained the observed pattern (Hourston et al., 2009; Lampadariou and Eleftheriou, 2018). Very limited information is available to date on the relationship between the body cuticle structure of nematodes with their habitat types and hydrodynamic condition. The cuticle represents a barrier between organisms and their outer environment. It also confers their body shape and supports locomotion along with the help of body muscle and pseudocoel (Cesaroni et al., 2017). Nematode assemblages in the present study area showed a preponderance of striated cuticle throughout the seasons with the lowest abundance of ornamented cuticle. Cuticle with ornamentations had proven to be related with sandy sediment, which was also reflected in PCA (**Figure 7E**). At the same time, ornamented cuticle might bestow advantages to thrive in physically harsh environmental conditions of the estuary (Vanreusel et al., 2010).

In this fashion, biological trait analysis added a new dimension in biodiversity study over solely taxonomical information, thereby enhancing our knowledge on ecological gradients existing within an estuary. Environmental variables, in concert with a prevalence of nematode species with non-selective deposit feeders, clavate tail, slender body, and striated cuticular structure with high colonization potential in combination, were able to sustain throughout the study period. Seasonal patterns in the functional structure of nematode assemblages were primarily related to differences in sedimentary conditions. In conjunction with dominant species with combination among different traits, low-abundance species were also contributed to the context of their ecological roles. With respect to their capabilities, they respond differentially to stressful environmental conditions, thereby corroborating resilience to community structure. Nevertheless, a 1-year temporal observation might not be enough to obtain a definite conclusion and obviously need more than a 1-year assessment if the same seasonal succession pattern is repeated annually.

Presently, SES is subjected to multiple anthropogenic environmental changes, e.g., mean sea level rise, salinity intrusion, and land loss., which rapidly transform the community structure and functioning of the estuarine benthic ecosystem. As a consequence, the entire Matla estuarine system is affected by reduced freshwater input, increased salinity, and siltation. In addition, acceleration of various extreme climatic events increases the vulnerability of estuarine biodiversity and causes local extinction of many species (Ghosh et al., 2015). Hence, a complete database about the meiobenthic, especially nematode diversity is essential before many species might get extinct due to loss of biodiversity and ecosystem stability. Seasonal macrobenthic dynamics across Matla River have been revealed in a very recent study by Bhowmik and Mandal (2020), howbeit knowledge of meiobenthic composition is presently lacking from this region. As meiobenthos occupy an important trophic position in the aquatic food web and in maritime countries like India, a large percentage of people rely on their coastal environment for their food security and livelihood; therefore, enhancement of biodiversity knowledge using BTA is indispensable to understand the health of this rapidly changing ecosystem in SES.

CONCLUSION

The assimilation of our results provided a first-time systematic description of biodiversity patterns of meiobenthic assemblages, exclusively free-living nematodes from pristine subtidal sediment of Matla River of SES in both spatial and temporal (seasonal) scales. This study highlighted that seasonally governed biotic and abiotic factors like salinity, dissolved oxygen concentration, and sediment properties play crucial roles in meiobenthic distribution. Our study also revealed diverse morpho-functional and ecological traits characterized by notable microhabitat and niche heterogeneity that leads to development of a wide array of adaptation in order to inhabit them. Finally, this work represents a reliable dataset on meiobenthic diversity and ecology, which will act as a roadmap for the future researchers and environmental policymakers for the design and implementation of sustainable management blueprints for this ecologically fragile ecosystem. In this respect, it would be fascinating to further investigate seasonal succession in meiobenthic diversity for a longer time frame with addition of more traits.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MG: conceptualization, field work, sample collection, laboratory analysis, statistical analysis, data interpretation, writing – original draft, and editing. SM: conceptualization, field work, sample collection, data interpretation, resources, and writing – review and editing, supervision, project administration, and funding acquisition. Both authors contributed to the article and approved the submitted version.

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The Distribution Pattern of Marine Bivalve Death Assemblage From the Western Margin of Bay of Bengal and Its Oceanographic Determinants

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The global pattern of shallow marine biodiversity is constructed primarily using the data from extra-tropical sites. A severe knowledge gap in the shallow benthic diversity exists for the tropical Indian Ocean, especially along the coastline of peninsular India. Latitudinal biodiversity gradient (LBG)—a poleward decrease in diversity, even though accepted as a pervasive global pattern, often differs from regional trends. Although several oceanographic variables are known to influence regional patterns, their relative effect in shaping the shallow benthic community in tropical seas remains unclear. The east coast of India bordering the Bay of Bengal (BoB) presents a 2,500 km stretch (8–22°N) of tropical coastline with a spatial variation in oceanographic parameters including freshwater mixing, primary productivity, temperature, and shelf area. Here, we documented the marine bivalve distribution using spatially-temporally averaged beach samples and evaluated their relationship with the oceanographic variables. Our data reveal the existence of a highly diverse fauna, comparable to other tropical shallow marine sites. Overall species composition reflects a typical assemblage of the Indian Ocean, dominated by Veneridae but shows an uncharacteristically low proportion of Tellinidae and Lucinidae. The latitudinal variation in diversity shows a mid-latitude drop at around 14°N—a pattern inconsistent with the prediction of latitudinal biodiversity gradient (LBG). The functional groups are dominated by infauna (65%), unattached groups (69%), and suspension feeders (87%). There is only a slight difference in species composition between southern and the northern sites pointing to a predominantly continuous circulation and considerable mixing within the BoB. Productivity range, shelf area, and salinity emerge as best predictors of the species richness. All environmental variables together explain the species composition across the latitudinal bins satisfactorily. The species composition of the east coast shows no distinct nature in comparison to the Indo-Malayan biodiversity hotspot; the proximity to this hotspot and biological exchange with it may have contributed to the high diversity of the east coast fauna. Our study highlights the complex interplay between multiple oceanographic variables in determining the distribution and diversity of tropical shallow marine benthos at a regional scale generating biodiversity patterns that are at odds with global trends such as LBG.

Keywords: latitudinal biodiversity gradient, macrobenthic invertebrate, ecological guilds, mollusca, Indo-Malayan Archipelago

INTRODUCTION

Recognizing the determinants of diversity and distribution of fauna at the global and regional scales is one of the important themes of ecological research, especially in the context of recent changes in the climate (Sankaran and McNaughton, 1999; Willig et al., 2003). The study of biodiversity is heavily dominated by the terrestrial ecosystem although the number of higher taxa is substantially greater in the marine realm than on land (Grassle et al., 1991). The lack of documentation of marine biodiversity is not homogeneously distributed and such spatial gaps often lead to substantial underestimation of the global biodiversity. Insufficiency in data is most pronounced in the tropical seas of Asia, especially along the coast of India even though this landmass harbors close to 6,100 km of tropical coastline (May, 1994). This area has been studied extensively for fishes and other macro-invertebrate groups of economic importance (Appukuttan, 1996; Kripa and Appukuttan, 2003) including molluscs. The primary goal of such studies was to identify and describe new species (Melvill, 1909; Hornell, 1922; Gravely, 1941; Ray, 1949; Satyamurti, 1956; Ganapati and Nagabhushanam, 1958; Kundu, 1965; Appukuttan, 1972; Subba Rao, 2017, ZSI, State fauna Series). The regional diversity pattern of molluscs is largely ignored except for studies focusing on specific species (Bharti and Shanker, 2021) or fauna of the west coast of India (Ingole et al., 2009, 2010). Present understanding of the factors controlling the molluscan distribution along the east coast of India is insufficient. The east coast of India bordering the Bay of Bengal (BoB) presents an example of a tropical coastline with a large latitudinal span (8–22°N) and a very high influx of terrestrial sediments through river runoffs influencing salinity profile along the coast (Shetye, 1993; Shetye et al., 1996). The coast also shows spatial variation in temperature, sediment input, and productivity (Bharathi et al., 2018). Molluscan assemblages have long been recognized to serve as a reliable proxy for diversity and ecosystem health in shallow marine systems (Kidwell, 2001). Hence the study of molluscan diversity is critical to appreciate the regional diversity pattern of shallow marine fauna and to recognize its drivers along the east coast of India.

Species richness of marine bivalves has been documented globally as part of a few large studies (Stehli et al., 1967; Crame, 2000a,b). Although measuring species richness is important for global-scale assessment, it cannot be taken as an absolute index, since it varies with habitat type, complexity and also does not reflect functional diversity. Furthermore, such indices do not reflect changes in species composition or even changes at higher taxonomic levels. Therefore, species richness, although useful for global studies, should be accompanied by more detailed information on species composition and ecology to capture the true essence of regional biodiversity. The only regional-scale studies to understand the drivers of molluscan distribution along the east coast of India are based on literature-based occurrence data (Sivadas and Ingole, 2016; Sarkar et al., 2019). Sarkar et al. (2019) attempted to also evaluate the functional diversity, community composition but recognized that the conclusions may have been affected by the sampling inconsistencies across the literature. A detailed sampling effort following a consistent protocol is necessary to evaluate the true pattern. It has been documented that “time-averaged” (temporally condensed record of multiple generations of fauna living in the same place) and “spatially-averaged” (spatially accumulated by random post-mortem transportation from different habitats at the same time) molluscan death assemblages could yield a near-perfect reflection of the true regional biodiversity despite the potentially different taphonomic history of the specimens (Kidwell and Bosence, 1991; Kidwell and Flessa, 1995; Kidwell, 2001; Warwick and Light, 2002; Mondal et al., 2021). A detailed within-habitat live sampling of marine molluscs along a ∼2500 km stretch of the east coast of India, while desired, proved to be logistically challenging. Sampling “spatially-temporally averaged” death assemblages as a surrogate for regional biodiversity is a technique suitable for the scale as vast as the present one.

In this study, we attempted to understand the regional pattern of bivalve diversity of the east coast of India by employing a detailed sampling of time-averaged death assemblages to minimize methodological inconsistencies. Using the specimens collected from beach samples from 17 localities spanning over 14 latitudinal bins along the east coast, we addressed the following questions:

1. What is the nature of spatial variation in diversity, ecology, and species composition?
2. How do the oceanographic variables influence shaping the patterns?

MATERIALS AND METHODS

Study Area

The BoB is a tropical semi-enclosed basin, bordered by India and Sri Lanka on the west, Bangladesh on the north, and Myanmar and Thailand on the east. A stretch of ∼2500 km coast of the Indian subcontinent marks the western margin of BoB (**Figure 1A**). Western BoB experiences seasonally reversing monsoons, severe cyclonic storms (SCS), a large amount of rainfall, and river run-off (Mohanty et al., 2008).

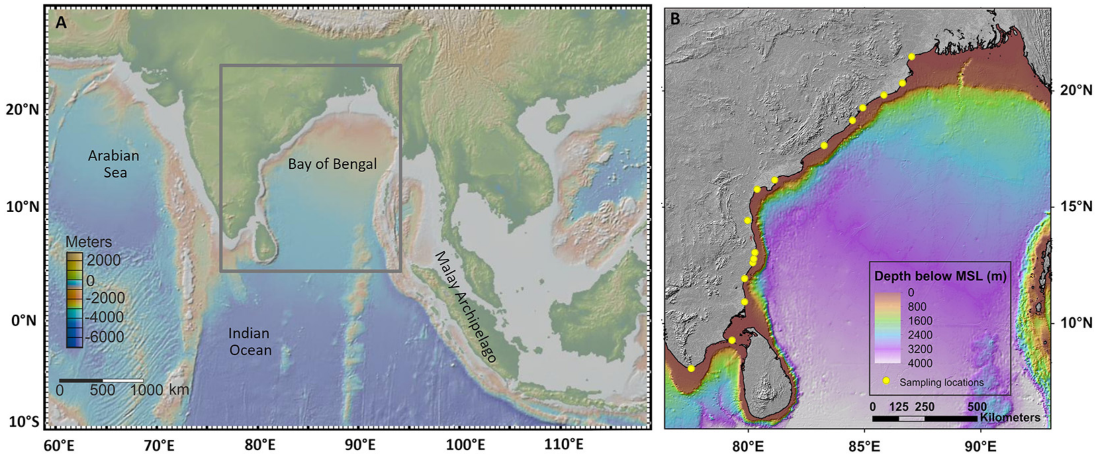

FIGURE 1 | Map of India **(A)** showing the sampling locations **(B)**. The map is based on Survey of India Outline map (1996).

The northwestern coastal BoB receives discharge mainly from glacial rivers (Ganges, Brahmaputra). Peninsular rivers (such as Godavari, Krishna) discharge in the southwestern coastal BoB. The high amount of annual freshwater discharge ($\sim$102 m^3) from the Ganges-Brahmaputra rivers system at the northwestern BoB especially during the monsoon (June-October), results in the development of an N-S gradient in salinity and temperature along the east coast of India; the northern Bay is characterized by low salinity and cooler temperature compared to the southern regions (Shetye, 1993).

Field Sampling and Identification

We selected 17 sampling localities that span from Kanyakumari (8.08°N) at the south to Sundarbans (21.94°N) at the north (**Table 1**) spread across 14 latitudinal bins (1° each, **Figure 1B**). Each bin is represented by at least one sampling locality. The minimum distance between two sampling localities is 5 km. For collecting bivalve specimens from each locality, we took a traverse of $\sim$1 km along the seashore; all visible molluscan shells were collected. Specimens that were damaged beyond recognition were ignored. We did not collect sediment samples during our collection. The sampling exercise was conducted during a period of five and half years, from July 2010 to December 2015.

All bivalve specimens were separated from the collected molluscan sample, washed, sun-dried. The individual number was calculated by counting the articulated valves and adjusting for the disarticulated valves. Each latitudinal bin was represented by a minimum of 200 individuals. Taxonomic nomenclature was primarily based on the published work by Subba Rao (2017) and the World Register of Marine Species (WoRMS Editorial Board, 2020). Because of the unavailability of authoritative monographs on Indian bivalves and controversy on species nomenclature, we used an internally consistent species nomenclature and used it as the operational taxonomic unit. Additional information on identification and ecology was derived from Apte (1998), Zuschin and Oliver (2003), Oliver (1992), ZSI, State fauna Series, and NMiTA[1]. The species occurrence of Indo-Malayan Archipelago (south-east Asian biodiversity hotspot) was collected from published literature (Dijkstra, 1991; Dolorosa et al., 2015; Lutaenko, 2016) and compared with the data along the east coast of India from the present study and literature-based occurrence compiled in Sarkar et al. (2019).

Raw species richness is defined as the direct count of observed species. Raw and rarefied species richness was calculated using the species abundance in each latitudinal bin. Additional indices of diversity and evenness were evaluated by Shannon–Wiener index (H), Pielou's evenness index (J), respectively, to account for sample size. The species were classified into three groups based on substrate relationship (epifaunal, infaunal, others to include borer

TABLE 1 | Details of the sampling locations used for the present study.

Name of location	Latitude	Longitude	Number of individuals
Kanniyakumari, Tamil Nadu	8.07	77.54	601
Rameshwaram, Tamil Nadu	9.28	79.3	1,124
Karaikal, Puducherry	10.93	79.83	424
Gandhi beach, Puducherry	11.93	79.83	422
Mahabalipuram, Tamil Nadu	12.61	80.19	325
Kovalam, Tamil Nadu	12.78	80.23	82
Chennai, Tamil Nadu	13.05	80.28	521
Nellore, Andhra Pradesh	14.43	79.97	732
Chirala, Andhra Pradesh	15.76	80.37	386
Machilipatnam, Andhra Pradesh	16.17	81.13	479
Visakhapatnam, Andhra Pradesh	17.65	83.26	1,217
Palasa, Andhra Pradesh	18.72	84.48	1,152
Gopalpur, Odisha	19.27	84.92	315
Puri, Odisha	19.81	85.83	57
Paradeep, Odisha	20.32	86.62	1,155
Chandipur, Odisha	21.47	87.02	2,358
Bakkhali, West Bengal	21.56	21.25	108

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[1] https://nmita.rsmas.miami.edu

and nestler on or within hard substrates), three finely subdivided substrate guilds (byssally attached, cemented, and unattached), and four trophic guilds (suspension feeders, deposit feeders, and chemosymbionts).

Oceanographic Variables

We have included oceanographic variables (productivity, sea surface temperature, and salinity) that are known to influence molluscan diversity (Roy et al., 1998; Valentine and Jablonski, 2015). We have collected pre-existing data on the annual mean and range of net primary productivity (NPP), sea surface temperature (SST), salinity from the Ocean Productivity database[2] for each latitudinal bin. Species diversity of shallow marine fauna is also known to vary with the available area of habitat (Smith and Benson, 2013) and we used shelf area as a proxy for available habitat. The shelf area for a latitudinal bin is calculated as a product of coastal length and the average distance from the coast to the shelf-slope break for specific locations. The coastal length and shelf width are obtained from GEBCO Compilation Group (2020). Cyclone frequency is known to affect the molluscan death assemblages especially in tropical siliciclastic settings (Bhattacherjee et al., 2021); we included it in our analyses to rule out the possibility of transportation-related influence on the observed species richness and to establish the reliability of our data. Cyclone frequency data were collected from the global-tropical-extratropical cyclone climatic atlas from the United States Navy National Climate Data Center cyclone records. The details of the processing are discussed at Bhattacherjee et al. (2021).

Statistical Analysis

We used the Spearman rank-order coefficient to measure the correlation of diversity with latitude. A significant negative correlation between diversity and latitude is consistent with predictions from LBG. To evaluate the relationship between various oceanographic variables and diversity, functional groups, we used the Spearman rank-order correlation test. We also estimated the effect of these variables on diversity and proportion of dominant functional group with multiple generalized linear models (GLMs) to analyze all parameters simultaneously and evaluating their partial contributions to the total variation in diversity (Quinn and Keough, 2002). We employed the Akaike information criterion (AICc) to rank alternative GLM models based on the trade-off between the model fit and its complexity (Burnham and Anderson, 2002; Grueber et al., 2011). We generated a set of models with all possible combinations of environmental predictors and scored them according to their relative support as measured by AICc. To account for the uncertainty in model selection, we performed model averaging, applying a cut-off criterion of $\Delta \text{AICc} \leq 2$ to choose the best set of models.

To recognize the compositional distinctness along the coast and between regional occurrences within the BoB, we used ordination analysis. The compositional similarities among latitudinal bins were calculated from an abundance matrix of species in bins using the Bray–Curtis similarity index. For biogeographic comparison between India and Indo-Malayan Archipelago, we used an occurrence matrix of species using the Sørensen similarity index. The similarity matrices were clustered by the unweighted pair group method using arithmetic averages (UPGMA) and visualized as a dendrogram. Two-dimensional ordination assembles were created with non-metric multidimensional scaling (NMDS) using the Bray–Curtis similarity indices for comparison among latitudinal bins and Sørensen similarity indices between sites from India and Indo-Malayan Archipelago. To assess the relative importance of environmental variables on the distribution of species along the coast, we used Redundancy Analysis (RDA) on the Hellinger distance-transformed species data (Legendre and Legendre, 1998).

All univariate and multivariate analyses were performed in R (R Core Development Team, 2012). The ecological analyses were done using the "Vegan" package in the R platform.

RESULTS

We have collected a total of 11,458 individual bivalves from 14 latitudinal bins (**Table 1**) that represent 287 species, 129 genera, and 35 families. The raw species richness is lower than the observed richness in Indo-Malayan Archipelago (518). There is no significant correlation between location-specific abundance and species richness (Spearman's rho = −0.06, $p = 0.82$) (**Figure 2**). The average raw species richness is 44 and rarefied richness is 36 (**Table 2**). The most common families are Veneridae, Cardiidae, Arciidae, Mactridae, and Donacidae (**Table 2**). The relative proportion of infauna (substrate relationship), unattached (attachment type), and suspension feeders (feeding style) seems to dominate various functional groups (**Figure 3**) (**Table 2** and **Supplementary Table 1**).

There is no significant correlation between species richness and latitude (Spearman's rho = 0.158, $p = 0.588$) (**Figure 4** and **Table 2**). However, the diversity appears to drop around 14°N. A similar trend is observed in rarefied richness, evenness, and Simpson diversity indices (**Figures 4A–D**). The species richness of the five most abundant families reveals no significant correlation with latitude, except for Mactridae (**Figures 4E–I** and **Table 2**). The latitudinal distribution of life modes also does not show a significant correlation (**Figures 4J–R** and **Table 2**).

In the NMDS plot (stress value = 0.155), the sites do not form latitudinally separated clusters, although sites north of 15°N show a slight separation along the NMDS axis 2 (**Figure 5A**). Some species that are abundant in the north of 15°N such as *Wallucina assimilis*, *Trapezium oblongum* are absent in the south. Similarly, a few dominant species of the south such as *Vepricardium coronatum* and *Timoclea costellifera* are absent in the northern region. A dendrogram constructed by UPGMA, however, does not show any distinct cluster of latitude-specific species composition (**Figure 5B**).

Productivity (range) shows a significant correlation with species richness (**Figure 6A** and **Table 3**). None of the environmental variables significantly correlated with the

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[2] http://www.science.oregonstate.edu/ocean.productivity/standard.product.php

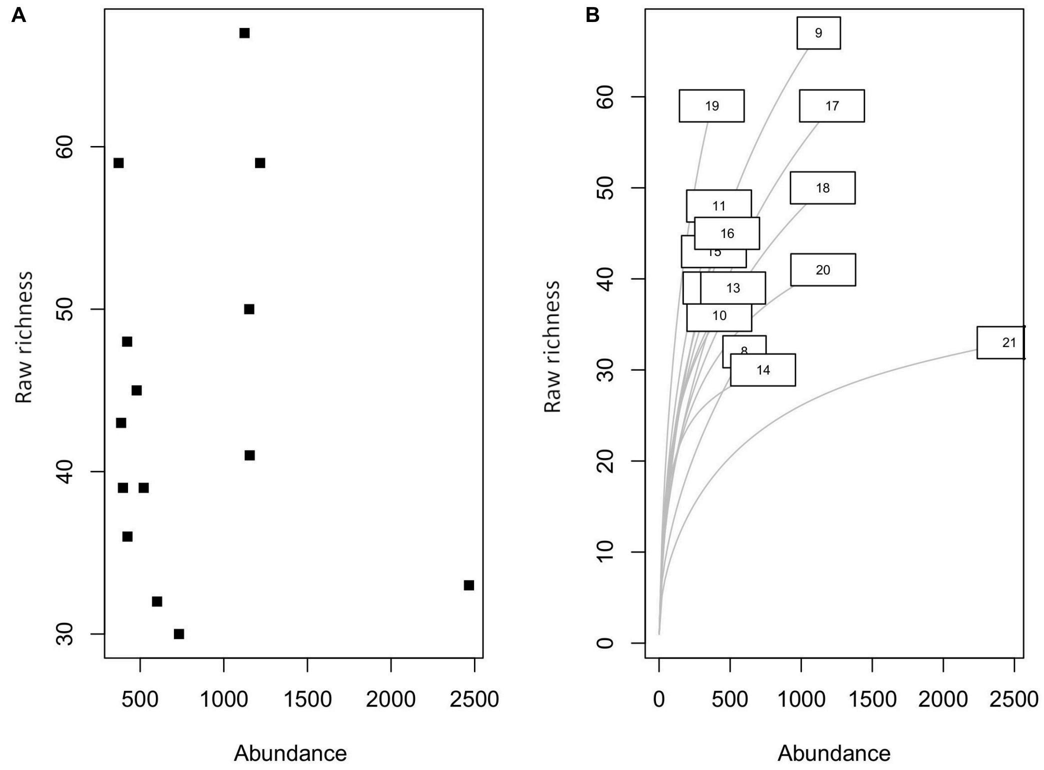

FIGURE 2 | **(A)** Relationship between species richness and abundance. **(B)** Rarefied species richness at different latitude bins.

TABLE 2 | Summary of the diversity of marine bivalve families and functional groups along with their correlation with latitude.

		Variable	**Total**	**Correlation with latitude**	
				rho	***p***
Overall		Species richness	44.36*	0.158	0.588
		Rarefied richness	36.13*	−0.151	0.605
		Evenness	0.64*	−0.156	0.594
		Simpson index	0.82*	−0.156	0.594
Individuals in common families		Veneridae	5,577	0.205	0.482
		Arcidae	1,813	0.045	0.879
		Cardiidae	1,085	0.189	0.516
		Mactridae	1,050	0.689	**0.006**
		Donacidae	823	−0.080	0.761
Species that belong to specific functional group	Substrate relationship	Infaunal	186	0.312	0.270
		Epifaunal	94	−0.170	0.560
		Others	7	−0.090	0.730
	Attachment type	Bysally attached	68	−0.380	0.172
		Cemented	22	−0.101	0.729
		Unattached	197	−0.131	0.655
	Feeding style	Deposit feeder	29	−0.101	0.729
		Suspension feeder	249	0.169	0.563
		Others	9	−0.131	0.655

The significant results are in bold.

proportion of infauna, unattached, or suspension feeders (**Figures 6B–D** and **Table 3**). Among the environmental variables, productivity (mean and range), temperature (mean and range), shelf area, and cyclone frequency do not show any relationship with any other environmental variables (**Supplementary Table 2**). After excluding the variables based

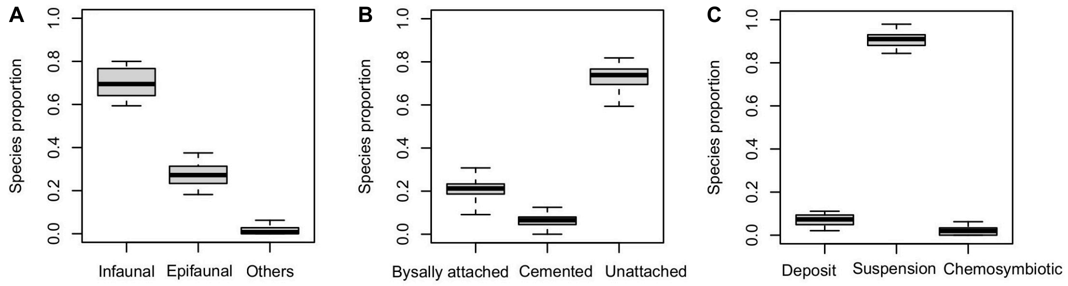

FIGURE 3 | Relative proportion of various ecological groups classified based on **(A)** substrate relationship, **(B)** attachment type, and **(C)** feeding type. The boxes are defined by 25th and 75th quantiles. The thick line represents median value within the box.

on autocorrelation, the GLM models show that the combination of productivity (range), salinity (mean), and shelf area were the most important predictors of species richness (**Table 4** and **Supplementary Table 3**). Shelf area and temperature (mean) emerge as important predictors for dictating the proportion of infauna. Shelf area, productivity (range), and mean value of salinity and temperature emerge as strong predictors for the proportion of unattached bivalves (**Table 4**). Salinity (range, mean), temperature (range), and productivity (mean) predict the proportion of suspension feeders (**Table 4**). Except for species richness, however, the variables have limited explanatory significance as indicated by the low or negative value of adjusted R^2.

About 79% of the variation in species composition is explained by all environmental variables considered together using RDA on the Hellinger distance-transformed species data (**Figure 7** and **Table 5**). The constrained variance of the global model with all environmental variables 0.66 and the unconstrained variance 0.34. Forward selection to choose a model with fewer variables, however, increases the unconstrained variance to 0.79 pointing to the limited explanatory power of the models with fewer environmental variables. The RDA plot also shows no significant influence of any single environmental variable in explaining the species composition across latitudinal bins.

In an occurrence-based NMDS plot (stress value = 0.131) comparing the present species composition with literature-based occurrence data of the east coast (Sarkar et al., 2019) and Indo-Malayan Archipelago, the sites do not form geographically separated clusters indicating a high degree of compositional similarity between the two regions (**Figure 8**).

DISCUSSION

Studies on bivalves from the Indian coast primarily focused on the detailed morphological description and identification at a local scale (Subba Rao, 2017, ZSI, State fauna Series among many others) barring a few (Ansari et al., 1977; Khan et al., 2010; Manokaran et al., 2015). Because local communities are an integral part of larger biogeographic regions, the diversity of local scale (spatial scale of meters to hundreds of meters) must be affected by regional-scale processes (spatial scale of 200 to thousands of kilometers) (Witman et al., 2004). The regional-scale studies on Indian bivalve diversity are primarily conducted on the west coast (Ingole et al., 2009, 2010). Regional analysis of the east coast fauna is based on data from literature compilation (Sivadas and Ingole, 2016; Sarkar et al., 2019) and hence suffers from potential sampling inconsistency. In contrast, the present study aims to understand the regional pattern of bivalve diversity instead of discrete local variations by employing a detailed sampling of time-averaged death assemblages to minimize methodological inconsistencies.

Reliability of Beach Sampling

Regional biodiversity assessments are strongly influenced by the sampling protocols. A regional-scale species richness is difficult to measure because the richness increases with the effort of sampling (Warwick and Light, 2002). Grab samples have often been considered to portray a true representation of the biological community (McKinney and Hageman, 2006). However, there are some limitations. A fundamental issue is that the megabenthos—benthic organisms that are large enough to be visible on seabed photographs, cannot be studied reliably from grab samples alone owing to their patchy distribution (Gage and Tyler, 1991). Comparison between grab samples and underwater studies revealed this difference for many regions including the Adriatic Sea (Zuschin et al., 1999; Stachowitsch et al., 2007; Riedel et al., 2008; Zuschin and Stachowitsch, 2009), and Antarctica (Dayton and Oliver, 1977) highlighting the role of sampling technique on the inferred diversity and ecological composition of a region.

Kidwell (2013) claimed that death assemblages are more diverse than the actual living fauna of an area due to time averaging. Owing to temporal accumulation of shifting patches and post-mortem transportation from proximal habitats, time-averaged assemblages tend to capture a more complete picture of biodiversity compared to ecological snapshots. However, post-mortem transport and reworking of older shells are most common in marine coastal areas and could potentially bias the time-averaged data. Processes such as abrasion, fragmentation, bioerosion, and decay could affect the death assemblages on recent marine fauna (Kidwell and Bosence, 1991; Warwick and Light, 2002; Nebelsick et al., 2011). Few marine shells, especially those that are extremely thin, dominated by a high-organic

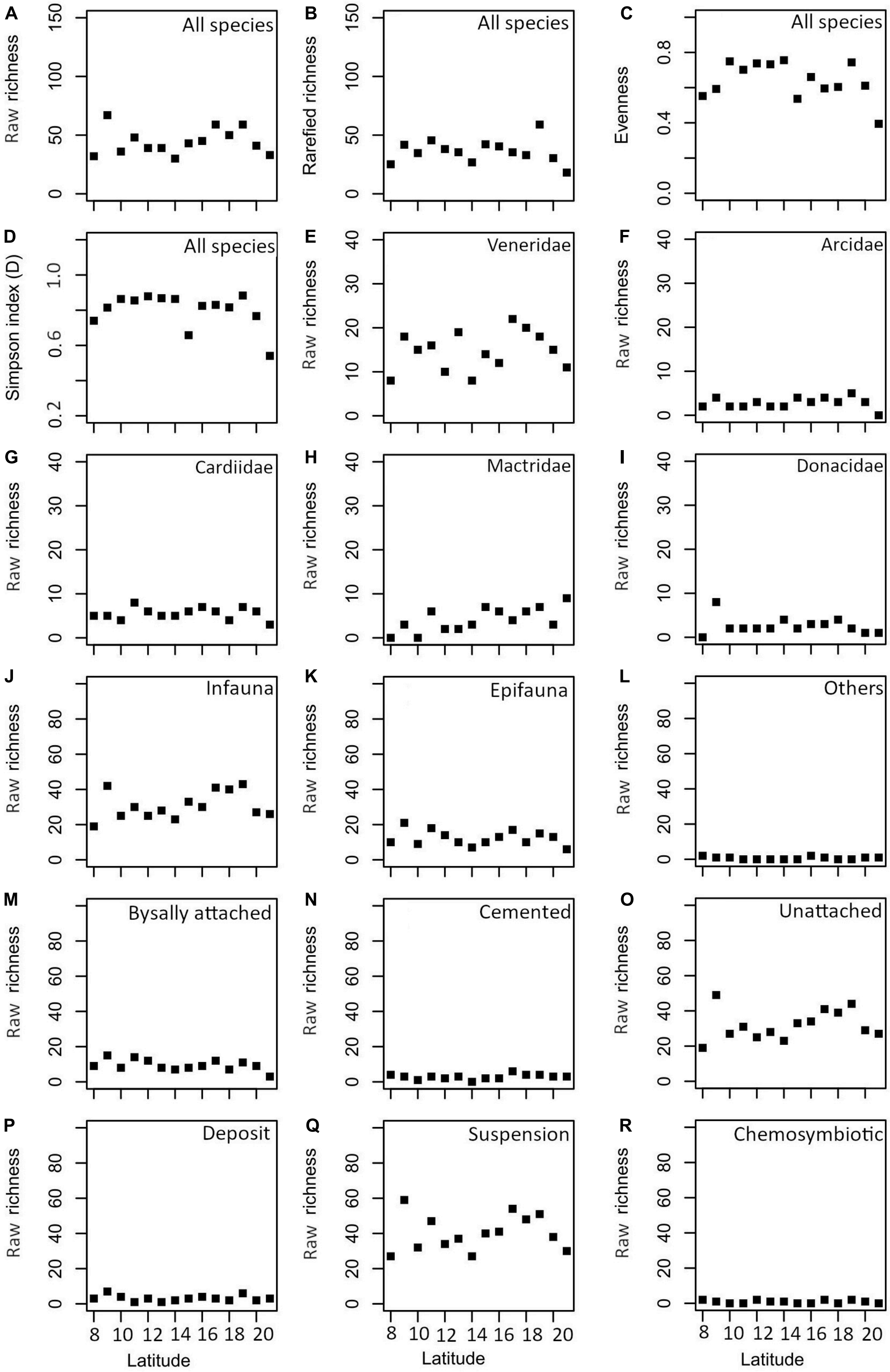

FIGURE 4 | Latitudinal variation in various diversity indices **(A–D)**, common families [**(E)** Veneridae, **(F)** Arcidae, **(G)** Cardiidae, **(H)** Mactridae, and **(I)** Donacidae] and functional groups based on substrate relationship [**(J)** infauna, **(K)** epifauna, and **(L)** others], attachment [**(M)** byssally attached, **(N)** cemented, and **(O)** unattached] and feeding [**(P)** deposit, **(Q)** suspension, and **(R)** chemosymbiotic].

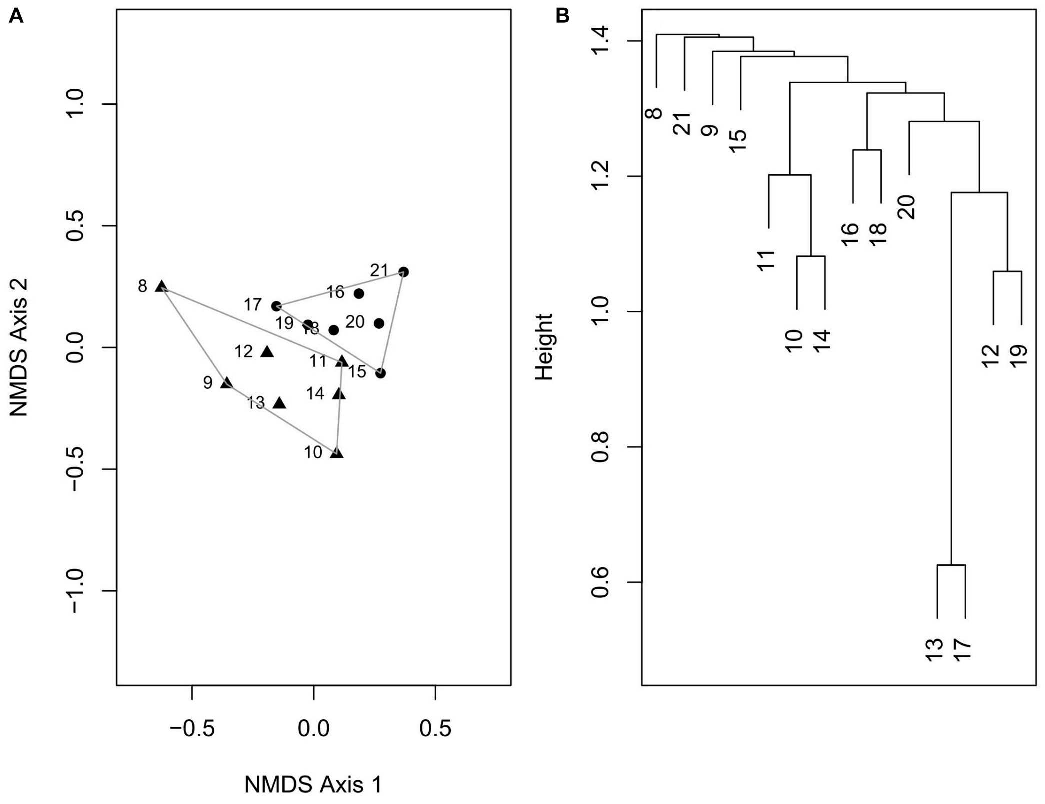

FIGURE 5 | (A) Ordination plot using non-metric multidimensional scaling, based on Bray–Curtis distance calculated from a matrix of marine bivalve species at different latitudinal bins. **(B)** Dendrogram constructed by UPGMA method using arithmetic averages.

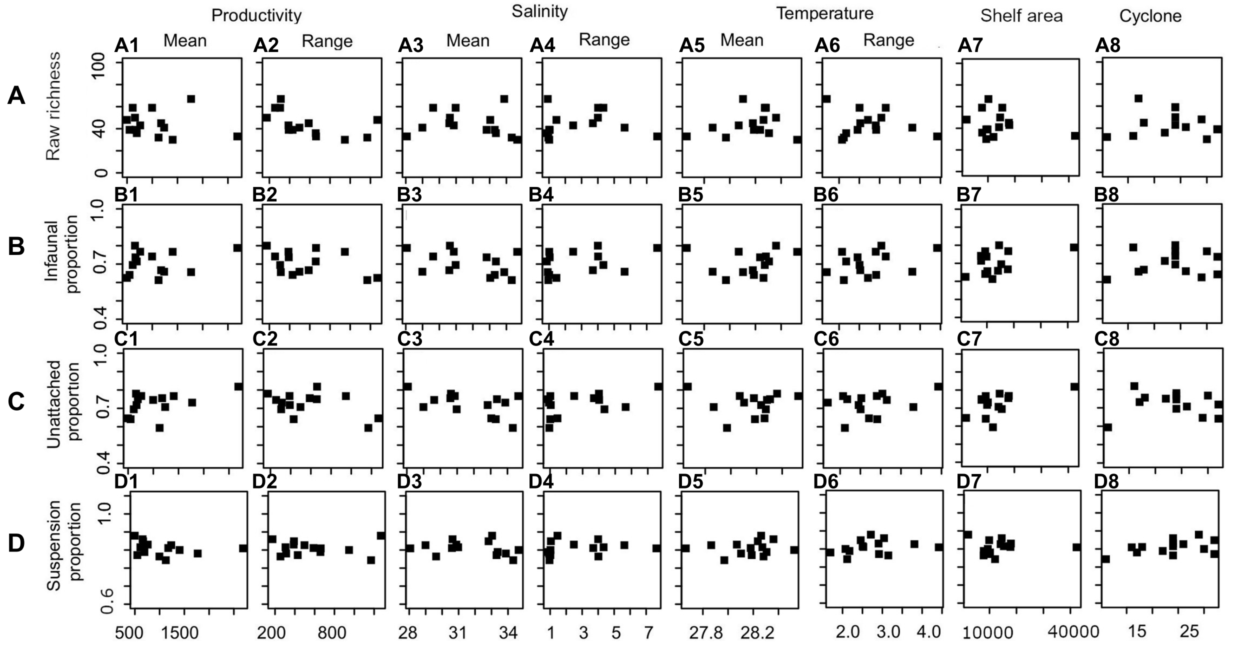

FIGURE 6 | The relationship between oceanographic parameters and species richness **(A)**, proportion of infauna **(B)**, unattached **(C)**, and suspension feeder **(D)**.

TABLE 3 | Correlation between species richness, proportion of ecological groups with environmental variables for latitudinal bins using Spearmann rank order correlation test.

Variables	Species richness		Proportion of infauna		Proportion of unattached		Proportion of suspension feeder	
	rho	*P*	*rho*	*p*	*rho*	*P*	*rho*	*P*
Productivity (mean)	−0.24	0.391	0.196	0.502	0.433	0.124	−0.396	0.161
Productivity (range)	**−0.69**	**0.005**	−0.402	0.155	−0.208	0.473	−0.127	0.663
Salinity (mean)	−0.28	0.317	−0.424	0.132	−0.393	0.165	−0.453	0.104
Salinity (range)	0.25	0.39	0.429	0.128	0.314	0.274	0.537	0.047
Temperature (mean)	0.12	0.69	0.288	0.317	0.134	0.649	−0.154	0.599
Temperature (range)	0.13	0.63	0.341	0.233	0.248	0.391	0.392	0.166
Shelf area	0.011	0.97	0.349	0.221	0.424	0.132	0.277	0.337
Cyclone frequency	−0.049	0.868	0.017	0.952	−0.231	0.426	0.113	0.699

The significant results are in bold.

TABLE 4 | Highest ranked logistic models (ΔAICc $\leq$ 2) investigating environmental correlates of the species richness and ecological categories of the marine bivalves.

Variable to be explained	Model	Intercept	AICc	ΔAICc	wAICc	R^2
Species richness	PR	54.565	109.814	0.000	0.416	0.290
	SM	299.707	111.193	1.379	0.208	0.413
	PR + SA	60.966	111.510	1.696	0.178	0.400
Proportion of infauna	SA + TM	−6.598	−39.368	0.000	1.000	−0.040
Proportion of unattached	SA + TM	−5.106	−38.423	0.000	0.558	−0.035
	PR + SM + TM	−5.066	−37.954	0.469	0.442	−0.043
Proportion of suspension feeder	SM	0.572	−76.868	0.854	0.190	0.000
	SR	0.486	−76.801	0.921	0.184	0.000
	TR	0.473	−76.788	0.935	0.182	0.000
	PM + SR	0.493	−76.443	1.280	0.153	−0.001

ΔAICc, difference in AICc from the best-supported model; wAICc, model weights; R^2, Nagelkerke's R^2. Predictors: PR, Productivity range; SA, shelf area; SM, salinity (mean); TR, temperature range; CF, cyclone frequency.

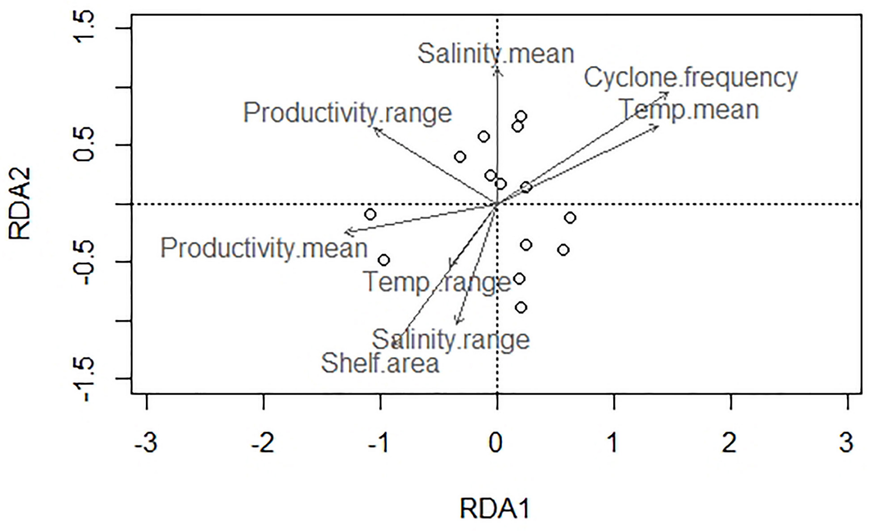

FIGURE 7 | Redundancy analysis (RDA) biplot of bivalve species composition and environmental parameters.

microstructure, with an exceptionally short lifespan, might be less represented in death assemblages due to differential post-mortem durability (Albano and Sabelli, 2011; Kidwell, 2013). High energy events such as tropical storms can also produce habitat mixing of shallow seafloors (Miller et al., 1992; Bhattacherjee et al., 2021). The small original sample size and severe analytical

TABLE 5 | Biplot scores for constraining variables derived from the redundancy analysis (RDA) to determine the relative contribution of each environmental variable for the compositional variation of bivalves.

Proportion of constrained variance = 66%				
Proportion of unconstrained variance = 34%				
	RDA1	**RDA2**	**RDA3**	**RDA4**
Productivity (mean)	−0.649	−0.125	0.037	−0.498
Productivity (range)	−0.525	0.322	0.193	0.521
Salinity (mean)	0.004	0.579	−0.464	0.587
Salinity (range)	−0.169	−0.514	0.431	−0.577
Temperature (mean)	0.691	0.337	−0.013	0.551
Temperature (range)	−0.204	−0.269	0.683	−0.591
Shelf area	−0.442	−0.607	0.244	−0.443
Cyclone frequency	0.735	0.481	0.321	−0.104

truncation of a data set can magnify the effects of such bias (Kidwell, 2013). Despite all these potential biases, time-averaged death assemblages from beach samples have been documented to substitute a conventional sampling effort of regional diversity (Kidwell, 2013) and may provide a stronger signal for species abundance compared to the original living community (Kidwell, 2001). Consequently, beach sampling is considered a valid sampling technique for diversity studies for Recent marine molluscs (Warwick and Light, 2002; Mondal et al., 2021). It is widely utilized for its logistical ease compared to other techniques for acquiring live community data (Warwick and Light, 2002; Zuschin and Ebner, 2015).

Beach sampling may present a few limitations in reconstructing the community structure of the east coast of India. In a siliciclastic setting frequented by storms in the northern east coast of India, Bhattacherjee et al. (2021) demonstrated a low life-dead fidelity of molluscan species in a local scale. Using the published literature data on bivalve occurrence, they also found that the frequency of cyclones may induce significant mixing at a regional scale. The abundance-based species diversity/composition of the present study, however, does not reveal significant dependence on cyclone frequency pointing to the preservation of the true biodiversity signature of the beach samples (**Tables 3**, **4**). Preservation of original ecological structure in beach samples is another point of worry. All infaunal bivalves have aragonitic shells and major epifaunal shells are calcitic. Due to the higher preservability of calcite, epifaunal shells may dominate a dead assemblage at the expense of the infaunal ones; this bias is prevalent among semi-lithified specimens (Cherns et al., 2011). Our specimens are less likely to suffer from such bias, primarily because of their pristine condition. More importantly, our results show a dominance of infauna—a pattern opposite of what would have been created by this specific preservation bias. This confirms the recent findings of Gupta et al. (2020) that the beach assemblages from the eastern coast of India preserve pristine shells pointing to an assemblage enduring the least taphonomic disturbance.

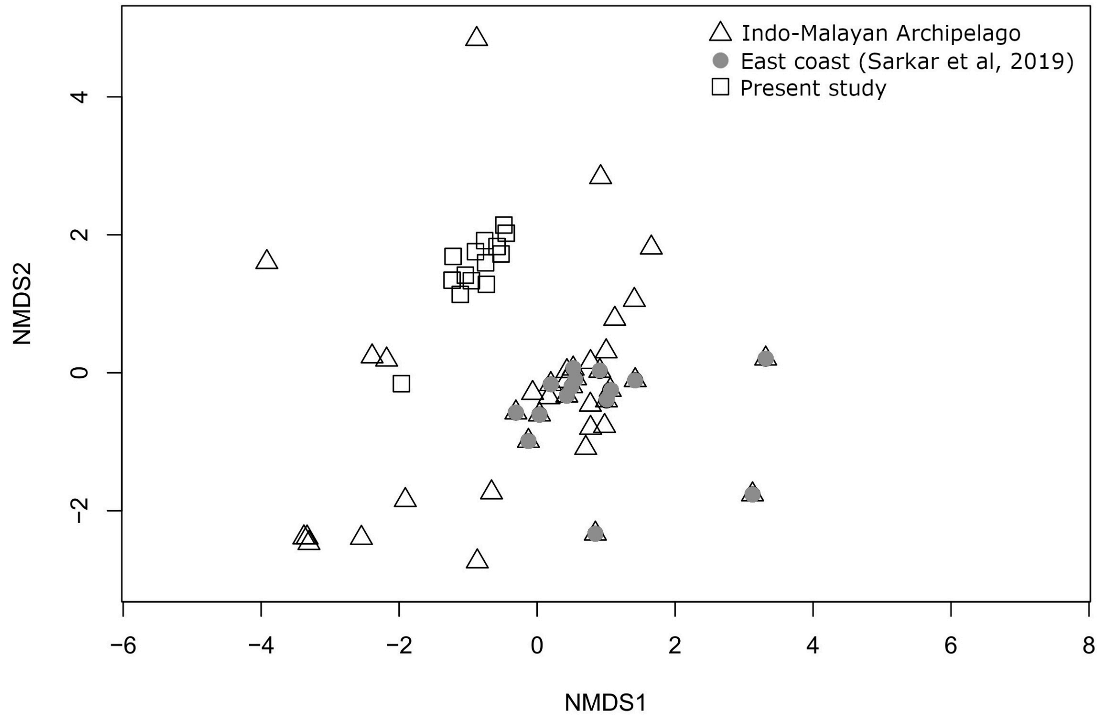

FIGURE 8 | Ordination plot using non-metric multidimensional scaling, based on Bray–Curtis distance calculated from a matrix of marine bivalve species occurrence from Indo-Malay Archipelago, literature-based data of east coast from Sarkar et al. (2019) and the present study.

Nature of Variation in Species Richness and Composition

Regional-scale studies of tropical shallow marine bivalve diversity are limited. The east coast of India is known to harbor a rich assemblage of molluscan fauna (Subba Rao, 2017). Our specimens, collected over 17 sites from the east coast, also show a high species richness of bivalve fauna (∼287), although slightly lower than the occurrence-based reports of 371 species (Sarkar et al., 2019) and 518 species reported from the biodiversity hotspot of Indo-Malayan Archipelago. The sampling protocol of the present study did not include the sediments and small bivalves therein. This exclusion may explain the lower observed diversity in comparison to the occurrence-based reports of BoB. The species richness of this region is comparable to other tropical hotspots such as the Red Sea (Zuschin and Graham Oliver, 2005).

Latitudinal biodiversity gradient is one of the most commonly accepted global patterns of regional faunal distribution including marine bivalve distribution (Roy et al., 1998; Jablonski et al., 2006; Roy and Goldberg, 2007). Global pattern documented for various temperate and polar marine regions often shows varying character; its true nature in species-rich intra-tropical region is still sparsely studied. The present study shows an interesting pattern of latitudinal variation in the tropics that does not follow the classical LBG. Instead of a monotonic increase leading to a peak at the southern point, it shows a low species diversity near 14°N followed by a symmetric increase (**Figure 5**). The drop in evenness near 14°N along with a change in diversity points to the contribution of multiple oceanographic parameters varying regionally as opposed to the monotonic variation in single variables such as sea surface temperature. In contrast to the claim of SST being the primary predictor of the global distribution of marine biodiversity, our study found a negligible role of temperature in dictating the variation in species richness at a regional scale (**Table 4**).

The distribution of species is influenced by a combination of species-specific traits (physiological tolerance, nature of reproduction, and dispersal) and the nature of the available habitat (oceanographic variables and geographic barriers) (Hesse et al., 1951). The overall composition of bivalve species of our study shows a characteristic assemblage of the Indian ocean, dominated by Veneridae. Species of *Timoclea*, *Sunetta*, *Meretrix*, *Anadara*, *Mactra*, and *Donax* constitute more than 70% of the overall species composition. The assemblage, however, differs from a typical Indian ocean assemblage by its uncharacteristically low proportion of Tellinidae and Lucinidae. It is important to note that these three families are the most important components of tropical infaunal bivalve communities in both species richness and individual abundance (Jackson, 1974). Species association along the coast neither shows a continuous change in diversity as predicted by LBG nor any distinct cluster reflecting the existence of any oceanographic barriers. Occurrence data on species composition points to the existence of such a strong barrier around 15°N along the west coast separating the species association of the northwestern sites from the rest of the Indian sites (Sarkar et al., 2019). This barrier on the west coast is primarily developed due to differences in salinity and productivity between the northern and southern Arabian Sea (Madhupratap et al., 2001; Sarkar et al., 2019). Based on the same occurrence data, Bhattacherjee et al. (2021) demonstrated a higher level of similarity in species associated with the northern part of the east coast compared to the southern part due to the high intensity of cyclone-induced mixing of the bottom fauna. Considering the methodological inconsistencies in sampling that may have influenced the literature-based occurrence data, we should take the results with caution. The abundance-based data of the east coast of the present study, in contrast, shows a more continuous variation in species composition along the east coast (**Figure 6**) pointing to a relatively well-mixed circulation of the BoB without any major oceanographic barrier in contrast to the western coast of India (Sarkar et al., 2019). The lack of sharp change in oceanographic variables along the coast (**Supplementary Figure 1** and **Supplementary Table 4**) also reaffirms our claim of predominantly continuous circulation.

The functional composition of the bivalve species is primarily dominated by infauna and bivalves without attachments. Among infaunal genera without any attachment, *Cardium*, *Sunetta*, and *Mactra* are the most common ones. The species of *Ostrea* dominates the epifauna with attachment. The species of *Sunetta*, *Donax*, and *Anadara* are the most common suspension feeders. Only a very few species of *Wallucina* represent chemosymbionts in this assemblage. Sarkar et al. (2019) did a preliminary analysis on the diversity and distribution of Indian marine bivalves based on occurrence data. A comparison of the major results between these two studies regarding the east coast, suggests a high degree of congruence despite possible methodological inconsistency and limitation in sampling effort in the first approach. Both the datasets revealed a higher richness at all taxonomic level in the east coast where the two most common families are Veneridae, Arcidae; both the studies showed a dominance of specific functional groups such as infaunal and unattached. The lack of a clear LBG and a non-monotonic increase in species richness along the east coast is demonstrated by both datasets.

Role of Physical Environment Influencing Diversity and Distribution

The eastern coast of India harboring the BoB displays variation in several oceanographic variables (**Supplementary Figure 1**). The northern region is characterized by high siliciclastic input from large rivers and variable salinity (Subramanian, 1993; Ganesh and Raman, 2007) while the southern region is characterized by relatively low siliciclastic input and presence of reefs (UNEP-WCMC, WorldFish Centre, WRI, TNC, 2010). The observed variation in bivalve distribution along this coast, however, is not controlled by any single physical parameter and points to the emergent influence of multiple oceanographic variables creating a complex biological response.

Productivity is widely believed to be a significant controller of marine benthic diversity which may increase between regions of low to moderate productivity, and then abruptly decline toward regions of higher productivity (Levin et al., 2001; Rex et al., 2005). A strong positive correlation is found between eutrophication and bivalve diversity throughout the Indo-West

Pacific tropical province (Vermeij, 1990; Taylor, 1997). At low levels of productivity, food limitation is thought to limit the number of species that can survive. The reason behind the decline in species diversity in regions of highly fluctuating productivity is attributed to demographic stochasticity that may bring about diversity declines (Levin et al., 2001). The highly diverse east coast is characterized by low but generally stable productivity. Despite a high riverine flux bringing nutrients, the productivity remains lower (Nair et al., 1973; Madhupratap et al., 2003; Kumar et al., 2007) because of the loss of nutrients in the deep ocean (Qasim, 1977; Sen Gupta et al., 1977; Radhakrishna et al., 1978). The chlorophyll α concentrations (10–20 mg m^{-2}) and primary productivity values (40–502 mg C m^{-2} d^{-1}), although lower than the Arabian Sea values for the same season, show significantly lower seasonal fluctuation in the east coast (Madhupratap et al., 2003). Our study identifies the important role of productivity variation in guiding species richness and proportion of dominant functional groups (**Table 4**). Although mean productivity is not correlated with richness, an increase in productivity range appears to cause a decrease in species richness. Such a decrease is probably caused due to the fluctuating oxygen concentration produced from the degradation of organic flux and related stress produced by the fluctuating productivity (Berger et al., 1989). This phenomenon is not unusual for benthic communities such as bivalves. Global data shows that a highly diverse benthic community is more likely to be supported by a stable primary production than a fluctuating production summing up to a higher value of annual productivity (Valentine and Jablonski, 2015). Moreover, productivity is also found to be correlated with change in dominance of functional groups for bivalves; oligotrophy supports a community of exposed sedentary suspension feeders in contrast to active benthic communities of highly productive regions (McKinney and Hageman, 2006). The dominance of mobile infauna (**Figure 4**) in our study also corroborates the same finding.

Temperature is known to play an important role in controlling the diversity, composition, and geographic distribution of marine species at a global scale (Barry et al., 1995; Walther, 2002; Parmesan and Yohe, 2003; Hiscock et al., 2004; Tittensor et al., 2010). Bivalves are exposed to a wide range of temperatures depending on their substrate relationship. Species that live at shallow depths (1 m or less) experience a greater range of temperature in a single locality than are most deep-water species over their entire geographic range (Jackson, 1972, 1973, 1974). Consequently, the shallow marine bivalves show a relatively high-temperature tolerance. Such inherent physiological tolerance of shallow marine bivalves along with a relatively narrow variation in temperature along the east coast (2.5°C) (**Supplementary Figure 1** and **Supplementary Table 4**) explains why temperature does not emerge as a strong predictor of diversity in our study (**Figure 7** and **Table 4**). This also supports the existing concerns about generalizing the effect of temperature on marine bivalves (Nawrot et al., 2017; Chattopadhyay and Chattopadhyay, 2020).

Another important factor influencing marine biodiversity is salinity. Salinity is found to play a role in guiding the species diversity of estuarine molluscs (Montagna et al., 2008). The relationship between salinity and diversity is more complex for marine ones (Sanders, 1968; Roy et al., 1998). An inverse relationship between bivalve species richness and salinity range is observed for global distribution (Valentine and Jablonski, 2015). The lack of correlation between salinity and overall species composition in our study may be influenced by the fact that marine organisms at high temperatures tend to tolerate the variation in salinity much more easily than in low temperatures (Panikkar, 1940; Sanders, 1968). Our results also show that salinity (mean) is the common factor influencing the richness and proportion of dominant functional groups (**Table 4**).

The long-held axiom in ecology states that larger areas hold more species than smaller areas (Rosenzweig, 1995) and predicts a positive influence of available area on diversity. Available habitat area plays an important role in shaping the community structure of shallow marine benthos through time and the continental shelf is recognized to be one of the most speciose habitats (Piacenza et al., 2015). Reconstructing the true shelf area is far from challenging and hence, several proxies are used (Holland, 2012). A few studies have used coastal length as a proxy (Cain, 1938; Connor and McCoy, 1979; Tittensor et al., 2010) and others estimated shelf area as a product of coastal length and width (Sanciangco et al., 2013). All of these global studies confirmed a positive correlation between habitat area and biological diversity of marine groups including bivalves (Valdovinos et al., 2003). Literature-based occurrence data shows a correlation between coastal length and marine molluscan diversity along the Indian coast (Sivadas and Ingole, 2016; Sarkar et al., 2019). Our results also show an influence of shelf area on species diversity (**Table 4**) supporting the validity of the habitat-area hypothesis in a small regional scale.

Among regional environmental parameters, no single environmental variable explains the major canonical axes of species variation satisfactorily (**Figure 7** and **Table 5**) indicating the influence of several environmental variables acting together in shaping the regional nature of species distribution. Occurrence-based data demonstrate a partitioning between northern and southern sites where the southern eco-region is characteristically dominated by borers like *Martesia striata*, and the northern eco-region is dominated by various species of *Donax* (Sarkar et al., 2019). Our abundance data, however, shows only a slight difference in species composition between southern and northeastern sites. The lack of strong compositional dissimilarity along the east coast probably owes to a highly mixed circulation pattern of the BoB.

Apart from the selected oceanographic variables considered in the study, the nature and amount of sediment influx may play an important role in guiding the distribution, especially influencing the distribution of functional groups in this region. The eastern coast of peninsular India is characterized by extremely high sediment influx (>1,350 million tons of suspended sediments/year) brought by the Ganges-Brahmaputra River systems together with other rivers to the BoB, especially toward the north (Milliman and Meade, 1983; Subramanian et al., 1985). This high riverine input makes it easier for the infaunal bivalves to thrive and flourish. The southern part of India (8–15°N) receives less than a fourth of the sediment supply brought by smaller rivers (Vamsadhara, Hyadri, Godavari, and

Krishna) compared to the larger rivers of the north (Bharathi et al., 2018). The presence of coralline hard substrate in the south (UNEP-WCMC, WorldFish Centre, WRI, TNC, 2010) along with relatively low riverine input make it more habitable for epifaunal forms—a slight increase in epifaunal proportion in the southern latitudinal bins (**Figure 3**) reflects this change in habitat. In contrast to the reported dominance of epifauna in the west coast (Sarkar et al., 2019), the east coast demonstrates the dominance of the infaunal sediment burrowers (**Figure 4**). A similar pattern is observed for the dominance of the unattached form in the east coast compared to that of the attached forms in the west coast. The dominance of infaunal, unattached species in the east coast is most likely a reflection of higher siliciclastic sediment input. Even though we did not measure the sediment load and the nature of substrate explicitly in this study, the observed pattern of coastal difference in dominant functional groups underscores the role of substrate in structuring shallow benthic communities.

Another important regional parameter, imparting a likely control over the species richness and composition, might be the location of the nearest biodiversity hotspot. Crame (2000a,b) has documented the presence of a bivalve biodiversity hotspot near the Indo-Malayan Archipelago and claimed that species are radiating from there. He put this as a mechanism to explain the clines of species richness decreasing radially from this area in a north-south latitudinal pattern and east-west longitudinal pattern. The higher species richness of the east coast may also be influenced by this proximity. It has long been recognized that the BoB faunal assemblage largely represents the Indo-Malayan archipelago and is considered a contiguous part of it. However, it has not been documented for bivalve fauna. Both occurrence data (Sarkar et al., 2019) and the present study reaffirm the lack of distinctness of bivalve fauna of the east coast from the Indo-Malayan species association (Hocutt, 1987). The present study suggests that the high-diversity regions in the east coast may have developed due to a combination of several oceanographic variables and influenced by larval transport with biodiversity hotspots like the Indo-Malayan Archipelago.

No single environmental predictor emerged to explain the diversity in the east coast. All the environmental variables together explain the species composition satisfactorily (**Figure 7**). This underscores the complex interplay between multiple oceanographic variables in determining the distribution and diversity of tropical shallow marine benthos in a regional scale—a pattern that is noted for benthic biodiversity in large marine ecosystems such as the western margin of the United States (Piacenza et al., 2015).

CONCLUSION

This study using "time-averaged" and "spatially-averaged" bivalve death assemblages from beach sampling is one of the first attempts to document regional species diversity of marine bivalves along the east coast of India and to investigate its oceanographic correlates. By following a rigorous and consistent sampling protocol, this study reveals the regional pattern of bivalve diversity and distribution in this largely unexplored region. The overall diversity is comparable to other tropical shallow marine sites. Bivalve assemblages along the east coast are characterized by a higher proportion of infauna and groups without any attachments than in the west coast. This difference points to the inherent difference in the physiography of the coasts; while the east coast receives a higher amount of riverine sediments that is conducive for infaunal bivalves, a low influx of sediments makes the west coast favorable for epifaunal groups. When compared to classical trends like LBG, the diversity change with latitude does not show a consistent pattern pointing toward a more regional nature of diversity variation. There is no strong distinction in species composition along the east coast indicating a continuous circulation and considerable mixing of water within the BoB. Productivity range, shelf area, and salinity appear to influence the species richness. Along with these oceanographic variables, salinity contributes significantly to determine the proportion of the dominant functional group (unattached, suspension feeders). All the environmental variables together explained the species composition across latitudinal bin pointing toward a complex interaction between multiple environmental variables and their contribution to species composition. Lack of distinctness in bivalve species composition in comparison to those of the Indo-Malayan archipelago suggests the influence of this biodiversity hotspot in the development and maintenance of the species-rich fauna of the east coast of India. Apart from demonstrating that regional patterns in bivalve distribution are influenced by a complex interplay between several environmental factors, our study also establishes the temporally-spatially averaged molluscan death assemblages as a reliable proxy for regional biodiversity studies.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

DC designed the research. DS collected the data. DS and MB analyzed the data. DC wrote the manuscript with input from DS and MB. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.675344/full#supplementary-material

Supplementary Figure 1 | Latitudinal variation in the oceanographic parameters along the east coast of India.

Supplementary Table 1 | Summary of Wilcoxon test comparing the proportion of various ecological types. The significant results are in bold.

Supplementary Table 2 | Significance of Spearmann correlation test between environmental variables. The significant results are in bold.

Supplementary Table 3 | Results of multiple GLM analyses to assess contribution of environmental variables in determining species richness, substrate relationship (infaunal proportion), attachment type (unattached proportion), feeding (suspension proportion). The significant results are in bold.

Supplementary Table 4 | Summary of the environmental variables used in the present study.

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Differential Symbiodiniaceae Association With Coral and Coral-Eroding Sponge in a Bleaching Impacted Marginal Coral Reef Environment

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Marginal reefs are known for severe stress-inducible perturbations such as high sedimentation, eutrophication, ocean warming, and acidification from anthropogenic climate change. The corals striving in such stressful environments develop physiological adaptations induced by differential genomic expressions or association with thermal stress-tolerant algal symbionts (Symbiodiniaceae). Despite such adaptations, corals are threatened by other space competitors such as algae and sponges. Coral-eroding sponges belonging to the *Cliona viridis* complex are one such space competitors that also associate with Symbiodiniaceae algal photosymbiont. The diversity of Symbiodiniaceae associates with the coral and sponge from the same ecosystems is scarcely known. In the present study, Symbiodiniaceae community structure in the coral *Turbinaria mesenterina*, a newly described coral-eroding sponge *Cliona thomasi*, and their surrounding seawater was determined from the nearshore marginal reef along the central west coast of India. The results revealed a significantly higher relative abundance of *Durusdinium* and *Gerakladium* than *Symbiodinium* and *Cladocopium* in the seawater. Interestingly, both investigated host species showed differential Symbiodiniaceae association with significantly higher abundance of *Durusdinium* in coral and *Gerakladium* in sponge. The beta diversity analysis by Permutational multivariate analysis of variance (PERMANOVA) confirmed significant differences in Symbiodiniaceae profiles between sponge and coral. *Durusdinium* and *Gerakladium* are thermotolerant genera known to associate with different hosts in suboptimal conditions. Our field surveys suggested the bleaching resistance of the coral *T. mesenterina* despite the fact that the sea surface temperature reached the coral thermal threshold of 31°C during different periods of the years 2015, 2016, 2017, 2018, and 2019. Therefore, the thermal tolerance of the investigated coral and sponge species may be attributed to their respective thermotolerant photosymbiont associations. Furthermore, the results also indicated the host-specific

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photosymbiont selection from the local environment. Although these observations provide valuable biological insight, more research is needed to understand the tripartite association of sponge-coral-symbiont together to evaluate the competitive fitness of holobionts.

Keywords: coral, sponge, *Cliona*, *Turbinaria*, Symbiodiniaceae, symbiont, ITS2, bioerosion

INTRODUCTION

Coral reefs harbor the most dynamic and complex plethora of microbial communities, including bacteria, fungi, viruses, archaea, and dinoflagellates (Mies et al., 2017; Osman et al., 2020; Pernice et al., 2020). Endosymbiotic dinoflagellates of the Symbiodiniaceae family have gained considerable attention as an indicator for the well-being of the coral reef health and ecosystem functioning (Silverstein et al., 2012; Osman et al., 2020). Symbiodiniaceae are present in the coral's ambient environment (seawater and sediment) as free-living form as well as in association with different host organisms like sponges, foraminifera, clams, etc. (Takabayashi et al., 2012; Granados-Cifuentes et al., 2015). Free-living Symbiodiniaceae are crucial pool of photosymbiont for host organisms, as they acquired new symbiont from the ambient environment at different life stages (Granados-Cifuentes et al., 2015; Nitschke et al., 2016). Endosymbionts of reef-building corals contribute to most of the energy requirement of coral through photosynthesis, enabling calcium carbonate accretion and growth (Al-Horani, 2016). In return, coral supports Symbiodiniaceae by providing a protective environment and necessary components required for photosynthesis (Williams and Patterson, 2020). The dynamics in coral-Symbiodiniaceae interaction influences the ability of corals to function under different environmental conditions (Jones et al., 2008; Ziegler et al., 2017). The association of coral with different Symbiodiniaceae is regulated by local environmental conditions (Thornhill et al., 2017; Baker et al., 2018). So far, obligatory symbiosis of corals with different Symbiodiniaceae genera has been documented from a broad geographical and environmental regimes, that include *Symbiodinium*, *Breviolum*, *Cladocopium*, *Durusdinium* and, occasionally *Fugacium* and *Gerakladium* (formerly clades A, B, C, D, F, and G, respectively) (LaJeunesse et al., 2018; Osman et al., 2020). Each symbiont genus provides a different degree of support to the host coral (Stat et al., 2008; Camp et al., 2020; Pernice et al., 2020). For instance, Symbiodiniaceae diversity in *Leptoria phrygia*, experiencing thermal instability showed an exclusive association with *Durusdinium* for coping with thermal stress (Carballo-Bolaños et al., 2019). Furthermore, D'Angelo et al. (2015) confirmed the specific association of different *Porites* spp. with *Cladocopium* (C3) type symbiont in the warm and hypersaline waters of the Persian/Arabian Gulf.

Recent studies have confirmed that some corals (e.g., *Montastraea cavernosa*, *Pocillopora damicornis*, *Stylophora pistillata*, and *Porites lutea*) can adapt, sustain, and survive against local environmental stressors by switching or shuffling their associated photosymbionts (Silverstein et al., 2015; Boulotte et al., 2016; Osman et al., 2018; Tan et al., 2020). Response to environmental stressors varies among coral species and endosymbiont communities (van Woesik et al., 2011; Cunning et al., 2017). The local environment exerts selection pressure which eliminates the sensitive Symbiodiniaceae taxa and results in the dominance of stress-resilient species (Cunning et al., 2015; Claar et al., 2020). This differential abundance of specific thermotolerant Symbiodiniaceae taxa affects the functional characteristics of their host (LaJeunesse et al., 2010a; Carballo-Bolaños et al., 2019), eventually leading to the emergence of a particular "space winner" genotype (LaJeunesse et al., 2010a; Stat and Gates, 2011).

Globally, coral reefs are under threat due to climate change induced thermal stress and anthropogenic impacts, which disrupt delicate coral-Symbiodiniaceae interaction, causing mass coral bleaching, mortality, and rapid health deterioration of reef ecosystems (Hughes et al., 2017, 2018). Moreover, increasing disturbance may contribute to the overgrowth of benthic space competitors like cyanobacterial mats, macroalgae, and sponges, which pose additional threats to stressed reef-building corals (Horwitz et al., 2017). Among these benthic space competitors, bioeroding sponges are one of the most aggressive competitors that are known to erode reef-building corals and destruct the reef (Schönberg, 2000; Zundelevich et al., 2007; Fang et al., 2018b). For instance, species belonging to *Cliona viridis* species complex accounts for significant erosion of corals at the rate of >10 kg/m sponge area/year (Schönberg, 2000; Achlatis et al., 2019). The cosmopolitan sponge genus *Cliona* consists of 86 species (Van Soest et al., 2020), and among those, only about 25% of species are known to harbor symbiotic dinoflagellate communities (Achlatis, 2018; Mote et al., 2019). Studies have shown that algal symbionts of *Cliona* species provide their host with energetic inputs needed for excavating calcium carbonate through investment in photosynthates and/or photosynthesis by-products (Marlow et al., 2018; Achlatis et al., 2019). These symbionts occur in high densities in *Cliona viridis* species complex and display remarkably rapid lateral expansion and high bioerosion rates (Schönberg et al., 2008; Hill et al., 2011). Therefore, Symbiodiniaceae family members support their bioeroding host in space competition as well as in coping with the fluctuating environmental conditions (Fang et al., 2017, 2018b).

A few studies have shown that some sponges are associated with algal symbionts from *Symbiodinium*, *Breviolum*, and *Gerakladium* genera (formerly clades A, B, and G) (Hill et al., 2011; Ramsby et al., 2017). Moreover, these Symbiodiniaceae diversity analyses were mainly based on specific and/or multiple gene amplification followed by sequencing (Hill et al., 2011; Ramsby et al., 2017). However, the application of the next-generation sequencing (NGS) approach to dissect the taxonomic diversity of Symbiodiniaceae family associated with sponges is sparsely studied compared with other invertebrates (Riesgo et al., 2014; Ramsby et al., 2018). In order to gain insights into the role of Symbiodiniaceae members in the reef ecosystem, it is essential to study the multifaceted association between coral-symbiont, sponge-symbiont, and sponge-coral.

Determination of the composition and variability of symbiont community in reef-building corals and space-competing sponges is crucial to get an insight into how the symbiont compositional change influences the host's physiology and competitive abilities in response to suboptimal environmental conditions. Although previous studies significantly contributed to our understanding of coral-symbiont diversity and the environmental-induced plasticity, the understanding of symbiosis between bioeroding sponges and Symbiodiniaceae is still sparse. Therefore, the present study employed a deep sequencing approach to elucidate the Symbiodiniaceae diversity associated with the coral *Turbinaria mesenterina* and the bioeroding sponge *Cliona thomasi*, both competing in a marginal coral reef environment on the west coast of India. Shallow water nearshore coral reefs in this region are subjected to a broad range of chronic and acute stressors, which are considered suboptimal for coral reef development, including thermal stress-driven recurrent coral bleaching episodes (De et al., 2015, 2021; Hussain et al., 2016), coral diseases (Hussain et al., 2016), monsoonal freshwater influx, and anthropogenic perturbations like, siltation, turbidity, nutrient input, fishing, and intensive tourism-mediated damage (De et al., 2020). *C. thomasi* investigated herein is a newly discovered ecologically important sponge species, abundant in the Indian Ocean coral reefs (Mote et al., 2019). Therefore, aggressive growth of this species on live corals raises serious concern about reefs health (Mote et al., 2019).

MATERIALS AND METHODS

Study Site and Field Surveys

The study was conducted at the nearshore shallow water patch coral reef in the Grande Island archipelago, Central West Coast of India (15° 21′ 14.2″ N, 73° 45′ 57.8″ E). This nearshore patch coral reef on the Eastern Arabian Sea is highly disturbed by a wide range of stressors due to ongoing frequent thermal stress, low pH, monsoonal dilution of coastal seawater, higher sedimentation, and turbidity as two major rivers (Zuari and Mandovi rivers) discharge large amount of terrigenous sediment runoff and organic matter enrichment (Purnachandra Rao et al., 2011; Shynu et al., 2015; Veerasingam et al., 2015; Manikandan et al., 2016; Hussain and Ingole, 2020). The coral community in this reef habitat is mainly dominated by stress-resilient genera like *Porites*, *Siderastrea*, *Pseudosiderastrea*, *Coscinarea*, *Turbinaria*, and *Goniopora*; notably, sensitive branching taxa like *Acropora* are absent in this region (Hussain and Ingole, 2020). In recent years, corals in this nearshore habitat experienced an adverse impact from mass coral bleaching event (∼50%) during 2014–2017 (Hussain and Ingole, 2020), along with overgrowth of coral-eroding *Cliona* sponges (Manikandan et al., 2016; Mote et al., 2019), algal turf, macroalgae (Manikandan et al., 2016), coral diseases like white plaque and trematodiasis (Manikandan et al., 2016), and bioinvasion of alien octocoral *Carijoa riisei* (Patro et al., 2015). The study area is under continuous monitoring for the coral reef health assessment program since 2015. The field surveys showed a massive bleaching of corals in 2015. These bleaching events were continuously observed under subsequent field surveys. Furthermore, an increase in the sponge prevalence was recorded during 2015–2017. The details of survey times, methodology applied to monitor and the prevalence of coral-eroding sponges, and coral bleaching from the study site are given in Supplementary Information.

Sample Collection

The samples of the bioeroding sponge *C. thomasi* (n = 4) growing over the coral (*T. mesenterina)* colonies and healthy coral species *T. mesenterina* (n = 4) were collected in January 2019 from the depth of 6–8m. Massive growth forms of sponge species *C. thomasi* over different individual coral species are shown in **Figures 1a–d**. Utmost care was taken while collecting the samples, wherein each sample was distinct and separated from the other by at least 5 m. The coral and sponge tissue samples of ∼1–2 cm^2 in diameter and 0.5–1 cm in thickness were collected using precleaned hammers and chisels. To compare the community with the ambient environment, surrounding seawater samples (n = 4) were collected from a distance of 2–4 m away from sponge-coral colonies. Samples were immediately brought on board, fixed in liquid nitrogen, and transported to the laboratory for further processing. The sponge species was identified by spicule morphology and molecular analysis following the established protocol (Mote et al., 2019).

DNA Extraction and Sequencing

The total DNA from each collected sample was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. About 500 ml of seawater for each sample was filtered using 0.22 μm polycarbonate membrane filter (Whatman), and the filter paper was used for DNA isolation. For the identification of the Symbiodiniaceae community, the internal transcribed spacer 2 (ITS2) region was selected for amplification and sequencing using the primer set as forward 5′-GTGAATTGCAGAACTCCGTG-3′ and reverse 5′-CCTCCGCTTACTTATATGCTT-3′ (Boulotte et al., 2016). PCR amplifications were carried out in a 50-μl reaction volume containing ∼50 ng of DNA, 25 μl of 2×Taq Platinum PCR Master, 200nM of each primer, and ddH$_2$O to make up the final volume. Reactions were performed at 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, 51°C for 30 s, and 72°C for 30 s, and a final extension at 72°C for 4 min using a Mastercycler (Applied Biosystems, Foster City, United States). Illumina MiSeq libraries for the ITS2 region were generated and validated using 2100 Bioanalyzer (Agilent Technologies) for quality, and samples were sequenced using the 2 × 250 paired—end chemistry according to the manufacturer's specification (HiSeq Reagent Kit). Sequencing was done on the MiSeq Illumina platform and produced 4,525,076 paired-end raw reads with an average read length of ∼350 to ∼ 420 bp.

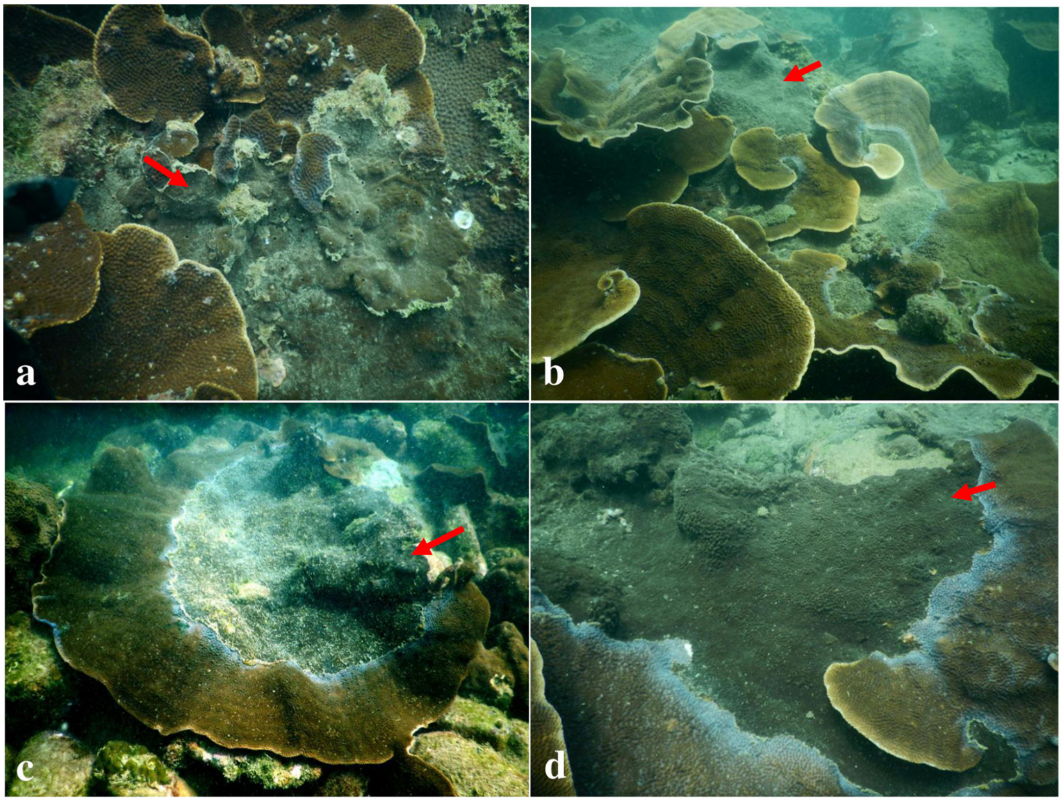

FIGURE 1 | Massive growth forms of *Cliona thomasi* observed over different live coral colonies of *Turbinaria mesenterina* **(a–d)** from the studied site Grande Island.

Bioinformatic Analysis

Sequence reads generated through the Illumina Miseq platform were demultiplexed, and primers were trimmed using Cutadapt (Martin, 2011). DADA2 pipeline recommended by Callahan et al. (2016) for ITS analysis based amplicon sequence variant (ASVs) generation was followed. The determined ITS2 ASVs were assigned a taxonomic identity using the RDP classifier (Wang et al., 2007) against reference database sequences. This study employed three different databases for taxonomic classification of ASVs: (i) Db1 (Claar et al., 2020), (ii) Db2 (Shi et al., 2021), and (iii) Db3[1]. To aid in the removal of non−Symbiodiniaceae sequences (e.g., non-target dinoflagellates), default RDP bootstrap value of 50 was used. The rank was set "unassigned" below this threshold, and these were hence removed from further analysis. The defined Symbiodiniaceae ASV table was utilized for downstream analysis, and abundance variations of Symbiodiniaceae genera and subtypes were analyzed.

The intragenomic variations (IGVs) among ITS2 regions challenged the Symbiodiniaceae diversity estimation. It is therefore important to determine the IGV profiles. The IGV profile for the Symbiodiniaceae diversity from the investigated samples was determined by SymPortal (Hume et al., 2019). For the SymPortal analysis, all sets of sequences were remotely submitted to SymPortal.org. SymPortal identify the specific sets of defining intragenomic variants (DIVs) that are used to characterize ITS2-type profiles (Camp et al., 2020; Hume et al., 2020).

Statistical Analysis

The vegan package v.2.5-6 in R (Oksanen et al., 2018) was used to calculate the alpha-diversity indices such as ASV richness, Shannon, Chao, and Simpson indices and to prepare a rarefaction curve for the investigated samples. The significant differences among the diversity indices values were determined by the Kruskal-Wallis test (with Dunn's *post hoc* test). Furthermore, the beta-diversity measures to test the statistical difference of Symbiodiniaceae community composition among the samples were determined by applying permutational multivariate analysis of variance (PERMANOVA) with 999 permutations using Bray-Curtis dissimilarity matrix in PRIMER v7 (Clarke and Gorley, 2015). Symbiodiniaceae community composition was ordinated using non-metric multidimensional scaling (nMDS), as implemented in vegan package in R using metaMDS function (Oksanen et al., 2018). Similarity percentage (SIMPER) analysis was performed to calculate the contribution of each ITS2 subtype to the dissimilarity within and between samples in the PRIMER v7. Analysis of similarity (ANOSIM) was carried out using 999 permutations with a Bray-Curtis distance in vegan package R

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[1] https://raw.githubusercontent.com/nitschkematthew/Symbiodatabaceae/master/Combining_databases/ITS2dbn1_Dinophy_Symbio.fasta

using Anosim function to test if there is a statistical difference between the Symbiodiniaceae communities of samples.

RESULTS

Diversity and Composition of Symbiodiniaceae Based on ITS2 Sequence Analysis

Deep sequencing analysis of ITS2 region recovered a total of 4,534,038 raw sequence reads from three compartment of the coral reef habitat, i.e., reef-building coral, bioeroding sponge, and seawater (**Supplementary File 1** and **Supplementary Table 1**). The raw amplicon sequencing dataset is available at the NCBI sequence read archive (SRA) database (accession PRJNA636097). After processing through DADA2 pipeline, the filtered sequence reads (3, 647, 450) were assigned to 1,008 unique ASVs (**Supplementary File 1** and **Supplementary Table 1**). The taxonomic classification of these ASVs showed high degree of variations when assigned against different Symbiodiniaceae databases investigated in this study. The ASVs with more than 50% confidence for their taxonomic assignments were 613, 594, 253 for the databases Db1, Db2, and Db3, respectively. The variations obtained at the genera level for the ASVs from different databases are shown in **Supplementary File 2** (**Supplementary Table 1**). The databases Db1 and Db2 showed similar results of taxonomic distribution and determined six Symbiodiniaceae genera (*Durusdinium*, *Gerakladium*, *Symbiodinium*, *Cladocopium*, *Breviolum*, and *Fugacium*) (**Supplementary File 2** and **Supplementary Table 1**). However, Db3 showed the lowest ASVs (253), which were mainly assigned only to *Durusdinium*, *Gerakladium*, and *Symbiodinium* (**Supplementary File 2** and **Supplementary Table 1**). At ITS2-subtype level, Db1 and Db2 identified more Symbiodiniaceae diversity than Db3 (**Supplementary File 2** and **Supplementary Figures 1–3**). Based on the higher diversity determination, we followed the Db1 database sequences to represent Symbiodiniaceae diversity in our samples.

The assigned 613 Symbiodiniaceae ASVs further distributed as 174 for coral, 180 for sponge, and 464 in seawater. The overlap of these ASVs between coral, sponge, and seawater is shown in **Figure 2**. The distribution of these ASVs among the samples with sequencing reads was investigated with a rarefaction curve (**Supplementary File 1** and **Supplementary Figure 1**). Shannon's diversity index determined for the studied samples was in the order of seawater (3.24 ± 0.29) > *T. mesenterina* (2.46 ± 0.23) > *C. thomasi* (2.03 ± 0.40) (**Supplementary File 1** and **Supplementary Table 2**). A similar, trend was observed in the Simpsons index as seawater (0.92 ± 0.02) > *T. mesenterina* (0.85 ± 0.03) > *C. thomasi* (0.78 ± 0.06) (**Supplementary File 1** and **Supplementary Table 2**). The alpha-diversity indices determined were found significantly different only between coral and seawater based on the Kruskal-Wallis test, followed by Dunn's *post hoc* test ($p < 0.05$). The beta-diversity measures for the investigated samples showed significant differences among the composition of the Symbiodiniaceae community associated with the coral species *T. mesenterina* and the

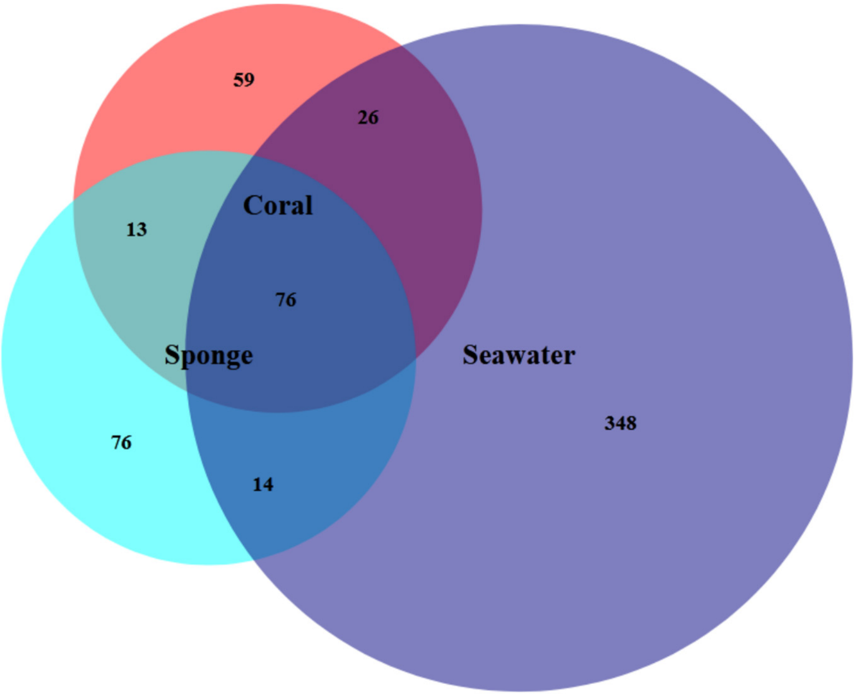

FIGURE 2 | Venn diagram shows the number of Symbiodiniaceae amplicon sequence variants (ASVs) present in each reef habitat compartment (coral, sponge, and seawater), as well as the amount of overlap between and among samples.

sponge species *C. thomasi* (PERMANOVA, $p = 0.04$; ANOSIM, $R = 0.854$, $p = 0.04$, see **Supplementary Tables 3, 4**). The Symbiodiniaceae communities between sponge-seawater and coral-seawater were also found to be significantly different (PERMANOVA and ANOSIM, $p < 0.05$, **Supplementary File 1** and **Supplementary Tables 3, 4**). The significant differences in beta-diversity between investigated coral and sponge species are mainly contributed by Symbiodiniaceae genus *Durusdinium* and *Gerakladium*. The results from the SIMPER analysis further confirmed higher dissimilarity in the Symbiodiniaceae community association between *T. mesenterina* and *C. thomasi* (average dissimilarity 58.3%) than *T. mesenterina*-seawater (average dissimilarity 42.4%) and *C. thomasi*-seawater (average dissimilarity 40%) (**Supplementary File 1** and **Supplementary Table 5**). The differential Symbiodiniaceae association was further confirmed by the clustering pattern obtained from nMDS analysis. The investigated host types were clustered distinctly and separately based on their associated Symbiodiniaceae community (**Figure 3**). The observed distinct variation among the Symbiodiniaceae species assemblage in bioeroding sponge and coral indicates the symbiont selectivity among two different hosts within the same reef habitat.

The most abundant Symbiodiniaceae genus found in the investigated coral species was *Durusdinium* (89.8 ± 11.7%), followed by *Gerakladium* (10.2 ± 11.7%) (**Figure 4A**). At ITS2 subtype level, *Durusdinium* sp. (89.1 ± 13.4%) was found to be the dominant, followed by G3.3 (9.9 ± 12.9%) in the coral species *T. mesenterina* (**Figure 4D**). The other types of *Durusdinium*, i.e., D1.8, D105, D106, D120, D124, and D2 were detected in lower abundance (**Figure 4D**). On the contrary, the sponge species *C. thomasi* contained a higher abundance of *Gerakladium* (83.3 ± 23.7%), followed by *Durusdinium* (16.6 ± 23.8%) (**Figure 4B**). Among *Gerakladium* types, the highest dominance determined was for *Gerakladium* G3.3 (78.5 ± 21.2%), followed by *Durusdinium* D1 (16.6 ± 23.7%) (**Figure 4E**). The other types of *Gerakladium* G100, G101, G3.1, and G3.2 were detected in lower abundance (**Figure 4E**). The most abundant Symbiodiniaceae taxa in seawater samples were *Durusdinium* (51.0 ± 10.1%) and *Gerakladium* (40.3 ± 3.3%), followed by *Symbiodinium* (3.5 ± 5.5%), *Fugacium* (3.0 ± 3.1%), and *Cladocopium* in (2.0 ± 3.5%) (**Figure 4C**). *Breviolum* was also detected in seawater in a very low abundance (<1%). Furthermore, at the ITS2 type level, seawater contained *Durusdinium* sp. (50.6 ± 13.9%) and *Gerakladium* G3.3 (36.3 ± 5.1%) (**Figure 4F**).

In order to define the intragenomic variants for the ITS2 region, SymPortal DIV profiles for the Symbiodiniaceae community in corals, sponge, and free-living habitats were determined. SymPortal analysis provided the complete ITS2 profile only for coral samples, which showed the dominance of ITS2 type profile D1 and lower dominance of types D4-D4c-D1c-D2-D6 (**Supplementary File 2** and **Supplementary Figure 4**).

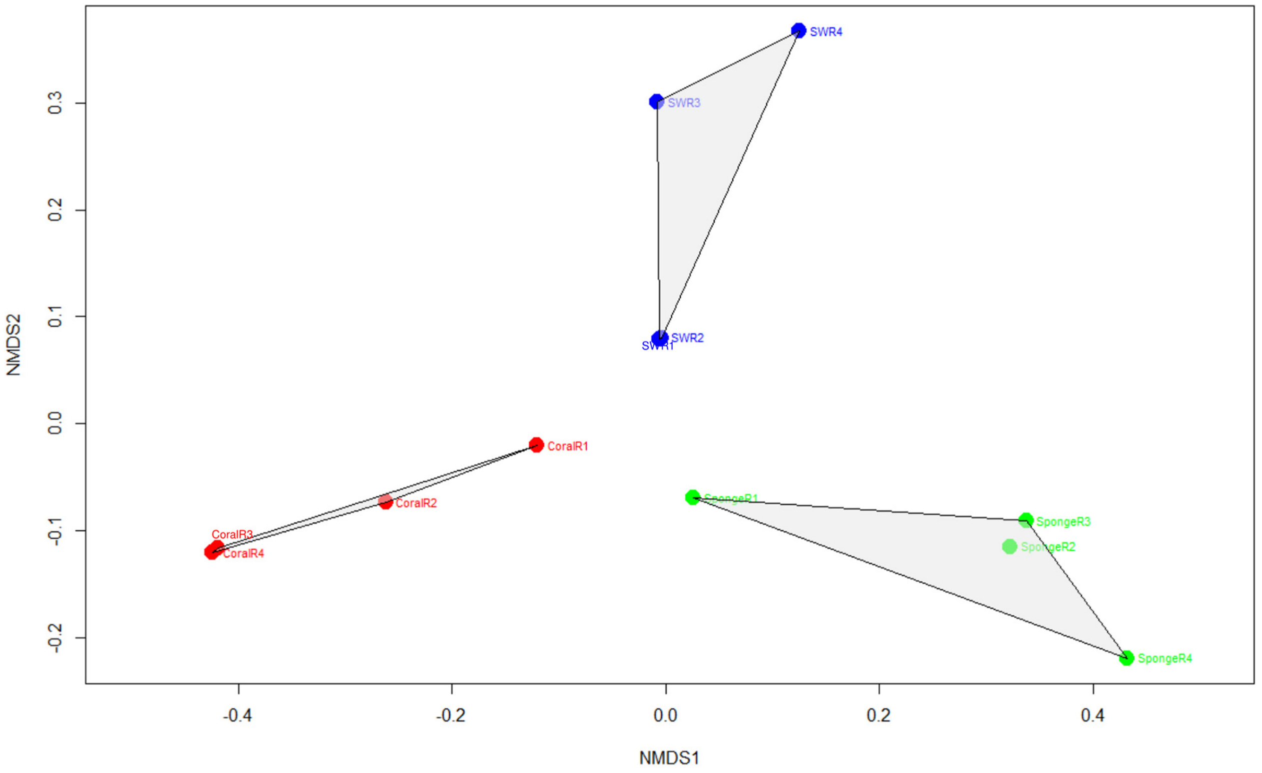

FIGURE 3 | Non-metric multidimensional scaling plots showing the pattern of Symbiodiniaceae communities recovered from the coral samples, sponge samples, and seawater (stress value: 0.12). Stress value <0.05 shows an excellent representation in nMDS analysis.

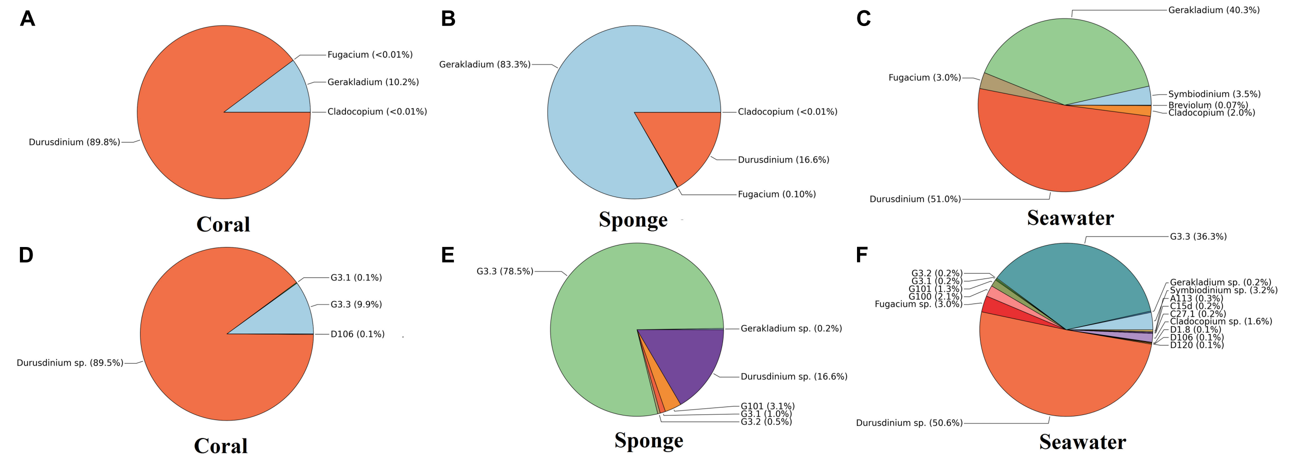

FIGURE 4 | Symbiodiniaceae community composition at Grande Island. **(A–C)** Relative abundances of Symbiodiniaceae genera in host (coral and sponge) and free living in seawater. **(D–F)** Relative abundances of Symbiodiniaceae at subtypes level in host (coral and sponge) and free living in seawater. Values represent mean relative abundances across group samples.

However, seawater and sponge samples could not show the complete ITS2 type profiles (**Supplementary File 2** and **Supplementary Figure 5**).

DISCUSSION

This study determined the Symbiodiniaceae diversity associated with the two space competitors (i.e., coral and sponge) in the same reef habitat using high-throughput sequencing of the ITS2 region. ITS2 marker is commonly used to analyze Symbiodiniaceae (Thornhill et al., 2007; Stat et al., 2011; Shi et al., 2021). The present study followed the ASV-based approach for defining the Symbiodiniaceae diversity over the conventional operational taxonomic units (OTUs) using 97% similarity clustering threshold to collapse sequence diversity into OTUs. The redundancy in ITS2 delineation has been well documented based on the reference database employed (Tonk et al., 2013; Shi et al., 2021). This study confirms the variations in ITS2 delineation and taxonomic assignment through three different reference databases. The difference in the results obtained may be attributed to the sequence length and ITS2 boundary variations in the databases. Furthermore, this study confirms the IGV level delineation called as DIVs for ITS2 subtypes using SymPortal. The DIV profiles to search for Symbiodiniaceae community of coral showed strong overlap with the sponge and free-living habitat due to the high relative abundance of *Durusdinium* (D1) (**Supplementary File 2** and **Figure 3**).

Symbiodiniaceae Community Associated With the Coral *T. mesenterina*

The investigated coral *T. mesenterina* showed a higher abundance of the genus *Durusdinium*. Interestingly, *Durusdinium* genus is widely known to be associated with scleractinian corals from the Caribbean and Indo Pacific reefs (Knowlton and Rohwer, 2003; Jones et al., 2008; Brener-Raffalli et al., 2018). Previous studies have suggested that the association of coral with *Durusdinium* may indicate local environmental stressors, such as high temperature, sedimentation, and light intensity (D'Angelo et al., 2015; Osman et al., 2020; Wall et al., 2020). Studies from different global reefs attribute the increased association of *Durusdinium* with corals to the adaptation against thermal stress (Oladi et al., 2019; Chankong et al., 2020; Williams and Patterson, 2020). *Durusdinium* communities in corals from the Andaman Sea with high host specificity were attributed to higher turbidity and high nutrient concentrations in the reef (LaJeunesse et al., 2010b). In general, the studies have confirmed that the *Durusdinium* type D1a or D1-4 (*Durusdinium trenchii*) are more frequently associated with corals in thermally challenged marginal habitats (Cooper et al., 2009; LaJeunesse et al., 2010a; Stat et al., 2013; Oladi et al., 2019; Qin et al., 2019; Williams and Patterson, 2020). *D. trenchii* is often referred to as an opportunistic symbiont which makes their association heterologous (Smith et al., 2017; Matthews et al., 2018).

The marginal coral reef of the present study was subjected to severe thermal stress-driven coral-bleaching events from 2014 to 2016. Sea surface temperature (SST) data of NOAA Coral Reef Watch (NOAA-CRW) platform revealed that the SST exceeded the thermal bleaching thresholds throughout the years 2015 to 2019 (**Supplementary File 1** and **Supplementary Figure 2**). The underwater field survey confirmed *in situ* coral bleaching during October 2014, April 2015, October 2015, and April 2016 (Hussain and Ingole, 2020). The years 2014–2017 were the warmest years in history, leading to mass coral mortalities globally (Eakin et al., 2019; Skirving et al., 2019). There have been reports of coral bleaching in all major reefs of India during this period (Hussain and Ingole, 2020). Such warming events in the last few decades have significantly altered the coral population and led to the emergence of non-reef-forming communities (Hughes et al., 2017; Lough et al., 2018). This clearly implies that temperature and local stressors remain important drivers of coral decline; therefore, the response of Symbiodiniaceae to stressors is crucial for predicting the response of the reef community as a whole.

Our *in situ* surveys confirmed high bleaching resilience in *T. mesenterina* (**Figures 5a–c**) while other coral genera such as *Coscinaria*, *Goniopora*, and *Porites* were susceptible to thermal bleaching (**Supplementary File 1** and **Supplementary Figure 3**). The determined association of stress-tolerant Symbiodiniaceae members belonging to *Durusdinium* with the coral *T. mesenterina* may be attributed to its stress tolerance and bleaching resistance. A detailed analysis of Symbiodiniaceae association with other coral species though is needed to confirm the thermal-tolerance adaptation of *T. mesenterina*. Increased stress on marginal reefs tends to shift the coral community toward low species heterogeneity and to increase the dominance of species well adapted to increasing temperature regime (van Woesik et al., 2011; Hoegh-Guldberg et al., 2019). The switching of endosymbiont from *Cladocopium* to *Durusdinium* has been reported in adults of *Acropora millepora* in response to heat stress and, more recently, in *Acropora* spp. from Palk Bay (India) after the bleaching event in 2016 (Thinesh et al., 2019). In the disturbed reefs in Singapore, the higher bleaching resilience of *Pocillopora* was attributed to its association with thermotolerant *Durusdinium* (Guest et al., 2016). The coral *Galaxea fascicularis* from the South China Sea was found to be more resistant to thermal stress because of its association with *Durusdinium* D1a (Zhou et al., 2017). In another report, *Pocillopora verrucosa* associated with *Durusdinium* D1a was found to be more resistant to thermal stress than *Pocillopora lutea* associated with *Cladocopium* (Qin et al., 2019). Interestingly, a decadal study with higher temperature variability in the Kenyan reef found that *Pavona* and *Pocillopora* were resistant to bleaching due to their association with *Durusdinium* (McClanahan et al., 2015). Similar results of higher temperature regime tolerance were reported for scleractinian coral *Leptoria phrygia* from Southern Taiwan (Carballo-Bolaños et al., 2019). Studies revealed that under high-temperature stress, *Durusdinium* D1a increases the coral bleaching thresholds by 1.0 to 1.5°C (Berkelmans and Van Oppen, 2006; Silverstein et al., 2015) by maintaining a high photochemical efficiency compared with *Breviolum* and *Cladocopium* (Cunning et al., 2017; Klueter et al., 2017). Therefore, our observations suggest that *T. mesenterina* is tolerant against the thermal bleaching events in the studied marginal reef habitat. Our finding implies that the higher thermal resilience in *T. mesenterina* was possibly due to the association with *Durusdinium*. A similar association of *Durusdinium* with

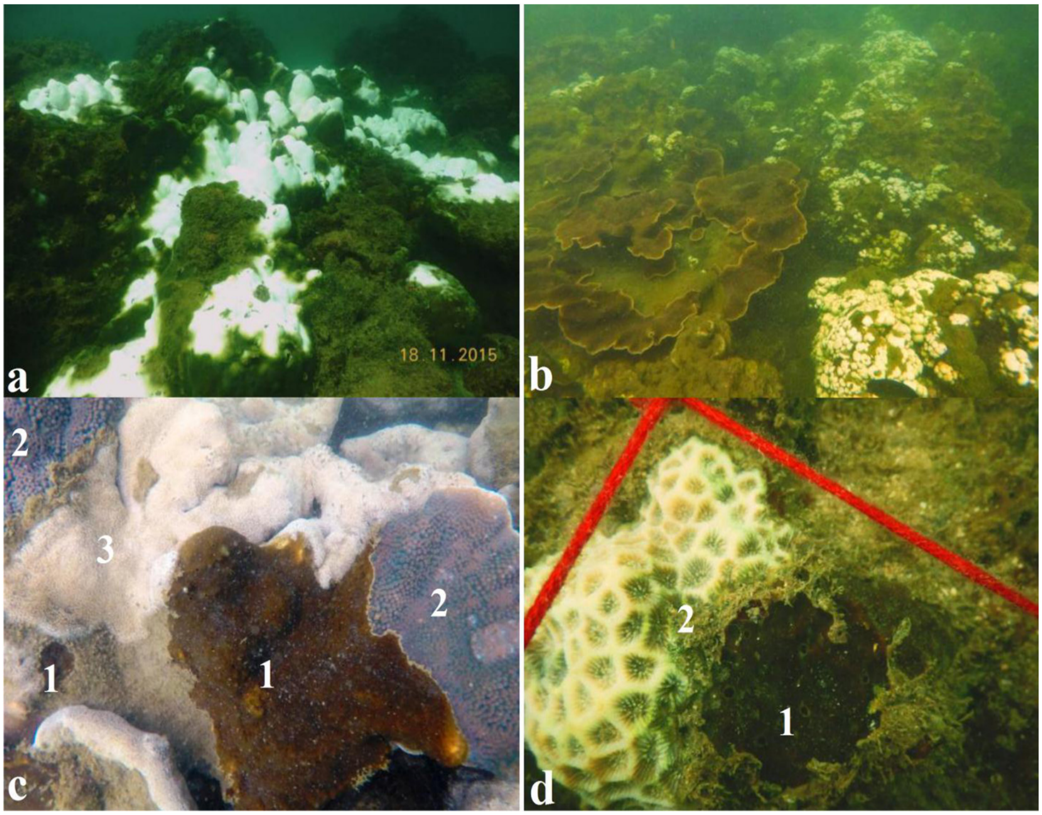

FIGURE 5 | Mass bleaching event observed during November 2015: **(a)** *In situ* observation of coral bleaching in 2015 [Photograph provided by Hussain and Ingole (2020)]. **(b)** *In situ* observation for bleaching resistance of *T. mesenterina* than the other coral species observed. **(c)** Thermal bleaching resistance observed in coral boring sponge *C. thomasi* and *T. mesenterina*: (1) healthy *C. thomasi*, (2) healthy *T. mesenterina*, and (3) partially bleached *Porites* sp. colony. **(d)** (1) Healthy *C. thomasi* and (2) partially bleached *Favites* sp.

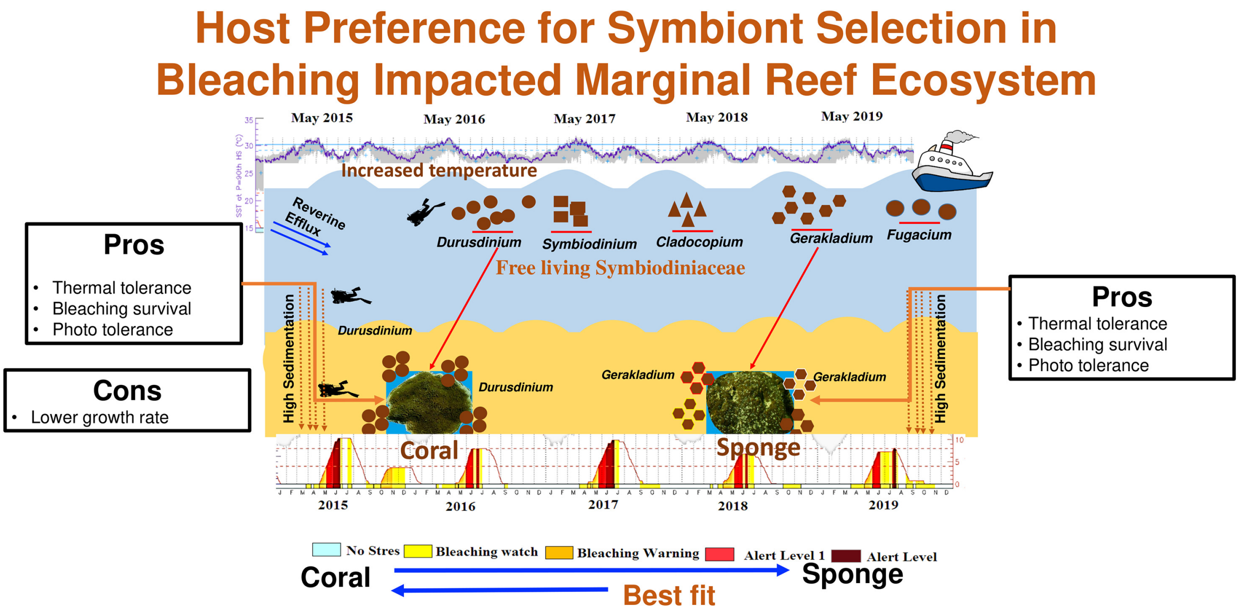

FIGURE 6 | Graphical representation of host-specific acquisition of Symbiodiniaceae and its benefit to the host survival in bleaching impacted marginal coral reef ecosystem.

T. mesenterina has been reported from the stressed marginal habitat of Taiwan (Chen et al., 2005).

Along with *Durusdinium*, *Gerakladium* (10.2%) was the subdominant genera in *T. mesenterina.* The association of *Gerakladium* with scleractinian coral is rare though a few studies reported its association with *Porites lobata* in Hawaii (Stat et al., 2013), *Orbicella annularis* from Virgin Islands (Edmunds et al., 2014; Pochon et al., 2014a), *Acropora* sp. from Western Australia (Thomas et al., 2014), and *Diploastrea heliopora* from the Great Barrier Reef (Chakravarti and van Oppen, 2018). *Gerakladium* is mostly associated with the specific group of sponges (Schönberg and Loh, 2005; Hill et al., 2011), soft corals (Van Oppen et al., 2005), and foraminifera (Pochon et al., 2014b). The simultaneous occurrence of *Durusdinium* and *Gerakladium* was reported in thermally tolerant *Porites lutea*, from the South China Sea (Qin et al., 2019). However, the *Gerakladium* association with *T. mensenterina* needs to be ascertained by increasing the range of study sites from different geographical locations.

Symbiodiniaceae Community Associated With the Sponge *C. thomasi*

The present study confirmed the dominance of *Gerakladium* in the encrusting sponge species *C. thomasi* unlike the dominance of *Durusdinium* in host coral *T. mesenterina.* The results indicated the host-specific association of Symbiodiniaceae members. The species-specificity and flexibility in the Symbiodiniaceae association have also been reported in some sponges (Hill et al., 2011; Ramsby et al., 2017). For instance, Caribbean clionaid species *C. aprica*, *C. laticavicola*, and *C. tenuis* are known to associate with *Symbiodinium* and *Breviolum*, while the other member of the family *C. caribbaea*, *C. varians*, and *C. tumula* are known for their multi symbiont association with *Gerakladium*, *Symbiodinium*, or *Breviolum* (Granados et al., 2008; Hill et al., 2011; Ramsby et al., 2017). The Indo-Pacific *Cliona orientalis* is known to harbor only *Gerakladium* (Hill et al., 2011).

The Symbiodiniaceae of sponges were studied earlier using Symbiodiniaceae-specific markers based on Sanger sequencing approach or denaturing gradient gel electrophoresis (DGGE) methods (Schönberg and Loh, 2005; Granados et al., 2008; Hill et al., 2011; Pochon et al., 2014b; Ramsby et al., 2017, 2018) and a study by Ramsby et al. (2018) by NGS. The available literature suggests the wide occurrence of *Gerakladium* genus in *C. viridis* species complex, but there is less information about cryptic species or subtypes of Symbiodiniaceae (**Supplementary File 1** and **Supplementary Table 6**). At the subtype level, only G2.1 was reported from the sponge *C. orientalis.* In the present study, we have utilized the high-throughput sequencing of the ITS2 region, which improved the detection of different Symbiodiniaceae subtypes from mixed populations and also determined community composition in the sponge. Within sponge *C. thomasi* samples, type G3.3 had the highest relative abundance (78.5%) followed by G101 (3.0%). In addition, the results detected type G3.1 and G3.2 at lower abundance (<1%), which indicates genetically distinct Symbiodiniaceae taxa in sponges. The advancement in detecting relatively rare Symbiodiniaceae subtypes reveals that sponge symbiont association can be flexible or specific within the same genus at the subtype level. The lower abundance of Symbiodiniaceae subtypes is known to play a significant role in coral holobiont resilience and response to perturbation (Ziegler et al., 2018). Therefore, the findings presented here indicate that there are additional sponge-associated species within *Gerakladium* genus which prove the great importance of the way that ITS2 sequence data are analyzed and interpreted in studies concerning the biological diversity. The knowledge of the dinoflagellate communities associated with bioeroding sponges is limited at the species level, with only two known species (*Gerakladium endoclionum* from *C. orientalis*, and *Gerakladium spongiolum* from *C. varians*) from sponges (Ramsby et al., 2017). Our ITS2 rDNA based analysis could not confirm the species identity of Symbiodiniaceae associated with *C. thomasi* due to lack of species-specific subtypes information in the revised taxonomy of *Gerakladium* (LaJeunesse et al., 2018).

Different studies have confirmed the ecological significance of *Gerakladium* in the bioerosion capabilities, survival, and growth rate of Clionaid sponges (Fang et al., 2016, 2018a; Achlatis et al., 2019). Furthermore, Chakravarti and van Oppen (2018) showed the *Gerakladium* genus as thermotolerant by *ex situ* analysis. Our *in situ* observations indicated the increased prevalence of *C. thomasi* from 6% in 2015 to 11% in 2017 (**Supplementary File 1** and **Supplementary Figure 4**) and bleaching resistance during mass bleaching events (**Figures 5c,d**). The thermal tolerance of sponges during mass bleaching events may be attributed to its association with *Gerakladium.*

Environmental Acquisition of Symbiodiniaceae

Symbiodiniaceae communities of the ambient seawater were predominantly represented by *Durusdinium* and *Gerakladium*, while *Symbiodinium*, *Fugacium*, and *Cladocopium* in were less dominant in the present study. Water column Symbiodiniaceae community may be exclusively free-living or symbiotic with different benthic hosts (Yamashita and Koike, 2013; Nitschke et al., 2016; Claar et al., 2020). Most of corals (∼80–85%) tend to acquire different symbionts from the surrounding environment at different life stages (Stat et al., 2008; Boulotte et al., 2016). The determined higher abundance of *Durusdinium* sp. in *T. mesenterina* and in ambient seawater (equal to *Gerakladium*) from the thermally challenged marginal sites indicates two possibilities of their association: (1) that the symbiont population in coral may have been retrieved from seawater or (2) the symbiont is typically associated with the coral hosts (Claar et al., 2020). Since horizontal acquisition is well established in corals, the former possibility appears a better fit. Unlike corals, vertical transmission of Symbiodiniaceae has been suggested in few sponges (Mariani et al., 2000, 2001). However, a few studies also suggested the environmental acquisition of free-living photosymbiont in sponges (Strehlow et al., 2016; Francis and Cleary, 2019). Also, it has been experimentally demonstrated that *C. varians* acquire symbiont from the ambient environment (Riesgo et al., 2014). The present study revealed the dominance of *Gerakladium* G3.3 in the sponge samples and also in ambient seawater.

Therefore, it can be inferred that there is a possibility for the acquisition of free-living symbiont from the ambient environment by *C. thomasi*, although detailed studies are required to understand their mode of acquisition. Our results support the possibility of host-specific acquisition of photosymbionts as *Durusdinium* in coral and *Gerakladium* in the sponge (**Figure 6**). Host-specific Symbiodiniaceae association in coral is well noted from different bioregions (Bernasconi et al., 2019; Howe-Kerr et al., 2020; Wall et al., 2020). The differential acquisition of symbionts by different hosts from the same environment can be attributed to various factors such as (1) cellular signaling to and from host and symbiont (Davy et al., 2012), (2) metabolic requisites of both the host and symbiont (Suggett et al., 2017), (3) microhabitat conditions of the host, (4) mode of transmission of the symbiont, i.e., horizontal or vertical (Stat et al., 2008), and (5) selection mediated reshuffling and/or re-switching of symbiont (Boulotte et al., 2016). Nevertheless, physiological, molecular, genetical, and signaling related detailed studies are needed to confirm the mode of host-specific Symbiodiniaceae association.

CONCLUSION

The present study provides an important insight into the coral-Symbiodiniaceae-sponge symbiosis in a data-deficient marginal coral reef habitat. Our results unveil a high abundance of thermal stress-tolerant Symbiodiniaceae *Durusdinium* and *Gerakladium* in an ambient environment experiencing severe temperature anomalies for the last 5 years. Furthermore, the study showed differential associations of Symbiodiniaceae between two hosts indicating a host-specific mode of selection. Since both the dominant Symbiodiniaceae members are well known for their thermotolerance, the determined thermal resistance by both the hosts in this habitat may be attributed to their association with the resistant Symbiodiniaceae *Durusdinium* and *Gerakladium*. Hence, the study highlights the influence of *Durusdinium* and *Gerakladium* and their possible role in enhanced acclimatization capacity of coral *T. mesenterina* and bioeroding sponge *C. thomasi* in a suboptimal environmental regime. At large, the stress-tolerant symbiont association may increase the resistance of few species and aid their survival, thereby increasing their dominance in space competition. Further studies on physiological, metabolic, and transcriptomic insights will help confirm the energetic tradeoffs by symbiont communities in the success of their respective hosts.

SAMPLING AND FIELD STUDIES

The authors have obtained all necessary permits for sampling and field observation from the competent authorities.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Nucleotide sequences have been submitted to the NCBI database under Bio project ID- PRJNA636097.

AUTHOR CONTRIBUTIONS

SM and VG conceptualized the study, designed the experiment, and analyzed the sequenced data. SM and KD performed sampling. SM performed DNA extraction experiments. KM performed the nMDS. AH did the field survey for bleaching and coral health assessment. MN, BI, and VG supervised the project and acquired the fund for the study. VG, SM, KD, and MN wrote the manuscript. KM and BI proofread the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.666825/full#supplementary-material

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REVIEW
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Diversity of Indian Barnacles in Marine Provinces and Ecoregions of the Indian Ocean

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The present study is the first completed and taxonomically validated literature review of the biodiversity of barnacles (Cirripedia) in India. A total of 144 species in 75 genera and 19 families have been recorded in India. The highest number of species has been recorded from the Bay of Bengal province, located on the eastern side of the Indian Peninsula, comprising the Eastern India ecoregion (76 species) and Northern Bay of Bengal ecoregion (34 species). The West and South India Shelf province has fewer species (Western India ecoregion: 29 species; South India and Sri Lanka ecoregion: 40 species; and Maldives ecoregion: 10 species) compared to the Bay of Bengal province. The Andaman province is composed of the Andaman and Nicobar Islands, and contains 65 species. Most of the coral-associated barnacles (family Pyrgomatidae) have been recorded in the corals reefs of the Andaman and Nicobar Islands (7 species), Eastern India (6 species), and Northern Bay of Bengal ecoregions (5 species). Sponge-associated barnacles (mostly in the subfamily Acastinae) were recorded in the Eastern India ecoregion, Southern India and Sri Lanka, and Andaman and Nicobar Islands ecoregions. Deepwater species were recorded the most extensively in the Andaman and Nicobar Islands ecoregion (21 species), followed by the South India and Sri Lanka ecoregion (9 species) and Eastern India ecoregion (7 species). Six Atlantic/boreal cold water species previously reported in India were removed due to incorrect identification, and some incorrectly identified species were validated and corrected.

Keywords: India, checklist, cirripedia, barnacles, biodiversity

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INTRODUCTION

India is one of the 12 mega-biodiversity countries and has 25 biodiversity hotspots, containing a considerable number of endangered species (Myers et al., 2000; Venkataraman and Wafar, 2005; Venkataraman and Raghunathan, 2015). India supports a rich diversity of marine habitats and invertebrate fauna (Aneesh et al., 2018; Trivedi et al., 2018; Kottarathil et al., 2019; Shih et al., 2019; Aneesh and Kappalli, 2020). India contains 7516.6 km of coastline—5422.6 km in the Indian Peninsula and 2094 km in islands (Andaman and Nicobar Islands: 1962 km; Lakshadweep Islands: 132 km) (Ahmad, 1972; Kumar et al., 2006; Trivedi et al., 2018).

More than 1400 species of barnacle were recorded from different oceanic regions across the world (Innocenti, 2006; Chan et al., 2009). Barnacles occur in almost all marine environments, from intertidal zones to the deepest parts of the oceans (Chan and Høeg, 2015). The greatest diversity of barnacles is observed in the tropical Indo-Pacific region (Newman and Abbott, 1980). Taxonomic studies of barnacles date back to the 16th century, when barnacles were identified as eggs of barnacle geese (Anderson, 1994). Burmeister (1834) was the first naturalist to classify barnacles into cirripedes which later attracted the attention of numerous taxonomists (Anderson, 1994). Darwin (1851, 1854) monographs on barnacles, written shortly after Burmeister's publication, became one of the major contributions to barnacle taxonomy.

Taxonomic studies on Indian barnacle fauna came out of the systemic work from one of these Darwin (1854) monographs, which included several species of barnacles from the Indian waters. Thomas Nelson Annandale, the first Director of the Zoological Survey of India, published a series of taxonomy papers (Annandale, 1905, 1906a,b, 1907, 1909, 1910a,b, 1911, 1913, 1914, 1916, 1924) based on the barnacle specimens deposited into the Indian Museum. Annandale (1906a) examined stalked barnacles collected from the R.I.M.S. (Royal India Marine Survey Ship) "Investigator" and described 11 new species. Later, Annandale (1909); (Annandale, 1910a,b) described eight new species and one new family (Poecilasmatidae; Annandale, 1909) of barnacles from Indian waters. Annandale (1924) published a list of cirripedia associated with Indian corals and described two new species. Sundararaj (1927) recorded five species of barnacles from the Krusadai Islands (Tamil Nadu). Nilsson-Cantell (1938) carried out a taxonomic study on barnacles of the Bay of Bengal, Arabian Sea and Indian Ocean, and listed a total of 139 species, 36 of which had a wide distribution beyond these three regions. Augustine Daniel of the Zoological Survey of India studied barnacle diversity of the Tamil Nadu state and recorded 42 species (Daniel, 1956). Daniel (1981) listed 15 species of barnacles collected from estuaries in both the east and south-west coasts of India. Fernando (2006) later published a monograph on Indian barnacles that contained more extensive records and listed 70 species.

Scientists at institutes and universities across Indian have contributed to our understanding of the taxonomy, diversity and biology of barnacles occurring in Indian waters (Gray, 1831; Gruvel, 1907; Hoek, 1913; Kemp, 1915; Pillai, 1958; Bhatt and Bal, 1960; Karande and Palekar, 1963, 1966; Daniel and Chakrabarathi, 1967; Prem-Kumar and Daniel, 1968; Balakrishnan, 1969; Wagh and Bal, 1969, 1974; Devaraj and Bennet, 1974; Karande, 1974; Desai and Senthilkumar, 1975; Fernando, 1978; Venkateswaran and Fernando, 1982; Wagh and Sawant, 1982; Newman and Killingley, 1984; Sudakaran and Fernando, 1987; Rao and Balaji, 1988; Frazier, 1989; Nandakumar, 1990; Rajaguru and Shantha, 1992; Ramakrishna and Talukdar, 2003; Karuppiah et al., 2004; Singh et al., 2004; Mitra and Misra, 2006; Sanjeeva Raj, 2006; Krishnamoorthy, 2007; Kumaravel et al., 2009; Pati et al., 2009; Mitra et al., 2010; Swami et al., 2011; Namboothri and Fernando, 2012; Patro, 2012; Ramamoorthy et al., 2012; Trivedi et al., 2015; Sahadevan, 2016; Roy and Rath, 2017; Desai et al., 2018; Parmar et al., 2018; Mondal et al., 2019). In addition to diversity research, there are a considerable number of studies focusing on the larval biology and settlement ecology of the common Indian intertidal barnacle *Amphibalanus amphitrite* (Gaonkar and Anil, 2010, 2012, 2013a,b; Gaonkar et al., 2012). In Goa and Kochi, on the west coast of India, settlement of cypris larvae have been investigated for their responses to diatom exopolymers (Patil and Anil, 2005), conspecific cues (Khandeparker and Anil, 2011), specific bacteria associating with the barnacle shells (De Gregoris et al., 2012), and sponge extracts (Mol et al., 2010). The reproductive cycle and population dynamics of *A. mphitrite* in Goa, India is affected by the interactions among monsoons, temperature and chlorophyll *a* concentration in seawater (Desai and Anil, 2005; Desai et al., 2006). The breeding and settlement patterns of *A. mphitrite* in Tamil Nadu, southeast coast of India are affected by tidal patterns, temperature and phytoplankton abundance (Karuppaiyan and Raja, 2007; Satheesh and Wesley, 2009). To date, there has not been a complete literature review on those extensive records of barnacle diversity in India or their accuracy. The objective of the present study is to provide the most taxonomically updated, validated and complete diversity records on barnacles in India. Species identities were validated based on morphological identifications using relevant taxonomic references, and supported by recent results of molecular taxonomic studies of barnacles in the Indo-Pacific waters.

MATERIALS AND METHODS

Provinces and Ecoregions in India

According to the definitions in Spalding et al. (2007), the coastline of India is comprised of four marine biogeographical provinces and six ecoregions (**Figure 1**). The West and South Indian Shelf province comprises the Western India ecoregion (from Kachchh district of Gujarat state to Ashtamudi Lake of Kerala state) and the South India ecoregion (Ashtamudi Lake of Kerala state to Karaikal, Puducherry of Tamil Nadu state) (**Figure 1**). The Central Indian Ocean Islands province includes the Maldives ecoregion, comprising Lakshadweep Islands and Minicoy. The Bay of Bengal province in India covers the Eastern India ecoregion (from Karaikal, Pondicherry of Tamil Nadu state to Konark of Odisha state) and the Northern Bay of Bengal ecoregion (Konark of Odisha state to Bidyadhari River Delta of West Bengal state). The Andaman province in India includes Andaman and Nicobar Islands ecoregion, which covers the Andaman and Nicobar Islands (**Figure 1**; Spalding et al., 2007).

Literature Review

The data on the barnacle fauna of India in the present study are based on peer-reviewed published literature and/or deposited material in marine collections. Only species present in Indian waters were recorded in the present study.

The collection site of each species is classified based on the Indian state and relevant marine provinces and ecoregions from Spalding et al. (2007). Species reported from adjacent

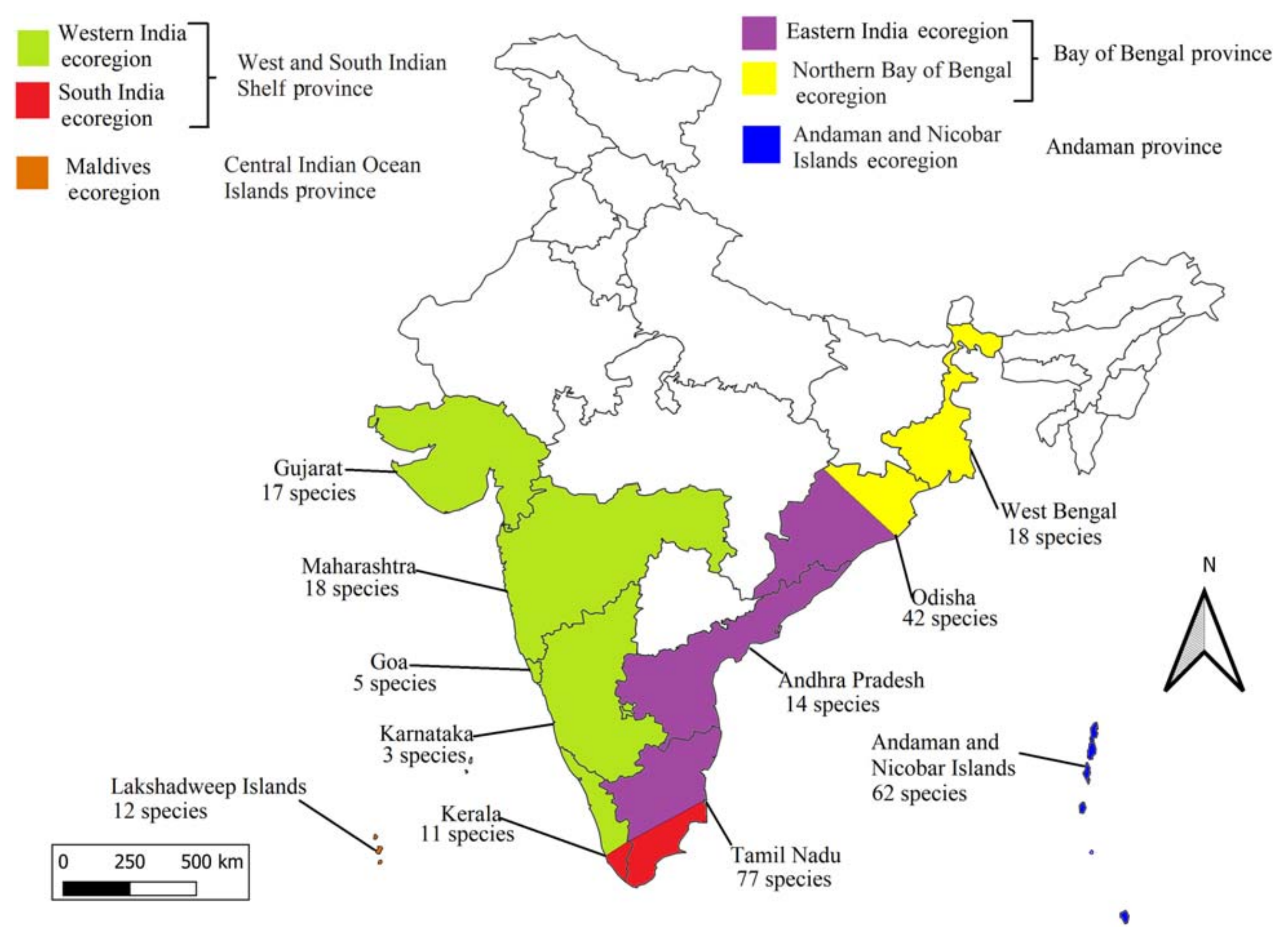

FIGURE 1 | Map of India (Sri-Lanka was not included) showing the states as well as ecoregions and provinces as defined by Spalding et al. (2007).

countries that formed a part of the former British Indian empire (Sri Lanka, Pakistan, Bangladesh, Maldives, and Myanmar) were excluded. A few old records without clearly stated collection sites were omitted. The synonyms, nomenclatural changes and classification of different species were validated based on Southward and Newman (2003), Chan et al. (2009), Jones and Hosie (2016).

Multivariate Analysis of Species Assemblages

Based on what is present and absent in the list of all recorded barnacle species, multivariate analysis (using species as variables) was performed using the PRIMER package (v6, Plymouth Routine in Multivariate Analysis, PRIMER-E Ltd; Clarke and Gorley, 2006) to examine variations in species assemblages among the ecoregions in India. Similarities among the ecoregions based on species data were calculated using the Sorensen similarity index. Non-metric Multidimensional Scaling (nMDS; Clarke, 1993) was conducted to generate two-dimensional plots on the species composition in all the ecoregions.

RESULTS

Diversity Patterns

A total of 155 barnacle species belonging to 75 genera and 19 families were reported from India (**Supplementary Appendix Table 1**). Of these, 40 species were described from Indian waters, of which 35 are valid species (**Table 1**) and five were synonymized: *Platylepas multidecorata* Daniel, 1962—described from Little Andaman, Andaman and Nicobar Islands—is now treated as a synonym of *Platylepas decorata* (Darwin, 1854). *Balanus longirostrum* var. *krusadaiensis* Daniel (1956), described from Tamil Nadu, is now treated as a synonym of *Membranobalanus longirostrum* (Hoek, 1913). *Balanus* (*Membranobalanus*) *roonwali* Prem-Kumar and Daniel (1968)—described from Chennai, Tamil Nadu—is now treated as a synonym of *M. longirostrum*. *Balanus amphitrite* var. *cochinensis* Nilsson-Cantell (1938)—described from Ernakulam, Cochin, Kerala—is now treated as a synonym of *Amphibalanus amphitrite* (Darwin, 1854). *Pollicipes polymerus madrasensis* Daniel, 1953—described from Royapuram, Chennai, Tamil Nadu—is now treated as a synonym of *Pollicipes polymerus* Sowerby (1833).

TABLE 1 | Barnacle species described from India.

Taxon name	Current identity	Type locality	World distribution
Lepas anatifera indica Annandale, 1909	*Lepas indica* Annandale, 1909	Off Ganjam coast, Orissa	India; Indian Ocean; Madagascar; South China Sea; East China Sea; China Jones and Hosie, 2016
Lepas bengalensis Daniel, 1952	*Hyalolepas bengalensis* Daniel, 1952	Madras (Chennai), Tamil Nadu	India Fernando, 2006
Conchoderma indicum Daniel, 1953	*Conchoderma indicum* Daniel, 1953	Krusadi Islands, Tamil Nadu	India Fernando, 2006
Lepas guanamuthui Daniel, 1971	*Dosima guanamuthui* Daniel, 1971	Great Nicobar, Andaman and Nicobar Islands	India; Northern Indian Ocean González et al., 2014
Oxynaspis celata indica Annandale, 1910	*Oxynaspis indica* Annandale, 1910	Odisha	India; Indo-Pacific; off Mauritius; Philippines to southwest Pacific; off New Zealand Rosell, 1991
Dichelaspis grayii var. *pernuda* Annandale, 1909	*Octolasmis grayii* var. *pernuda* Annandale, 1909	Chennai, Tamil Nadu	India Fernando, 2006
Platylepas indicus Daniel, 1958	*Platylepas indicus* Daniel, 1958	Chennai, Tamil Nadu	India Fernando, 2006
Tetraclitella karandei Ross, 1971	*Tetraclitella karandei* Ross, 1971	Madh Islands, Maharashtra	India; Taiwan; Phillipines Chan et al., 2009
Acasta sulcata var. *spinosa* Daniel, 1956	*Acasta sulcata akanthosa* Daniel, 1956	Royapuram, Chennai, Tamil Nadu	India Fernando, 2006
Balanus (*Semibalanus*) *madrasensis* Daniel, 1958	*Semibalanus madrasensis* Daniel, 1958	Chennai, Tamil Nadu	India Daniel, 1972
Balanus (*Semibalanus*) *sinnurensis* Daniel, 1962	*Semibalanus sinnurensis* Daniel, 1962	Chennai, Tamil Nadu	India Fernando, 2006
Dichelaspis rhinoceros Annandale, 1909	*Octolasmis rhinoceros* Annandale, 1909	Bay of Bengal	India Nilsson-Cantell, 1938
Dichelaspis stella Annandale, 1909	*Octolasmis stella* Annandale, 1909	Bay of Bengal	Indian Ocean Zevina, 1982
Heteralepas (Heteralepas) nicobarica Annandale, 1909	*Heteralepas nicobarica* Annandale, 1909	Nicobar Island, Andaman and Nicobar Islands	India Buhl-Mortensen and Newman, 2004
Scalpellum lambda Annandale, 1910	*Annandaleum lambda* Annandale, 1910	Bay of Bengal near Andaman and Nicobar Islands (13°54′15″N 94°02′15″E)	India; Indo-west Pacific; Indian Ocean; Zanzibar; Sumbawa; Indonesia; Malay Archipelago; South-West of Calatagan Pt; Philippines; South Japan; South-West Pacific Jones and Hosie, 2016
Scalpellum bengalens Annandale, 1906	*Scalpellum* (*Smilium*) *bengalens* Annandale, 1906	Ganjam coast, Odisha	India Annandale, 1906b
Scalpellum Alcockianum Annandale, 1906	*Alcockianum alcockianum* Annandale, 1906	Gulf of Manaar, Tamil Nadu	India; Indian Ocean; Mozambique Channel; Indonesia; Malay Archipelago; Australia; New Zealand; South-West Pacific and mid-Pacific guyots Jones and Hosie, 2016
Scalpellum laccadivicum Annandale, 1906	*Annandaleum laccadivicum* Annandale, 1906	Laccadive sea	India; Gulf of Oman; Sri Lanka; Indonesia; Japan; Taiwan Chan et al., 2009
Scalpellum subflavum Annandale, 1905	*Annandaleum laccadivicum laccadivicum* Annandale, 1906	Cochin, Kerala and Gulf of Manaar, Tamil Nadu	India; Indian Ocean; Sumbawa; Indonesia; Malay Archipelago; South-West of Calatagan Pt; Taiwan; Philippines; South Japan (South of Honda Island); South-West Pacific Jones and Hosie, 2016
Alepas xenophorae Annandale, 1906	*Paralepas xenophorae* Annandale, 1906	Kerala	India; Japan Utinomi, 1958
Megalasma striatum minus Annandale, 1906	*Megalasma minus* Annandale, 1906	Andaman Sea	Cosmopolitan: India; Atlantic Ocean; Indo-west Pacific; East coast of Africa (Zanzibar); Indian Ocean; Indonesia; Malay Archipelago; Philippines; Taiwan; S Japan; Pacific Ocean Jones and Hosie, 2016
Scalpellum gruvelii Annandale, 1906	*Annandaleum gruvelii* Annandale, 1906	Gulf of Mannar, Tamil Nadu and between Lakshadweep and mainland	India; Atlantic Ocean; Indo-west Pacific: Indian Ocean; South China Sea; Pacific Ocean Jones and Hosie, 2016
Annandaleum gruvelii var. *quadratum* Annandale, 1906	*Annandaleum gruvelii quadratum* Annandale, 1906	Gulf of Mannar, Tamil Nadu	India Annandale, 1906b
Creusia spinulosa forma *transversalis* Nilsson-Cantell, 1938	*Cantellius transversalis* Nilsson-Cantell, 1938	North Bay, Port Blair, Andaman and Nicobar Islands	Indo-west Pacific: India; Indian Ocean; Malay Archipelago; Taiwan; Philippines Jones and Hosie, 2016
Balanus cymbiformis Darwin, 1854	*Conopea cymbiformis* Darwin, 1854	Tuticorin, near Chennai, Tamil Nadu	India; Indian Ocean; Gulf of Aden; Indonesia; North Australia; Malay Archipelago; China; Philippines; South Japan; Fiji Island Jones and Hosie, 2016
Pyrgopsis annandalei Gruvel, 1907	*Pyrgopsella annandalei* Gruvel, 1906	Andaman Islands, Andaman and Nicobar Islands	India; Israel Achituv and Simon-Blecher, 2006, 2014

(Continued)

TABLE 1 | Continued

Taxon name	Current identity	Type locality	World distribution
Verruca plana Gruvel, 1907	*Altiverruca plana* Gruvel, 1907	Andaman and Nicobar Islands	Andanman and Nicobar Islands Gruvel, 1907
Verruca cristallina Gruvel, 1907	*Cristallinaverruca cristallina* Gruvel, 1907	Andaman and Nicobar Islands	India; Indian Ocean; Indonesia; Malay Archipelago; China; Philippines; New Caledonia; Loyalty Islands; Chesterfield Islands; Vanuatu; Wallis & Futuna Islands Jones and Hosie, 2016
Verruca multicostata Gruvel, 1907	*Newmaniverruca multicostata* Gruvel, 1907	Andaman and Nicobar Islands	India; Indian Ocean; Malay Archipelago Jones and Hosie, 2016
Pyrgoma indicum Annandale, 1924	*Galkinius indica* Annandale, 1924	Bay of Bengal	India; Indian Ocean; Mergui Archipelago; Kei Islands; Singapore; Malay Archipelago; Vietnam; China; Taiwan; Philippines; Japan; Palau Islands Jones and Hosie, 2016
Creusia spinulosa forma *transversalis* Nilsson-Cantell, 1938	*Cantellius transversalis* Nilsson-Cantell, 1938	Andaman and Nicobar Islands	India; Indian Ocean; Malay Archipelago; Taiwan; Philippines Jones and Hosie, 2016
Acasta funiculorum Annandale, 1906	*Eoatria funiculorum* Annandale, 1906	Tamil Nadu	Gulf of Mannar Van Syoc and Newman, 2010
Balanus (*Megabalanus*) *squillae* Daniel and Ghosh, 1963	*Notomegabalanus squillae* Daniel and Ghosh, 1963	Tamil Nadu	Tamil Nadu, India Daniel and Ghosh, 1963
Lithotrya nicobarica Reinhardt,1850	*Lithotrya nicobarica* Reinhardt,1850	Andaman and Nicobar Islands	India; Indian Ocean; Australia; Timor; Malay Archipelago; Ream and Dama Islands (Cambodia); Gulf of Thailand; Vietnam; Condor Islands; South China Sea; Philippines; Taiwan; South Japan; Tuamotu, Caroline Islands; Fiji; Paumotu Islands; Pacific Ocean Jones and Hosie, 2016
Balanus patelliformis Bruguière, 1792	*Fistulobalanus patelliformis* Bruguière, 1792	South coast of India Henry and McLaughlin, 1975	India; Malacca; Java Sea, Malay Archipelago; Philippine Archipelago Jones and Hosie, 2016
Platylepasmultidecorata Daniel, 1962	*Platylepas decorata* Darwin, 1854	Little Andaman, Andaman and Nicobar Islands	India; West Australia; South China Sea; China; Pacific Ocean, Galapagos Islands Jones and Hosie, 2016
Balanus longirostrum var. *krusadaiensis* Daniel, 1956	*Membranobalanus longirostrum* Hoek, 1913	Tamil Nadu	India; Indian Ocean; Singapore; Malay Archipelago; Fu Kuoh Islands, Cambodia; Gulf of Siam; Vietnam; Condor Island; Lien Chien, Tourane; Bay of Along; China Jones and Hosie, 2016
Balanus (*Membranobalanus*) *roonwali* Prem-Kumar and Daniel, 1968	*Membranobalanus longirostrum* Hoek, 1913	Chennai, Tamil Nadu	India; Indian Ocean; Singapore; Malay Archipelago; Fu Kuoh Islands, Cambodia; Gulf of Siam; Vietnam; Condor Island; Lien Chien, Tourane; Bay of Along; China Jones and Hosie, 2016
Pollicipes polymerus madrasensis Daniel, 1953	*Pollicipespolymerus* Sowerby, 1833	Royapuram, Chennai, Tamil Nadu	India; Mexico, Baja California; North American coast; North Pacific; Aleutian Islands; Russia Van Syoc et al., 2010
Balanus amphitrite var. *cochinensis* Nilsson-Cantell, 1938	*Amphibalanus amphitrite* Darwin, 1854	Ernakulam, Cochin, Kerala	Cosmopolitan in tropical and subtropical waters: India; Bermuda and southeast United States to Brazil; England and W Europe to S coast of Africa Red, Black and Mediterranean Seas; Suez Canal; southeast Africa; Indian Ocean; Australia; Indonesia; Singapore; Malaysia; Réam (Cambodia); Gulf of Siam; Vietnam; Condor Islands; Tang Trien (South Annam); Cauda Nhatrang; Hongay, Tonkin; South China Sea; Hong Kong; China; Bohai Sea; Taiwan; Philippines; Japan; South Honsyu, Kyusyu and Ryukyu Islands; Vladivostok; Hawaii; central California to southeast Mexico Jones and Hosie, 2016

At the family level, the highest number of species were reported from the family Poecilasmatidae Annandale (1909) (mostly epibiotic on crustaceans; 27 species, 8 genera), followed by Archaeobalanidae Newman and Ross (1976) (epibiotic in various organisms; 25 species, 12 genera); Balanidae Leach (1817) (mostly intertidal and subtidal, 21 species, 6 genera); Pyrgomatidae Gray (1825) (coral-associated, 15 species, 12 genera); Scalpellidae Pilsbry (1907) (deepwater; 15 species, 7 genera); Lepadidae Darwin (1852) (pelagic; 8 species, 4 genera); Tetraclitidae Gruvel (1903) (8 species, 4 genera); Verrucidae Darwin (1854) (deepwater; 6 species, 4 genera); Chthamalidae Darwin (1854) (intertidal; 6 species, 3 genera); Calanticidae Zevina (1978) (deepwater; 5 species, 3 genera); Heteralepadidae Nilsson-Cantell (1921) (deepwater; 5 species, 3 genera); Platylepadidae Newman and Ross (1976) (epibiotic on turtles; 5 species, 2 genera); Chelonibiidae Pilsbry (1916) (epibiotic on turtles; 2 species, 1 genus); and Oxynaspididae Pilsbry (1907) (epibiotic on corals; 2 species, 1 genus). The following families each contain only one species in one genus: Coronulidae Leach (1817) (on cetaceans); Iblidae Leach (1825) (intertidal); Lithotryidae Gruvel (1905) (intertidal); Pollicipedidae Leach (1817) (intertidal); and Sacculinidae Lilljeborg (1861) (parasitic).

State-wide data revealed that the highest number of species were reported from Tamil Nadu (77 species, 39 genera, 15 families) followed by Andaman and Nicobar Islands (62 species, 40 genera, 15 families), Odisha (42 species, 26 genera, 12 families), Maharashtra (18 species, 12 genera, 8 families), West

Bengal (18 species, 11 genera, 6 families), Gujarat (17 species, 11 genera, 7 families), Andhra Pradesh (14 species, 8 genera, 5 families), Lakshadweep Islands (12 species, 8 genera, 7 families), Kerala (11 species, 9 genera, 7 families), Goa (5 species, 4 genera, 3 families), and Karnataka (3 species, 3 genera, 2 families) (**Figure 1** and **Supplementary Appendix Table 2**).

The Eastern India ecoregion has the highest number of species (76 species), followed by Andaman and Nicobar Islands ecoregion (65), South India and Sri Lanka ecoregion (40), Northern Bay of Bengal ecoregion (34), Western India ecoregion (29), and Maldives ecoregion (11) (**Figure 2A** and **Supplementary Appendix Table 1**). The low number of species recorded in the Maldives ecoregion is probably due to the low number of studies conducted there.

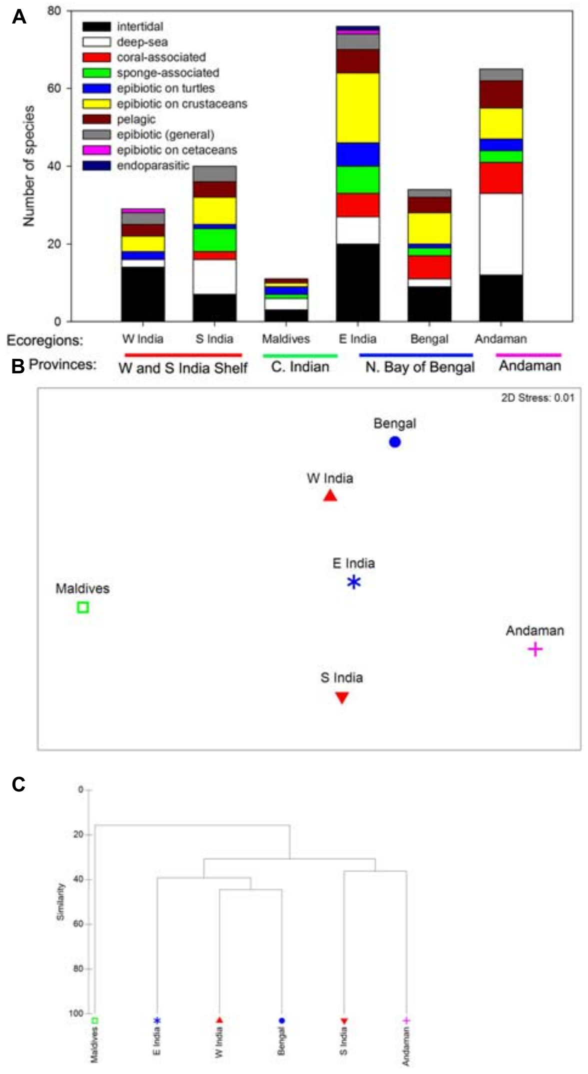

FIGURE 2 | (A) Species richness of barnacles from different life styles/habitats in different ecoregions and provinces. For clarity, names of ecoregions were abbreviated. W India – Western India Ecoregion, S India – Southern India and Sir Lanka ecoregion, Maldives – Maldives ecoregion, Bengal – Bay of Bengal ecoregion, Andaman – Andaman and Nicobar Islands ecoregion. **(B)** nMDS plot on the ordination of ecoregions based on species assemblage data. **(C)** Cluster analysis on the similarity of species assemblages among ecoregions.

Most of the coral-associated barnacles (family Pyrgomatidae) were recorded in the Andaman and Nicobar Islands ecoregion (7 species), Eastern India ecoregion (6 species) and Northern Bay of Bengal ecoregion (5 species), which contain a great diversity of coral reefs (Venkataraman and Wafar, 2005; Venkataraman and Raghunathan, 2015; **Figure 2A**). The Maldives ecoregion covers the Lakshadweep Islands, which have extensive coral reefs; however, due to a lack of studies conducted in this ecoregion, only two coral barnacle species were recorded here. No coral-associated barnacles were recorded in the Western Indian ecoregion, the coastlines of which are characterized by mangroves and soft-bottomed shores and rocky shores in the urbanized Mumbai. There are, however, coral reefs in the Gulf of Kachchh of Gujarat state, but no detailed coral barnacle studies have been conducted there so far. Sponge-associated barnacles (mostly in the subfamily Acastinae) were recorded in the Eastern India, Southern India and Sri Lanka, and Andaman and Nicobar Islands ecoregions. Sponge diversity appears to be high in these three regions, supporting such diversity in barnacles (Ubare and Mohan, 2018; **Figure 2A**).

The deepwater scalpellid, calanticid and verrucid species were relatively extensively recorded in the Andaman and Nicobar Islands ecoregion (**Figure 2A** and **Supplementary Appendix Table 1**), followed by the Eastern India ecoregion (21 species) and the South India and Sri Lanka ecoregion (9 species). These three ecoregions contain deep-sea ecosystems and are often reported to contain deepwater crustaceans (Macpherson et al., 2020; Padate et al., 2020).

Multivariate Analysis of Species Assemblages

Based on the multivariate analysis, the distribution of the ecoregion clusters does not reflect clear separations among the provinces (**Figure 2B**). The Eastern India, Western India, and Northern Bay of Bengal ecoregions were located in the same cluster with 40% similarity (**Figure 2C**). The Andaman ecoregion is closer to the South India ecoregion. The Maldives ecoregion is separate from the other ecoregions (**Figures 2B,C**).

DISCUSSION

Diagnostic Species in Ecoregions

Some species are specific to certain ecoregions. *Chthamalus barnesi*, *Tetraclita ehsani* are Arabian species and are only recorded in the Western India ecoregion. The stalked barnacle *Lithotrya nicobarica,* which lives in the burrows of calcareous rocks, is only recorded in the Andaman and Nicobar Islands ecoregion, where the intertidal rocks are mostly coral formations and calcareous (Bandopadhyay and Carter, 2017). *Tetraclita squamosa,* which has green shells, is only recorded in the mid intertidal shore of the Eastern India ecoregion and Andaman and Nicobar Islands ecoregion; it is absent from the Western India ecoregion, the mid intertidal shore of which instead harbors *Tetraclita ehasani* and *Tetraclitella karandei*. These two species were only reported in the Gujarat state in the Western India ecoregion (Trivedi et al., 2021). Differences in diagnostic species between the South India Shelf province (Western India ecoregion) and the Northern Bay of Bengal provinces may be a result of differences in major oceanographic currents between these two provinces. The Bay of Bengal is affected by monsoon gyres. Large anti-cyclonical gyres are generated in the Bay of Bengal during the winter months and weaken in summer (Potemra et al., 1991). On the other hand, the western coast of India faces the Arabian Sea, where the hydrography is affected by the counter flows of the northeast Monsoon Current and the Indian Monsoon Current during different seasons. This resulted in Northern Bay of Bengal province is different from South India Shelf province from the cluster analysis (**Figures 2B,C**).

Validating Incorrect Species Identification

There are several records of Atlantic cold-water species reported in India that are apparently misidentifications or have taxonomic ambiguities. Daniel (1956) and Krishnamoorthy (2007) recorded *Semibalanus balanoides* (Linnaeus, 1767) in Tamil Nadu. This species is a boreal intertidal barnacle in the Atlantic and Arctic waters (Southward, 2008), and therefore cannot live in the tropical Indian waters. Subsequently, Daniel (1958, 1962) described two new species from Tamil Nadu, namely *Semibalanus madrasensis* (Daniel, 1958) and *S. sinnurensis* (Daniel, 1962), and it is suggested that *S. balanoides* might be either one of these species. Ramamoorthy et al. (2012) identified *Balanus balanus* (Linnaeus, 1758), a boreal-arctic subtidal barnacle in the northern Atlantic (Southward, 2008), from a coral reef invertebrate survey on Pirotan Island, Gujarat, western India. This record, too, may be a misidentification, and hence was not considered as a valid record.

Daniel (1956) identified *Perforatus perforatus* (Bruguière, 1792), another Atlantic species, in Tamil Nadu, but its presence in the Indian waters has not been confirmed. A recent survey in Korea reported this to be an invader in southern Korean waters, probably through ballast water, that has established itself as an ecologically important species (Choi et al., 2013; Kim et al., 2020a,b). Another doubtful record is that of *Balanus glandula* Darwin (1854) from shrimp ponds in Odisha (Nayak and Berkes, 2014; Nayak, 2017); the species is an inhabitant of the temperate northeast and North West Pacific, so we considered the record to be invalid in the present study.

The high shore barnacle *Chthamalus challengeri* Hoek (1883)—a cold-water inhabitant of the West Pacific, including Japan and far-east Russia—was reported by Bhatt and Bal (1960) and Daniel (1972) from Maharashtra. However, a recent review of the genus *Chthamalus* Ranzani (1817) by Southward and Newman (2003) refutes the above record. Only *C. malayensis* was recorded from Tranquebar and Mumbai by Southward and Newman (2003). The presence of *C. malayensis* Pilsbry (1916) along the eastern and western coasts of India was further confirmed from molecular evidence (Tsang et al., 2012; **Figures 3A,B**). Based on the above, the record of *C. challengeri* in Maharashtra is believed to actually be *C. malayensis*. In Mumbai, another chthamalid barnacle, *Microeuraphia withersi* (**Figures 3E,F**), was also recorded. *Microeuraphia* have three teeth on their mandible, whereas *Chthamalus* have four teeth on their mandible. It is therefore not possible that Daniel (1972) identified *Microeuraphia withersi* to *C. challengeri* due to such big morphological differences in mandibles between the two species.

Another chthamalid barnacle, *Chthamalus stellatus* (Poli, 1791), was recorded from Gujarat, North West India by Parmar et al. (2018) and is an intertidal species in the Atlantic Ocean and Mediterranean Sea (Pannacciulli et al., 1997). The record of *C. stellatus* in Gujarat appears to be erroneous. A recent examination of *Chthamalus* from Diu, Gujarat revealed that only *C. barnesi* Achituv and Safriel, 1980 is present on the rocky intertidal zone in this region (Trivedi et al., 2021). Geographical distribution of *C. barnesi* range from North Western India to the Persian Gulf (Shahdadi and Sari, 2011). The record of *C. stellatus* from Gujarat should be *C. barnesi* (**Supplementary Appendix Table 1**). Similarly, records of *Chthamalus malayensis* in Maharashtra, Gujarat (Karande and Palekar, 1963; Daniel, 1972; Wagh and Bal, 1974) should also be *C. barnesi* (**Supplementary Appendix Table 1**).

The stalked barnacle *Pollicipes polymerus* Sowerby (1833) is common in the intertidal regions of the northeast Pacific coast (Newman and Abbott, 1980). However, Daniel (1953b) recorded eight specimens of this temperate species attached to floating wood in Tamil Nadu as *Pollicipes polymerus madrasensis*. Newman and Abbott (1980) tried to investigate why such a temperate species is present in India by analyzing variations in the oxygen-18 stable isotope at different positions on its shell plates relative to the basal margin of the type specimen of *P. polymerus madrasensis*. Oxygen-18 stable isotope on shells can reflect the growth pattern of barnacle shells from different climatic environments. Results of the isotope analysis found that the type specimens of *Pollicipes polymerus madrasensis* found in India grew up in cold temperate waters, meaning that this species is not native to India. The present study did not consider this record to be an Indian record.

Tetraclita Schumacher (1817) is a common acorn barnacle on mid-intertidal shores of tropical and subtropical regions (Chan et al., 2007a). In India, several species of *Tetraclita* have been recorded, but a few of these records need clarification. In the Eastern India ecoregion, the green *Tetraclita squamosa* (Bruguière, 1792) was identified by Bruguière (1792) from Tranquebar, east coast of India (**Figures 3C,D**), which was a Danish colony in the 17th century. The illustration of *T. squamosa* in Bruguière (1792) shows an empty external shell without opercular plates. Bruguière (1792) probably collected an empty shell of *Tetraclita* that had washed onshore. The identification of *Tetraclita* could not be confirmed based on the external shell as identification requires the shapes of the scutum and tergum, and cirral morphology (Chan et al., 2007a). The third author (BKKC) visited several seashores in Tamil Nadu, including Pondicherry and Tranquebar, in 2007 (**Figures 3A–D**) and attempted to collect specimens of *Tetraclita squamosa* from its type locality for comparative studies, but he did not find any. Fernando (2006, 77) commented that *T. squamosa* "occurs

FIGURE 3 | Indian coastlines and barnacles. **(A)** Mamahariprum, eastern coast of India. Most of the hard substrates are large boulders. **(B)** *Chthamalus malayensis* is the dominant intertidal species on eastern coast of India. **(C)** Tranquebar, the remnants of Danish fort on coastline. **(D)** Coastline of Tranquebar is composed of large brick walls deteriorated from the Danish fort and large boulders. **(E)** Mumbai, large extent of rocky shores just below the urbanized city. **(F)** *Microeuraphia withersi* on the Mumbai coastline. **(G)** Diu, Gujarat showing the sandstone rocky shores. **(H)** *Tetraclita ehsani* in northwest India. **(I)** *Tetraclitella karandei* at Diu, Gujarat.

not so commonly in Tranquebar and it takes about an hour to locate a single specimen," thereby suggesting that it occurs in very low abundance and is not common on the Eastern coast of India. The above on-field observations and published reports suggest that the species identity of *T. squamosa* in eastern India is still uncertain.

In the Western Indian ecoregion, the pink *T. rufotincta* Pilsbry (1916) was recorded in Gujarat (Wagh and Bal, 1969; Daniel, 1972; Fernando, 2006; Parmar et al., 2018). However, a detailed revision of *Tetraclita* in the West Indian Ocean using a molecular approach revealed that *T. rufotincta* is distributed in the Red Sea and the Persian Gulf; *Tetraclita ehsani* Chan et al., 2011 is common in the Gulf of Oman and Arabian Sea (Shahdadi et al., 2011; Tsang et al., 2012). In India, *T. ehsani* and *T. karandei* are only present in Gujarat, and absent south of Gujarat (Trivedi et al., 2021; **Figures 3G–I**).

In the Andaman and Nicobar Islands ecoregion, the pink *Tetraclita japonica formosana* (Hiro, 1939) was recorded in the Andaman and Nicobar Islands (Malakar et al., 2015). *Tetraclita japonica formosana* is only common along the east coast of Taiwan and the Pacific coast of Japan (Chan et al., 2007b; Tsang et al., 2007). The records from Andaman and Nicobar Islands need further investigation and clarification.

Suggestions for Further Studies

The present study revealed that most of the species reported from India are intertidal and epibiotic species of crustaceans and common fishery catches in India. More specialized species, including coral-associated barnacles, remain understudied. Previous coral barnacle records in India were mainly from old publications dating back as much as from 48 to 96 years ago (Annandale, 1924; Nilsson-Cantell, 1938; Daniel, 1972). No coral-associated barnacles were collected from the extensive corals in the Lakshadweep Islands and Minicoy or the Gulf of Kachchh of Gujarat state. The diversity of coral-associated barnacles in Indian waters is clearly a knowledge gap that requires more attention. There are presently no records of barnacles in the superorder Acrothoracica, and only one in the parasitic superorder Rhizocephala (**Supplementary Appendix Table 1**). More research is needed to understand the species diversity of these two superorders.

The Indian Exclusive Economic Zone (EEZ) is characterized by deepwater basins, including the Bay of Bengal to the east and the Arabian Basin to the west. The deepwater barnacle fauna of the Indian EEZ and the Indian Ocean are less studied than their Pacific counterparts. Recent deep-sea sampling in the Indian Ocean revealed the first deep-sea hydrothermal vent barnacles from the region (Watanabe et al., 2018; Chan et al., 2020). Long-term dedicated exploration of the deepwater basins in the Indian EEZ waters would certainly offer a richer perspective on the species composition of deep-sea barnacles in the region.

AUTHOR CONTRIBUTIONS

JT, KP, BKKC, and VP wrote the manuscript. All authors involved in collection of barnacle specimens and literature review.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.657651/full#supplementary-material

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Distribution Pattern of the Benthic Meiofaunal Community Along the Depth Gradient of the Western Indian Continental Margin, Including the OMZ and Abyssal Plain

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The continental margin harbors a variety of habitats that support incredible biodiversity and the function of their oceans' ecosystems. The meiofauna is considered a significant component of the benthic faunal community from the polar to the tropical regions. The meiofaunal community in the deep Indian Ocean, especially along the depth gradient, is poorly investigated. The present study aims to explore the benthic meiofaunal community structure along the depth gradients and its associated environment in the western Indian continental margin (WICM) and abyssal plain in the eastern Arabian Sea. Sediment samples were collected from seven different depths (111–3,918 m) along the WICM including the oxygen minimum zone (OMZ) and abyssal plain. A total of 22 taxa (groups) were encountered along the WICM. The nematodes (85%) were the most dominant taxa in all the depths, followed by copepods (11%), nauplii (5%), and polychaetes (1.36%). Our results suggest that (a) the organic matter has accumulated in OMZ sites; (b) a high amount of total organic carbon did not influence the meiofaunal density or biomass; (c) oxygen and depth gradients were significant drivers of the meiofaunal community, low levels of oxygen contributed to lower taxa diversity and density at 485 and 724 m depths; (d) a significant relationship of meiofaunal density and biomass with chloroplastic pigment equivalent (CPE) values indicates pelagic-benthic coupling. Copepods, nauplii, tanaidaceans, isopods, kinorhynchs, and cumaceans were affected by the low-oxygen conditions at the OMZ sites. Enhanced meiofaunal diversity, density, and biomass at deeper sites (non-OMZ-D) was attributed to increased abundance of copepods, nauplii, tanaidaceans, isopods, kinorhynchs, and cumaceans and were mostly concentrated on the surface sediment (0–4 cm) triggered by enhanced bottom-water oxygen and freshness of available food outside the OMZ except 3,918 m. Therefore, the present study showed the meiofaunal community pattern with respect to depth gradients and their related environmental changes, including the OMZ along the WICM and abyssal plain in the Arabian Sea. Based on this study, the future extent of these underestimated marine ecosystems must be considered a priority to understand its functional consequences.

Keywords: meiofauna, rare taxa, benthic diversity, continental margin, oxygen minimum zone, Arabian Sea, Indian Ocean

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INTRODUCTION

The deep sea is one of the world's most biologically diverse ecosystems. The deep sea starts from about 2,000 m and extends to the Challenger Deep, the deepest ocean trench (10,927 m) in the world. The variations in depth and associated altered environments are a primary factor for the diversity of life. Moreover, this biodiversity has been less explored, and perhaps most of the undiscovered species may still be covered from the oceans (Costello et al., 2012). The continental margin is a geophysical layer covered by the thick continental crust and a thin oceanic crust that extends from the coastal to the deep sea and is comprised of the shelf (0–200 m), slope (200–3,000 m), and rise (3,000–4,000 m). Its surface area covers about 11% of the oceans' total Earth area (Menot et al., 2010). In the past few decades, a variety of habitat scale levels has been identified based on their characteristic such as geomorphological, hydrographical, geochemical and biological along the continental margin (Levin and Sibuet, 2012). Collectively, these features create unique ecological settings such as coral reefs, methane seeps, canyons, oxygen minimum zones (OMZs), seamounts, and hydrothermal vents. These hotspots and the habitat heterogeneity along the continental margin create an environment to host surprisingly high rates of population (Etter et al., 2005), biomass, physiological adaptation, species endemicity (Menot et al., 2010), and some of the most diverse array of benthic life forms on the planet (Grassle and Maciolek, 1992).

Benthic meiofauna represents a group of small-sized animals (between 31 and 500 μm) with a high turnover rate (Zeppilli et al., 2018). They are used as a food source for higher trophic levels, such as several fishes, shrimps, and shellfishes (Danovaro et al., 2007). Apart from their contribution to the food chain, meiofauna also plays a crucial role in sediment energetics and bio-indicators to assess environmental health (Heip et al., 1984; Danovaro et al., 2002; Zeppilli et al., 2015). Meiofauna act as vertical conveyors between the sediments, known as the bioturbation process (Coull, 1999). Further, they contribute to modifying the sediment hydrodynamics and biogeochemical fluxes (Aller and Aller, 1992; Schratzberger and Ingels, 2018). The understanding of the meiofaunal community along the continental margin and the abyssal plain is comparatively lower than that of shallow waters. The quantitative research of the benthic meiofaunal community below the shelf and the continental slope and abyssal depths began in the 1970s (Wigley and McIntyre, 1964; Thiel, 1966). Although, since then, the exploration of meiofauna along the continental margin has increased across all the oceans, this research is relatively limited in the Indian Ocean (Soltwedel, 2000). In the 1970s to the 1990s, the meiofaunal research along the continental margin spread to the marginal slope of East Africa in the northwestern Indian Ocean (Thiel, 1966, 1979; Romano and Dinet, 1981; Duineveld et al., 1997) and western India in the eastern Arabian Sea (Ansari et al., 1980).

The present study demonstrates the meiofaunal community along the Western Indian continental margin (WICM) is impinged upon by the OMZ. The OMZ is one of the most prominent features found in the Arabian Sea, the North Indian Ocean, which hosts about 40% of the global denitrification (Al Azhar et al., 2017). The Arabian Sea is characterized by a very pronounced midwater oxygen minimum zone (OMZ), between 150 and 1,250 m, where, the dissolved oxygen levels were observed below 0.05 $\mathrm{mL.L^{-1}}$ (Reichart et al., 1998) and were frequently changing the OMZ in space and time (Schulz et al., 1996; Lachkar et al., 2018). The western half of the Arabian Sea evidenced cyclonic and anticyclonic quasi-geostrophic mesoscale eddies and fronts with their associated meandering currents (Flagg and Kim, 1998; Shankar et al., 2002; Artamonov, 2006; Resplandy et al., 2011). The highest primary production was observed about 380 g C $\mathrm{m^{-2}}$ $\mathrm{year^{-1}}$ in the eastern part of the Arabian Sea, which was mainly driven by transition phases between SW and NE monsoon (Ivanova et al., 2003). Similarly, high primary productivity was observed off Trivandrum (Malik et al., 2015). The high organic carbon content were mainly associated with a depth of 200–1,200 m (Schulz et al., 1996). A vertical supply of nutrients is driven by eddies (Resplandy et al., 2011) with active nitrate reduction and denitrification (Morrison et al., 1999). Thus, the Arabian Sea is a very dynamic ecosystem—one of many OMZs in the world.

The benthic biodiversity along the WICM, including OMZs and abyssal plain, are poorly understood. Few studies discussed benthic macrofaunal community structure along the WICM (Ingole et al., 2010; Levin et al., 2013), while understanding meiofauna along the continental margin depths below 200 m and extended abyssal plain in the Arabian Sea is sparse. Ansari et al. (1980) studied the meiofaunal community at depths between 20 and 840 m along the continental slope in a 15°N transect. Further, Ansari et al. (2017) showed the meiofaunal community along the depths ranged 500–1,956 m off Ratnagiri region. These studies did not generate any meiofaunal data from the abyssal plain in the Arabian Sea. Further, there is a lack of continuous study from the shelf (non-OMZ), slope (including OMZ) and abyssal plain in the Arabian Sea. Therefore, the present study aims to understand the benthic meiofaunal community structure with their surrounding environment along the WICM (depths between 111 and 2,054 m), including the OMZ and abyssal plain (3,918 m).

Over the past few decades, research and reviews have shown that the abundance of benthic meiofauna generally decreases as the depth increases (Soltwedel, 2000). It has also been observed that the diversity and evenness of meiofauna are highly localized and associated with small-scale geochemical changes (Levin and Mendoza, 2007; Thurber et al., 2010; Van Gaever et al., 2010; Vanreusel et al., 2010). Generally, nematodes are the dominant groups among all meiofaunal communities and tend to be most tolerant than any other groups including polychaetes, to the lower concentration of dissolved oxygen concentration (Levin et al., 1991). Therefore, we are hypothesizing based on the previous studies that (1) the benthic meiofaunal density, biomass, and group diversity will vary due to depth gradients and changes in the concentration of DO; (2) the population will decrease with the increasing depths; and (3) rare taxon groups will be at a minimum in lower DO conditions.

MATERIALS AND METHODS

Study Area and Sampling Strategy

The sample collection was carried out onboard R/V Sindhu Sadhana maintained by the CSIR-National Institute of Oceanography. The multidisciplinary cruise (SSD068) was conducted from December 7, 2019, to January 6, 2020, along the WICM, eastern Arabian Sea. The hydrographic properties (temperature, salinity, and dissolved oxygen) of the water column were measured with a CTD profiler (SBE 25, Seabird, United States) cast. The study area was categorized based on (i) geophysical features, such as the continental margin (111–2,054 m) and abyssal plain (3,918 m), and (ii) hydrographic properties, i.e., oxygen concentration: Non-OMZ-S (Shelf) (111 m), OMZ (202, 484, and 764 m), and Non-OMZ-D (Deep) (1,204, 2,054, and 3,918 m).

Onboard, sediment samples were collected with a multicore (inner diameter of 10 cm core liners) at seven different water depths (111, 202, 485, 764, 1,204, 2,054, and 3,918 m) along the 15°N transect in the Arabian Sea (**Figure 1**; **Table 1**). A single multicore with eight-core liners was deployed at each site, and three replicates (independent undisturbed core liners) were used for the meiofauna study. Another independent undisturbed core liner was used simultaneously from the same multicore deployment for measuring the various environmental conditions in the sediment. The sediment cores were sectioned vertically at every 2 cm till 10 cm depth (0–2, 2–4, 4–6, 6–8, and 8–10 cm) immediately after the multicore came onboard. All vertical sections were preserved in 4% buffered formalin with few drops of Rose Bengal (0.5 $g.L^{-1}$) for meiofauna analysis (Giere, 2009). For sediment analysis, sections were frozen (−20°C) until analysis at the laboratory.

Laboratory Analysis

Total organic carbon (TOC) in sediment was estimated through wet-oxidation technique using standard potassium dichromate and ($K_2Cr_2O_3$) and Sulfuric Acid (H_2SO_4), thereby titration against Ferrous Ammonium Sulfate $(NH_4)_2Fe(SO_4)_2$ (Walkley and Black, 1934). Analytical precision was checked through replicate analyses of selected samples ($n = 10$) produced precision (percentage standard deviation) of $< 5\%$ for TOC. Sediment chlorophyll (Chl *a*) and phaeopigments (Phaeo) were determined spectrophotometrically after extraction with 90% acetone from the sediment (Danovaro, 2010). The ratio Chl *a* to phaeopigments was used as the "freshness" of the organic matter (OM) (García and Thomsen, 2008). The sum of Chl *a* and Phaeo was used to measure an organic matter of phytodetrital origin, also known as Chloroplastic pigment equivalent (CPE). The ratio of Chl *a*/TOC was used to indicate the bioavailability of the bulk organic matter representing the contribution of phytoplanktonic originated organic carbon (Ramalho et al., 2014). The sediment pore water was extracted by centrifuge technique (Giere, 2009). Inorganic nutrients (NO_2^-, NO_3^-, NH_4^+, PO_4^{3-}, and SiO_4^-), total nitrogen (TN), and phosphorous (TP) in all the samples were analyzed in duplicates by colorimetric method (Grasshoff et al., 1999) using a UV-Visible spectrophotometer (UV 3200). Seawater nutrient standards (OSIL, UK) and in-house standards were used to check nutrient measurement reproducibility. Analytical precision was checked by repetitive measurements for NO_2^-, NO_3^-, NH_4^+, PO_4^{3-}, and SiO_4^-, obtained at 0.01, 0.07, 0.1, 0.02, and 0.2 μM, respectively. Analytical precisions for TN and TP were found as 10 and 5%, respectively.

For meiofauna, each sediment section was sieved through a stack of 300 and 32 μm mesh size for extraction of metazoan meiofauna from the rest of the fauna. Before sieving, sediments were suspended and poured on the sieve following the suspension-decantation method (Pfannkuche and Thiel, 1988). The procedure was repeated at least five times to increase extraction efficiency. Further, residual sediment was examined for leftover fauna. All individuals were counted and identified up to the group taxon level under a stereo zoom microscope (Leica S8APO, Nikon SMZ18) and images captured using an upright microscope Nikon Ei with camera attachment (Digital Sight 1000). The taxon nauplii were counted separately and then merged with copepods (Itoh et al., 2011; Neira et al., 2018). The nauplii and copepods were used for relative percentage abundance and density comparison. The taxa that contributed <1% of the total meiofaunal abundance of the study area was defined as rare taxa at each depth (Bianchelli et al., 2010).

For biomass estimation, less abundant faunal groups were picked out entirely onto slides; wherever the abundance of the faunal group was high, 100 individuals per group per core were randomly picked out for biomass estimation (Nozais et al., 2005). The sorted organisms' length and width were then computed using camera-based software IS-Capture, pre-calibrated using a standard scale. The length-width measurements were then used to determine the organisms' biomass following the formulae given by Nozais et al. (2005). Biomass of 10 groups (viz., Nematoda, Ostracoda, Kinorhyncha, Polychaeta, Oligochaeta, Arachnida, Nauplii, Tardigrada, and Turbellaria) was computed. The remaining groups were excluded from biomass calculations due to less density per core and lack of conversion factors.

Statistical Analysis

The principal component analysis (PCA) was performed to show the distribution of environmental variables (Euclidean distance) between sampling stations. Before PCA, the environmental data was normalized by transforming with Log(X+1). Pearson correlation was performed to examine multicollinearity among environmental variables and possible inter-relationships between each other. The univariate and multivariate methods have been applied as benthic assessment tools. Univariate indices were calculated for biological data, such as Species richness (S), Margalef index (d) (Margalef, 1968), Pielou's index (J′) (Pielou, 1969), and the Shannon-Wiener index (H′) (Shannon and Weaver, 1949). For multivariate analysis, non-metric multidimensional scaling (n-MDS) was implemented on meiofauna community data. Square root transformation applied on the meiofauna community with Bray–Curtis Similarity was used for n-MDS.

PERMANOVA tests were used to test the significant differences within the factors based on the total meiofauna abundance matrix (square root transformed and Euclidean distance). Similarity percentage (SIMPER) analysis was used to

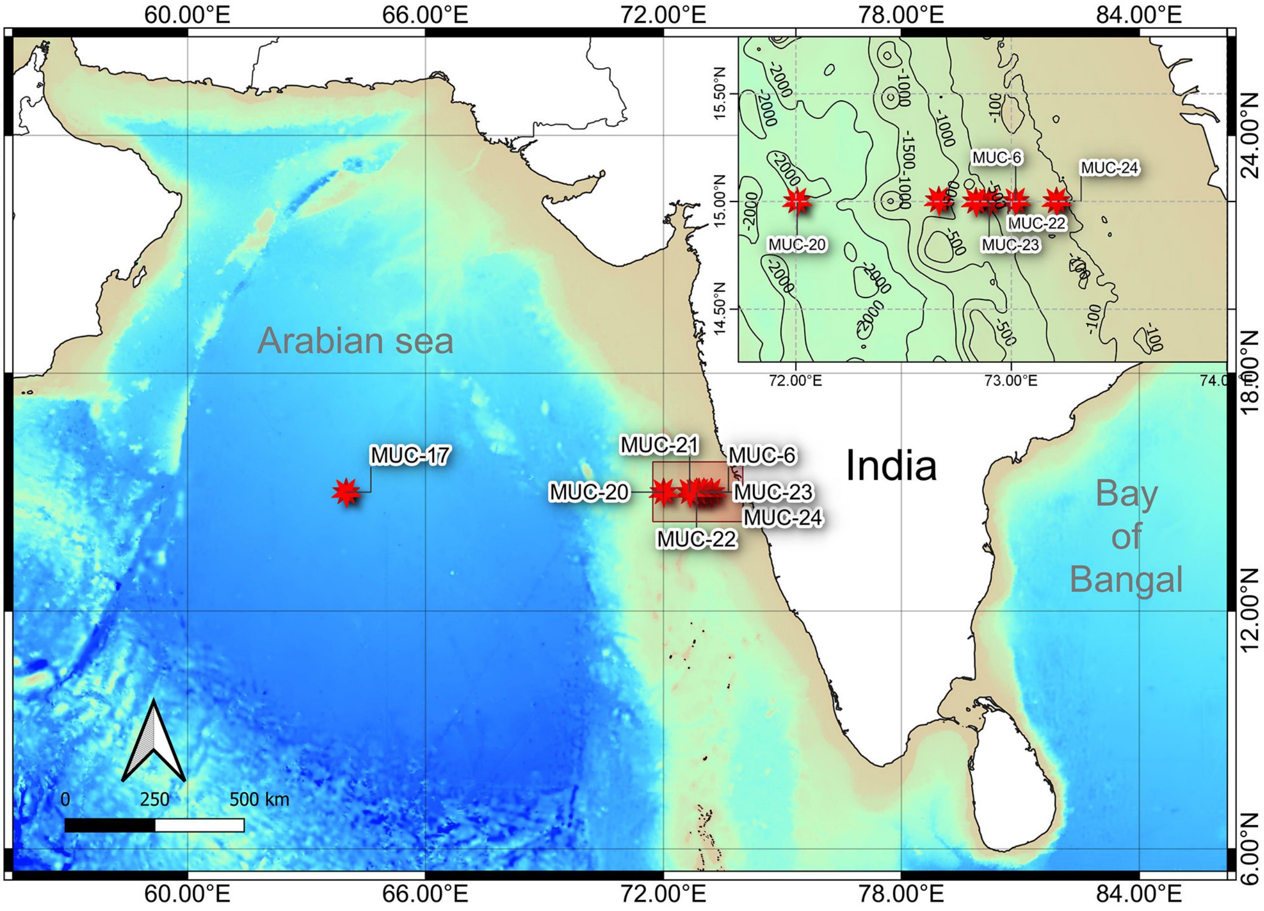

FIGURE 1 | Bathymetric map showing the sampling locations along the Western Indian Continental Margin (WICM) and in abyssal plain, Arabian Sea. Map data: GEBCO 2019 (access date: 21.01.2021).

know the contribution of taxa within each group. Redundancy analysis (RDA) was performed to explain the relationship between meiofaunal community composition, biomass and diversity indices, and environmental variables. According to an established protocol, prior to RDA, the gradient lengths were estimated in a detrended correspondence analysis (DCA) (ter Braak and Šmilauer, 2002). No transformation was used for further analysis. The RDA explained the above 95% species-environment relationship, including both the axes. Monte Carlo permutation test used to determine significant relationships between the meiofaunal taxa and environment variables at 499 permutations under the full model. However, the significance was found very low. Therefore, the BIOENV procedure was followed to determine the best explanatory environmental variables (Euclidean distance) shaping the meiofauna community (Bray Curtis similarity) using Spearman's correlation (Clarke et al., 2014).

The univariate and multivariate methods have been applied using the PRIMER *v6* software package (Clarke and Gorley, 2006) with the PERMANOVA add-on (Anderson et al., 2008). The Spearman's rank correlations were performed using XLSTAT (Version 2009.6.01, Addinsoft). DCA and RDA were performed in CANOCO *v*4.53 (ter Braak and Šmilauer, 2002). The study area map was constructed in QGIS *v*3.10 (QGIS, Development Team, 2020). Mapping data are courtesy of the General Bathymetric Chart of the Oceans Digital Database (Weatherall et al., 2019). Map contours were drawn with 15-arc resolution GEBCO 2019 data downloaded from OpenDEM public domain.

RESULTS

Environmental Parameters

The bottom water temperature and salinity decreased proportionately with increasing depth along the WICM and abyssal plain. Bottom water temperature ranged from 1.7 °C at 3,918 m to 23.6°C at 111 m depths, and similarly, salinity ranged from 34.7 to 35.7 PSU, respectively (**Table 1**). The bottom water dissolved oxygen varied widely along with the depth due to intense OMZ in the WICM. The OMZ extended from the water depth of 202 m to 764 m in the present study. The depth 485 m has been considered core OMZ due to the least concentration (0.04 mL.L^{-1}) of dissolved oxygen, while the maximum (2.71 mL.L^{-1}) was at the abyssal plain (3,918 m) water depth during the present study. The bottom water dissolved

TABLE 1 | Environmental parameters along the different depths in the study area.

Sites	**Non-OMZ-S (shelf)**	**OMZ**			**Non-OMZ-D (deep)**		
Depth	**111 m**	**202 m**	**485 m**	**764 m**	**1,204 m**	**2,054 m**	**3,918 m**
Water							
Temperature (°C)	23.60	15.20	11.86	9.31	6.80	2.90	1.70
DO (mL.L^{-1})	1.19	0.05	0.04	0.21	0.56	1.97	2.71
Salinity (ppt)	35.70	35.40	35.40	35.20	35.10	34.80	34.70
Sediment							
TOC (%)	1.68	3.05	12.25	5.38	3.73	1.30	0.55
Chl *a* (μg/g)	0.12	0.66	0.95	0.38	0.45	0.15	0.01
Phaeo (μg/g)	0.40	2.07	3.02	1.18	1.35	0.43	0.00
Chl *a*/Phaeo	0.30	0.32	0.32	0.32	0.33	0.35	0.00
CPE (μg/g)	0.52	2.73	3.97	1.56	1.80	0.58	0.01
Chl *a*/TOC	0.07	0.22	0.08	0.07	0.12	0.12	0.02
PO_4^{3-}-P (μM)	41.86	56.98	83.70	66.80	27.62	29.40	65.65
SiO_4^--Si (μM)	243.28	211.64	257.48	284.74	48.02	97.08	145.93
NO_2^--N (μM)	7.04	7.44	20.70	21.48	5.08	5.90	15.63
NO_3^--N (μM)	21.80	19.02	16.96	33.20	16.98	11.96	18.85
NH_4^+-N (μM)	78.20	46.04	266.68	383.42	70.68	48.20	64.28
TP (μM)	151.38	118.42	222.60	323.22	72.10	53.44	136.90
TN (μM)	918.44	1085.86	994.36	998.70	1220.46	1058.52	599.95

Sediment parameters representing the average data of vertical sections.

oxygen concentration increased gradually below the OMZ toward deeper depths.

Enrichment and variability of TOC in sediments of WICM were associated with oxygen minima (**Table 1**). Food availabilities by quality and quantity varied along with the depths. The quantity of TOC and CPE was higher in the OMZ region than in the most profound oxygenated depth sites. The CPE value and the phaeopigment concentration at the core OMZ (485 m) were highest. The quality of available OM (Chl *a*/TOC) was found lowest at 485 m and 764 m within the OMZ in the WICM and in the abyssal plain (3,918 m) in the non-OMZ-D site. The ratio of Chl *a*/Phaeo was found to be increased with depth. The highest freshness was recorded at 2,054 m and about zero at the abyssal plain (3,918 m) (**Table 1**).

The pore water nutrients were found to be influenced due to the OMZ. The nutrients phosphate, silicates, nitrite, nitrate, ammonium, and total phosphorus were maximum at the OMZ site. It tends to decrease toward the non-OMZ-D sites. In contrast, total nitrogen depicted a peak at 1,204 m and its lowest point at 3,918 m.

Several environmental variables were significantly correlated with each other (**Supplementary Table 1**). TOC showed a significant positive relation with Chl *a,* phaeophytin, and CPE. Bottom water DO showed a significantly negative relation with Chl *a,* pheophytin and CPE. Water depth illustrated a significant positive relation with dissolved oxygen while inversely correlated to salinity, bottom water temperature, and OM freshness (Chl *a*/Pheo) (**Supplementary Table 1**).

The PCA ordination constructed from the environmental variables related to food, nutrients, and bottom water dissolved oxygen showed that the first two components accounted for about 53.6% (PC1 explained 34.6% and PC2 19%) of the data variability (**Figure 2**). The OMZ region (6–20) was clustered together as they were characterized by enrichment of CPE and TOC and high contribution of pore water solute, i.e., phosphate, silicate, ammonium, nitrite, nitrate, and total phosphorus, while non-OMZ-S (1–5) was separated due to enrichment of fresh and phytoplanktonic rich OM and total nitrogen. The non-OMZ-D sites were characterized by a higher value of bottom-water dissolved oxygen, CPE, and phaeophytin.

Meiofaunal Communities and the Distribution Patterns

Overall, 22 taxa (groups) were recorded in the present study. Bathymetric patterns of meiofaunal density appeared to be similar to those for meiofaunal biomass at WICM (**Figure 3**). The average meiofaunal density was 272.08 ± 48.06 ind. 10 cm^{-2} in along the transect (including continental margin and abyssal plain). The average meiofaunal density at the continental margin (111–2,054 m) was 278.26 ± 83.97 ind. 10 cm^{-2} and 234.99 ± 61.60 ind. 10 cm^{-2} at the abyssal plain (3,918 m). The highest density was recorded at non-OMZ-S (111 m) and declined afterwards in the OMZ sites up to 485 m, but it showed a gradual increase toward non-OMZ-D (2,054 m) depth. Density was generally lower than the sites of comparable depths in other OMZ regions worldwide but higher than the OMZ region of the northeast Arabian Sea. In the OMZ region, an average density ranged from 151 ± 11 (485 m) to 303 ± 16 ind. 10 cm^{-2} (202 m). The mean lowest abundance of the nematode was observed at 1,204 m (115 ± 111 ind. 10 cm^{-2}) and the relative percentage

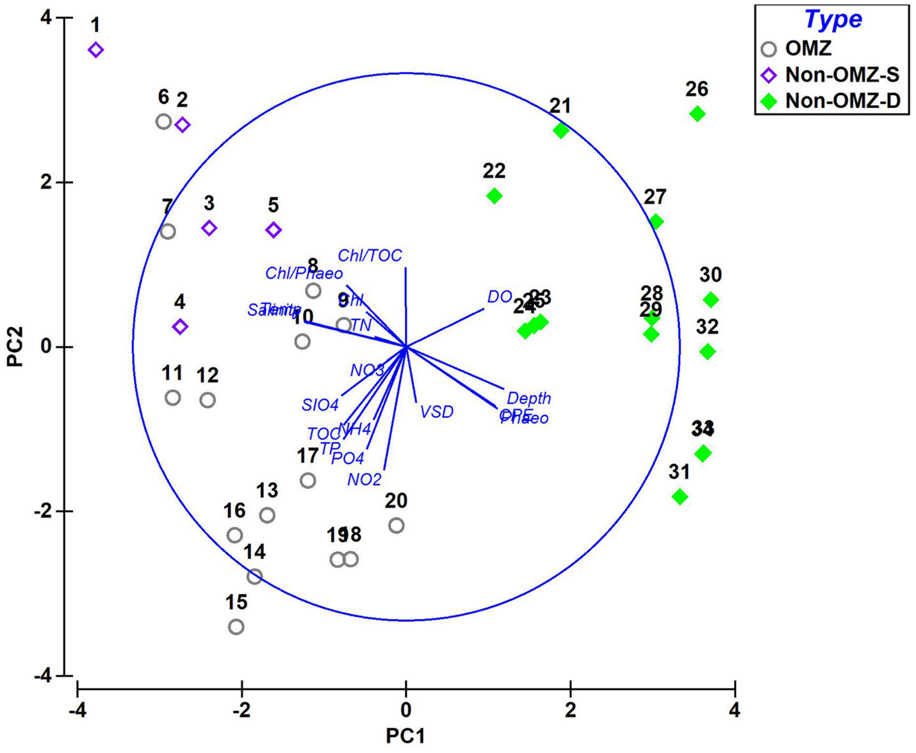

FIGURE 2 | Principal-component analysis (PCA) derived from the contribution of parameters in each benthic zone. PC 1 and 2 accounted for 53.6% of the total variation present. Type: non-OMZ-S – 111m (1–5); OMZ – 202 m (6–10), 485 m (11–15), 764 m (16–20); non-OMZ-D – 1,204 m (21–25), 2,054 m (26–30), 3,918 m (31–34). Numerical codes represent the sequential number of vertical sections such as 1 = 0–2 cm, 5 = 8–10 cm.

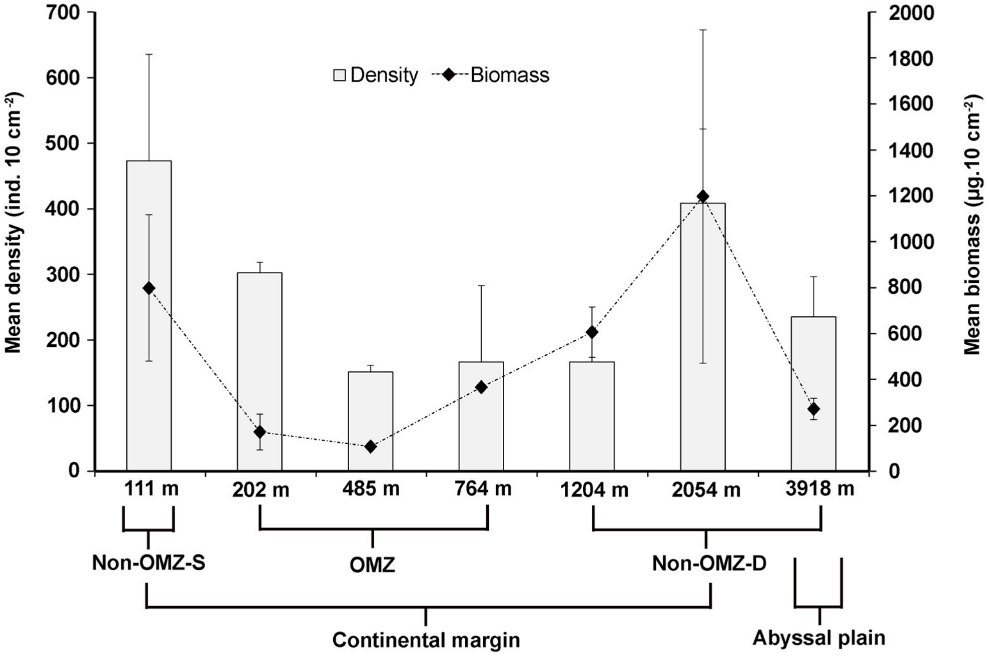

FIGURE 3 | Distribution of total meiofaunal density, and biomass (mean ± SD) in the sediment (0–10 cm) along the depth gradient of WICM.

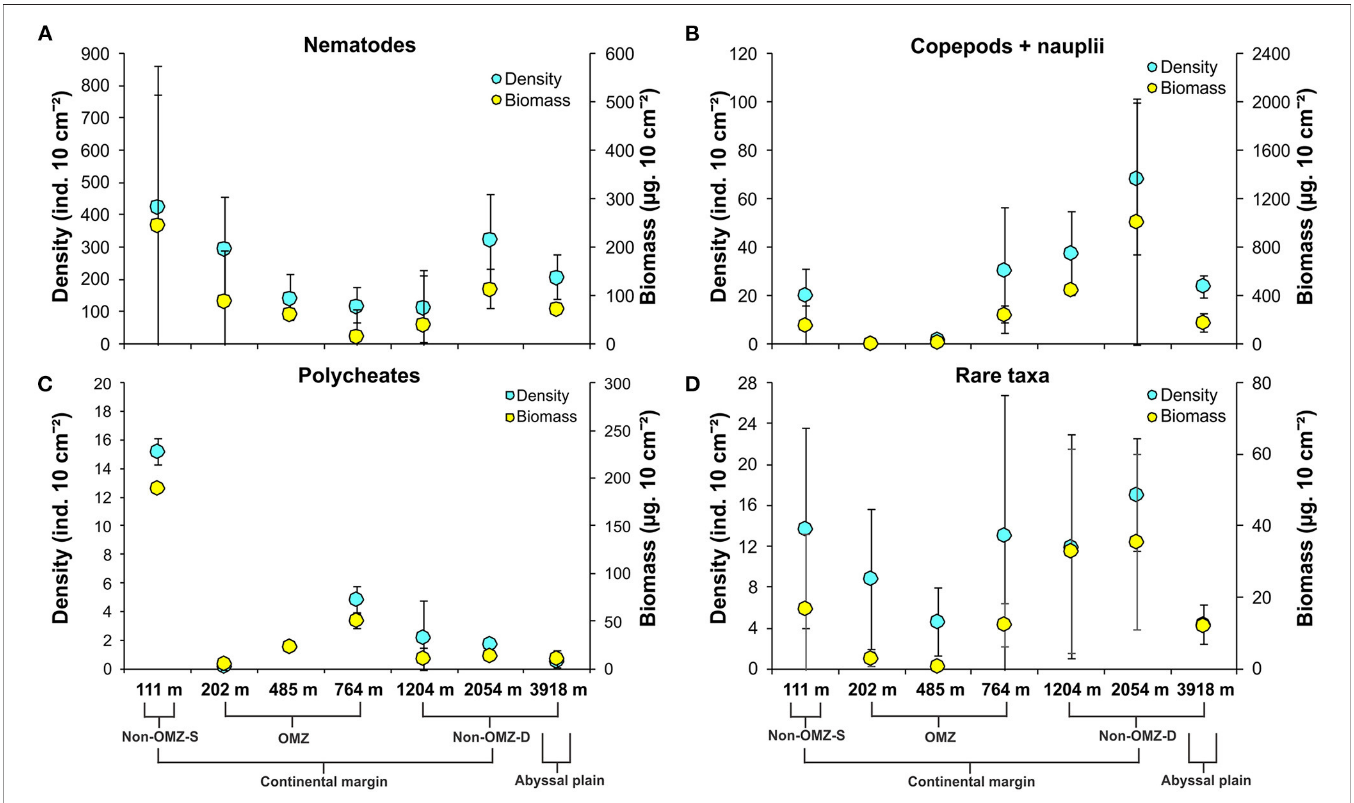

FIGURE 4 | Distribution of density (mean ± SD) and biomass (mean ± SD) of major meiofaunal taxa along the depth gradient of the WICM and abyssal plain. **(A)** Nematoda; **(B)** Copepoda + Nauplii; **(C)** Polychaeta; **(D).** Rare taxa include nemerteans, ostracods, bivalves, kinorhynchs, gastropods, arachnids, minor phyla, tardigrades, tanaids, turbellarians, insects, oligochaetes, gastrotrichs, sipunculids, cumaceans, isopods, cnidarians, and holothurians.

composition reported maximum (97%; 294 ± 161 ind. 10 cm^{-2}) at 202 m, while copepod and nauplii were absent (**Figure 4A**; **Table 2**). The meiofaunal density showed a marked variation between the depths while considering the non-OMZ conditions. The non-OMZ-S (111 m) was recorded with 474 ± 164 ind. 10 cm^{-2}, while density at non-OMZ-D ranged from 166 ± 84 ind. 10 cm^{-2} (1,204 m) to 409 ± 113 ind. 10 cm^{-2} (2,054 m). All the depths were dominated by nematodes with an overall mean relative abundance of 85%, followed by copepods (11%), nauplii (5%), and polychaetes (1.36%). Copepods and nauplii were absent at 202 m, and their density increased with increasing depths (**Figure 4B**). The polychaetes were recorded highest 15 ± 0.9 ind. 10 cm^{-2} at 111 m (non-OMZ-S) and lowest 0.13 ± 0.18 ind. 10 cm^{-2} at 202 m within OMZ (**Figure 4C**). The mean meiofaunal biomass was highest (1198.84 ± 729.11 µg. 10 cm^{-2}) in non-OMZ-D site (2,054 m), followed by (798.01 ± 320.26 µg. 10 cm^{-2}) in the non-OMZ-S (111 m) and the least 104.46 ± 8.02 µg. 10 cm^{-2} at core OMZ site (485 m) (**Figure 3**). Copepods were dominant at non-OMZ-D (764–3,918 m) with an overall mean relative biomass of 55.18%. They were absent at the 202 m, where nematodes were found to be dominated. The second highest contributor to biomass were nematodes, followed by polychaetes and nauplii (**Figure 3**).

The taxa that contributed < 1% of the total meiofaunal density are considered as rare taxa in this study (**Figure 4D**). The relative percentage of rare taxa found in the present study followed in decreasing order include ostracods, bivalves, kinorhynchs, gastropods, arachnids, minor phyla, tardigrades, tanaidaceans, turbellarians, insects, oligochaetes, gastrotrichs, sipunculids, cumaceans, isopods, cnidarians, and holothurians listed. These taxa were represented 3.84% cumulatively of total abundance. Nematodes and copepods were recorded as the dominant taxa in meiofaunal assemblages. Generally, this could increase the negligence in the rare taxa's relative changes and mask the presence of different taxa presence in different habitats. Therefore, taxa contributing <1% were considered rare taxa to understand their distribution pattern along the WICM.

The rare taxa distribution is shown in **Figure 5**. The number of rare taxa was abundant at 764 cm, falling into the OMZ region. The composition of meiofaunal assemblage inhabiting OMZ differed from the non-OMZ-S and non-OMZ-D sites. Moreover, some taxa were mainly present in a specific habitat. Tardigrades were found only at non-OMZ-D depths (2,054 and 3,918 m), while gastrotrichs and turbellarians were present below 764 m (**Figure 6**). Kinorhynchs were absent at OMZs depths of 202 and 485 m. The abundance of temporary meiofaunal taxa like isopods and tanaidaceans were found below 764 m. In comparison, cumaceans were founds only at non-OMZ-S (111 m) and non-OMZ-D (1,204 m).

TABLE 2 | Relative percentage abundance (%) of meiofaunal taxa at seven sites sampled along the Western Indian Continental Margin (WICM) and abyssal plain.

Sites	Non-OMZ-S (shelf)	OMZ			Non-OMZ-D (deep)		
Depth (m)	**111**	**202**	**485**	**764**	**1,204**	**2,054**	**3,918**
Bivalvia	0.62	0.08	0.08	0.23	0.31	0.40	0.11
Cnidaria	–	–	–	0.08	–	–	–
Copepoda	3.53	–	1.10	11.54	17.44	10.39	6.48
Cumacea	0.01	–	–	–	0.08	–	–
Echinoderm	–	–	–	–	0.04	–	0.03
Gastropoda	–	0.82	–	–	0.04	0.33	–
Gastrotricha	–	–	–	0.04	–	–	0.11
Arachnida	0.11	0.17	0.13	0.34	0.38	0.14	0.19
Insecta	0.01	–	–	0.11	0.11	–	–
Isopoda	–	–	–	0.04	–	0.03	–
Kinorhyncha	0.19	–	–	0.65	1.19	0.40	0.08
Nauplius	0.70	–	0.17	6.90	5.10	6.33	3.69
Nematoda	89.69	97.05	94.72	70.83	68.99	78.70	87.77
Nemertea	1.61	1.73	2.62	4.45	3.49	1.03	0.79
Oligochaeta	–	0.08	–	0.04	0.04	–	0.03
Ostracoda	0.31	–	0.08	0.04	0.88	1.06	0.41
Polychaeta	3.20	0.04	1.01	2.87	1.30	0.42	0.22
Sipuncula	–	–	0.04	0.11	–	0.02	–
Tanaidacea	–	–	–	0.19	0.08	0.20	0.08
Tardigrada	–	–	–	–	–	0.53	–
Turbellaria	–	–	–	0.23	0.50	0.02	–
Minor phyla	0.03	0.02	0.04	1.30	0.04	-	–

Univariate indices showed marked variation between OMZ and non-OMZ sites. The highest number of taxa (S) was evidenced at 764 m in OMZ and 1,204 in the non-OMZ-D site, while the least S was found within OMZ (202 and 485 m) (**Supplementary Figure 1A**). Other indices, i.e., d, J′, and H′, showed a similar variation to number of taxa and differed significantly between the depth gradients (**Supplementary Figures 1B,C**).

The n-MDS ordination of meiofaunal density was similar to meiofaunal biomass (**Figure 7**), comprising two groups. Group A comprises non-OMZ-S and all non-OMZ-D sites and 764 m from OMZ region, while group B included 202 m and 485 m of OMZ region. PERMONOVA carried out based on meiofaunal density, which illustrated significant effects on the depth gradient ($p < 0.05$). The SIMPER analysis specified the dissimilarity of 34% between groups A and B due to variation in the density of four main taxa as mentioned earlier, which highlighted copepods, nematodes, nauplii and polychaetes. The kinorhynchs, tanaidaceans, and turbellarians were absent in group B, while ostracods and bivalve showed higher densities in group A compared to group B, where gastropods density was higher at group B compared to group A (**Supplementary Table 2**).

Vertical Distribution in the Sediments

The vertical profile depicted 80% of the meiofauna was concentrated in the upper 0–2 cm layer followed by the 2–4 cm layer (**Figure 8** and **Supplementary Figure 2**). The core OMZ (485 m) was observed 93% faunal concentration at 0–2 cm layer while other depths of OMZ (202 and 764 m) found density up to 4–6 cm depth in the sediment. Nematode was the dominant taxa recorded throughout the sediment core, from a sediment depth of 0 to 10 cm, but this gradually declined with increasing depth in the sediment. Nematodes contributed 67–98% to the total abundance at all the stations, while the other groups were restricted to the upper few centimeters. Copepods and nauplii were found in the upper 4 cm layer. The relative importance of copepods and nauplii increased in non-OMZ-D sites (**Supplementary Figure 3**). Meiofaunal biomass was maximum at the upper 0–2 cm layer (42–97%). In the shelf region (111 and 202 m), the meiofauna, was found penetrated up to 6 cm depth below the surface sediment (**Figure 8** and **Supplementary Figure 2**). Below the shelf region, Nematodes were dominant taxa in terms of density, copepods and nauplii dominated here however it contributed higher to biomass at deeper depths (764, 1,204, 2,054, and 3,918 m) and were limited to 0–4 cm of surficial sediment depth.

Meiofaunal Response With the Environment

The results of BIOENV analysis based on the depth gradient indicated that the TOC, Chl *a,* phaeophytin, CPE, quality of total available OM, depth, dissolved oxygen, phosphate, and ammonia were the primary predictor variable in the best-fit regression model for meiofaunal density that explained 73% of significance

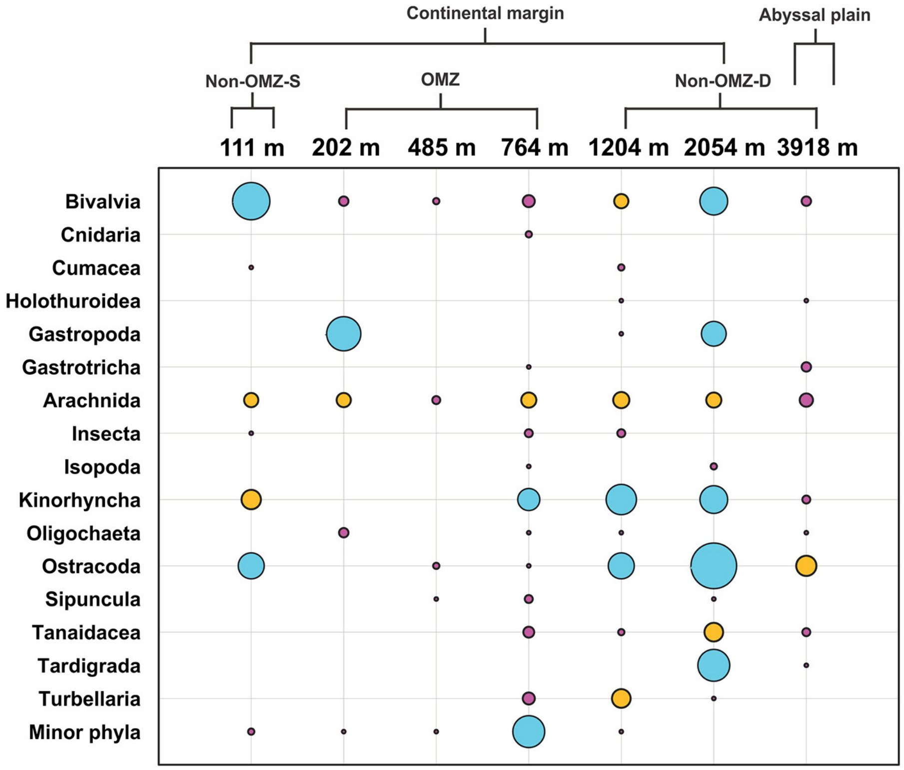

FIGURE 5 | Structure of meiofaunal rare taxa along the depth gradient of WICM and abyssal plain. The bubble size is equivalent to the density of meiofauna in ind. 10 cm^{-2}, the blue bubble signifies value ranges between 1 and 4.5, while the yellow ranges between 0.5 and 1, and pink <0.5.

according to the permutation test (**Supplementary Table 3**). The forward stepwise selection method based on Monte Carlo test was not significant for meiofaunal density with environmental variables. Therefore, the best predictor variables influenced meiofaunal densities based on BIOENV procedures were considered. The first two axes of RDA explained 99.8% of the total variance between meiofaunal community structure and environmental variables. The vectors' direction specifies that TOC-related signifiers (Chl *a*, Phaeo, CPE, phosphate) decreased along the first axis, which was distinctly at the OMZ core site (**Figure 9A**). Copepods, nauplii, and other crustaceans such as isopods, kinorhynchs and ostracods mainly were reported from the surface sediment layer (0–2 cm), where they are likely associated with increased DO availability, the freshness of OM and depth. Nematodes, polychaetes, gastropods and bivalve were related to the quality of available OM, which was found at non-OMZ-S. Other taxa such as cnidarians, sipunculids, gastrotrichs, turbellarians, minor phyla appear to be associated with Depth, $NH4^+$ and Chl *a*/TOC (**Figure 9A**).

For meiofaunal biomass in WICM, Chl *a,* phaeophytin, quality of total available OM, depth, and phosphate emerged as the variable in the best-fit regression model, explaining 70.8% of significance (**Supplementary Table 4**). The stepwise forward selection was not significant with meiofaunal biomass and environment variables; thus, the BIOENV best explanatory variables were considered. The RDA analysis illustrated similar variables responsible for distributing the meiofaunal community with meiofaunal biomass (**Figure 9C**).

Meiofaunal diversity was best explained by TOC, pheophytin, Chl *a,* CPE, depth and $NH4^+$ (**Supplementary Table 5**). The RDA analysis illustrated that taxon richness, diversity, and evenness were best explained by depth vector, which were distinctly increased at 1,204 m of non-OMZ-D. The vectors associated with TOC were found maximum toward the OMZ core site, while total meiofaunal density and biomass were inversely related to TOC (**Figure 9B**).

DISCUSSION

The circulation of dissolved oxygen in the world oceans differs spatially with zones of the low oxygen water centered around the tropics (Stramma et al., 2008). The Arabian Sea, including the WICM, was among the near anoxic condition concentrations at its transitional depths in the oceans. Generally, the West Indian shelf and slope is influenced by the West Indian underwater current flow, which leads to slightly above anoxic condition. However, off Goa region was found anoxic and very static throughout the year (Naqvi et al., 2009). The Arabian Sea OMZ extends between longitudinal 60° and 75° E and latitudinal between 10 and 25° N (Naqvi and Noronha, 1991) and vertically between 150 and 1,200 m depths. In the present study, the OMZ

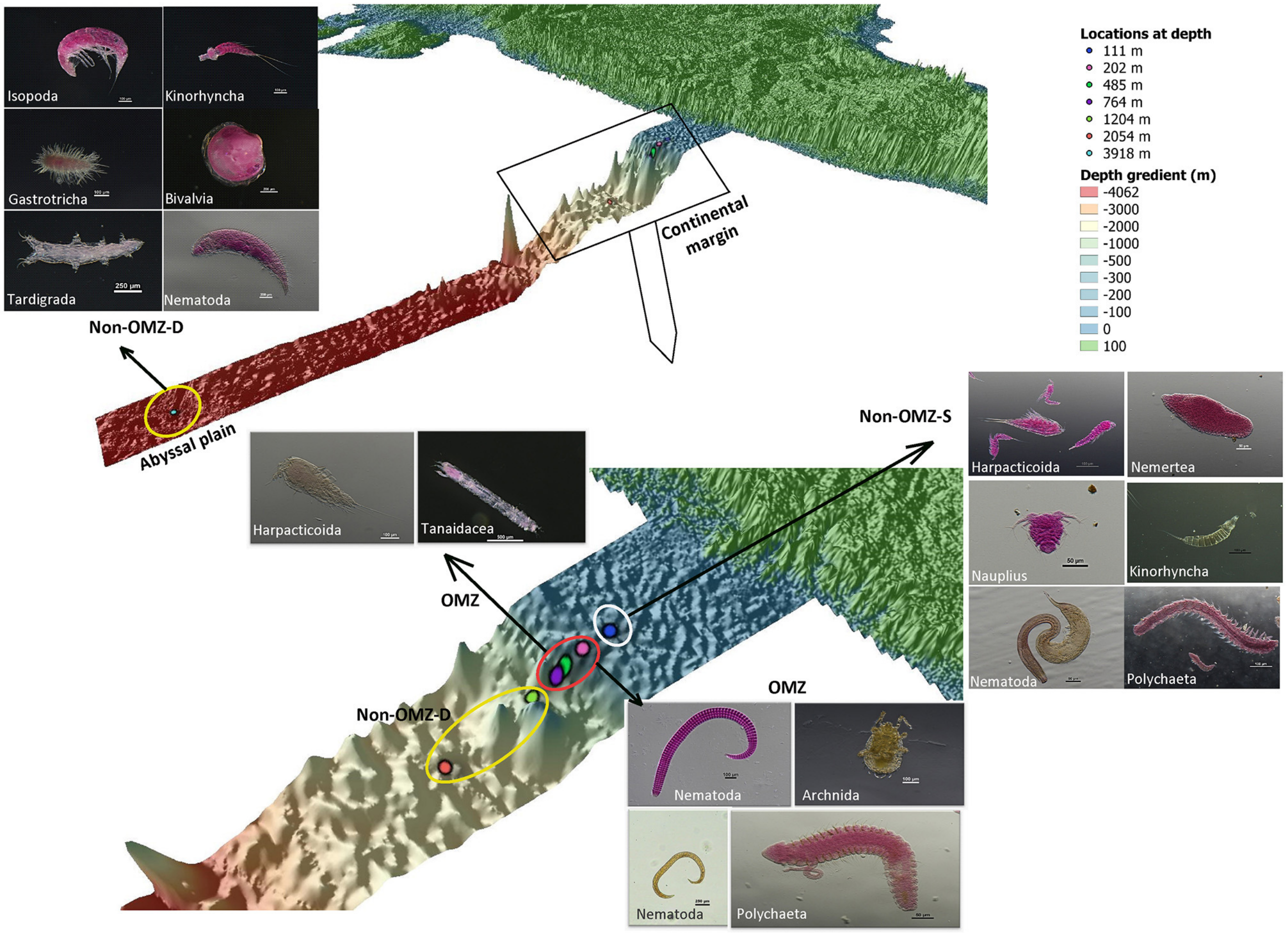

FIGURE 6 | The schematic representation of the distribution of meiofaunal taxa along the depth gradient of WICM and abyssal plain. The stations encircled with colors denotes a particular geomorphological character as White: non-OMZ-S, Red: OMZ and Yellow: non-OMZ-D.

was extended from a depth of 202 to 764 m, where 485 m was considered as the core of OMZ due to the least bottom water DO concentration.

Sediment TOC were significantly higher within the OMZ area than those at the non-OMZ-D, which were oxygenated. The strong inverse correlations between TOC and DO was observed, which was evidenced by earlier studies around the globe, such as Peru (Neira et al., 2001a), Central Chile (Neira et al., 2001b), off Costa Rica (Neira et al., 2018), and the western Indian continental margin (Ingole et al., 2010). The CPE was correlated strongly ($r = 0.87$), with TOC showing similar depth gradient observations. Therefore, the relationship of TOC, DO, and CPE suggest that the flux of sinking CPE on to the benthic sediment was greater in the oxygen-deficient water columns than in oxygenated waters. Correspondingly, the attenuation coefficient for sinking OM has been reported to be weak beneath OMZs off Peru (Martin et al., 1987), in the Arabian Sea (Haake et al., 1993), and off Mexico (Devol and Hartnett, 2001). This reduced attenuation of sinking OM may be attributed to reduced low oxygen conditions and microbial activity (Fenchel and Finlay, 1995). The high levels of dissolved phosphate in pore water at the OMZ site enhance phosphorite deposition by preserving organic sediments at low oxygen concentrations (Frank et al., 1975). The Chl *a*/Phaeo ratio was observed similar in OMZ sites (202, 485, and 764 m) with 0.32, which were lower than those of non-OMZ-D and higher than of non-OMZ-S. The higher values of Chl *a*/Phaeo ratio at two depths of non-OMZ deeper sites (1,204–2,054 m) suggest that the organic matter deposited was relatively fresh. The high TN values at 202 m and non-OMZ-S sites could indicate preferential use of nitrogen during the remineralization of organic matter of phytoplanktonic origin (Sánchez and Carriquiry, 2007).

The role of DO in structuring the benthic meiofauna, especially nematodes from the continental margins, as evidenced earlier in few studies (Cook et al., 2000; Neira et al., 2001a, 2018; Singh and Ingole, 2016). The environmental parameters including DO and meiofaunal taxa other than nematodes and meiofaunal biomass considered in the present study demonstrated new addition to the studies of meiofaunal community patterns along the WICM and abyssal plain in the

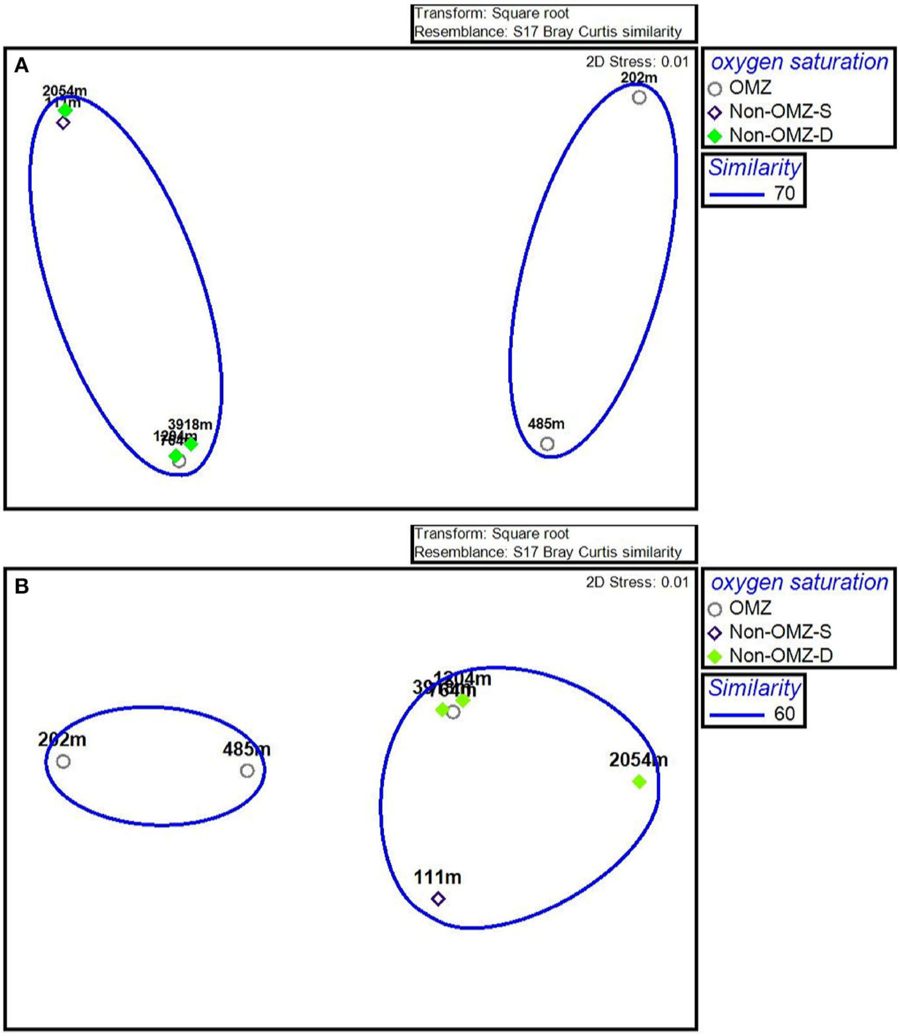

FIGURE 7 | The n-MDS ordination depicting the meiofaunal community on the WICM. **(A)** Meiofaunal density grouped on 70% similarity and **(B)** Meiofaunal biomass grouped on 60% similarity.

Arabian Sea. The present study reports the remarkable changes in the meiofaunal taxa's diversity, density, and biomass along the depth gradient. The density was observed to be lower in the present study than OMZ off Chile (Veit-Köhler et al., 2009). The depth gradient as well as OMZ influenced overall density and biomass. Meiofaunal density and biomass usually decreases with increasing water depths (Rex and Etter, 2010). Differing diversity indices were also observed between OMZ v/s non-OMZ sites, where oxygen is the main limiting factor (Sellanes et al., 2010). In the OMZ site, the nematode density was at its maximum while crustacean density and diversity decreased (**Table 2**; **Figure 5**), which was also recorded by earlier studies from off Ratnagiri, eastern Arabian Sea (Ansari et al., 2017). Taxa diversity was reduced at 485 and 202 m. In contrast, it was found higher with a gradual increase in oxygen levels at 764 and 1,204 m depths. Similar results were represented by earlier studies (Gooday et al., 2009a; Levin et al., 2009). This resulted from favorable oxygen concentration and abundant food availability, described as the "edge effect" by earlier studies from the Pakistan margin (Levin, 2003; Gooday et al., 2010). Similarly, influence of DO on benthic community structure was reported from off Chile and Peru (Thiel, 1978), Mexico (Levin et al., 1991), and the Black Sea (Rhoads and Morse, 1971).

In the present study, the average density of nematode (114.66–425.39 ind. 10 cm^{-2}) was recorded higher than the previous study (62.9–176.6 ind. 10 cm^{-2}) carried out at 14°N (Singh and Ingole, 2016). The lower density of nematode encountered at 14°N may be variation in sampling gears where spade box corer (50 × 50 × 50 cm) was used for 14°N and multicore has been used in the present study. However, the reported nematode density of Oman margin ranged from 494 to 2495 ind. 10 cm^{-2} was higher than the present study (Cook et al., 2000). The higher density on Oman margin could be related to the DO ranges (0.13–2.99 $mL.L^{-1}$), while in present study

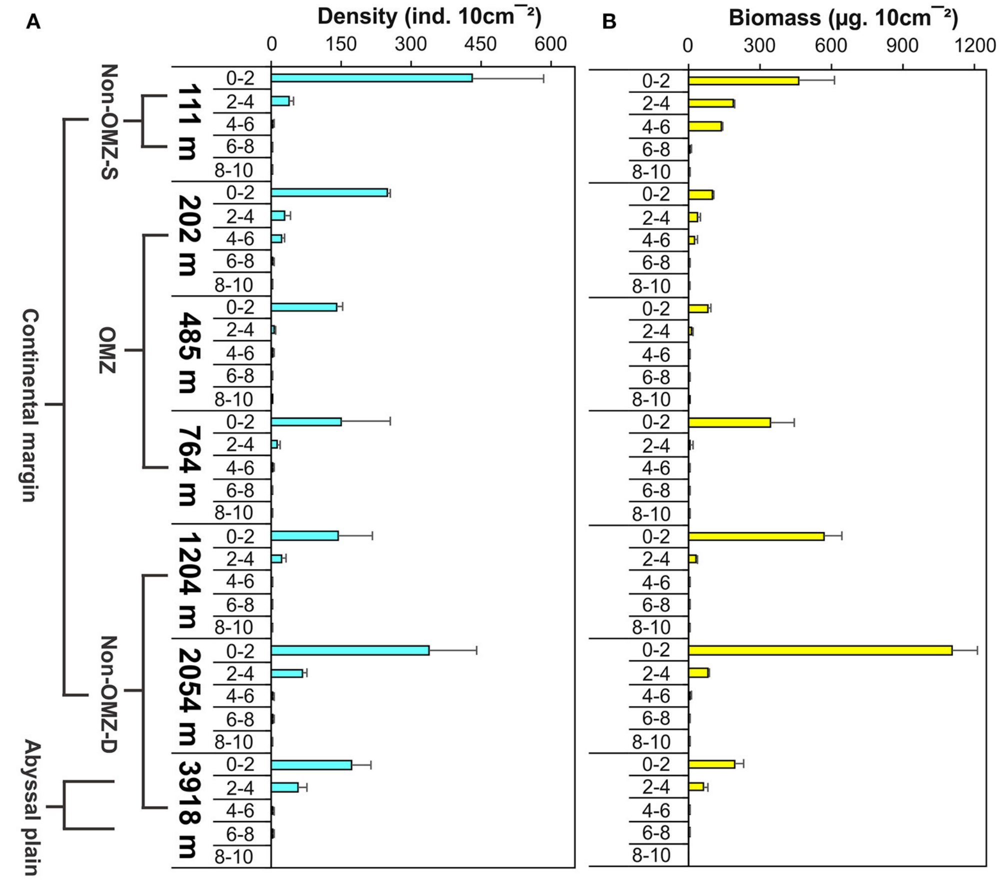

FIGURE 8 | Vertical distribution of meiofauna within the sediment column along WICM and abyssal plain. **(A)** Meiofaunal density and **(B)** Meiofaunal biomass.

DO was reported lower (0.04–2.71 mL.L^{-1}) than Oman margin. The reported nematode density of the core OMZ in the present study was comparable to the core OMZ (upper and lower summit of Volcano 7) of the eastern Pacific Ocean (Levin et al., 1991). The relative percentage composition of nematodes was negatively impacted by bottom water oxygen concentration (**Supplementary Figure 3**). The nematode relative percentage composition at 202 and 485 m was strongly enhanced due to the effect of low oxygen concentration, which led to decrease in the density of other meiofaunal taxa. The absence of harpacticoid copepods, nauplii, and kinorhynchs shows inability to tolerate low oxygen concentrations (Murrell and Fleeger, 1989) at 202 m, and their consistent increase with the increasing DO in non-OMZ-D suggest that oxygen limitations directly control meiofaunal composition at higher taxonomic levels. Similar results were observed from off Peru and Costa Rica (Neira et al., 2018), and the Arabian Sea (Ansari et al., 2017).

The mean meiofaunal biomass was highest in non-OMZ-D (2,054 m) followed by 111 m (non-OMZ-S) and was lowest at the core OMZ (485 m), which was affected by the low DO. These findings may have attributed to a process, where low oxygen concentrations may influence the body size of individuals across the whole community related changes or within specific taxa (Rex and Etter, 2010). The effect on body size at the deficient oxygen levels was documented by earlier studies in the Arabian Sea (Levin et al., 1991; Gooday et al., 2009b; Rohal et al., 2014). The biomass of copepods was more dominant at non-OMZ-D than any other taxa from metazoan meiofauna. The experimental studies have shown that crustaceans were the most susceptible to changes in oxygen levels. The LC_{50} (in mg O_2 L^{-1}) of crustaceans were higher than for other organisms studied (Vaquer-Sunyer and Duarte, 2008). The predictions were made that the fishes should be the first to be affected among benthic fauna, followed by crustaceans, worms, echinoderms, and molluscs as oxygen lowers (Vaquer-Sunyer and Duarte, 2008). A similar effect was also documented through experimental studies, where crustaceans such as shore crabs *Carcinus maenas* (L.) and shrimp *Crangon crangon* (L.) in the Danish fjords (Jørgensen and Jorgensen, 1980) and amphipod *Monoporeia affinis*, harpacticoids *Microarthridion littorale*, and *Pseudobradya* sp. in the Baltic Sea (Modig and Ólafsson, 1998) were wiped out due to low oxygen levels.

Results showed marked variations in the assemblages of rare taxa between OMZ and non-OMZ sites. The masking of the relative importance and the distribution of rare taxa in different habitats was caused by the dominance of nematodes and copepods (Bianchelli et al., 2010). Moreover, some taxa

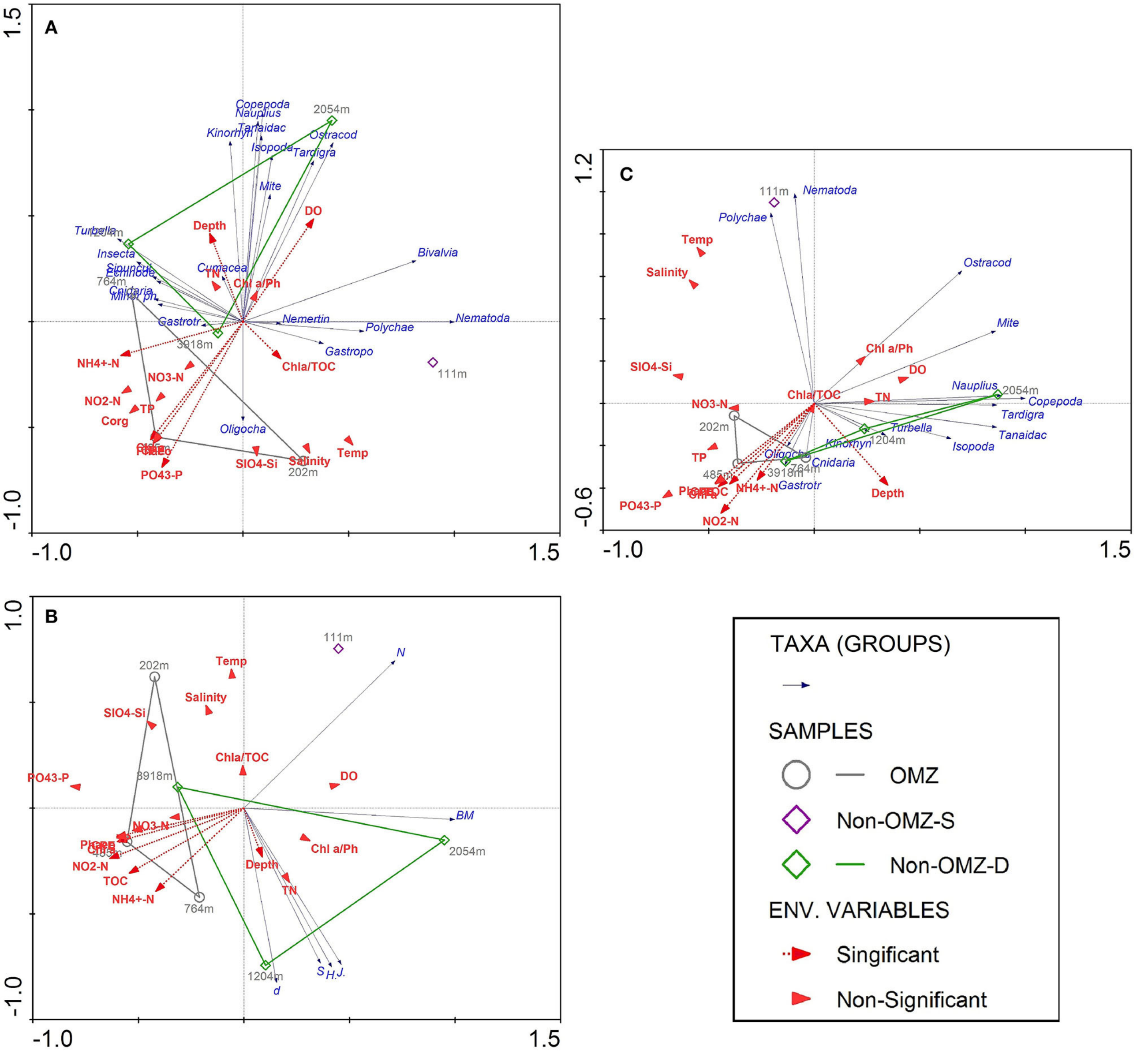

FIGURE 9 | Redundancy analysis (RDA) depicting the meiofauna community of seven sites sampled along the WICM and abyssal plain in relation to environmental variables and depth. Dashed red arrows represent the environmental significant variables (vectors) based on BIOENV procedures. Solid blue arrows are the meiofaunal taxa (responses). Arrows pointing in the same direction are correlated, and longer arrows indicate increasing values. **(A)** The first two axes explained 99.8% of the total variance of taxon abundance-environment variance; **(B)** The first two axes explained 100% of the total variance of meiofaunal diversity-environment variance; **(C)** Biomass-environment variance was explained by 99% of the first 2 axis variance.

were exclusively observed in specific depths and their associated habitat. The isopods and tanaidaceans were found below 764 m at non-OMZ-D depths. However, cumaceans were recorded at 111 and 1,204 m, which were subjected to lower food quality and freshness (Cartes and Sorbe, 1996). Therefore, it seems like oxygen was the limiting factor for distribution of isopods, tanaidaceans and cumaceans, was supported by study in the OMZ off Chile (Veit-Köhler et al., 2009). However, tardigrades, gastrotrichs, turbellarians, and kinorhynchs were utterly absent in OMZ sites. Gastrotrichs and kinorhynchs were also absent in the low oxygen concentration sites Ant-7104 and Con-7161 off Chile (Veit-Köhler et al., 2009).

The sediment vertical distribution of meiofaunal density and biomass at WICM ranged similar to OMZ off Costa Rica (Neira et al., 2018), due to the approx. homologous environmental conditions and geographical location (latitude) among both regions. The maximum fauna was found in the upper 4 cm of the sediment depth, where the OM flux is low (Lambshead and Hodda, 1994). The community size structure was smaller, evidenced by the decrease in biomass wherever nematodes were dominant at the OMZ site. The annelids and their function (bioturbation) were reported in a few studies from OMZ and mainly contributed via tolerant annelids to hypoxic conditions (Levin et al., 2000; Smith et al., 2000). This may enhance the sediment layers' reworking and induce mixing downward (Levin et al., 1991), which supports nematode survival rates in the subsurface and deeper sediments (Braeckman et al., 2010). The enhanced relative proportion of copepods at non-OMZ-D sites influences the total meiofaunal biomass because of their comparably high average individual body weight (Jensen, 1988).

The meiofaunal density and biomass were known to influence by several aspects, for example, habitat heterogeneity (Gooday et al., 2010), bathymetric patterns (Gambi et al., 2010), food availability (Cook et al., 2000), and oxygen concentration (Levin, 2003; Neira et al., 2018). In the present study, the RDA plot signifies the role of dissolved oxygen (**Figure 9**), where a positive correlation of meiofaunal density, biomass and a number of crustacean's taxa was shown. The meiofaunal taxon richness (S and d), diversity (H′) and taxonomic evenness (J′) was found to be distinctly lower at 202 and 485 m of OMZ stations (**Supplementary Figure 1**), while depth also showed significant positive relation (**Figure 9C**). Furthermore, the meiofaunal density and biomass were observed to be positively related to food input and quality. A strong positive relation of TOC and its signifiers Chl *a*, phaeophytin, CPE, at OMZ (**Figure 9**) affect meiofaunal density, diversity and biomass which is represented by BIOENV results (**Supplementary Tables 3–5**). The influence of organic matter perturbation in the sediment on meiofaunal biomass has been recorded in earlier studies (Soltwedel, 2000).

OM quality and bioavailability generally decrease with depth due to degradation in the water column process. Due to this, an increase in meiofaunal density was observed at the shelf area due to OM's freshness and bioavailable OM quality (**Figure 3**). Nematodes and polychaetes density and biomass showed a positive relationship with OM's freshness and quality, which were illustrated in RDA plot (**Figure 9**). Therefore, meiofaunal density and biomass decrease with increasing depths. The CPE values were comparatively high, and meiofaunal density and abundance were found to be low at the core OMZ. Similar results were recorded at NW African margin (Soltwedel, 1997), and it has been suggested that phytodetritus deposits in that area had been transported over long distances and, therefore, were more degraded. Several investigations in OMZs from other parts of the world have noted a correlation between food quality and the lack of oxygen (Danovaro et al., 2000; Neira et al., 2001a). Therefore, food availability is a regulating factor along with the vertical sediment profile (Ingels et al., 2009). The importance of food quantity and availability on nematode abundance and diversity has been emphasized by Cook et al. (2000) from the Arabian Sea.

CONCLUSION

The present study reveals several characteristics of benthic meiofaunal communities and their response to changing depths and associated environmental factors primarily DO along the WICM. The study area was classified and summarized below with corresponding meiofaunal community characteristics based on the geophysical and hydrographic characters. The depth ranges and their related changes in environmental characteristics recorded along the WICM. The continental margin was observed with different DO concentrations, including intense OMZ with higher TOC and CPE. The density and biomass of the meiofaunal community were low within the OMZ region, where phytodetritus (CPE), TOC, and pore water nutrient were accumulated in higher amounts. The meiofaunal density showed a higher value in non-OMZ-S, while the lowest recorded at the intense OMZ (485 m) region. The diversity was observed moderate at non-OMZ-S and D, while the highest recorded at lower OMZ (764 m). The rare taxon showed the minimum richness at the lowest DO concentration along the OMZ while increasing in developing DO values. However, the result of the present study did not support our third hypothesis, as the population density did not show a trend of decreasing with increasing depths along the WICM, which could be due to several factors like OMZ and different geophysical structure in the study area. OMZs represent a principal barrier for benthic species between abyssal plain (food limitation) and continental shelf (plenty of food). These ecosystems may hold an answer to unaddressed questions such as diversified genetic speciation through evolutionary adaptations to ever reducing oxygenation of the world ocean due to global warming and eutrophication. Moreover, this study suggests that more exploration of the meiofaunal community will allow us to understand how the community patterns influence the ecosystem functioning along the heterogenous WICM and abyssal floor in the Arabian Sea.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**; further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

SS designed this study. SS and SG carried out the field sampling. SK, SA, AC, and SC analyzed the meiofauna. UP, BS, SG, and SC estimated environmental variables. SS, SG, and SK performed statistical analysis, plotted map, figures, and wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.671444/full#supplementary-material

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frontiers in Marine Science

REVIEW
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Marine Macrobenthos of NorthWest India-Reviewing the Known and Unknown

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Tropical ecosystems sustain higher biodiversity and face faster species extinction. However, baseline information of these areas is either inadequate or scattered due to various reasons. The 2,360 km long coast of North West India (NWI), is a heavily industrialized and urbanized zone. This coast with unique biogeographical and climatic features with two notified marine protected areas also supports rich biodiversity. This review was motivated by a need to construct a synoptic view on marine benthic ecology and functioning by consolidating available information of macrobenthos. Two thousand seventy-eight macrobenthic taxa belonging to 14 phyla were compiled from 147 references and were composed mostly by Polychaeta (*n* = 617), Gastropoda (*n* = 602), and Bivalvia (*n* = 216). Habitat wise, intertidal and subtidal zones were more intensely studied and contributed most to the diversity records. Sediment texture and salinity were the major drivers of macrobenthic community structure in the subtidal areas and estuaries, respectively. In the intertidal zones, zonation patterns related to the tidal levels and time of exposure were distinct with the high water zones being sparsely populated and lower intertidal zones sustaining higher species and functional diversities. All zones of NWI coast were distinctly impacted to various extent by anthropogenic activities affecting the resident macrobenthos. Decline in species richness and species substitution due to pollution were reported in urbanized zones. Non-monsoonal months favored a more conducive environment for the macrobenthic diversity and functionality. Hypoxia tolerant polychaete species mainly belonging to Spionidae and Cossuridae dominated during the low oxygen conditions of upwelling and OMZ zones of NWI. Inadequate identification and inconsistency of sampling methods were major deterrents for concluding trends of distributions. Suggestions for future macrobenthic research include focusing on lesser studied groups and areas, seasonal as well anthropogenic hypoxic zones and well planned long-term monitoring studies. Major data lacunae were identified in the taxonomy, molecular, functional aspects, and bioinvasive studies of macrobenthos in this geographical zone despite clear evidence of high diversity of extant macrofauna. This compendium should help prioritize research areas and objectives aimed at enhancing our understanding of macrobenthos and improve predictive capabilities of community shifts that may occur due to global climate change scenarios.

Keywords: review, macrobenthos, biodiversity, functioning, India

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INTRODUCTION

Coastal ecosystems host some of the most diverse, extensive, and complex floral and faunal assemblages and the sustainability of these systems is maintained by the myriad functional roles of the constituent biota. Biodiversity plays an important role in maintaining ecosystem services and possible losses of biodiversity can certainly interrupt key ecological processes (Harrison et al., 2014). Ecological consequences of biodiversity loss on the efficient functioning of ecosystem are now firmly established (Loreau et al., 2001; Danovaro et al., 2008) and this reaffirms the need to quantify and evaluate available information of various facets of biodiversity.

The species diversity of marine systems are majorly constituted by sediment dwelling flora and fauna (Radulovici et al., 2010) accounting for 98% of all known marine species. Marine benthos includes living members of the 29 non-symbiont animal phyla described thus far, except one (Porifera, Placozoa, Cnidaria, Ctenophora, Platyhelminthes, Gnathostomulida, Nemertea, Kinoryhncha, Nematoda, Loricifera, Rotifera, Priapula, Gastrotricha, Pogonophora, Tardigrada, Echiura, Mollusca, Chaetognatha, Kamptozoa, Phoronida, Sipuncula, Brachiopoda, Annelida, Echinodermata, Arthropoda, Hemichordata, Bryozoa, and Chordata) (Ray and Grassle, 1991). The dominant component of marine benthic assemblages is macrobenthos (larger than 500 μm) which includes some of the most speciose groups i.e., annelids, crustaceans, molluscs, etc. (Snelgrove, 1999). Macrobenthic investigations have garnered most scientific attention among the benthic groups due to its distinctive community characteristics and complex functional role at the water–sediment interface. They are key components in the benthic functioning of coastal ecosystems and are a vital link in global carbon, nitrogen, and sulfur cycling (Snelgrove, 1998). They are major food sources for varied demersal predators occupying the same ecosystem (Griffiths et al., 2017). Macrobenthos also are potential biological indicators due to their sedentary nature, long-life spans, environmental plasticity, ability to integrate the environmental quality status, and effectively reflect the system condition at spatio-temporal scales (Fitch and Crowe, 2010). Also, they have diverse species composition and show marked responses to several stressors such as hypoxia and anthropogenic disturbances (Dauvin et al., 2012; Peng et al., 2014).

Benthic faunal diversity is a stepping stone for exploring the relationships between biodiversity and ecosystem functioning. Understanding the biodiversity in marine sediments and its linkages to various ecosystem processes is important for maintaining ecological services and to estimate the species being lost or extinct due to various pressures. A decrease in benthic biodiversity may have a concomitant negative impact on key ecosystem functions and biogeochemical cycling particularly in shelf regions that are known to contribute to the bulk of benthic productivity (Field et al., 1998). Unknown diversity exceeds much more than known information (Venkataraman and Wafar, 2005). Global trends in macrobenthic diversity distributions and its causes can be successfully evolved only if sufficient and reliable data from lesser studied areas are made available within a cogent framework. Efficient evaluation of biodiversity and functioning losses of nearshore habitats is dependent on the availability of adequate data banks, which is largely lacking in many geographical regions owing to a host of reasons (Konar et al., 2010). The lacunae are all the more conspicuous in case of tropical coastlines, despite these zones constituting one-third of the world shelf area (Muniz et al., 2005) and supporting high biodiversity (Olsgard et al., 1998). Coastal systems are more vulnerable than deep sea systems due to the dual impacts of anthropogenic pressures and global warming. Projected catastrophic ecosystem responses of climate change are mostly expected to be individualistic (i.e., at species level) and may include modification of species assemblages, alteration of species interactions, species shifts, or even extinctions (Gayton, 2008). This necessitates planning and implementation of sound ecosystem management procedures focusing on areas most vulnerable to climatic vagaries.

The Arabian Sea, located in the northeast Indian Ocean, is a geochemically active area along the western boundary of India. The coast of North West India (NWI) (15–24°N) is one of the most productive zone with unique characteristics. NWI has two of the biggest, highly industrialized and urbanized coastal states, Maharashtra and Gujarat (**Figure 1**). The NWI is about 2,320 km which is nearly 29% of the nation's total coastal length and has the most extensive shelf and slope areas that translate into one of the richest fishing grounds of India. The marine fish production of NWI for 2019 was 3.56 million tones accounting for 26.6% of the total marine fish production from the country (CMFRI, 2019). The coast presents a variegated coastal physiography and geomorphology that provides diversity of habitats like mangroves abounding estuary mouths and creeks, coral reefs, mudflats, vast sandy, and rocky intertidal areas. There are two notified Marine Protected Areas (MPAs) with coral formations i.e., Malvan along Maharashtra coast and the Gulf of Kachchh Marine National Park and Sanctuary (GoK MNPS) in the state of Gujarat.

The western Indian continental shelf is one of the five major upwelling zones of the world (Benguela, Humboldt, California, Canary, and Somali) (Naqvi et al., 2009). The characteristic upwelling process during the southwest monsoon leads to the development of coastal hypoxia along the west coast, forming one of the world's largest natural oxygen-deficient systems (Naqvi et al., 2000). This has implications on the coastal productivity and influences benthic biological processes as well (Jaleel, 2012). During the last few decades, this coastal region has been experiencing rapid industrial developments and burgeoning urbanization (Sachs et al., 2002) while sustaining high commercial fish landings. Some of the major problems faced are related to rapid industrialization and associated urbanization resulting in coastal erosion, siltation, habitat loss, and deterioration of water quality in some zones.

The Arabian Sea is experiencing a secular warming since 1995 as a response to regional climate change which has manifested in the form of disruption of seasonal cycles and increased frequency of extreme events in the adjacent Indian mainland in the last decade (Prasanna et al., 2009). Continued warming in sea surface temperatures will have long term implications

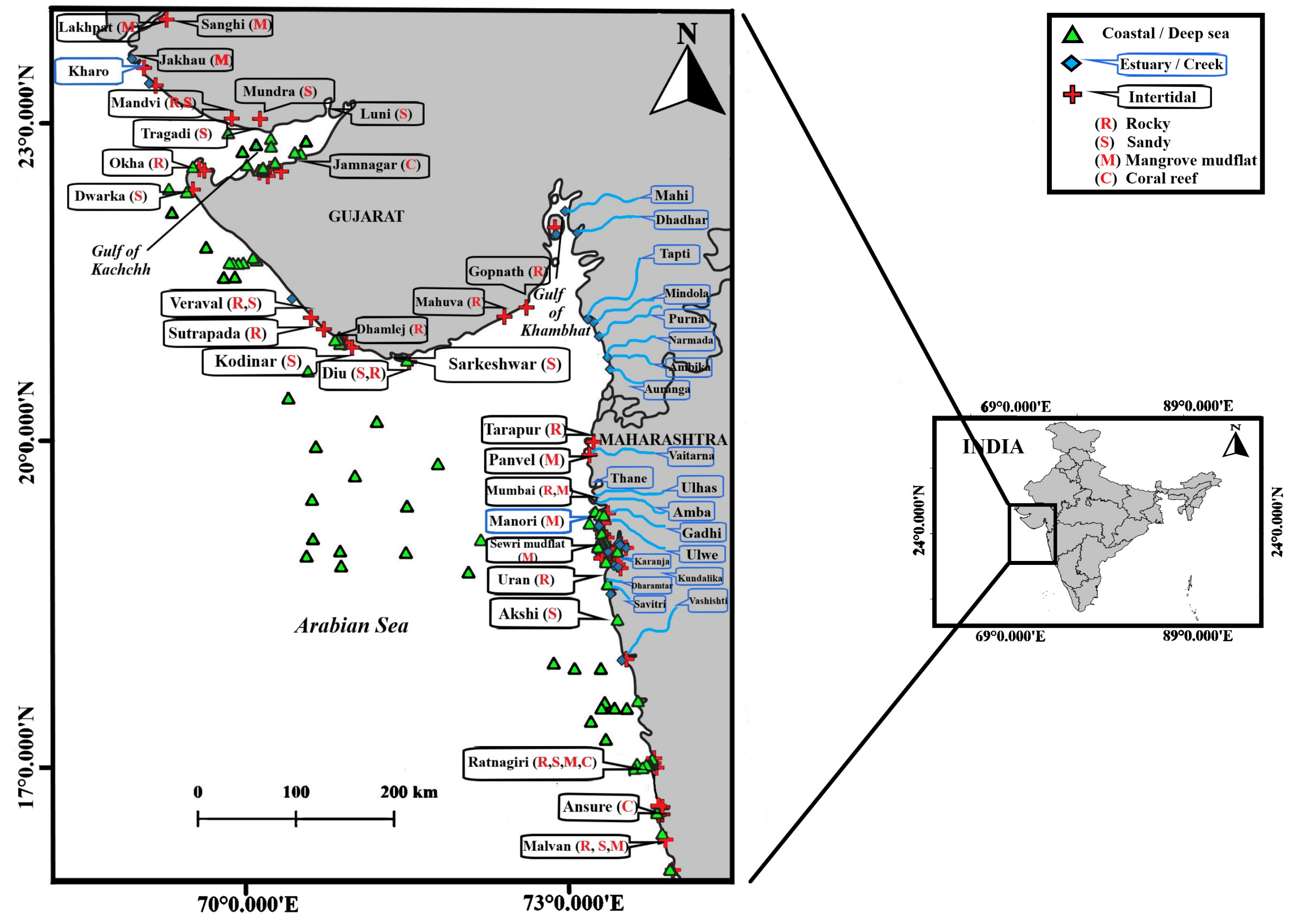

FIGURE 1 | Map of the study locations of macrobenthic investigations along North West coast of India.

on the coastal biodiversity. In a scenario wherein the coastal systems are increasingly facing the detrimental effects of climate change and exponential anthropogenic pressures, it is vital to co-ordinate global monitoring efforts, gather the baseline data of extant biodiversity and analyze them proactively. Gaps in present monitoring and reporting systems require to be identified and rectified to strengthen existing programs (Mawdsley et al., 2009). In this review, we have attempted to collate all available information pertaining to the vital aspects of macrobenthic assemblages of the NWI, encompassing varied habitats such as the continental shelf, creeks, estuaries, intertidal zones including coralline. Furthermore, we have summarized the studies carried out thus far, inventoried the recorded species, deduced general trends, examined environmental factors determining macrobenthic community structure and endeavored to identify data lacunae, and areas that merit further investigations. While several government sanctioned macrobenthic surveys have been executed, the data acquired have been largely scattered, random, and in disparate forms. This makes evolving of an overarching holistic view of macrobenthic research largely unsuccessful, thus weakening efforts to plug knowledge voids. The review would benefit managers of the coastal zone in drawing up conservation plans and expend resources toward areas identified as diversity hotspots or least studied.

DATA COLLECTION AND TAXA INVENTORY

The meta data for this review was compiled from published research papers on the various aspects of macrobenthos. Totally, 185 scientific articles were gathered from various sources, the oldest references dating to the 1940s (**Figure 2A**). The articles were categorized based on the type of zone. The comprehensive checklist of macrobenthic taxa identified at least till the generic level along with the corresponding references is presented in **Supplementary Table 1**. All the names were verified with the WoRMS (World Register of Marine Species) database. Around 105 species names were not found on any of the verified online databases (tagged with an asterisk). Thirty-nine species could not be traced on WoRMS, but were mentioned on other Google databases. Thirteen species were tagged as *nomen dubium* (a name of uncertain taxonomic significance) on WoRMS. Totally, 2,078 macrobenthic taxa belonging to 14 phyla have been

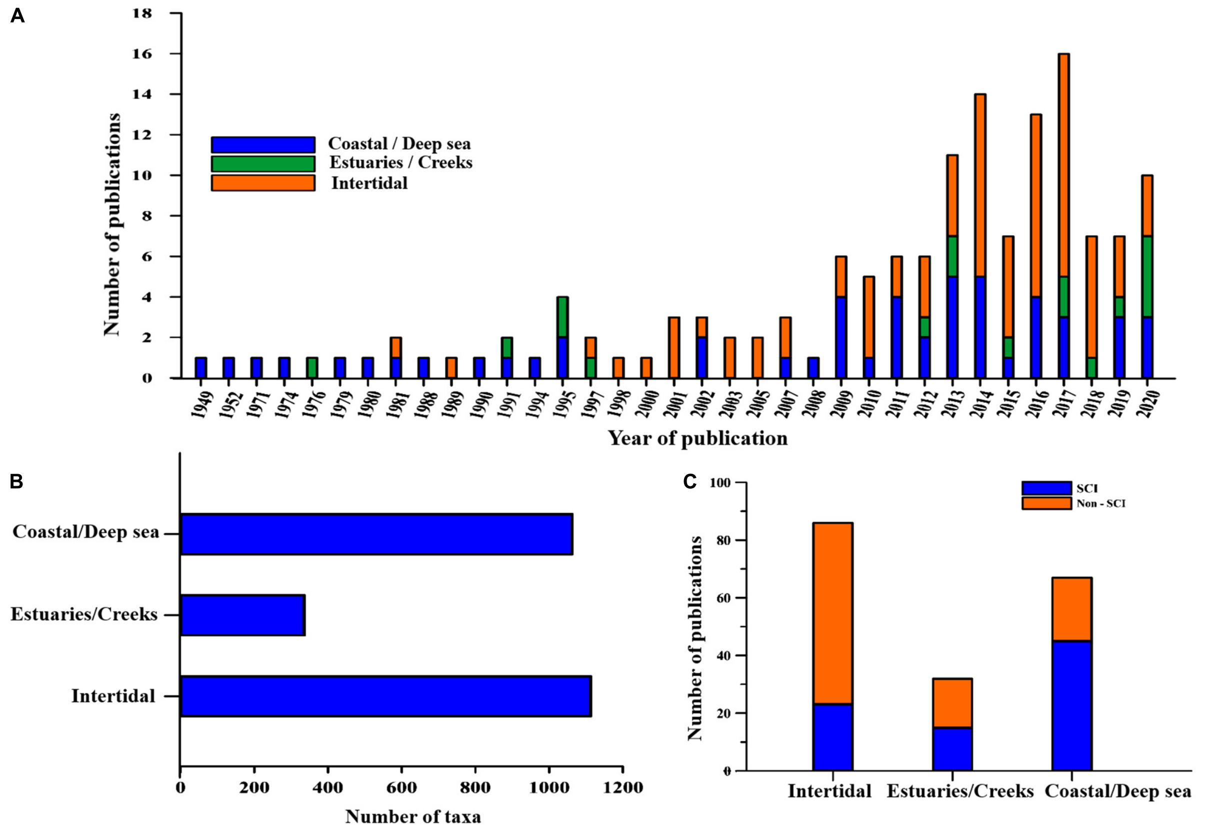

FIGURE 2 | (A) Annual number of publications indicating zonal categorization (1949–2020). **(B)** Zonal categorization of macrobenthic taxa along North West coast of India. **(C)** SCI and non-SCI literature of macrobenthic studies along North West coast of India presented zone-wise.

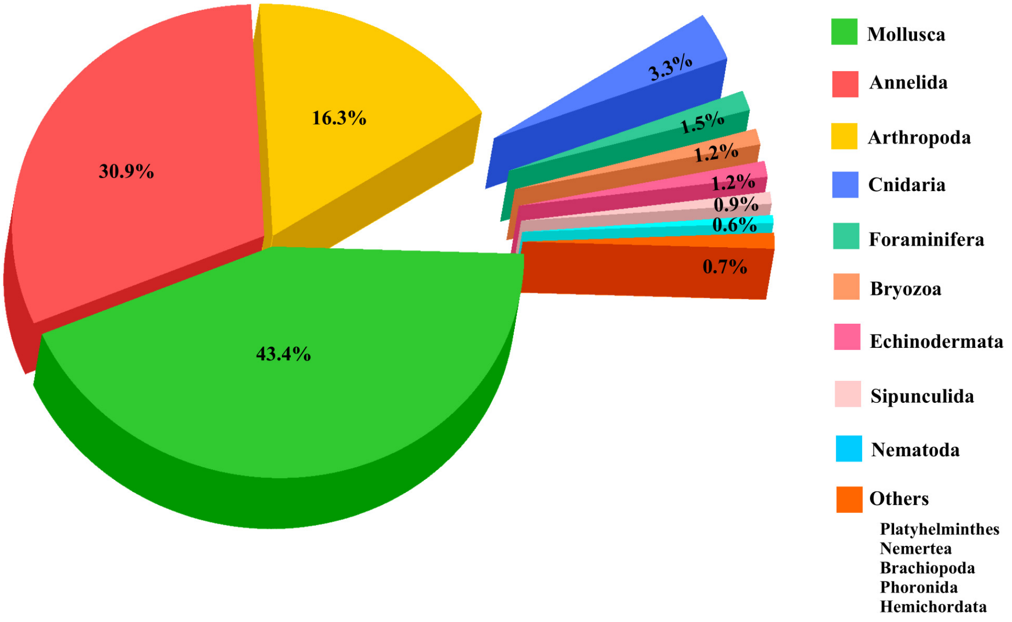

FIGURE 3 | Phylum level composition percentage of macrobenthic taxa recorded and listed in **Supplementary Table 1**.

identified from various realms of the NW coast of India. More number of species was identified from the intertidal (1,113) and coastal (1,063) zones as compared to estuaries (**Figure 2B**). Also, comparatively lower number of species were reported from estuaries (336). The inventory was detailed in the case of polychaetes (617 species), gastropods (602 species), bivalves (216 species), brachyurans (109 species), and amphipods (107 species) (**Figure 3** and **Supplementary Table 1**).

THE INTERTIDAL ZONE

Among the intertidal categories of NWI, the dominant types are tidal mudflats and mangroves. The Maharashtra coast is dotted by sandy and rocky beaches flanked by promontories. Intertidal mudflats abound along the estuarine mouth and creeks which sustain substantial mangrove patches. While the Maharashtra coast is mainly linear, the Gujarat coast has two major indentations, the Gulf of Kachchh and the Gulf of Khambhat, each having its distinct physico-chemical and hydrodynamic characteristics. The Gujarat coastline has varied geomorphology having a network of tidal creeks with abundant mangroves, rocky shores, vast mudflats, coral reefs, sandy beaches, calcium carbonate cliffs, and sand dunes. The following account summarizes the macrobenthic studies of intertidal locations by categorizing data into four major habitat types. The various locations mentioned in this compilation are marked in **Figure 1**.

Rocky Intertidal

The Malvan coast of Maharashtra has exceptionally high biodiversity due to its multifarious habitats which has earned it the MPA status. Therefore, this intertidal ecology has been the subject of several investigations related particularly to sea anemones (Parulekar, 1966, 1969, 1971a,b), polychaetes (Parulekar, 1973), and molluscs (Joshi, 1969). Gaikwad and Ranade (1979) provided a checklist of 72 polychaete fauna collected from Ratnagiri, of which 19 were new records from the west coast as well as Indian waters, respectively. Around 92 and 56 species of intertidal fauna were identified from the rocky pool and rocky shore environments of Malvan coast, respectively (Parulekar, 1981). From the Ratnagiri coast, Wadkar (1989) reported five species of polychaetes. Eight hydroid species from eight rocky intertidal locations of the Konkan coast were described by Nagale and Apte (2013a). In a comprehensive study on the vertical diversity, density, distribution, and ecological aspects of Gastropoda at 14 predominantly rocky intertidal sites along the Ratnagiri coast, 127 species belonging to 20 families were recorded (Kurhe et al., 2014). Pioneering taxonomic studies on crabs of the Maharashtra coast were conducted by Chhapgar (1957) after which very little was discovered on this group. The crabs, *Xenophthalmus wolfii, Xenophthalmus garthii*, and *Ozius tuberculosus* were reported from both rocky and sandy beaches of Maharashtra (Khot et al., 2016b,a, Khot et al., 2019).

Very high biodiversity was reported from different types of intertidal zones of Mumbai megacity located in Maharashtra, as early as 1959 (260 species; Bhatt, 1959). Earlier accounts on the molluscan diversity along the then Bombay Presidency were given by Abercrombie (1892), Melvill and Abercrombie (1893), Melvill and Standen (1901), and Rai (1931). Hornell (1949) identified 225 gastropod species and 199 bivalve species. Bhatt (1959) had reported 58 live gastropod and 35 bivalve species. During a survey along the Mumbai coast line, 38 and 51 molluscan species were identified from two different rocky beaches (Jaiswar and Kulkarni, 2005).The rich biodiversity of the rocky intertidal zone of Mumbai, despite the anthropogenic stressors prevalent, have been accounted by Datta et al. (2010). From three rocky beaches, around 50 macrobenthic species were reported which included 41 gastropods and 5 pelecypods. In a later study, 70 macrobenthic taxa, were identified in the rocky pools of the intertidal area of Colaba, Mumbai (Sukumaran et al., 2014). Around 30 and 34 species of macrobenthos dominated by molluscs were identified from the Haji Ali and Marine Drive intertidal zones (Balasaheb et al., 2017).

From the rocky intertidal zones near an effluent outfall at Uran bordering the eastern side of the Thane Creek, Ram et al. (1998) reported nine gastropod species though the major groups were amphipods, barnacles, and polychaetes. Macrofaunal density and diversity were higher in rocky intertidal zones as compared to nearby sandy shores and the subtidal areas. From the Uran coast of Maharashtra, about 60 species belonging to 25 families of Gastropoda was listed by Pawar and Al-Tawaha (2017a), mostly collected from rocky stretches. Further studies by Pawar and Al-Tawaha (2017c) reported 170 species belonging to 83 families dominated by gastropods, brachyurans, pelecypods, etc. from the same intertidal areas at Uran, though the species checklist was not provided. Twenty-five macrobenthic groups including 16 polychaete families were recorded from the sand interspersed rocky intertidal zones of Tarapur coast around an atomic power station, Maharashtra (Kubal et al., 2016).

The Gulf of Khambhat at Gujarat has very high turbidity owing to high tidal amplitude and the heavy load of suspended sediments channelized through the perennial rivers emptying into the Gulf. From the littoral sites of Mahuva, Gopnath (bordering the Gulf), and Veraval (away from the Gulf), 32 macrobenthic species belonging to 24 families were recorded (Raghunathan et al., 2003). In the rocky zones of Veraval, Sutrapada, Okha, and Dwarka, molluscs (28 species), arthropods (14 species), and annelids (3 species) were observed to be associates of zoanthids (Pandya et al., 2014). Similarly, Trivedi et al. (2014) studied the macrobenthos associated with the zoanthid, *Palythoa mutuki* at four different sites (Sutrapada, Dhamlej, Kodinar, and Veraval) along the Saurashtra coast of Gujarat. Sixty-seven species belonging to Arthropoda, Mollusca, Cnidaria, Annelida, etc. were identified. Seven species of opisthobranch were reported from intertidal habitats of south Saurashtra by Poriya et al. (2015) among which five species were first records from the coast. Vakani et al. (2016) recorded 38 molluscan species from rocky intertidal region of Veraval. A comparative study undertaken at Tragadi (muddy substratum), Nana Layja (rocky), and Luni (sandy) along the northern coast of the GoK recorded 15 species with gastropods forming the dominant group (Naz et al., 2016). The highest species diversity was recorded at the rocky shore. Twenty-four species belonging to 18 families of bryozoans were identified from the rocky intertidal zones of Gujarat and Maharashtra by Venkatraman et al. (2018) and 23 species of limpets were reported from the same coastal stretch by Vakani and Kundu (2018) and Vakani et al. (2020). Vadher et al. (2020) provided a checklist of 95 sea slug species from the intertidal region of Gujarat coast.

Sandy Intertidal

From the sandy shores of Malvan, 57 macrobenthic species were reported by Parulekar (1981) during surveys spanning different seasons during several years. Forty-seven molluscan species were identified from a predominantly sandy intertidal zone interspersed with rocky patches along the Akshi coastline of Maharashtra by Kurve and Kurve (2010). Fifty-six macrobenthic taxa were reported from a sandy beach at Ratnagiri where the intertidal macrofauna were dominated by crustaceans, gastropods and polychaetes (Sivadas et al., 2012). Shannon Wiener index varied from 0.094 to 0.92 indicating low diversity in the polluted sandy beaches of Versova, Mumbai (Anandan et al., 2003). Major macrobenthic groups were polychaetes, amphipods followed by isopods, crabs, hermit crabs, decapods, pelecypods, and gastropods. Seven macrobenthic species were reported from the sandy Girgaon intertidal zone (Balasaheb et al., 2017). The molluscan species, *Cellana radians* (Gastropoda), *Chiton* (Amphineura), *Trochus intercostalis* (Gastropoda) were the most abundant species reported from the sandy intertidal zones at Veraval and Diu (Misra and Kundu, 2005; Agravat and Raval, 2019). The distribution pattern, community structure of the sabellariid worm, *Neosabellaria clandestinus* from the biogenic reef of Gulf of Khambhat, Gujarat was studied by Chaudhari et al. (2016). The Mandvi in the northern GoK coastline is wide, sandy with various landforms and distinct geomorphological features. 18 species of crustaceans, 15 species of polychaetes, one nemertea were investigated for their bioturbatory activities and the resultant micro-environment (Patel and Desai, 2009). From the sandy rocky intertidal zones of Mandvi, 25 gastropod species were reported by Kardani et al. (2014).

Mangrove Mudflats

The mangrove mudflats of Malvan had comparatively lesser species diversity (29 species) as compared to other intertidal habitat types (Parulekar, 1981). In the intertidal zones of Ansure creek at Ratnagiri, 17 benthic species were recorded dominated by the mollusc, *Cerithideopsilla cingulata* (Apte et al., 2014). A recent study on the polychaete diversity and seasonal variation in the mangrove covered intertidal area of Shirgaon, Ratnagiri revealed 6 species (Karhale et al., 2018). From the mangrove sites around Mumbai coast, 46 genera of macrobenthos belonging to Mollusca, Polychaeta, Brachyura, etc. were identified (Takar et al., 2020). Eighteen macrobenthic species including molluscs and brachyurans were reported from the mudflats of Gorai creek having extensive mangroves (Balasaheb et al., 2017). Kantharajan et al. (2017) identified 61 molluscan species from eight mangrove ecosystems along Mumbai coast. This included 46 species of Gastropoda, 14 species of Bivalvia, and 1 Polyplacophora. Higher presence of gastropods was attributed to the superior tolerance of this group to adverse conditions in mangroves. Only 9 polychaete species were identified from the vast intertidal mudflats of Thane creek that borders the Mumbai metropolis (Quadros et al., 2009). Expectedly the diversity indices were poor indicating low diversity and evenness.

Previously, Awati and Karandikar (1948) were the earliest to record three *Onchidium* species from the Mumbai coast. Three species of *Onchidium* were recorded along the Uran intertidal zone, *Onchidium verruculatum* and *Platevindex* sp. were abundant in marshy loamy substratum and *Onchidium peronni* was mostly associated with mangroves (Patil and Kulkarni, 2013). From the mangrove mudflats at Uran, Pawar et al. (2019) identified 86 macrobenthic species belonging to 45 families. At two intertidal locations along the Karanja creek in Maharashtra, a two year study reported high densities of the polychaete, *Perinereis cultrifera* along with other species of polychaetes, gastropods, crustaceans, pelecypods, etc. and it was concluded that the area supported good diversity and abundance of macrobenthos (Pawar and Kulkarni, 2009). Pawar et al. (2019) assessed the macrobenthic species composition and abundance from the intertidal zones of the Panvel creek.

Pandya (2013) investigated the biogenic structures of macrobenthos due to their bioturbatory activities in the tidal mudflats of Mahi estuary and coastal Gulf of Khambhat. The author suggested that the ichnological evidences can be used as indicators of animals even in their absence, which can be useful for biodiversity, ecological, and functional studies. Marine gastropod fauna from a large ship breaking yard of Alang was studied by Baxi et al. (2017) with prevailing environmental parameters. The intertidal region, despite being industrially influenced, sustained a good molluscan diversity with 77 species. Around 62 species of mangrove associated macrofauna consisting of crustaceans, gastropods, bivalves, polychaetes were recorded from three locations in the GoK (Saravanakumar et al., 2007). A study on the macrobenthos in mangrove zones of the Jakhau coast at the mouth of the GoK identified 27 macrobenthic species (Rohit et al., 2016). Another survey on the brachyuran diversity at 8 different locations in this area yielded 19 species belonging to eight families (Trivedi et al., 2012) where the crabs preferred open mud flats as compared to other habitats. Three crab species all belonging to the family Campantriidae from the intertidal mangrove areas of Jakhau and Lakhpat were described by Trivedi et al. (2017). From the mangrove rich intertidal zones of Mundra and Sanghi in the northern GoK, 13 and 17 gastropod species respectively were reported by Kardani et al. (2014). Dominant species were *Cerithidea cingulata, Cerithidea fluviatilis, Umbonium vestarium*, and *Assiminea* sp. Further north, three brachyuran crab species from the intertidal mangrove mudflats of Lakhpat and Jakhau located in the GoK mouth, were new records for Indian waters (Trivedi et al., 2017). Kachhiya et al. (2017) described seven species of hermit crab belonging to genus *Clibanarius* from intertidal zones of Gujarat of which six were first records from Indian west coast.

Coral Reefs

The Marine National Park and Sanctuary (MNPS) at Jamnagar, GoK has highly heterogeneous intertidal habitats that support multitude of species including corals. Sedimentation is a major natural threat in this area that adversely affects the coral species and its associated organisms. Several reef associated species have been listed by many workers (Kundu, 2001; Vaghela et al., 2010; Ramamoorthy et al., 2012; Adhavan et al., 2014). A new species of echiurid *Acanthobonellia pirotanensis* was described by Jose (1964) from Pirotan islands of the MNPS. Records of some rare species like *Bonnelia* (Echiuroidea), *Coeloplana* (Ctenophora), *Convoluta* and *Leptoplana* (Platyhelminthes), and *Lineaus* (Nemertea) were also made (Kundu, 2001). A checklist of opisthobranch (mollusca) fauna of GoK by Apte et al. (2010) reported 33 species belonging to 19 families of which 21 were new records to Gujarat and 13 were new records for the Indian coast. Hydroid diversity records (17 species) from the intertidal zones of Gujarat were earlier contributed by Thornely (1916) whereas Nagale and Apte (2013b, 2014) added new records of hydroids from the intertidal zones of GoK. Kamboj (2014) reported the occurrence of about 30 crab species and more than 200 molluscan species from the shallow intertidal areas and deeper waters of the MNPS. Five species of hermit crabs from the area were described by Jhala et al. (2017). Three species of sea anemone and one species of crab belonging to the rare category were reported by Mirza et al. (2017) from the GoK. Four sea anemones, one crab, and one polychaete species were described by Mirza et al. (2019) from another survey in the GoK. The detailed description and taxonomical details of two minute gastropods (*Pseudoliotia henjamensis* and *Cyclostrema ocrinium*) were reported from the MNPS by Mukhopadhyay et al. (2019). New taxon records for the GoK were contributed by Padate et al. (2018). Seventy-one species of intertidal amphipods belonging to 23 families were identified from the coralline zones of the MNPS (Srinivas et al., 2020). Five functional traits of these amphipods were also studied to understand the spatial patterns in amphipod functioning.

THE ESTUARIES AND CREEKS

The estuaries along the NW India are vulnerable to various anthropogenic activities and the resultant deteriorating ecology has raised concerns in the local administration and general public. They are also subject to pronounced natural variations caused by the distinct monsoon season resulting in significant freshwater inflow and flushing (Rao et al., 2019). Indian estuaries receive heavy freshwater discharge during the seasonal rainfall period that often exceeds the total capacity of the estuaries resulting in fresh water domination (Sarma et al., 2011). The strong flushing during monsoon alters the abiotic variables such as water temperature, pH, DO, and salinity causing natural stress in the estuarine environment (Feebarani et al., 2016). Significant freshwater inputs during monsoon cause reduction in the macrobenthic fauna of the estuary due to abrupt salinity fluctuations and increased turbidity (Alongi, 1990). The mortality and recruitment of macroinvertebrates during different seasons result in continuous seasonal variation in their abundance and composition.

The macrobenthos of Vashishti estuary in Maharashtra, mainly constituted by Polychaeta, Mollusca and Crustacea, was lower than that of the nearshore coastal system off the estuary (Nair et al., 1998). Benthic foraminifera were used to assess the ecological status of Gadhi and Ulwe estuaries by Kale (2017), wherein 23 live species were identified. The diversity and distribution of macrobenthos of Ulhas estuary and Thane creek were studied by Govindan et al. (1976), Athalye (1988), Athalye and Gokhale (1991), Gokhale and Athalye (1995), Mathew and Govindan (1995) and Athalye et al. (2003). In the abovementioned studies, Polychaeta, being the dominant macrobenthic taxon, was the focus group. A comprehensive account on the polychaete diversity of Indian estuaries was provided by Khan and Murugesan (2005). The first comprehensive seasonal study of the amphipod community structure and their spatio-temporal distribution in four estuarine (Ulhas, Amba, Savitri, and Kundalika) sediments of Maharashtra was provided by Srinivas et al. (2019b). The study investigated the species composition, diversity and distribution, functional traits of amphipods, and the influence of hydrosedimentological variables on community structure. Altogether, 57 amphipod taxa were recorded from these estuaries and majority of the taxa belonged to the functional group that was characterized by detritivory and domiculous behavior. Overall, 189 macrobenthic taxa were identified from the Ulhas, Amba, and Savitri estuaries (Mulik et al., 2020c) during the three seasons, wherein Polychaeta was the most dominant group.

Benthic studies along south Gujarat estuaries (Purna, Auranga, Ambika, Purna, Mindola, and Narmada) were undertaken (Varshney et al., 1981; Govindan et al., 1983, Dange, 2018). A study from Kharo creek, Kachchh (Gujarat) (Nigam and Chaturvedi, 2000) revealed 47 foraminiferal species of which 44 were benthic (only seven were live). The brachyuran crab diversity and distribution was studied out by Pandya and Vachhrajani (2013), Shukla et al. (2013), Gadhavi (2015) and Gadhavi and Vachhrajani (2015) in Mahi estuary, Gulf of Khambhat. Two species i.e., *Dotilla intermedia* and *Macrophthalmus brevis*, were recorded for the first time from this region. Meetei et al. (2020) investigated the macrobenthic community structure of Tapi estuary and recorded 49 taxa from 13 sites of this river wherein Mollusca was the dominant group.

THE COASTAL ZONE

The Indian west coast, especially, contributes to >70% of the marine capture fishery of the country (Ingole et al., 2009). In the Indian subcontinent, the integral relationship of the demersal fishery with benthos was well established by Harkantra et al. (1980) and Parulekar et al. (1982). These studies established a direct relation between benthic fauna and the distribution of exploited demersal fisheries, especially the shrimps and proposed that the quantitative data on benthos can be used as an efficient tool for the assessment of demersal fishery resources. Subtidal macrobenthic fauna off Dabhol, Maharashtra was studied by Ingole et al. (2002) who concluded that the coastal environment was favorable for feeding and breeding of commercially important prawn and crab species. Joydas and Damodaran (2009), investigated the NWI shelf and established that the benthic community played a key role in dictating the demersal fishery production of the vast western Indian shelf. Investigations in the inner shelf of central west Indian coast by Parulekar (1973) and Ansari et al. (1977) indicated presence of rich macrobenthic density near the coasts (dominated by polychaetes) that progressively decreased with depth. Kasinathan et al. (1974) studied macrofauna off Dwarka and Okha (GoK) that were characterized by different substrate types. A study in the subtidal region off Versova, Mumbai by Varshney et al. (1988) suggested that the macrobenthic species diversity was poor in nearshore stations due to the coastal pollution and higher in the unpolluted offshore region. A comprehensive work by Nair (2002) provided the status of flora and fauna of GoK including macrobenthic communities.

"Taxonomy" forms the "root" of any ecological study. Several workers have contributed toward taxonomic analysis of different macrobenthic groups along the NWI. Rao and Soota (1981) provided a list of 37 polychaete species collected from intertidal and subtidal habitats of various parts of Gujarat. Most of the collected species formed the first locality records from the respective areas while two species i.e., *Ceratonereis costae* and *Cirriformia tentaculata* were recorded for the first time from Indian waters. A new polychaete species, *Serpula indica* and six new records of *Serpula* sp. associated with variety of flora and fauna of Ratnagiri coast were reported by Parab and Gaikwad (1989). Kurhe et al. (2009) recorded 75 species of marine gastropods from Ratnagiri coast. Pati et al. (2015) provided an updated list of all the valid polychaete species with their distribution along the Maharashtra coast. A bi-operculate form of fouling polychaete, *Hydroides operculatus* was recorded from Diu by Kubal et al. (2012). Yokoyama and Sukumaran (2012) reported three polychaete species of family Spionidae i.e., *Paraprionospio cordifolia, Paraprionospio cristata*, and *Paraprionospio patiens* from NWI coast. The species were previously misidentified as *Paraprionospio pinnata.* Saiz et al. (2015) described a new subspecies of the sipunculid, *Phascolion pacificum denticulatum* from shallow waters off Malvan and Ratnagiri that represented the first record of any *Phascolion* species from the Indian coast. A new polychaete species, *Heterospio indica* was described from the NWI coast by Parapar et al. (2016). Mirza et al. (2017) reported three sea anemone and one crab species from the southern GoK. Recently Sivadas and Carvalho (2020) provided an updated checklist of annelid fauna from India comprising 727 species belonging to 334 genera and 72 families. The study also provided an overview of species with "erroneous" or "cosmopolitan" status. Nerurkar et al. (2020) provided species inventory of the gastropod family Nassariidae of India.

Limited macrobenthic studies were conducted along the NWI coast that provided information on the functional aspects. Sivadas et al. (2013) studied the functional diversity of macrofauna of Kalbadevi Bay, Ratnagiri, using three traits like feeding, mobility, habitat with temporal variations. Ingole et al. (2014) studied the feeding behavior of the macrobenthic fauna off Ratnagiri and Mumbai and observed that surface deposit feeders, carnivores and interface feeding spionids dominated the sediments during interfall monsoon. Sukumaran et al. (2016) also studied the feeding strategy of polychaetes and registered dominance of microphagous feeders, post the disturbance of cyclone Phyan, however, recovery was observed by re-establishment of multiple feeding guilds later. Vijapure et al. (2019a) studied five functional traits like feeding mode, motility, body size, bioturbation mode, and habitat of macrobenthic polychaete species. This is the only extensive study that employed "Fuzzy coding" procedure to understand the functioning of polychaete species of a large geographical zone.

EXTENSIVE ECOLOGICAL SURVEYS

In the past decade, many extensive macrobenthic studies were undertaken in broad geographic areas along the western continental shelves (Jayaraj et al., 2007, 2008; Joydas and Damodaran, 2009, 2014; Joydas et al., 2009; Anilkumar, 2017). These workers documented the macrobenthic diversity, distribution, abundance, and community structure in relation to the environmental influences on them. Parulekar and Wagh (1975) reported occurrence of 9 macrobenthic groups, dominated by Polychaetes from the NWI coast in the depth range of 20–140 m. Harkantra et al. (1980) studied the distribution, abundance of benthos, and sedimentological properties in depth range of 10–70 m from western Indian shelf (covering a decent length of NW coastline). The study revealed that the benthic diversity was rich in nearshore habitats while it decreased toward deeper waters. Joydas and Damodaran (2009) sampled a vast area of Indian west shelf, covering varying depths (30–1,000 m), along as many as 17 transects, covering the NWI shelf. The investigation recorded 165 species of polychaetes belonging to 33 families from the entire west Indian shelf while 106 were identified from the NW region exclusively.

Studies by Jayaraj et al. (2007, 2008) and Anilkumar (2017) were confined to the NWI shelf from Dwarka to Mumbai at a depth of 30–200 m. In the same area, Jayaraj et al. (2007, 2008) reported the presence of 133 polychaete species, belonging to 39 families. An extensive temporal sampling effort by Sukumaran et al. (2016) demonstrated the impact of tropical cyclone *Phyan* on the polychaete community of the Malvan MPA, followed by a complete recovery. Rengaiyan et al. (2017) carried out a study in the coastal waters of the south-eastern Arabian Sea, including Ratnagiri and Mumbai transects from the NWI coast. The study determined spatial variations in the polychaete assemblage that consisted of 16 families and 71 species, mainly governed by substrate composition. The diversity and distribution patterns of polychaete species along the NWI coastline were surveyed during the three major seasons and overall 140 species belonging to 42 families were identified by Vijapure et al. (2019a).

MOLECULAR STUDIES AND PHYLOGENY

The molecular approach not only assigns appropriate molecular tags to named or unnamed entities but also helps to reveal cryptic species and understand the role of cryptics in ecological and evolutionary processes. With the help of molecular lens, a number of studies worldwide have delineated cryptic species diversity of wide range of macroinvertebrate phyla (Kawauchi and Giribet, 2014; Nygren et al., 2018; Fauvelot et al., 2020) that were hidden under the umbrella of single morphospecies. Few molecular studies have been carried on the macrobenthos along the NWI coastal region. Magesh et al. (2014) redescribed a nereid, *Namalycastis glasbyi* from the Gorai creek, Mumbai with COI sequences. An interesting work by Joseph et al. (2014) revealed the presence of three cryptic species of limpet *Cellana karachiensis* from Veraval with different shell color banding pattern and indicated a close molecular resemblance to Oman species populations using the COI gene. The research was extended further by Joseph et al. (2016b) in terms of coverage of study area (five sites along Gujarat coast) and genetic markers (COI and 16S). The study demonstrated the existence of six haplotypes of *C. karachiensis* with phenotypic plasticity in the study region, suggesting initiation of the speciation. Phylogenetic analysis by Joseph et al. (2016a) proved efficacy of COI gene in distinguishing six zoanthid species from the Saurashtra coast. Detailed taxonomic investigation of a new polychaete species *Heterospio indica* from NWI coast by Parapar et al. (2016) was complemented with molecular analysis where 18S and COI genes were deposited in GenBank and represented the first sequencing of the species of *Heterospio* belonging to monogeneric family Longosomatidae. Rengaiyan and Ingole (2018) in the eastern Arabian Sea, sequenced 18S rDNA gene from 54 polychaetes species. Barcodes of five markers COI, 18S, 28S, cytb, ITS2 were generated from *Hydroides inornata* by Sun et al. (2017) from Ratnagiri for the phylogenetic analysis of *Hydroides operculata*-complex. Vijapure et al. (2019b) generated a comprehensive reference library of 58 COI barcodes of thirty-one polychaete species from NWI coast. The effectiveness of molecular characterization and phylogenetics in distinguishing the polychaete species, including invasive, pollution indicator *Streblospio* sp. was proven by this investigation. The genetic scrutiny facilitated the identification of a prospective new *Streblospio* species by segregating them from the closely related congeners. Trivedi et al. (2019) suggested a modified protocol for genomic DNA extraction and amplification of foraminifera *Ammonia* sp. from intertidal region of Nana Layja, GoK. In order to resolve the masked phenotypic differences of invaders and early detection of bioinvasion, DNA barcoding (Miralles et al., 2016; Sun et al., 2017), and metabarcoding (Rey et al., 2020; Westfall et al., 2020) efforts have proved effective worldwide. However, these advanced molecular methods will work effectively only if species are taxonomically identified and corresponding sequences are deposited in public reference library (Brasier et al., 2016) with constant updates of the repository (Curry et al., 2018).

APPLICATION OF MACROBENTHOS IN ENVIRONMENTAL MONITORING

Expectedly, most studies pertaining to the application of macrobenthos in environmental monitoring along the NWI coast have been concentrated in and around heavily urbanized and industrialized coastal zones like Mumbai, estuaries that are the hub of a plethora of anthropogenic activities or protected zones like the GoK MNPS. Further on, the various studies are discussed under broad anthropogenic categories for ease of comprehension.

Univariate and Benthic Biotic Indices

Univariate indices were applied more frequently in environmental studies, probably due to the ease of application (Quadros et al., 2009; Kulkarni et al., 2010, 2011; Sukumaran et al., 2013, 2014, 2016; Naz et al., 2016; Dias et al., 2018; Takar et al., 2020). Several diversity indices (Shannon-Wiener, Index of frequency, Rarity index, Dominance and Evenness Indices, Margalef Richness Index) were applied to the macrobenthic density in various studies (Varshney and Govindan, 1995; Pawar and Kulkarni, 2007; Pawar et al., 2019). A lot of interest has been evinced in the usage of Benthic Biotic Indices (BBIs) during the last two decades in evaluating the ecological quality status of marine and estuarine waters. The unawareness of the taxonomic characteristics of macrobenthos has impeded the application of benthic indices in assessing the ecological quality status of the tropical environment (Bigot et al., 2008). Studies investigating the efficacy of BBIs in determining the estuarine ecological status along the NWI India have gathered momentum in the past decade. AZTI's indices (AMBI/M-AMBI) were successful in discerning an appropriate ecological status of most of the salinity zones across four estuaries (Ulhas, Amba, Savitri, and Kundalika) (Mulik et al., 2017, 2020a,b; Dias et al., 2018) and coastal zones (Nandgaon coastal waters, adjacent to the atomic power station in Maharashtra, Sivaraj et al., 2014; Mumbai and Ratnagiri coastal waters; Sivadas et al., 2016). The exclusion of monsoon data and averaging the status of the non-monsoonal seasons for the efficient application of benthic indices was recommended. Data transformations were observed to have no influence on the efficiency of AMBI (Dias et al., 2018; Mulik et al., 2020b; Mulik et al., 2020a).The Benthic Opportunistic Polychaeta Amphipoda (BOPA) index was applied to tidal pool communities of a tropical shore to evaluate the impact of an oil spill on intertidal ecology (Sukumaran et al., 2014).

Habitat Modification and Loss of Species

A comparison of the polychaete diversity of the intertidal flats of the anthropogenically stressed Thane creek with past available data indicated the deteriorating environmental conditions of the creek had resulted in species substitution. The changing sediment texture and increase in hypoxic conditions and nutrients resulted in resilient polychaetes like *Namalycastis senegalensis* and *Polydora tentaculata* being replaced by even more pollution tolerant types like *Ceratonereis burmensis* (Quadros et al., 2009). Khot et al. (2016a) have remarked that many species which were earlier recorded from Maharashtra coast during the nineties were not observed in recent times possibly due to increasing anthropogenic stress. Vaghela et al. (2010) compared the intertidal chemistry and macrobenthic assemblages of the industrialized zone of Sikka, GoK with previous data and concluded that while the abiotic parameters remained unchanged, the macrofaunal diversity indices were significantly lower than that reported previously. This decline was attributed to the habitat modification brought about by the anthropogenic pressures in that area. An example of diminishing diversity due to anthropogenic pollution was provided by Jaiswar and Kulkarni (2005) from the heavily polluted Mahim intertidal zone where gastropod species were absent. Previously, from the same area, 90 species of gastropods were reported (Subrahmanyam et al., 1952). The absence of the previously reported *Aplysia benedicti*, from most of the coastal zones of Mumbai was noted by the authors who attributed this species loss to the severity of pollution in Mumbai.

Oil Pollution

North West India coast is especially vulnerable to oil spills on account of the heavy ship traffic, presence of oil terminals and Single Point Moorings (SPMs). An intertidal study conducted in the vicinity of the waste water discharge of an oil terminal at Uran revealed a localized marginal impact on intertidal organisms characterized by low biodiversity and dominance of stress tolerant macrobenthic species (Ram et al., 1998). Gajbhiye et al. (1995) studied the impact of oil spill on the biological characteristics and also reported complete recovery of marine environment off Murud, Maharashtra after a year from oil spill. An oil spill that occurred in the mouth region of Mumbai Harbor affected the rocky intertidal region of Colaba. A 15 month long study using macrobenthic diversity concluded that the area was only temporarily affected (Sukumaran et al., 2014). Another study that evaluated the impact of an oil spill on intertidal communities in the rocky beach of Uran, reported large scale mortality of brachyurans, decapods and large polychaetes at the high water line (Vijapure et al., 2016). However, the low water line had live macrobenthic groups like tanaidaceans, gastropods, amphipods, isopods, etc.

Discharge of Pollutants

While examining the health of the coastal marine environment around the Mumbai region, Zingde and Govindan (2000) observed increased macrobenthic abundance and reduced diversity. However, the impact of anthropogenic stress decreased from coast to offshore region and was minimal beyond 5 km from the coastline. Thane creek is amongst the major water bodies in an enclosed area in India and it disconnects Mumbai from mainland (Vijay et al., 2015). Various studies were carried out on the biotic and abiotic components of Thane creek (Virkar et al., 2004; Poojary et al., 2012; Quadros and Athalye, 2012; Athalye, 2013). It was reported that the water and sediment quality of Thane creek had deteriorated due to the discharges of pollutants from industrial and domestic sources. The shells of *Paphia textile* were observed to have been blackened by deposition of hydrogen sulfide due to domestic waste discharge at Girgaon along the Mumbai coast (Balasaheb et al., 2017). An assessment of the macrobenthic communities in the intertidal zones around an atomic power plant functional for more than four decades at Tarapur, Maharashtra concluded that the impact of discharges from the power plant was minimal (Kubal et al., 2016).

Harbors and Ports

Harbors and ports form the "hearts" of the coasts that aid in building a large share of the economy for the country. However, they are also areas where industrial and domestic effluents dominate the spectrum of anthropogenic inputs. A number of macrobenthic studies were undertaken in the harbor and port waters along NWI coastline (Ingole et al., 2009; Sukumaran and Saraladevi, 2009; Swami and Udhayakumar, 2010). Sukumaran and Saraladevi (2009) suggested spionids as a biological indicator for cost-effective and rapid environmental assessment of highly disturbed environments like ports. Ingole et al. (2009) examined the health status of three ports of central west India including Ratnagiri harbor from NWI coast. The stressed conditions at these areas were reflected by a number of biotic indices like Polychaete: Amphipod ratio, ABC curve, and geometric class abundance. Reduced gastropod diversities in areas subject to human intervention apropos to those away from such influences were observed at coastal areas of Uran which has a large marine container terminal (Pawar and Al-Tawaha, 2017a). Sukumaran et al. (2013) provided a valuable baseline data of macrobenthos and polychaetes (family level) along with prevailing environmental conditions in and around oil terminals situated in the GoK MNPS. The investigation concluded that although pockets of higher stress to benthic fauna could occasionally occur, the impact of oil and gas activities on macrobenthic communities in this eco-sensitive region was probably low.

Increased maritime transportation has in turn posed a risk to the environment from both pollution and bioinvasions (Seebens et al., 2013). Introductions of alien biota could pose a threat to local coastal and marine ecosystems with both economic losses and reduction in native biodiversity. Some biofouling studies have been undertaken along the maritime states of Maharashtra and Gujarat that have commercially important harbors and ports. Few studies have investigated biofouling by deploying different types of test panels/coupons at harbors of Vijaydurg (Srinivas et al., 1992, Mumbai (Swami and Chhapgar, 2002; Swami and Udhayakumar, 2010), and also at Bombay High (Venugopalan and Wagh, 1990). The busiest and commercially important Mumbai and Jawaharlal Nehru ports of Maharashtra were rigorously sampled by Gaonkar et al. (2010a) and 29 benthic species of hard substratum fauna and 14 associated fauna were recorded. *Protula tubularia*, a tube dwelling polychaete species, was a new introduction in the region. Invasive species of bivalve *Mytilopsis sallei* was also recorded from the enclosed habitats of the port. Another work in the Mumbai harbor, reported the introduction of 14 polychaete species (Gaonkar et al., 2010b). The study provided an account of bioinvasion and highlighted the risks of ship-mediated introductions and proliferation of tolerant invasive species in near future. Biofouling by the oyster, *Saccostrea cucullata* in mangrove forests of the Vashishti estuary was reported by Panchang (2014). Srinivas et al. (2019a) reported the first occurrence of a possible alien caprellid, *Phtisica marina* from the coastal waters off Vadinar and Sikka in Indian waters.

OVERVIEW AND GENERAL TRENDS

Some common trends of the macrobenthic assemblages of NWI that have emerged from the above compiled literature are (a) Polychaeta was the dominant macrobenthic group; (b) anthropogenic impact on macrobenthos was reported across all zones; (c) sediment texture and salinity were the major drivers of macrobenthic community structure in the coastal waters and estuaries, respectively; (d) typically, the mesohaline and oligohaline zones of all estuaries were anthropogenically impacted, hence subject to the "Estuarine Quality Paradox"; (e) distribution of tolerant species was largely influenced by salinity as they inhabited specific salinity zones; and (f) sharper distributional trends were visualized in more polluted zones vis-a-vis moderately disturbed types.

In the intertidal studies conducted along the NWI, Mollusca has received more academic interest than other groups like Polychaeta and Amphipoda. This phylum contributed majorly to the intertidal species diversity of the NWI coast. Molluscs were the major taxonomic group of macrobenthos observed at different intertidal areas elsewhere too (Barnes and Barnes, 2012; Petracco et al., 2012). Habitat preferences were evident with more gastropod species being reported from rocky shores than sandy and muddy areas. Alongi (1989) had opined that tropical sandy intertidal communities were dominated by brachyurans and bivalves and mudflats were inhabited by mainly polychaetes and microcrustaceans citing superior behavioral escape mechanisms to avoid environmental extremes. The present review indicated that this generalization may not work for this geographical zone. Sandy zones had abundance of polychaetes and crustaceans while mangrove mudflats had molluscs and gastropods.

Alongi (1989) compared tropical macrobenthic literature with temperate macrobenthic ecosystems and conceptualized that (a) tropical species diversities were not essentially greater in tropics on account of greater environmental stress and (b) infaunal communities were mostly comprised of opportunistic species. The species list compiled herein (**Supplementary Table 1**) of only macrobenthic invertebrates (which automatically excludes six meiobenthic phyla) included 2,078 taxa that belonged to 14 of the 28 known non-symbiont animal phyla that comprises all known marine benthic taxa (Widdicombe and Spicer, 2008), thus re-iterating that tropical ecosystems supported high biodiversity (Gray, 1997; Hillebrand, 2004). This also raises the possibility of novel species yet to be described from this biogeographical zone. From **Supplementary Table 1**, it was also evident that infaunal communities of NWI included more sensitive species (62.2%) than opportunistic (37.8%), thus diverging from the view held by Alongi (1989). The comparison in **Table 1** is indicative and may be viewed with the caveat that the studies have employed different sampling scales, sizes, and techniques. However, from the compilation of studies conducted in other geographical zones (**Table 1**), it appears that the first concept may not hold firm in the case of intertidal zones. The species diversities of intertidal zones presented in this study were certainly not lesser than that reported from temperate areas. In the case of estuaries, macrobenthic diversity along NWI was comparable with values reported elsewhere with Polychaeta being the dominant group in most of the studies (**Table 1**). Since the extensive macrobenthic studies in the coastal waters of NWI primarily focused on Polychaeta, the relative evaluation was based on this taxon. **Table 1** suggested that the diversity of Indian polychaete fauna was comparable or relatively lower than other regions. This could be due to the bias in sampling methodology, gear, stations surveyed. Spionidae was one of the common speciose families, in the majority of the studies. Spionidae is known to be one of the most ubiquitous benthic taxa (Fauchald, 1977; Blake, 1996) with cosmopolitan species assemblage (Dix et al., 2004).

In the intertidal zones of NWI, zonation patterns with relation to tidal levels and time of exposure were distinct with the high water zones being sparsely populated due to high degree of exposure and desiccation (**Table 1**). Higher species and functional diversities were observed at the lower intertidal zones of the GoK MNPS which had structurally complex habitats. The species distributional patterns in the intertidal zone were net effect of various physiological needs, limits and adaptations at different tidal levels (Srinivas et al., 2020). The type of substratum, shorter durations of exposure and moderate wave action of the intertidal zone contributed toward higher distribution of species rather than abiotic parameters like water temperature, pH and salinity (Misra and Kundu, 2005). Similarly, Karhale et al. (2018) concluded that the intertidal polychaete abundances were not dictated by water quality parameters. However, others (Anandan et al., 2003; Rohit et al., 2016; Pawar and Al-Tawaha, 2017c) have reported that intertidal macrobenthic biomass and abundances were influenced by water and sediment quality parameters. Other reported driving factors influencing the diversity, distribution and abundance of intertidal organisms were food availability, organic carbon, pheophytin, and sediment texture (**Table 1**). In general, the spatial patterns of intertidal assemblages in all the studies have by and large followed the general model described by Menge and Sutherland (1987) who postulated that in stressful environments, organisms were directly regulated by environmental stress and less impacted by competition-predation activities.

While a panoply of factors have been ascribed importance in influencing macrobenthic community structure of intertidal zones, all studies agreed on the primacy of salinity and sediment structure as determinants of macrobenthic assemblages of estuaries along NWI (**Table 1**). The significance of the salinity and sedimentary texture in influencing macrobenthic community structure has been well documented in the estuaries of north Queensland, Australia (Inglis and Kross, 2000), estuaries of South Africa (Teske and Wooldridge, 2003), Schelde estuary, NW Europe (Ysebaert et al., 2003; Hampel et al., 2009), Nueces estuary, Texas (Ritter et al., 2005), Amazon estuary, Brazil (Silva et al., 2011) and Yangtze estuary, China (Yan et al., 2017). This was collectively attributed to the drought and flood events that change salinity and sediment properties and thus impacting macrobenthic communities and the functioning of the estuarine ecosystems. This suggests that the salinity gradient is the most influential parameter of estuaries belonging to different biogeographical regions, climatic conditions and diverse macrobenthic species composition. Majority of estuaries along the NWI coast were distinctly impacted to various extent by

TABLE 1 | Comparison of the dominant macrobenthic taxa and major factors exerting influence on the macrobenthic community structure from some indicative studies reported elsewhere with investigations included in this review (indicated by the shaded region).

Location	Species richness (Dominant taxa)	Major factors	References
Rocky intertidal areas			
Lough Hyne Marine Nature Reserve, Ireland	39 (Mollusca)	Species migration	Davidson et al., 2004
Changdao Archipelago, Shandong Province, China	68 (Mollusca)	Sediment type	Wang et al., 2009
Yangtze River,China	20 (Gastropoda)	–	Dong et al., 2016
3.5–13.5° South East Pacific, Peru	239 (Mollusca)	Nutrients, water temperature	Ibanez-Erquiaga et al., 2018
Malvan, Maharashtra, India	148 (Polychaeta)	Intertidal zonation	Parulekar, 1981
Gopnath, Mahuva and Veraval, Gujarat, India	32 (Mollusca)	–	Raghunathan et al., 2003
Mumbai coast, Maharashtra, India	50 (Gastropoda)	–	Datta et al., 2010
Ratnagiri coast, Maharashtra, India	127 (Gastropoda)	Intertidal zonation	Kurhe et al., 2014
Saurashtra Coast, Gujarat, India	67 (Arthropoda)	Intertidal zonation	Trivedi et al., 2014
Uran coast, Maharashtra, India	170 (Gastropoda)	Salinity, temperature, SGS, OM	Pawar and Al-Tawaha, 2017c
Sandy intertidal areas			
Barnstable harbor, MA, United States	47 (Polychaeta)	Temperature, SGS	Whitlatch, 1977
Manukau Harbour, New Zealand	95 (Polychaeta, Mollusca)	SGS	Pridmore et al., 1990
De Panne beach, Belgium	39 (Polychaeta)	Intertidal zonation	Degraer et al., 1999
Shuangtaizi Estuary, China	29 (Mollusca)	SGS, OM	Zhang et al., 2016
Port of Mandvi, Gujarat, India	33 (Polychaetea, Crustacea)	Intertidal zonation	Patel and Desai, 2009
Akshi village, Raigad, India	47 (Mollusca)	–	Kurve and Kurve, 2010
Kalbadevi beach, Ratnagiri, India	56 (Polychaeta)	SGS, phytopigment, Corg	Sivadas et al., 2012
Northern gulf of Kachchh, Gujarat, India	36 (Gastropoda)	Substratum, wave action	Kardani et al., 2014
Mangrove intertidal areas			
Port Swettenham, Malaysia	85 (Polychaeta, Gastropoda)	Tidal regime, SGS, pH	Sasekumar, 1974
Sydney, Australia	29 (Mollusca, Crustacea, Annelida)	–	Kelehar et al., 1998
Mai Po, Hong Kong	46 (Crustacea, Gastropoda)	Salinity, season	Lui et al., 2002
Sydney, Australia	22–31 (Oligochaeta,Polychaeta)	No effect of sediment	Chapman and Tolhurst, 2004
Gulf of Kachchh, Gujarat, India	62 (Polychaeta)	Temperature, pH, salinity	Saravanakumar et al., 2007
North coast of Mumbai, Maharashtra, India	59 (Gastropoda, Bivalvia)	Anthropogenic activities	Balasaheb et al., 2017
Mumbai, Maharashtra, India	61 (Mollusca)	Anthropogenic activities	Kantharajan et al., 2017
Mumbai coast, Maharashtra, India	46 (Bivalvia, Gastropoda, Polychaeta)	Physico-chemical parameters	Takar et al., 2020
Coral Intertidal areas			
Coast of Argentina,Southwestern Atlantic	118 (Bivalvia, Polychaeta)	Coralline turf, coralline fronds	Liuzzi and Gappa, 2008
Carigara Bay Eastern Visayas, Philippines	121 (Mollusca)	–	Dandan and Diocton, 2019
Larak Island, Persian Gulf	20 (Polychaeta, Mollusca, Arthropoda)	Reproductive behaviour, SGS	Tavanayan et al., 2021
Pirotan Island, Gujarat, India	89 (Gastropoda)	Anthropogenic activities	Ramamoorthy et al., 2012
Gulf of Kachchh, Gujarat, India	71 (Amphipoda)	Intertidal zonation	Srinivas et al., 2020
Estuaries			
Douro estuary, Spain	19 (Oligochaeta, Polychaeta)	Metals	Mucha et al., 2003
Schelde estuary, NW Europe	47 (Polychaeta, Amphipoda)	Salinity	Ysebaert et al., 2003
Lima estuary, NW of Portugal	54 (Bivalvia)	Salinity, SGS	Sousa et al., 2006
Odiel-Tinto estuary, SW Spain	86 (Polychaeta)	Salinity, SGS, Corg	Sánchez-Moyano et al., 2010
Caeté estuary, Brazil	83 (Polychaeta)	Salinity, SGS, hydrodynamics	Silva et al., 2011
Subaé, Paraguaçu and Jaguaripe estuary, Brazil	87 (Polychaeta)	Salinity, SGS	Barros et al., 2012

(Continued)

TABLE 1 | Continued

Location	Species richness (Dominant taxa)	Major factors	References
Kundalika estuary, Maharashtra, India	78 (Polychaeta)	Salinity	Dias et al., 2018
Ulhas estuary, Maharashtra, India	86 (Polychaeta)	Salinity, nutrients	Mulik et al., 2020c
Amba estuary, Maharashtra, India	118 (Polychaeta)	Salinity	Mulik et al., 2020c
Savitri estuary, Maharashtra, India	72 (Polychaeta)	Salinity	Mulik et al., 2020c
Coastal			
Northwest coast of Mexico	210 (Polychaeta; Spionidae)	SGS, depth, Corg	Rodríguez-Villanueva et al., 2003
Levantine coast of Turkey	184 (Polychaeta; Spionidae)	SGS, depth, Corg	Mutlu et al., 2010
Black Sea	301 (Polychaeta)	Salinity, food availability	Surugiu et al., 2010
Portuguese continental shelf	319 (Polychaeta; Spionidae)	SGS, OM	Martins et al., 2013
Aegean and Levantine coasts of Turkey	358 (Polychaeta; Spionidae)	–	Çinar and Dagli, 2013
Northwestern coast of Baja California, Mexico	231 (Polychaeta; Spionidae)	–	Hernández-Alcántara et al., 2017
Northwest Indian shelf	133 (Polychaeta)	SGS, temperature, DO	Jayaraj et al., 2007
Western Indian Shelf	165 (Polychaeta; Spionidae)	Depth, DO, temperature	Joydas and Damodaran, 2009
South-eastern Arabian Sea	71 (Polychaeta)	SGS	Rengaiyan et al., 2017
Northwest Indian coast	140 (Polychaeta; Spionidae)	SGS, DO	Vijapure et al., 2019a

SGS, sediment grain size; OM, organic matter; Corg, total organic carbon; DO, dissolved oxygen.

anthropogenic activities affecting the resident macrobenthos (Govindan et al., 1983; Shukla et al., 2013; Kale, 2017; Dias et al., 2018; Mulik et al., 2020c). It was also discerned from various studies that anthropogenic factors influenced macrobenthic assemblages mostly in the poly-mesohaline and oligohaline zones where the salinity was lower leading to what experts have termed as "Estuarine Paradox" (Elliott and Quintino, 2007). The role of both the natural and anthropogenic factors in determining the estuarine macrobenthic community structure have been documented in other tropical and temperate estuaries as well [Douro estuary, Spain, Mucha et al. (2003); Lima estuary, Portugal, Sousa et al. (2006); Odiel-Tinto estuary, Spain, Sánchez-Moyano et al. (2010); Cachoeira River estuary, Brazil, Ourives et al. (2011); Santos estuary, Brazil, Abessa et al. (2019)]. Sediment texture appeared to be the overwhelming consensual determinant parameter of macrobenthos structure in the subtidal zones along the NWI coast which resonated well with studies in other geographical zones too (**Table 1**). Sediment characteristics were found to govern the distribution pattern of polychaete taxon in different habitats, followed by some hydrological parameters. It was thus evident from **Table 1** that both sedimentary and hydrodynamic parameters (with different subset of variables) have significant role in determining the diversity and distribution of polychaete community structure in different geographic locations.

Extinction rates are higher in tropical species as they are more susceptible for disturbance which is referred to as the "tropical biodiversity crisis" (Vamosi and Vamosi, 2008). Documenting species loss due to various stressors and comprehending the ramifications are daunting tasks by itself; the difficulty compounds in the absence of inventories of extant species. Declining biodiversity around urbanized zones like Mumbai was clearly evidenced by decline in gastropod species from 1893 (227 species) to 1996–1998 (67 species). Similarly, pelecypod species reduced from 199 species to 30 species during the same duration (Jaiswar and Kulkarni, 2005). Datta et al. (2010) reported that fewer species than those reported previously were observed in the rocky intertidal zones of Mumbai and attributed this loss partly to the anthropogenic activities. In the Mahim creek and Bay area, where previously 90 species of gastropods were recorded by Subrahmanyam et al. (1952), gastropods had completely disappeared as the areas became polluted due to indiscriminate disposal of industrial and domestic effluents leading sometimes to the development of hydrogen sulfide (Jaiswar and Kulkarni, 2005). Similar decline of species richness due to increasing pollution have been have been reported by Simboura et al. (1995). Such biodiversity losses may lead to loss of genetic diversity, functioning and sustainability of ecosystems in the long run (Battaglia et al., 1980; Danovaro et al., 2008).

The NWI coast has a marked monsoonal season which influences the abiotic parameters of the coastal waters and underlying sediments thereby influencing the macrobenthos (Alongi, 1989). Different distribution studies of macrobenthic fauna reviewed in this compendium have unequivocally stated that non-monsoonal months favored a more conducive environment for the macrobenthic diversity and functionality as compared to the monsoon season. Higher values of macrobenthic abundance, diversity and biomass were obtained during the non-monsoonal seasons in many studies (Pawar and Kulkarni, 2009; Sukumaran et al., 2014; Pawar et al., 2019; Mulik et al., 2020c, Takar et al., 2020). The pre and post-monsoon periods present a more stable environment that is suitable for macrobenthic organisms, already stressed from the natural variations in the environment. An exception to this general trend was visualized from the mangrove, rocky, sandy intertidal zones in the northern Gulf of Kachchh. Here the gastropod densities were higher during monsoon, which was contradictory to the general trend of lower macrobenthic standing stock during monsoon observed for the west coast of India. One reason could be the less precipitation occurring in the arid Kachchh area resulting in little or no fluctuation in salinity (Kardani et al., 2014). However, Vijapure et al. (2019a) have also observed lower macrobenthic abundances during monsoon in the coastal waters of GoK even though signatures of upwelling were not recorded here.

The extended work by Joydas and Damodaran (2014) reported Oxygen Minimum Zones (OMZ) at 200 m depth of entire western shelf of India that was more pronounced in the northern continental shelf edge. Decline in macrobenthic density, biomass, polychaete species richness and diversity with the dominance of species belonging to polychaete families like Spionidae, Cirratulidae, and Paraonidae were reported in the OMZ. Levin (2003) extensively studied macrobenthos from OMZ around the world that included Indian western shelf enclosing NWI coast. The investigation stated that the species residing in OMZ could survive in hypoxic environments through morphological and physiological adaptations for improved oxygen uptake. Besides the OMZ, seasonal hypoxic events have become a fact of concern worldwide (Briggs et al., 2017) that alter both the structure and function of benthic communities. The episodic event generally involves proliferation of soft bodied annelids, especially opportunistic polychaetes that can tolerate the extreme environmental conditions (Levin et al., 2009). Vijapure et al. (2019a) reported that the monsoonal coastal hypoxia had altered taxonomic and functional composition of polychaete assemblages along NWI coast. It was evident from the comparison presented in **Table 2** that Polychaeta was the dominant macrobenthic group in the hypoxic settings described globally. The overview suggested that hypoxia tolerant polychaete species mainly belonged to the genera (Family) *Paraprionospio* (Spionidae) and *Cossura* (Cossuridae) that are morphologically and physiologically adapted to sustain low oxygen levels (Lamont and Gage, 2000; Levin, 2003).

Several studies conducted in temperate zones have recommended the application of multiple indices to get a better assessment of the ecological status of estuaries considering that the macrobenthic communities are complex and geographically unlike (Salas et al., 2006; Kröncke and Reiss, 2010; Wetzel et al., 2012) and that indices were originally developed for particular stressors (Afli et al., 2008). However, the NWI studies as well as a number of other tropical estuaries have successfully applied AMBI for ecological quality status assessment (Borja and Tunberg, 2011; Valença and Santos, 2012; Brauko et al., 2015; Mulik et al., 2017, 2020a,b). The ecological assignments made available by European databases for the application of AMBI may not work in a tropical setting. Therefore, some of the Indian studies required the re-assignation of species to appropriate ecological groups based on expert judgment and knowledge of study area as recommended by Teixeira et al., 2010. In the Ulhas estuary, the opportunistic species, *Streblospio gynobranchiata* was classified to EG V from EG IV (Mulik et al., 2017, 2020a,b). In another study from the Mandovi and Zuari estuaries, *Magelona* sp. (II), *Protodorvillea* sp.(II), and *Staurocephalus* sp. (IV) were considered as EG III (Sivadas et al., 2016) so as to improve the sensitivity of AMBI. The tropical estuaries along the NWI are generally affected by heavy urbanization and industrialization (Dias et al., 2018; Mulik et al., 2020c). Hence, it becomes challenging to derive reference conditions for these estuaries because of heterogeneous sediment unavailability of sites with minimal impact, lack of historical data and absence of numerical models (Feebarani et al., 2016; Sivadas et al., 2016). Considering the above mentioned criteria, in the estuaries of NWI, the reference conditions are set by increasing the highest diversity and richness to 15% for each salinity zone as a preventive approach for the reliable use of the M-AMBI index (Borja et al., 2012).

GAPS AND LIMITATIONS

It is well known that intertidal habitats provide the most heterogeneous habitats than any other realm and thus supports high species diversity. Investigations into the intertidal macrobenthic diversity were plentiful and more intensive than other habitats possibly due to the ease of access to the study areas, higher species diversity and also lower costs involved in sampling. Of the 1,113 species reported from the intertidal zones, 438 belonged to Gastropoda, 140 to Polychaeta, 105 to Bivalvia, whereas no species records were available for groups like tanaidaceans, isopods, etc. Thus it was concluded that while the expertise of macrobenthic taxonomy was limited to some major groups, groups like nematodes, cumaceans, sergestids, mysids, tanaidaceans, and sipunculids were largely ignored. This could be due to the paucity of taxonomical experts and available taxonomical keys. Also, it is possible that groups like gastropods and bivalves were more abundant, visibly sized and therefore easier to collect. Many of the molluscan species were identified from empty shells too.

It was also observed that the intensity and type of sampling and the availability of taxonomical keys could significantly increase the species diversity statistics. For example, in the comparatively unpolluted rocky beach at Colaba in Mumbai, Sukumaran et al. (2014) identified 70 macrobenthic taxa. The previous study by Datta et al. (2010) reported 48 species, however in this account only the epifauna were accounted for and the identification of many groups were not resolved upto species. These kinds of disparities make any logical long term comparison and evaluation of macrobenthic diversity redundant.

Contrary to the easily accessible intertidal regions, assessment of subtidal regions along the coast and offshore habitats requires specialized logistical support thus making it an expensive task (Fitch and Crowe, 2010). Majority of the efforts were made by the Council of Scientific and Industrial Research-National Institute of Oceanography (CSIR-NIO) as a leading organization to undertake this challenge along with few other regional research/educational institutes. Due to the requirement

TABLE 2 | Responsive species to hypoxia in different geographical settings (Shaded region indicates studies from NWI).

Location	Responsive Species	References
Louisiana continental shelf	Polychaete: *Paraprionospio pinnata*	Qu et al., 2015
Southeastern Arabian Sea	Polychaete: *Paraprionospio cordifolia*	Ingole et al., 2016
Mississippi Bight	Polychaetes: Maldanids, *Cossura delta*, *P. pinnata*	Rakocinski and Menke, 2016
Louisiana continental shelf	Polychaete: *Cossura soyeri*, Mollusc: *Nuculana acuta*	Briggs et al., 2017
Valparaiso Bay, Continental shelf of central Chile	Polychaete: *Cossura chilensis*	Soto et al., 2017
Kochi, southwest coast of India	Polychaetes: *P. pinnata*, *C. coasta*, foraminifera: *Bolivina* sp.	Pandiya rajan et al., 2021
Central west Indian coast	Polychaete: *Paraprionospio pinnata*	Ingole et al., 2014
Indian western continental shelf	*Prionospio pinnata*, *P. cirrifera*, *P. cirrobranchiata*, *Aricidea fauveli*, *Paraonis gracilis gracilis*, *Cirriformia* sp. 1	Joydas and Damodaran, 2014
Northwest Indian coast	Polychaetes: Maldanid *Leichone* sp., *Cossura coasta*, Spionid *Paraprionospio cristata*, *Paraprionospio* sp.1, *P. patiens*	Vijapure et al., 2019a

of extensive and exhaustive sampling efforts, many of these studies have relied on one time sampling. However, this has lead to data lacunae of seasonal fluctuations of benthic structural and functional diversity patterns. As the NWI region is subject to upwelling related hypoxia during monsoon, it is important to capture the macrobenthic response during this characteristic phenomenon.

Many of the studies investigating macrobenthos in the NWI coast have been concentrated around certain regions, whereas large tracts remain to be investigated. Few places than others have attracted more studies i.e., Malvan, Ratnagiri Mumbai, Uran, Sikka-Vadinar etc. It appears that areas subject to severe pollution on account of increasing urbanization like Mumbai and areas of high biodiversity like the Malvan Marine Sanctuary and the GoK Marine National Park have been studied more frequently than other locations. Also, the proximity of a coastal zone to biological research/educational institutions probably encouraged more studies. For example, Mumbai and Uran studies were mostly undertaken by scientific personnel belonging to research/educational institutions present in the city. The macrobenthic ecology of coastal zones between Malvan and Ratnagiri, Ratnagiri and Uran, Mumbai to Saurashtra, Gulf of Khambhat, inner and northern shores of Gulf of Kachchh remain mostly unknown.

The estuarine macrobenthos are very much under surveyed, which is surprising considering that the estuaries of the NWI zone have industrial and urban clusters along its banks and receives most of the disposals of these establishments. Some sort of information on macrobenthos is available from 17 estuaries out of 43 major estuaries along the NWI. However, detailed macrobenthic species level data are available only for four major estuaries (Ulhas, Amba, Savitri, and Kundalika) along the Maharashtra coast. In tropical ecosystems, there is still an urgent need to identify consistent spatio-temporal patterns and influencing parameters of estuarine benthic assemblages in order to understand the ecological processes which in itself is a major challenge in ecology. It was also observed that the studies dealing with macrobenthic assemblages in estuarine systems often sample pockets from the entire estuary, making it difficult to understand the broad general patterns. Estuarine organisms are frequently confined to distinct zones of salinity gradients, resulting in clear distribution patterns (Wolff, 1983). Hence, it is of utmost importance to know the distribution pattern of macrobenthos along the entire salinity gradient of the estuary to understand the general functioning of these ecosystems. Only few studies on the complex interaction between chemical parameters, sediment dynamics and hydrodynamics in controlling the estuarine macrobenthic distribution patterns of NWI have been undertaken thus far.

Despite the Indian coast being rich in macrobenthic diversity, only a handful of molecular studies have been carried so far. The contribution of sequence depositions from multiple loci of Indian macrobenthic species at GenBank is meager. Thus, there exists a pressing need than ever before, to widen the taxonomic coverage and capture the information in the genetic database. It is important to add molecular tools like DNA barcoding and metabarcoding techniques along with traditional microscopy for improving accuracy and speed of species analyses. Toward this, a well- equipped library of DNA barcodes needs to be constructed for the NWI coast. The literature from NWI region suggests that DNA metabarcoding approach has not been implemented along this region so far. Hence, the sensitivity and breadth of the biodiversity assessment should be revitalized with advanced, sensitive and cost effective, high throughput DNA sequencing technique like metabarcoding in future. From the literature, it was also evident that very few biofouling studies have been undertaken in the past in the area. Ignoring problems caused by biofoulers and invasive introductions could pose a threat to harbors and ports with potentially unending tide of invaders. Hence, these studies need to be undertaken in future with adaptation of advanced molecular techniques as timely detection of biofoulers will allow us to apply preventive measures to stop the aggregation of macrofoulers.

From the literature, it was apparent that many macrofaunal groups from the NWI coast still remain understudied and therefore the marine biodiversity of India is presently under-reported (Venkataraman and Wafar, 2005). In order to improve this state, awareness for taxonomic studies in India requires to be cultivated in the research communities. Building taxonomic capacity at national, regional and sub-regional levels with relevant faunal identification guides and manuals in both printed as well as electronic versions is also a crucial measure. While putting efforts in compiling the database for the present study, we also faced problems in obtaining printed manuals that were not available readily online. These manuals are not only important for researchers focusing on a particular faunal group of interest but also for cultivating the taxonomy interest in contemporary generations of researchers. Unfortunately, these valuable literature are often conserved in institutional custody and unavailable to readers in the present era of digitization. Hence, it is important to facilitate the online availability of valuable old literature/manuals/identification keys/thesis to improve the ease of taxonomic research. While this account has tried to compile all topic related information available via the digital media, efforts were taken to obtain the hard copies of those manuscripts that were unavailable. A perusal of the literature review of many of the older papers made one conclude that a considerable amount of data was available in the form of Ph.D. thesis, majorly which were not available in a digital format. Therefore, such data which was not in a published form were left out in this compilation which may underestimate the number of species reported.

Tropics with warmer temperatures are known to boost early larval developments and hence shorter pelagic larval durations than the temperate regions (Álvarez-Noriega et al., 2020). However, the century is facing a rapid climate change where issues like global warming is not only altering the reproduction patterns, spawning time of benthic marine invertebrates (Bronstein et al., 2016) but also affecting their sensitive planktonic life stages (Nguyen et al., 2012). Hence, compilations such as this one will help researchers and ecologists to undertake studies on reproductive traits of already known marine invertebrate taxa of the ecoregion and recognize the alterations in the life history patterns and trace the changes in the future, if any, due to climatic events. Oceanographic processes also have a huge impact on larval dispersal including upwelling phenomenon (Bashevkin et al., 2020). It would be interesting to understand benthic larval ecology in upwelling regions along NWI coast that is not undertaken thus far.

A noteworthy lacunae would be the absence of long term consistent times series seasonal data which could be used to derive long term changes and trends in ecology due to the climate change and anthropogenic interventions. Even in areas like Mumbai, Malvan, GoK, etc., which have been studied more intensively, the sampling size and methodology, analytical, and statistical tools applied were varied in different studies making long term comparisons cumbersome and difficult. The most commonly used diversity index was (*H*'). However, some studies employed the base as $\log_2$ whereas others applied $\log_{10}$. Additionally, Shannon index have been calculated on various data formats i.e., species, genus, family abundances or even a mixture of various taxonomical levels resulting in problematic comparisons. The limitations imposed by discrete studies, such as those reviewed here, will have to be overcome by undertaking carefully planned improved observational studies at known biodiversity hotspots and also at areas previously not studied. In conjunction with observations on the macrobenthos, it is equally important to measure similar abiotic parameters using same standard methodologies so as to derive meaningful conclusions. Long -term monitoring studies are a must for evaluating changes in the ecosystem and ascribe reasons for these changes (anthropogenic vs climate change), test the efficacy of present biodiversity regulations, assign "biodiversity hot spot" to a region and to measure recovery processes from disturbances (Crowe et al., 2000; Hawkins et al., 2002).

Extensive monitoring studies with a broad geographic coverage require enormous resources like project funding, sampling effort and several man-hours to generate the species level data. Economic constraints have taken a toll on biomonitoring programs in several countries, despite their importance (Borja and Elliott, 2013). Likewise, there has been a lack of funding (that is likely to happen more than before due to the pandemic situation) from the Indian government to undertake large-scale environmental monitoring programs. This may limit the number of transects surveyed and hamper the sampling periodicity that will ultimately end up in data lacunae. A possible solution to this is to apply the Taxonomic Sufficiency (TS) approach that can effectively reduce the analytical man-hours and resultant monetary costs for species identification. However, extreme caution needs to be taken to avoid loss of information while employing TS (Fiori and Soares-Gomes, 2002; Bevilacqua et al., 2009). Dissimilar response of the constituents within higher taxa to environmental changes may also limit the applicability of TS (Bertasi et al., 2009). Despite the practical applicability of this approach, only two studies have employed TS approach in the Indian waters using macrobenthic polychaetes thus far (Joydas and Damodaran, 2013; Vijapure and Sukumaran, 2019). Both the TS studies indicated that generic as well as family level data could reliably detect the distribution patterns analogous to that of species, in spite of differences in sampling areas/depths, periodicity and influential data transformation types. Despite apprehensions of loss of information on biodiversity by several studies (Terlizzi et al., 2003; Giangrande et al., 2005), the TS worked successfully in this region due to consistent and sizable proportion of monotypic polychaete taxon and uniformity in responses of the constituents of higher polychaeta.

Of late, multivariate indices like AMBI and M-AMBI are considered to be more effective in evolving the ecological status of estuaries and coasts (Sivaraj et al., 2014; Sivadas et al., 2016, Mulik et al., 2017, 2020a; Dias et al., 2018) and are more reliable than the application of *H*'. Few studies have applied any BBI other than the Shannon Diversity index. For accurate environmental assessment it is important to apply a BBI which is impervious to seasonal perturbations, especially in coastal zones of NWI, where many authors have emphasized the deleterious effects of the monsoon on benthic species diversity and abundances. As taxonomical records keep updating, some species may be merged under a common species name. For example, Quadros et al. (2009) reported a decline in the abundance of polychaete species, *Nereis glandicincta* and *Ceratonereis burmensis* in the intertidal zones of the heavily polluted Thane creek. At present both species have been merged into a single species, *Neanthes glandicincta* on WoRMS. Further there are considerable alterations and updations to other species as well. Almost all studies referred in this review have dealt with either species/group diversity/species descriptions/distribution with some giving species checklists. Studies dealing with the molecular taxonomy, phylogenetics, benthic food web dynamics of macrobenthos are completely missing. Hence it would be beneficial if the next level of benthic ecological studies involved these omitted aspects of benthic research.

A good proportion of information for this review was extracted from non-Science Citation Index (SCI) journals particularly those pertaining to the intertidal zones (**Figure 2C**). Publishing in SCI journals may need to be encouraged so that the entire information is peer-reviewed in the best possible manner that can provide reliable baseline for future studies. Some of the studies considered for this review, while reporting high number of species have not included the checklist in their reports making it difficult for this compilation to add to the cumulative species list. Some authors have also included groups like seaweeds in their macrofaunal list. And finally, it is quite possible that the macrobenthic species of NWI may be vastly under reported due to lack of well planned surveys. The NWI coast, particularly has potential for new species occurrences (Vijapure et al., 2019a). Hence, there exists a scope for exploring the undescribed diversity with taxonomic as well as molecular efforts that will aid the future ecological studies effectively. As evident from the above compilation of literature, great effort needs to be put forward for improving taxonomic research in India.

AUTHOR CONTRIBUTIONS

SS, TV, and JM contributed to the conception, design, collation and analyses of data, and preparation of the manuscript. HR contributed to the collation of data, data analysis, and preparation of table and figures. SS wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.671245/full#supplementary-material

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Bacterial and Fungal Diversity in Sediment and Water Column From the Abyssal Regions of the Indian Ocean

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The deep sea is the largest environment on Earth, comprising important resources of commercial interest. It is composed of a wide variety of ecosystems, which is home to often unique organisms that are yet to be described. The deep-sea is one of the least studied environments, where research is strongly linked to technological access and advances. With the recent advances in the next-generation sequencing and bioinformatics tools, there is an enhanced understanding of microbial diversity and ecological functions in deep sea. Multidisciplinary programs are being undertaken to investigate into microbial communities in diverse marine environments. As compared to other Oceans, the deeper parts of Indian Ocean are still poorly sampled and studied for bacterial, and more so fungal diversity. The studies reporting usage of modern sequencing tools to describe uncultured microbial diversity have seen a rise in numbers in the last decade. In this review, we summarize the important findings of research works carried on bacterial and fungal diversity from the abyssal regions of the Indian Ocean and provide our views on possible future paths.

Keywords: benthic, bioinformatics, deep sea, metagenomic, next-generation sequencing

INTRODUCTION

The Deep-Sea – What Lies Beneath?

The abyssal plain (also referred to as the deep-sea) is normally located between 3000 and 6000 m deep in the global ocean. It includes biogenic sediments, ocean waters from the bathypelagic (ranging from 1000 to 4000 m) and abyssopelagic (ranging from 4000 to 6000 m) zones, and occasionally manganese nodules (da Silva et al., 2013; Corinaldesi, 2015). The deep-sea environment plays important roles in nutrient cycling, carbon sequestration and biomass production (Barbier et al., 2014; Danovaro et al., 2014, 2017). Light intensity decreases with depth within this region, and photosynthetic production is arrested due to the absence of sunlight. The temperatures nearing freezing (−1°C to 4°C) and the paucity of organic matter at the seafloor bed are the key features of the deep sea that control benthic productivity and biomass (Jørgensen and Boetius, 2007). Characteristically, the biota of the deep-sea are "food limited," since it is solely dependent on organic matter input from the photic zone (Danovaro et al., 2017).

Despite the "harsh" conditions, there is a large variety of deep-sea organisms. The diversity of deep-sea benthic communities has intrigued researchers. Over the last two decades, deep-sea explorations have led to the discovery of novel ecosystems and diverse microbes. Gartner et al. (2011) studied the effect of hydrostatic pressure on the microbial communities from the deep sea sediments of Eastern Mediterranean and revealed that Gamma-proteobacteria had selective advantage over others under mimicked nutrient supply in elevated pressure conditions. Marine microbial communities are important for the structure and dynamics of food webs, global biogeochemical cycles, and the remineralization of organic matter (Jørgensen and Boetius, 2007; Parvathi et al., 2020; Wei et al., 2020). The microbial processes occurring along the seafloor are essential in sustaining primary and secondary production in the water column. In deep-sea sediments, the most significant fraction of taxonomic richness and biomass is contributed by the Bacteria and Archaea, which represent around 90% of the total benthic biomass. Multidisciplinary efforts across the globe are undertaken to characterize the microbial communities in different marine environments. For example, the *Sorcerer II* Global Ocean Sampling expedition (2003–2004) carried out in the Atlantic and Pacific Oceans; the TARA Ocean expedition (2009–2013) carried out in the Atlantic, Pacific and Indian Ocean. Despite this, the deep-sea environment remains one of the most understudied ecosystems on earth.

The total microbial counts in the marine sediments is estimated to be 2.9×10^{29} – 5.4×10^{29} cells, contributing to 3.6% of the entire living biomass on Earth (Kallmeyer et al., 2012; Parkes et al., 2014), and bacterial endospores in the upper kilometer of marine sediment are estimated between 2.5×10^{28} and 1.9×10^{29} (Wörmer et al., 2019). Stratification of the microbial communities is dependent on the depth of the sediment; wherein cell counts are inversely proportional to depth (Inagaki et al., 2003; Parkes et al., 2005; Inagaki et al., 2006; Biddle et al., 2008; Fry et al., 2008; Teske, 2013; Ciobanu et al., 2014; Inagaki et al., 2015; Chen et al., 2017). Additionally, microbial abundance is inversely proportional to the age of marine sediments and is higher in organic-rich anoxic sediments than oligotrophic oxic sediments (Kallmeyer et al., 2012; D'Hondt et al., 2015). Studies carried out on pore-water suggested that the microbial activity in the sub-seafloor environment is extremely low, with means respiration rates ranging between 2.8×10^{-18} and 1.1×10^{-14} moles of electrons per cell per year (D'Hondt et al., 2004; Hoehler and Jørgensen, 2013; D'Hondt et al., 2015).

Although efforts are there to develop newer methods for studying deep sea organisms, the biodiversity in abyssal plains remains one among the least understood (da Silva et al., 2013). In addition, commercial mining of marine mineral resources has regained attention in recent times due to rising global demands and the belief that marine resources would someday replace land-based resources (Molari et al., 2020). The Indian Ocean has attracted attention as a potential mining site for polymetallic nodules; enriched in minerals such as manganese, iron, copper, cobalt, nickel and rare-earth elements (Wegorzewski and Kuhn, 2014). This has increased the curiosity among the scientific community in gaining insights about 'sedimentary life' in the Indian Ocean. The Indian Ocean is the third largest ocean, yet it remains among the most underexplored oceans in terms of biodiversity, especially microbial diversity (Hood et al., 2009; Wang et al., 2018). Mining of the deep sea nodules might result in perturbations in the deep-sea environments (Miller et al., 2018); hence, it is important to explore and record the biota present in deep-sea sediments. Among the biota present, microbes are considered important as they are believed to play a key role in organic matter mineralization, thereby affecting the global biogeochemical cycles and carbon sequestration capacity of oceans. This review is aimed at highlighting the bacterial and fungal diversity derived from the abyssal deep-sea environments (including water, hydrothermal vents, polymetallic nodules and sediment) of the Indian Ocean.

BACTERIAL DIVERSITY OF THE ABYSSAL REGIONS OF THE INDIAN OCEAN INFERRED USING CULTURING METHODS

The deep sea microbes are difficult to isolate due to poor understanding about their nutritional requirements and lack of novel methods and incubation conditions. Despite this, considerable efforts have been invested in culturing of deep-sea bacteria, mainly to under their taxonomic novelty, physiological adaptations and biotechnological potentials (Zengler et al., 2002).

The first study, by Johnson et al. (1968), investigated the bacterial composition in the sediments of the Indian Ocean. After this, extensive studies have been carried out to gain an understanding about the topography and benthic life in deep-sea sediments of the Central Indian Ocean Basin (CIOB) (Parulekar et al., 1982; Chandramohan et al., 1987; Nath and Mudholkar, 1989; Sharma and Rao, 1992; Sharma and Kodagali, 1993; Ingole et al., 1999; Ingole et al., 2001). The microbial standing stock in the CIOB was measured (Raghukumar et al., 2001) and the results showed a relatively homogenous distribution of bacteria, indicative of possible active microbial processes and a stable ecosystem. The bacterial counts in the sediments were found to be in the range 10^{10}–10^{11} cfu g^{-1}, higher than those found in sediments of the Pacific and Atlantic Oceans. Furthermore, perturbations in the CIOB stimulated the retrievable bacterial counts from sediments. This resulted in an increase in the culturable bacterial diversity, wherein *Acinetobacter* and *Moraxella* species that were dominant before the disturbance were replaced by *Acinetobacter*, *Coryneforms*, *Enterobacter*, *Marinococcus*, *Pseudomonas,* and *Staphylococcus* (LokaBharathi and Nair, 2005). Disturbances in the sediment caused by anthropogenic influence could result in a re-emergence of the buried sedimentary organic material accessible for microbial degradation. This could result in the alteration of bacterial communities therein and thereby impact the ecological process within the ecosystem.

In recent times, researchers have focused on isolation, cultivation and screening of deep-sea microbes for biotechnological applications. Aiming to identify bacteria with potential biotechnological applications, Gawas et al. (2019) isolated 43 heterotrophic bacteria belonging to the phyla Proteobacteria, Actinobacteria, and Firmicutes, from nodule associated sediments of the first generation mining site and preservation reference zone of the CIOB. This is among the first reports of *Oceanobacillus* (Firmicutes) and *Brachybacterium* (Actinobacteria) in the CIOB, although these genera have been previously reported from deep-sea sediments of the Pacific and the Atlantic Oceans. Padmanaban et al. (2019) investigated the metabolic potential of bacteria isolated from deep-sea sediments of the Indian Ocean, mainly from the Bay of Bengal and the Andaman Sea. They isolated and screened 34 bacteria for their potential to produce extracellular hydrolases such as caseinase, α-amylase, urease, gelatinase, lipase, DNase and the production of anti-bacterial metabolites against human clinical pathogens. These 34 bacterial isolates were affiliated to Firmicutes, Proteobacteria and Actinobacteria, with Firmicutes and Actinobacteria being the dominant phyla, which was also confirmed through metagenomic studies.

Fifty-one bacteria capable of degrading polyaromatic hydrocarbons, belonging to 29 genera, were isolated from the deep seawater column (3946 – 4746 m) above the South-West Indian Ridge. The majority of the isolated bacteria were grouped under Proteobacteria (88%), followed by Bacteroides (6%), Actinobateria (4%), and Firmicutes (2%). Of these isolates, 34 isolates showed the ability to use phenanthrene as a sole carbon source, wherein 20 isolates belonged to Alpha-proteobacteria within the genera, *Alterierythrobacter*, *Citricella*, *Erythrobacter*, *Kaistia*, *Lutibacterium*, *Maricaulis*, *Martelella*, *Mesorhizobium*, *Novosphingobium*, *Pseudomonas*, *Phenylobacterium*, *Roseovarius*, *Rhodobacter*, *Salipiger*, *Stappia*, *Sphingopyxis*, *Sphingomonas*, *Tistrella*, and *Thalassospira*. Within the Gamma-proteobacteria, isolates belonged to the genera *Alkaligens*, *Alkanovorax*, *Halomonas*, *Idiomarina*, *Marinobacter, Pseudoidiomarina,* and *Pseudomonas. Muricauda* and *Salegentibacter* (Bacteroides), *Bacillus* (Firmicutes) and *Microbacterium* (Actinobacteria) also showed phenanthrene-degrading potential (Shao et al., 2015). Moreover, in addition to bioprospecting, isolation of bacterial cultures could yield novel findings with respect to new species within the environment or an undocumented functional role. Yuan et al. (2009) isolated a novel hydrocarbon-degrading bacterium from the deep sea waters of the Indian Ocean and named it *Novosphingobium indicum*, referring to the Ocean from which the type strain was isolated. Another study reported a unique lineage of *Aquificales* in the Edmon hydrothermal vent and the Kairei vent field of the Central Indian Ridge (Reysenbach et al., 2002). *Bhargavaea cecembensis*, a novel Gram-positive, sporulating bacterium, was isolated from sediments of the Chagos-Laccadive ridge system in the Indian Ocean (Manorama et al., 2009). *Acuticoccus sedimeni* was reported from sediments collected from Indian Ocean from a depth of 2946 m (Lai et al., 2019). This strain was isolated from sediments enriched with poly aromatic hydrocarbons (PAHs) as sole source of carbon and energy. This also shows that the novel strains obtained from deep-sea sediments could have applications in field of bioremediation too like PAH degradation. Cao et al. (2017) reported a novel thermophilic sulfur-reducing bacterium, *Desulfurobacteium indicum* from sulfide sample collected from a depth at 2771 m from a high temperature hydrothermal vent in the Indian Ocean. Ren et al. (2014) reported a Mn-oxidizing bacterial strain, *Fulvimarina manganooxydans* from a Fe and Mn-rich hydrothermal plume in the south-west Indian Ocean. Wang J. et al. (2020) reported a novel planctomycete, *Gimesia benthica*, from the bottom water samples collected with a multi-corer from a depth of 4213 m in Northwest Indian Ocean. Most of the Planctomycetes strains are known for their role in global carbon and nitrogen cycles (Wagner and Horn, 2006). Shivaji et al. (2007) and Bhadra et al. (2008) have reported novel *Brevibacterium oceani* and *Microbacterium indicum* species, respectively, from Chagos Trench in Indian Ocean. Qiu et al. (2021) reported a halotolerant *Halomonas sedimenti* from the deep sea sediment (2699 m) of the Southwest Indian Ocean. Xie et al. (2021) have reported a novel hydrogen and sulfur-oxidizing chemolithoautotroph, *Sulfovorum indicum*, from deep sea hydrothermal plumes in the Northwestern Indian Ocean. This reiterates the fact that there is a lot more to be explored from the abyssal depths of the Oceans, and it is a very good source of novel bacterial isolates for understanding the diversity and also useful for biotechnological applications.

All the research findings discussed above underline the importance of traditional isolation and cultivation of bacteria, as they allow the possibility of genome sequencing and bioprospecting for biomolecules and industrially relevant processes. Although isolation and culturing of bacteria help us provide holistic information regarding the microorganism, this may not always be feasible due to the stringent nutritional requirements and limited methods available for their isolation. For these reasons, researchers are now focusing on culture-independent methods to gain insights into diversity and ecological roles of deep sea life forms. Additionally, these tools allow for detection of the viable but non-cultivable fraction of the sedimentary microbial community (Polymenakou et al., 2009; Schauer et al., 2010).

BACTERIAL DIVERSITY IN THE ABYSSAL REGIONS OF THE INDIAN OCEAN BASED ON CULTURE-INDEPENDENT METHODS

Despite technological advances, only 5% of the ocean floors have been scientifically explored. There is a lacuna in understanding the distribution patterns, diversity and ecological roles played by microbes within the infinite seafloor (Corinaldesi, 2015).

Describing marine microbial communities is vital to catalog the genetic diversity in a region and understand the functional roles of these organisms in the ecological processes of marine ecosystems. Deep-biosphere bacteria are extremely difficult to cultivate due to their incredibly slow growth rates, hence the number of pure cultures available for in-depth studies does not exceed a few hundred (Jørgensen and Boetius, 2007). Microbial communities interact with each other to exchange nutrients, biochemical products and chemical signals. The presence of this complex community cannot be detected based on traditional cultural methods. Recent developments in molecular fingerprinting techniques have been instrumental in providing new insights into bacterial diversity and their response to environmental heterogeneity (Varliero et al., 2019). The use of molecular methods has made it possible to analyze microbial communities without the conventional isolation and culturing techniques. Molecular analysis using rRNA as a marker began in the early 1970s based on Sanger's sequencing. This was replaced by the next-generation sequencing (NGS) techniques such as Illumina, Ion Torrent and Roche/454, which are reliable and efficient tools for studying microbial communities. **Table 1** summarizes select studies carried out using NGS in the last decade from the abyssal regions of the Indian, Pacific and Atlantic Oceans. This shows that abyssal regions of the Indian Ocean are less explored as compared to the Pacific and Atlantic Oceans.

Marine bacteria, being metabolically diverse, significantly impact the nutrient composition and energy flow in both:

TABLE 1 | Un-cultured bacterial and fungal diversity reported (last 10 years) from the abyssal regions of different Oceans using different next-generation sequencing platforms.

S. No.	Area	Sample	Depth (m)	NGS platform	Gene	References
1	Indian Ocean	Sediment	5000	454 pyrosequencing	16S rRNA (V6)	Zinger et al. (2011)
2	Indian Ocean	Sediment	2784	454 pyrosequencing	16S rRNA (V3–V4)	He et al. (2016)
3	Indian Ocean	Sediment	4800	Illumina HiSeq	16S rRNA (V3–V4)	Wang et al. (2018)
4	Indian Ocean	Sediment	3000	Illumina MiSeq	16S rRNA (V3–V4)	Parvathi et al. (2020)
5	Indian Ocean	Sediment	3776	Illumina MiSeq	16S rRNA (V3)	Sinha et al. (2019)
6	Indian Ocean	Water	3000–4000	Ion S5 TM XL	16S rRNA (V3–V4)	Gao et al. (2021)
7	Indian Ocean	Sediment	2086	Illumina MiSeq	ITS1	Zhang et al. (2016a)
8	Indian Ocean	Sediment	2813	Illumina HiSeq	ITS	Xu et al. (2018)
9	Pacific Ocean	Sediment	3953	454 pyrosequencing	16S rRNA (V6)	Zinger et al. (2011)
10	Pacific Ocean	Sediment	2982	454 pyrosequencing	16S rRNA (V3–V4)	He et al. (2016)
11	Pacific Ocean	Fe-Mn nodules	3573	Illumina MiSeq	16S rRNA (V4)	Zhang et al. (2015)
12	Pacific Ocean	Water	2665	Illumina HiSeq	16S rRNA	Anantharaman et al. (2016)
13	Pacific Ocean	Sediment	4970–5620	Illumina MiSeq	16S rRNA	Dong et al. (2016)
14	Pacific Ocean	Water	3000	Illumina MiSeq	16S rRNA	Lindh et al. (2017)
15	Pacific Ocean	Sediment	4200	Illumina MiSeq	16S rRNA	Lindh et al. (2017)
16	Pacific Ocean	Water	3000	Illumina HiSeq	16S rRNA	Li et al. (2018)
17	Pacific Ocean	Sediment	2980	Illumina HiSeq	16S rRNA	Wu et al. (2019)
18	Pacific Ocean	Water	5000	Illumina MiSeq	16S rRNA	Wei et al. (2020)
19	Pacific Ocean	Sediment	4129	Illumina MiSeq	16S rRNA (V3–V4)	Molari et al. (2020)
20	Pacific Ocean	Water	4000	Illumina HiSeq	16S rRNA (V3–V4)	Wang M. et al. (2020)
21	Pacific Ocean	Sediment	6000	Illumina HiSeq	16S rRNA (V3–V4)	Wang M. et al. (2020)
22	Pacific Ocean	Sediment	4700–10902	Illumina MiSeq	16S rRNA (V4–V5)	Hiraoka et al. (2020)
23	Pacific Ocean	Sediment	3156–7837	Illumina MiSeq	16S rRNA (V3–V4)	Zhang et al. (2021)
24	Pacific Ocean	Sediment	4500, 5315	Illumina HiSeq	ITS2	Xu et al. (2019)
25	Pacific Ocean	Sediment	3500–5500	Illumina HiSeq	ITS2	Luo et al. (2020)
26	Pacific Ocean	Sediment	5527	Illumina HiSeq	ITS1	Yang et al. (2020)
27	Pacific Ocean	Sediment	3200	Illumina MiSeq	18S rRNA (V7–V8)	Rojas-Jimenez et al. (2020)
28	Atlantic Ocean	Water	4600	454 pyrosequencing	16S rRNA (V6)	Zinger et al. (2011)
29	Atlantic Ocean	Sediment	3860	454 pyrosequencing	16S rRNA (V6)	Zinger et al. (2011)
30	Atlantic Ocean	Water	4000	454 pyrosequencing	16S rRNA (V6)	Ghiglione et al. (2012)
31	Atlantic Ocean	Water	2990	454 pyrosequencing	16S rRNA (V3–V4)	He et al. (2016)
32	Atlantic Ocean	Sediment	2949	454 pyrosequencing	16S rRNA (V3–V4)	He et al. (2016)
33	Atlantic Ocean	Sediment	3760–4869	Illumina MiSeq	16S rRNA (V3–V4)	Varliero et al. (2019)
34	Atlantic Ocean	Sediment	2728	Ion Torrent PGM	16S rRNA (V3–V4)	Queiroz et al. (2020)
35	Atlantic Ocean	Water	4000	Illumina MiSeq	16S rRNA	Coutinho et al. (2021)
36	Atlantic Ocean	Fe-Mn Crust	4000	Illumina MiSeq	16S rRNA (V3–V4)	Bergo et al. (2021)
37	Atlantic Ocean	Sediment	2720	Ion Torrent PGM	ITS	Nagano et al. (2017)
38	Atlantic Ocean	Sediment	3734	Illumina MiSeq	ITS1	Vargas-Gastélum et al. (2019)

the sediments as well as the overlaying water column; thus, governing the critical biogeochemical cycles (Arrigo, 2005; Fennel et al., 2005; Emerson et al., 2010). Distinct biological patterns have been revealed in marine environments due to the advances in sequencing techniques. For example, Proteobacteria is found to be dominant in the Atlantic Ocean sediments and the deeper depths of the Arctic and Pacific Oceans (Fuhrman et al., 1993; Schauer et al., 2010). Seasonal changes have been reported in the Pacific Ocean, with Bacteroidetes being more abundant than Proteobacteria in winter (Suh et al., 2014). Compared to other Oceans, studies with respect to the Indian Ocean are in their infancy (Wang et al., 2016).

The first culture-independent molecular study in the Indian Ocean was carried out in the Edmon hydrothermal vent (3300 m) on the Central Indian Ridge (Hoek et al., 2003). Sequencing of 150 clones of the amplified 16S rDNA revealed the incidence of 26 unique bacterial phylotypes. The majority of the clones were affiliated with the Epsilon-proteobacteria. Among the Epsilon-proteobacteria, more than 40% of the phylotypes were closely related to *Nautilia lithotrophica*, a thermophilic chemoautotrophic sulfur reducer isolated from deep-sea vents; while the majority of the remaining sequences clustered with uncultured clones. Epsilon-proteobacteria displays wide metabolic diversity, but most are hydrogen- and sulfur-oxidizing chemolithoautotrophs. They play significant roles in carbon and sulfur cycles and are also dominant in the active hydrothermal vents in the Pacific and Atlantic Oceans. One of the 150 clones analyzed was identified as *Hydrogenobacter thermolithotrophum*, which is the first report of the incidence of this genus in deep-sea hydrothermal environments.

Studies on sediments obtained from the Afanasiy- Nikitin seamount in the Equatorial East Indian Ocean revealed a unique bacterial diversity depending on the depth of the sediment (Khandeparker et al., 2014). Sixty-four clones obtained from the top surface sediments classified into Firmicutes (63%) and Gamma-proteobacteria (37%). Within the Firmicutes, *Bacillus* was dominant, followed by *Dolosigranulum*. *Pseudomonas,* and *Shigella* or in some cases *Escherichia* were prominent among the Gamma-proteobacteria. The 58 clones obtained from deeper sediments (200 m) were dominated by the Gamma-proteobacteria (66%) represented by *Pseudomonas* and *Enterobacteriaceae,* followed by Beta-proteobacteria (34%) represented by *Limnobacter* and *Burkholderiales*. Hence, it can be said that bacterial communities are stratified based on the depth of the sediment. Gamma-proteobacteria members are metabolically versatile and abundant in various environments, including the cold deep ocean, hydrothermal region, nodule province, polluted continental area, and water column. Gamma-proteobacteria is known to mediate sulfide reduction and oxidation, which is one of the most important microbial chemosynthetic pathways in deep-sea hydrothermal ecosystems.

Li et al. (2014) examined the microbial diversity inhabiting the exterior (black Fe-Mn oxides) as well as the interior (white carbonates) of carbonate sediments of the Southwest Indian Ridge (SWIR). Analyses of the 16S rRNA gene of the 145 clones indicated that diverse bacteria are associated with the exterior and interior of the sediments. Ninety-three phylotypes were obtained from the clone analysis, among which a large majority belonged to the Proteobacteria (alpha, beta, gamma, and delta), followed by the Acidobacteria (22.07%), Actinobacteria and Bacteroidetes (6.9%); and a small fraction classified as Chloroflexi, Deferribacteres, Nitrospirales, Planctomycete, Verrucomicrobia, and uncultured taxonomic groups WS3. *Nitrospira*, which plays a role in nitrogen cycling in the conversion of nitrites to nitrates, is widespread in marine environments and has been reported from metal-rich sediments of Pacific Ocean. Deferribacteres and Nitrospirales are known metal reducers and could play a role in the formation of metal oxides. These bacterial groups detected are common in deep-sea sediments and participate in various biochemical processes such as recycling nutrients (carbon, nitrogen, sulfur) and trace metals (iron and manganese).

Another study conducted in the SWIR, analyzed the bacterial communities within inactive hydrothermal vents (Zhang et al., 2016b). Samples were collected at two different sites for comparison using the Illumina MiSeq2500 platform, and it was found that the Proteobacteria and Bacteroidetes were dominant at both locations. The major classes in the two samples were α-proteobacteria, followed by Gamma-proteobacteria, Sphingobacteria, Beta-proteobacteria, and Flavobacteria. Alpha- and Gamma-proteobacteria are known to mediate sulfide reduction and oxidation. Sphingobacteria and Flavobacteria are known degraders of biopolymers in sedimentary organic matter. Thus, the bacterial community identified could be involved in nitrogen and sulfur cycling and metal metabolism, suggesting that they may play important ecological roles in inactive deep-sea hydrothermal vents (Zhang et al., 2016b). Furthermore, the diversity and abundance varied between the two samples isolated from the two adjacent sites (E 50.9277°, S 37.6251°, and E 50.9643°, S 37.6174°), suggesting that the ambient environmental parameters probably influence the formation of microbial communities, even within the same oceanic ridge. Environmental conditions are considered to have a strong influence on microbial biogeography (Li et al., 2009). Several studies in Pacific and Atlantic Oceans have also previously shown that spatial distances affect microbial diversity (Papke et al., 2003; Whitaker et al., 2003; Martiny et al., 2006; Ramette and Tiedje, 2007; Schauer et al., 2010; Zinger et al., 2011).

Bacterial diversity from rare earth elements-rich sediment (4800 m) in the Indian Ocean was characterized using the Illumina HiSeq platform (Wang et al., 2018). The results revealed the occurrence of 49 different phyla, among which the most abundant bacteria were Proteobacteria, with Gamma-proteobacteria being present in all sections of the core; followed by Firmicutes (27.95%), Actinobacteria (5.45%), Bacteroidetes (4.03%), Cyanobacteria (1.71%), and Chloroflexi (0.68%). The major genera included, *Lactobacillus*, *Profundibacterium*, *Shigella*, *Escherichia, Pseudoalteromonas*, *Vibrio*, *Propionibacterium*, *Alteromonas*, *Enterobacter*, *Sphingomonas*, and *Staphylococcus*. The results also revealed that the microbial diversity at this site was less sensitive to changes in the vertical depth within the sediment core; however, the abundance of bacteria changed with the vertical depth profile. *Pseudomonas* and *Alteromonas*, which are predicted to play a role in building matrix outside cells to induce or control mineralization, suggest that these bacteria possibly play a role in the formation of polymetallic nodules in the Indian Ocean. Another study using the Illumina MiSeq platform was conducted on sediments from the Bay of Bengal region of the Indian Ocean also showed that bacterial diversity within the deep-sea sediments is quite similar (Parvathi et al., 2020). Proteobacteria dominated the sediments, followed by Firmicutes, Cyanobacteria, Bacteroidetes, Actinobacteria, Chloroflexi, and Planctomycetes. Alpha-proteobacteria was the most abundant class among Proteobacteria, followed by Gamma-proteobacteria and Delta-proteobacteria, and are known to mediate sulfide reduction and oxidation. Planctomycetes have a suggestive role in methane oxidation. *Wolbachia* belonging to α-proteobacteria was found to be the dominant genus in the deep-sea. Functional analysis revealed that dehalogenation activities were higher in *Wolbachia* dominated sediments, hinting at the role of these bacteria in biogeochemical cycles of chlorine, iodine, bromine and halogenated carbon substrates.

All of these findings portray the importance of diversity studies within an environment. Bacteria are highly adaptive and sensitive to environmental perturbations. The bacterial community structure differs depending on the features of the environment, the nutrient profiles, the vertical zonation, and the interior and exterior of sediments obtained from the same ecological niche. Therefore, cataloging the diversity of bacteria is of paramount importance to fully understand the processes taking place in a particular environment. Unfortunately, the Indian Ocean is yet to be explored, and a large portion of the Indian Ocean remains under-explored and under-sampled (**Figure 1**).

FUNGAL DIVERSITY IN THE ABYSSAL REGIONS OF THE INDIAN OCEAN

Compared to the exploration of bacterial diversity in the Indian Ocean, fungal diversity studies are still in their infancy. The first report on the isolation of deep-sea fungi from a

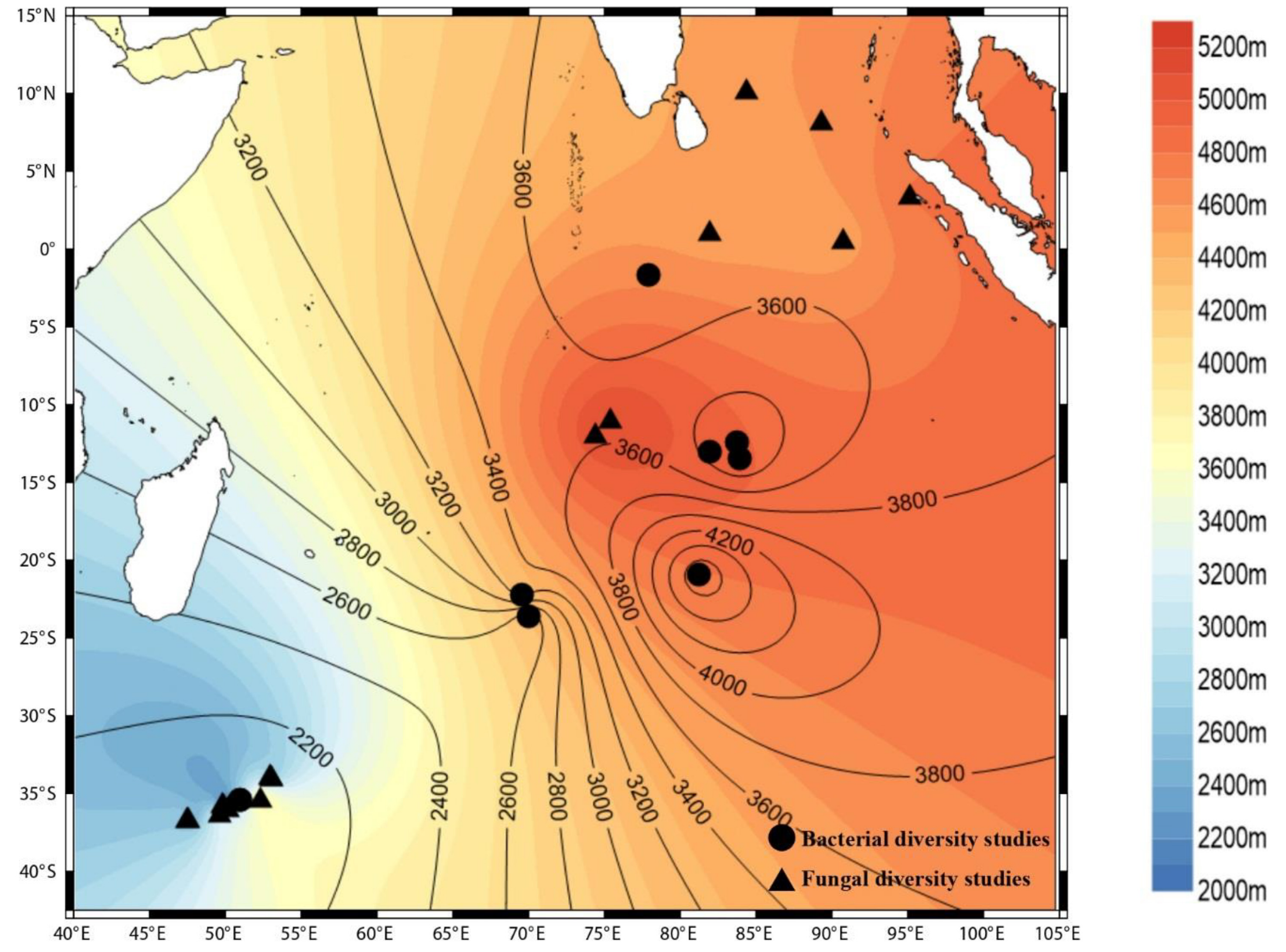

FIGURE 1 | Culture-independent studies carried out at various locations in the Indian Ocean. The circles depict the bacterial diversity studies; the triangles depict the fungal diversity studies. (Surfer, Golden software LLC).

depth of 4450 m from the Atlantic Ocean was published by Roth et al. (1964). Although the role and diversity of deep-sea fungi remains largely ambiguous, their ecological significance is being recognized. Numerous studies have reported isolation of fungal isolates from deep-sea environments including hydrothermal vents and the Mariana Trench (Takami et al., 1997; Gadanho and Sampaio, 2005; Nagahama et al., 2006, 2008). Fungal diversity in the deep-sea realm has been investigated by both traditional culturing and modern culture-independent methods.

The ability of fungi to adapt/thrive under deep-sea conditions in the Indian Ocean was first discussed by Raghukumar and Raghukumar (1998). Wherein two isolates, *Aspergillus ustus* and *Graphium* sp. obtained from calcareous shells in the sediments from the Arabian Sea and the Bay of Bengal, demonstrated conidial germination and hyphal growth at conditions mimicking the deep-sea environment, i.e., high pressures and low temperature. Following this, another study, based on culturing, reported the presence of fungi at a depth of 5904 m in the Chagos trench of the Indian Ocean (Raghukumar et al., 2004). They comprised non-sporulating as well as sporulating forms, identified as *Aspergillus sydowii*, and present up to 370 m depth of the core subsection mbsf. A total of 181 fungal cultures were isolated from 5000 m depth in the CIOB, most of which were terrestrial sporulating species belonging to *Aspergillus*, *Penicillium*, and *Cladosporium* genera (Damare et al., 2006). The presence of *Aspergillus terreus* in the sediments was confirmed in these studies using immunofluorescence techniques. Singh et al. (2010) isolated 16 filamentous and 12 yeast cultures, belonging to the Ascomycota and Basidiomycota, from sediments of the CIOB at depths of 5000 m. This was the first report of isolation of filamentous fungi (*Capronia, Exophiala, Sagenomella*, and *Tilletiopsis*) from deep-sea sediments, showing that the Indian Ocean basin is a host to a unique diversity of fungi.

The first culture-independent report on fungal diversity from the Indian Ocean sediments was published by Singh et al. (2011). A total of 39 OTUs, belonging to 32 fungal taxa, majorly the Ascomycota and Basidiomycota, were retrieved from 5000 m depth. Within the Ascomycota, members of Sordariomycetes, Dothideomycetes, and Saccharomycetes were identified. Members belonging to Tremellomycetes, Microbotryomycetes, and Ustilaginomycetes were identified within the Basidiomycota. This study revealed heterogeneity with respect to the fungal diversity in deep-sea sediments. In a comparative study using culture-dependent and culture-independent techniques, it was found that the fungal diversity altered vertically with the increase in the depth of the sediment (Singh et al., 2012a,b). Furthermore, 19 fungi belonging to 12 genera were obtained via culture-based methods, wherein a higher diversity was obtained (42 unique OTUs) using sequencing techniques. This was also confirmed in another study in the Eastern Indian Ocean, wherein 45 OTUs were obtained using sequencing approaches compared to 20 culturable fungal phylotypes (Zhang et al., 2014). The culturable fraction was dominated by filamentous fungi, including *Aspergillus*, *Penicillium*, *Simplicillium*, *Cladosporium*, and *Phoma*. Moreover, six of the twenty culturable fungal isolates and 20 of the 45 OTUs were first time reports from deep-sea sediments. A more significant fraction of fungal phylotypes was recovered using targeted environmental sequencing than the conventional culturable techniques from deep-sea sediments of hydrothermal vents in the Southwest Indian Ridge (Xu et al., 2018). In this study, 79 fungal taxa were identified from sediments, whereas isolates belonging to only 14 taxa could be cultivated. In a recent study, 42 OTUs and 10 different fungal phylotypes belonging majorly to *Aspergillus*, *Penicillium*, *Ophiocordyceps*, and *Phoma* could be recovered (Tang et al., 2020). All the findings discussed here suggest that sediments from the abyssal regions of the Indian Ocean are dominated by Ascomycota and Basidiomycota. Fungi detected in deep-sea sediments are similar to those present in the terrestrial environment, indicating the possibility of connectivity between these two environments, mediated by either aerial dispersal or terrestrial runoff.

CONCLUSION

The deep-sea is a largely unexplored area and is attracting attention in recent times due to the presence of polymetallic nodules. The mining of polymetallic nodules found in the Indian Ocean has been viewed as an alternative to terrestrial mining; therefore, it is important to understand the marine life existing in these regions. However, the knowledge about the inhabitants of the deep-sea ecosystem is limited. Furthermore, information on possible effects of anthropogenic disturbances due to deep-sea mining on the ecosystem and its dwellers is yet to be generated. Although newer technology such as submersibles and drilling tools are made available, similar efforts have not yet been made to explore the microbial diversity thoroughly in the Indian Ocean deep-sea.

This review has summarized the important findings on distribution and diversity of bacterial and fungal communities in the abyssal regions of the Indian Ocean. The deep-sea environments of the Indian Ocean possess diverse assemblages of bacteria and fungi, including novel taxa and new records of species that could be endemic to the region (For example, *Novosphingobium indicum*). The bacterial distribution in the Indian Ocean differs with respect to the depth of the sediment as well as spatial distances between the sampling locations, probably due to the differing environmental conditions. A variety of bacteria, with unique metabolic abilities for biotechnological potentials such as industrial and medical applications (extracellular hydrolases and anti-bacterial metabolites), have been retrieved from the Indian Ocean. Moreover, bacteria (*Pseudomonas* and *Alteromonas*) that may play a key role in formation of polymetallic nodules have been detected in sediments from the Indian Ocean. The presence of metal-utilizing bacteria (*Acinetobacter*) in samples from the Indian Ocean suggest for an environmentally induced adaptation mechanism due to the richness of metals in sediments. Although the third largest Ocean in the world, only a small fraction of the Indian Ocean deep-sea environments has been sampled, most of the high-throughput sequencing studies carried out mainly focus on the water column. Metagenomic and functional gene studies are lacking from the abyssal depths. Therefore, extensive sampling and functional gene characterization and quantification of microbes and their activities in the abyssal regions of the Indian Ocean need to be carried out to build the knowledge with respect to their diversity and the ecological processes they affect.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Benthic Foraminiferal Response to the Millennial-Scale Variations in Monsoon-Driven Productivity and Deep-Water Oxygenation in the Western Bay of Bengal During the Last 45 ka

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In this study, we presented a high-resolution benthic foraminiferal assemblage record from the western Bay of Bengal (BoB) (off Krishna–Godavari Basin) showing millennial-scale variations during the last 45 ka. We studied temporal variations in benthic foraminiferal assemblages (relative abundances of ecologically sensitive groups/species, microhabitat categories, and morphogroups) to infer past changes in sea bottom environment and to understand how monsoon induced primary productivity-driven organic matter export flux and externally sourced deep-water masses impacted the deep-sea environment at the core site. Our records reveal a strong coupling between surface productivity and benthic environment on glacial/interglacial and millennial scale in concert with Northern Hemisphere climate events. Faunal data suggest a relatively oxic environment when the organic matter flux to the sea floor was low due to low primary production during intensified summer monsoon attributing surface water stratification and less nutrient availability in the mixed layer. Furthermore, records of oxygen-sensitive benthic taxa (low-oxygen vs. high-oxygen benthics) indicate that changes in deep-water circulation combined with the primary productivity-driven organic matter flux modulated the sea bottom oxygen condition over the last 45 ka. We suggest that the bottom water at the core site was well-ventilated during the Holocene (except for the period since 3 ka) compared with the late glacial period. At the millennial timescale, our faunal proxy records suggest relatively oxygen-poor condition at the sea floor during the intervals corresponding to the cold stadials and North Atlantic Heinrich events (H1, H2, H3, and H4) compared with the Dansgaard/Oeschger (D-O) warm interstadials. The study further reveals oxygen-poor bottom waters during the last glacial maximum (LGM, 19–22 ka) which is more pronounced during 21–22 ka. A major shift in sea bottom condition from an oxygenated bottom water during the warm Bølling–Allerød (B/A) (between 13 and 15 ka) to the oxygen-depleted condition during the cold Younger Dryas (YD) period (between

10.5 and 13 ka) is noticed. It is likely that the enhanced inflow of North Atlantic Deep Water (NADW) to BoB would have ventilated bottom waters at the core site during the Holocene, B/A event, and probably during the D-O interstadials of marine isotope stage (MIS) 3.

Keywords: oxygen minima zone, primary productivity, organic matter flux, Indian monsoon, ventilation, epifaunal and infaunal benthic foraminifera

INTRODUCTION

The potentiality of fossil benthic foraminifera in deciphering past changes in sea bottom oceanographic conditions has long been recognized. Studies have shown a strong relationship between distribution patterns of benthic foraminifera and bottom water oxygen condition coupled with surface productivity-driven organic matter flux to the sea floor (e.g., Bernhard, 1986; Gooday, 1986; Lutze et al., 1986; Corliss and Chen, 1988; Altenbach and Sarnthein, 1989; Jorissen et al., 1992; Kaiho, 1999). Benthic foraminifera strongly responds to the variation in benthic environment by showing variations in their abundances, diversity, microhabitats, and adaptive morphologies (e.g., Corliss, 1985; Corliss and Chen, 1988; Corliss and Emerson, 1990; Corliss and Fois, 1990; Kaiho, 1994; Almogi-Labin et al., 1996; Gupta and Thomas, 1999; Nigam et al., 2007; Singh et al., 2015; Verma et al., 2018; Ma et al., 2019). Therefore, temporal variations in benthic foraminiferal assemblage in terms of these faunal parameters are extensively used to reconstruct past deep-sea environments (e.g., Corliss, 1986; Schnitker, 1994; Otto et al., 1995; Thomas and Gooday, 1996; Schmiedl et al., 1998; Drinia et al., 2004; Ma et al., 2019).

Arabian Sea (AS) and Bay of Bengal (BoB) are the two basins in the northern Indian Ocean with different oceanographic features. The fossil records of deep-sea benthic foraminiferal assemblages in the AS have been extensively used to reconstruct the history of past changes in the deep-water environment (primarily oxygen and trophic conditions) and to understand its linkage with monsoon and deep-water circulation (Hermelin and Shimmield, 1990; Otto et al., 1995; den Dulk et al., 1998, 2000; Schmiedl et al., 1998; Gupta and Thomas, 1999; von Rad et al., 1999; Schmiedl and Leuschner, 2005; Arumugm et al., 2014; Sarkar and Gupta, 2014). Results of earlier studies provided deep insight into the surface ocean circulation, deep-water ventilation through externally sourced water masses impacting development of oxygen minimum zone (OMZ) and benthic environment in AS and its atmosphere–ocean teleconnections with climatic fluctuations at different timescales. In recent years, significant contributions on the oxygenation history and OMZ variability at millennial timescale were made using benthic foraminiferal records from the eastern AS, a region of an intensified OMZ (Bharti and Singh, 2013; Singh et al., 2015; Verma et al., 2018).

The existing paleoceanographic reconstructions based on benthic foraminiferal assemblages in BoB are limited mainly to the longer timescales (Sharma, 1970; Singh, 1979; Srinivasan and Rajshekhar, 1981; Gupta, 1987; Raju and Mishra, 1991). The Quaternary benthic foraminiferal assemblage records on a high-resolution timescale are very sparse from the bay (Ma et al., 2019). Most of the sea bottom paleoceanographic reconstructions made earlier were based on the stable isotope records and geochemical tracers (Ahmad and Labeyrie, 1994; Piotrowski et al., 2009; Ahmad et al., 2012; Pattan et al., 2013; Raza et al., 2014; Ma et al., 2019). Here, we present a first high-resolution benthic foraminiferal assemblage record from the western BoB (off Krishna—Godavari Basin) showing millennial-scale variation during the last 45 ka. We used temporal variations in faunal proxies (abundances of ecologically sensitive groups/species, microhabitat categories, morphogroups) to decipher past changes in the benthic environment and to understand how monsoon-induced organic matter fluxes and global deep-water circulation influenced the deep-sea environments of BoB.

MATERIALS AND METHODS

Core Location and Regional Oceanographic Settings

Gravity core SK 218/1 (8.2 m length) was collected from 3,307 m water depth in the western BoB (14°02′06″ N, 82°00′12″ E; ∼204 km offshore) by ORV *Sagar Kanya* in 2005 (**Figure 1**).

BoB is a semi-enclosed basin in the eastern part of the northern Indian Ocean. Surface hydrography of BoB is driven by seasonally reversing monsoon wind circulations. During the summer season (June–September), a huge amount of freshwater and sediments are discharged into the bay through major rivers Ganga–Brahmaputra, Irrawaddy–Salween from the Himalayas and Mahanadi, Krishna–Godavari, Cauvery rivers from the Indian peninsula (Bird et al., 2008). The freshwater discharge and overhead precipitation freshen the surface layers by 3–7 psu, inducing strong stratification in the upper water column (Prasanna Kumar et al., 2002). The surface stratification restricts the wind driven mixing to a shallow depth (<20 m), thereby, inhibits the injection of nutrients from the subsurface into the euphotic zone leading to an oligotrophic condition and low primary productivity in BoB. In the winter season (December–February), surface stratification weakens and winter monsoon winds induced mixing invokes vertical transport of nutrients to the surface, enhancing primary productivity (Kay et al., 2018).

The water masses in BoB are a combination of locally and externally sourced (Schott and McCreary, 2001). The upper 100 m of the water column consists of low-saline Bay of Bengal waters (BBW) derived mainly from river discharge into the bay. The water masses at thermocline depth up to about 1,000 m are Red Sea Intermediate Water (RSIW) and Indonesian Intermediate Water (IIW). IIW is derived from North Pacific Central Water, which enters BoB via the Indonesian Throughflow

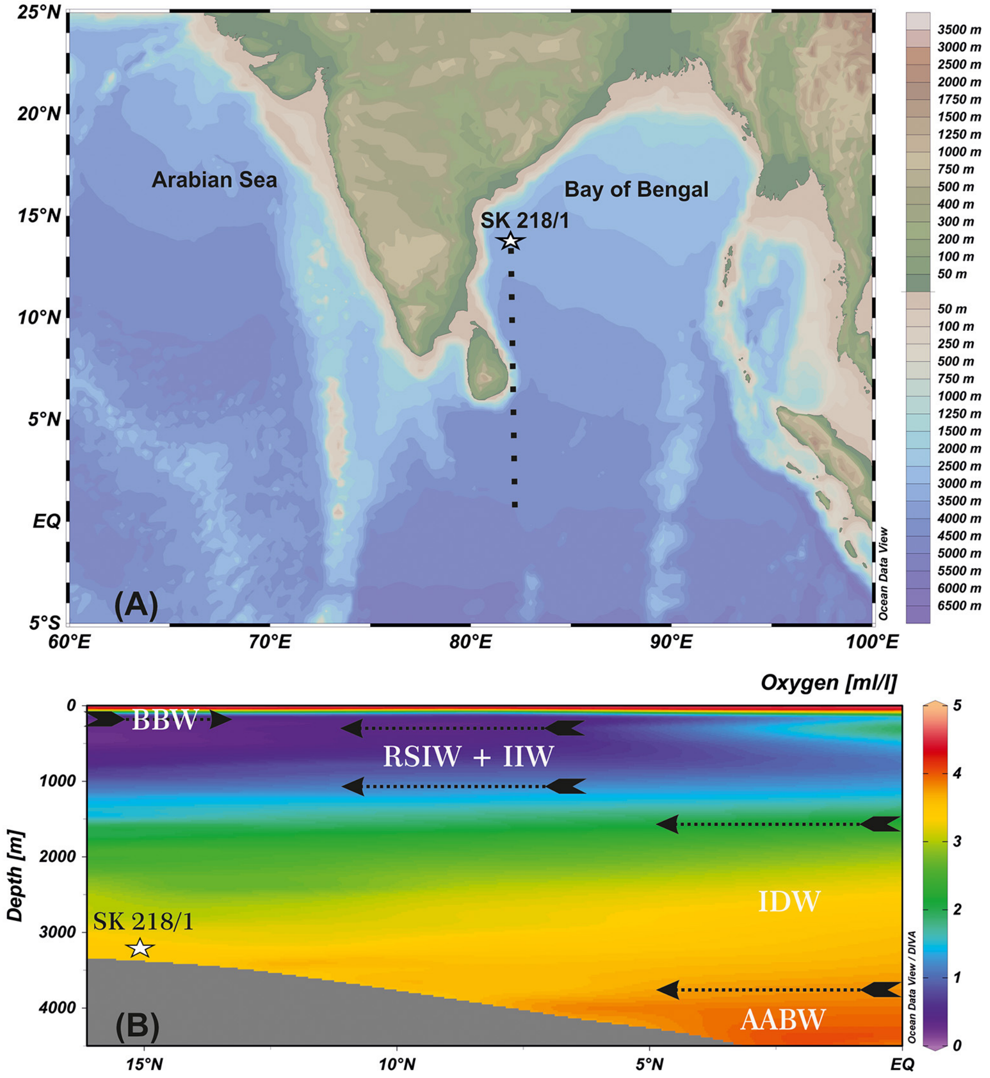

FIGURE 1 | (A) Map showing the location of studied core (SK 218/1) in the Bay of Bengal (BoB). **(B)** Oxygen (ml/L, color shading) depth (m) latitude section and vertical structure of water masses in the BoB [N–S cross-section represented by black dashed line in **(A)**]. Map source Ocean Data View (ODV; Schlitzer, 2015). BBW, Bay of Bengal Water; RSIW, Red Sea Intermediate Water; IIW, Indonesian Intermediate Water; IDW, Indian Deep Water; AABW, Antarctic Bottom Water.

(You, 1998). The water mass between 1,500 and 3,800 m is the Indian Deep Water (IDW) comprising mainly of North Atlantic Deep Water (NADW) and Circumpolar Deep Water (You and Tomczak, 1993; Tomczak and Godfrey, 2003). The Antarctic Intermediate Water (AAIW) lies just above the NADW at 1000–1500 m depth in the Indian Ocean up to 10° S (Lynch-Stieglitz et al., 1994). The Antarctic Bottom Water (AABW) is reported from water depths below 3,800 m (Tomczak and Godfrey, 2003; **Figure 1**).

Benthic Foraminiferal Analysis

A total of 158 sediment samples at regular intervals of 2–4 cm were taken for benthic foraminiferal studies to obtain an average temporal resolution of ~288 years. For separation of foraminiferal tests, sediment samples were processed following the standard micropaleontological techniques (e.g., Singh et al., 2018). Census counts of benthic foraminifera were made on >125 µm size fraction. Based on census data, the relative abundances of each benthic foraminiferal species were calculated. The taxonomic classification of benthic foraminiferal species is based on Schwager (1877) revised by Srinivasan and Sharma (1980), Brady (1884) revised by Barker (1960), Loeblich and Tappan (1988, 1990), and Sen Gupta (2002).

Age Model

The age model of the core adopted in this study was established by Govil and Naidu (2011) based on 8 AMS ^{14}C dates and δ^{18}O record of *Globigerinoides ruber* correlated with $\delta^{18}O_c$ global isostack curve of Martinson et al. (1987) (**Table 1**).

RESULTS

Temporal Variations and Environmental Preferences of Abundant Benthic Foraminifera

A total of 136 species representing 78 genera of benthic foraminifera is recorded (**Appendix 1**). Temporal variation in relative abundances of major benthic foraminiferal groups and their important constituent species are shown in **Figures 2–4**. Selected ecologically sensitive benthic species recorded in this study are illustrated in **Plate 1**.

TABLE 1 | AMS ^{14}C dates and calibrated ages (in calendar years before present) for core SK 218/1 (Govil and Naidu, 2011).

Depth (cm)	^{14}C ages (years BP)	Calibrated calendar age (years)
68	1,055 ± 30	300
150	3,840 ± 100	3,311
266	10,400 ± 60	10,976
322	13,940 ± 90	15,948
350	16,410 ± 100	18,772
498	22,100 ± 410	25,478
550	29,300 ± 330	32,822
638	33,060 ± 780	36,884

The AMS radiocarbon dates measured on monospecific samples of G. ruber were converted to calendar ages by using CALIB 6.0 software (Stuiver and Reimer, 1993) and considering a reservoir age of 400 years (Southon et al., 2002).

The benthic foraminiferal assemblage comprises of various taxa belonging mainly to uvigerinids, buliminids, cibicidids, miliolids, cassidulinids, and bolivinids (in decreasing order of relative abundances). Other quantitatively significant taxa of the assemblage are *Gyroidinoides* spp., *Oridorsalis* spp., *Chillostomella oolina*, *Eggrella brady*, *Pullenia* spp., and *Fursenkoina* spp.

The uvigerinid group, a major component of benthic assemblages is represented mainly by *Uvigerina peregrina, Uvigerina hispida,* and *Neouvigerina proboscidea*. The relative abundance of total uvigerinids in the core varies between 0 and 76 % with maximum abundances occurring during 21–23 and 26–27 ka (**Figure 4**). There has been a significant reduction in the abundance of uvigerinids during 14–15, 23–24 ka, and between 38 and 40 ka. The Holocene in general is characterized by a very low abundance of the uvigerinids. The constituent species *U. peregrina* and *U. hispida* both follow a pattern similar to that of the total uvigerinids (**Figures 2**, **4**). The uvigerinid taxa are known to be related to both the organic carbon flux and sea bottom oxygen level (Lutze et al., 1986; Hermelin and Shimmield,

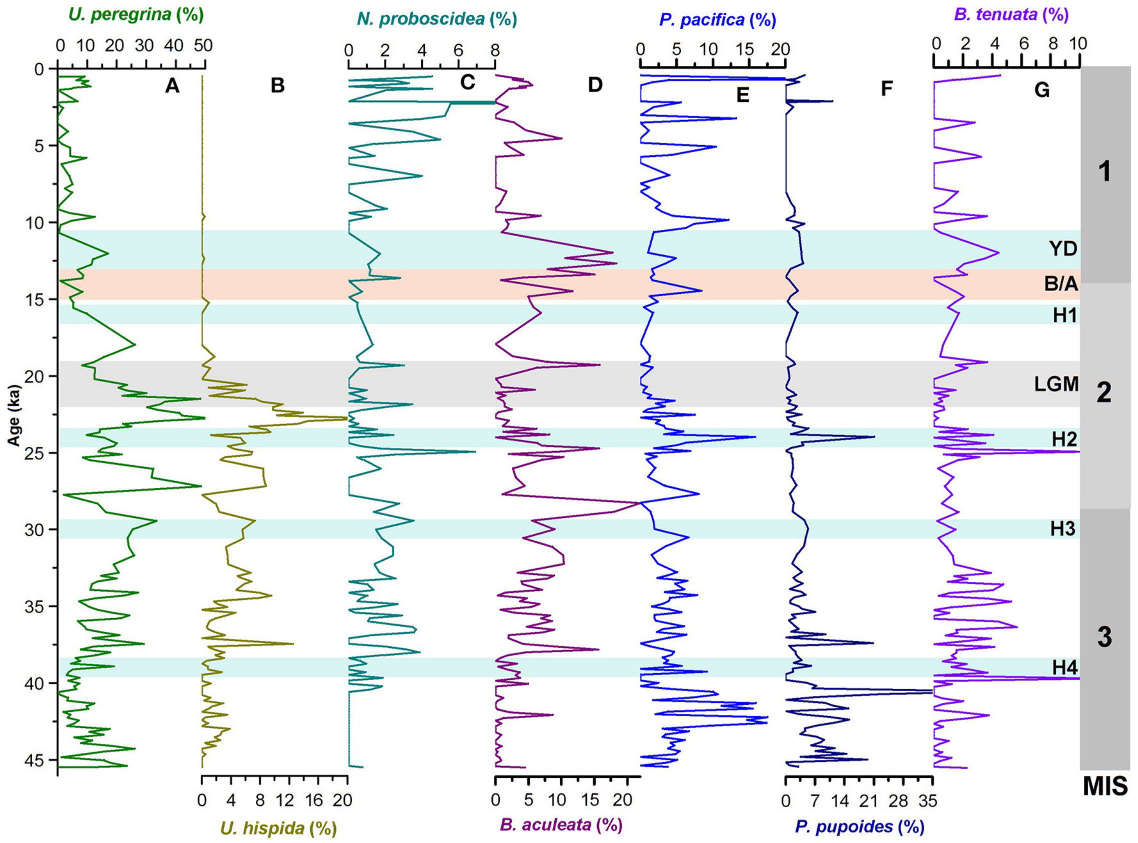

FIGURE 2 | Temporal variations in relative abundances of **(A–C)** uvigerinid species (*U. peregrina, U. hispida*, and *N. probscidea*) and **(D–G)** buliminid species (*B. aculeata, P. pacific, P. pupoides*, and *B. tenuata*) in the core SK 218/1. MIS 1–3 denotes the Marine Isotope Stages, H1–H4, Heinrich Events; YD, Younger Dryas; B/A, Bølling/Allerød; LGM, Last Glacial Maxima.

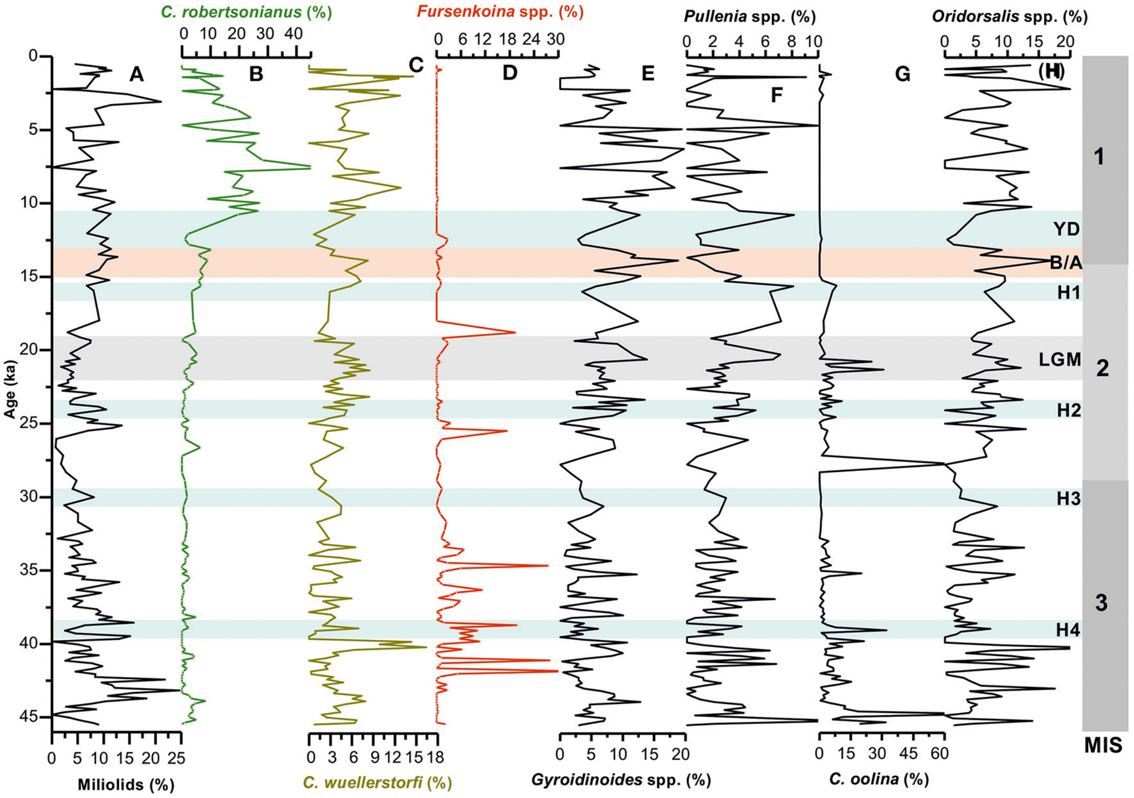

FIGURE 3 | Temporal variations in relative abundances of **(A)** total miliolids; **(B,C)** cibicidid species (*C. wuellerstorfi* and *C. robertsonianus*); **(D)** *Fursenkoina* spp., **(E)** *Gyroidinoides* spp., **(F)** *Pullenia* spp., **(G)** *Chillostomella oolina*, and **(H)** *Oridorsalis* spp. in core SK 218/1. MIS 1–3 denotes the Marine Isotope Stages; H1–H4, Heinrich Events; YD, Younger Dryas; B/A, Bølling/Allerød; LGM, Last Glacial Maxima.

1990; Jannink et al., 1998; Singh et al., 2015). The uvigerinids have preference for high organic carbon flux to the sea floor and low-to-moderate oxygen levels.

The buliminid group comprising genera *Protoglobobulimina* and *Bulimina* is the next important component of the benthic assemblages. The major constituent species of this group are *Bulimina aculeata, Protoglobobulimina pacifica, Protoglobobulimina pupoides*, and *Buliminella tenuata*. The buliminid group shows its high abundances during 12–13, 24–25, around 28 ka, between 30 and 37 ka and between 40 and 43 ka (**Figure 4**). Its abundance declines significantly during the Holocene (except for the period since 3 ka) and the last glacial maximum (LGM; 19–22 ka). However, *B. aculeata, P. pacifica*, and *B. tenuata* show an increase in their abundances during brief intervals within the Holocene (**Figure 2**). The tapered/cylindrical tests of the buliminids are suggestive of their preferences for infaunal habitat. Hence, their distribution pattern in the core is possibly controlled by the organic matter content in sediment and dissolved oxygen concentrations (e.g., Phleger and Soutar, 1973; Kaiho, 1994). *B. aculeata,* the major constituent of the buliminid population is considered to be a tolerant species to the low-oxygen environment (den Dulk et al., 2000).

The cibicidid group, which is represented mainly by *Cibicides wuellerstorfi* and *Cibicides robertsonianus* shows large variation in its abundance down core. The total abundance of cibicidids was very low between 16 and 45 ka, as compared with the Holocene (**Figure 4**). There has been a rapid increase in its abundance from 11 ka, reaching to its maximum during 6–8 ka. The variation pattern of *C. robertsonianus* abundance appears to be almost similar to that of the total cibicidids. The pattern of *C. wuellerstorfi* abundance, however, is slightly different with its abundance maxima occurring between 40 and 41, 19 and 22, 13.5 and 16 ka, and during 8–9 and 1–3 ka (**Figure 3**). *Cibicides* generally prefer epifaunal habitat (Kaiho, 1994; 1999) and are known to be associated with the high-oxygen sea bottom condition (Corliss and Fois, 1990; Singh et al., 2015; Verma et al., 2018; Verma and Singh, 2019).

The miliolids are relatively abundant in the Holocene when compared with the late glacial period. Its high abundance is also recorded during 42–44 ka of MIS 3 (**Figure 3**). The miliolids are known to have epifaunal habitat and are considered to be associated with oxic environment and low organic carbon flux (Kaiho, 1994, 1999; Singh et al., 2015; Verma et al., 2018).

Temporal variations in abundance patterns of other important groups (cassidulinids and bolivinids) and *Gyroidinoides* spp., *Pullenia* spp., and *Oridorsalis* spp. all show significant changes in their abundances down-core (**Figures 3**, **4**) and the interval of major changes (highs and lows) are associated possibly to

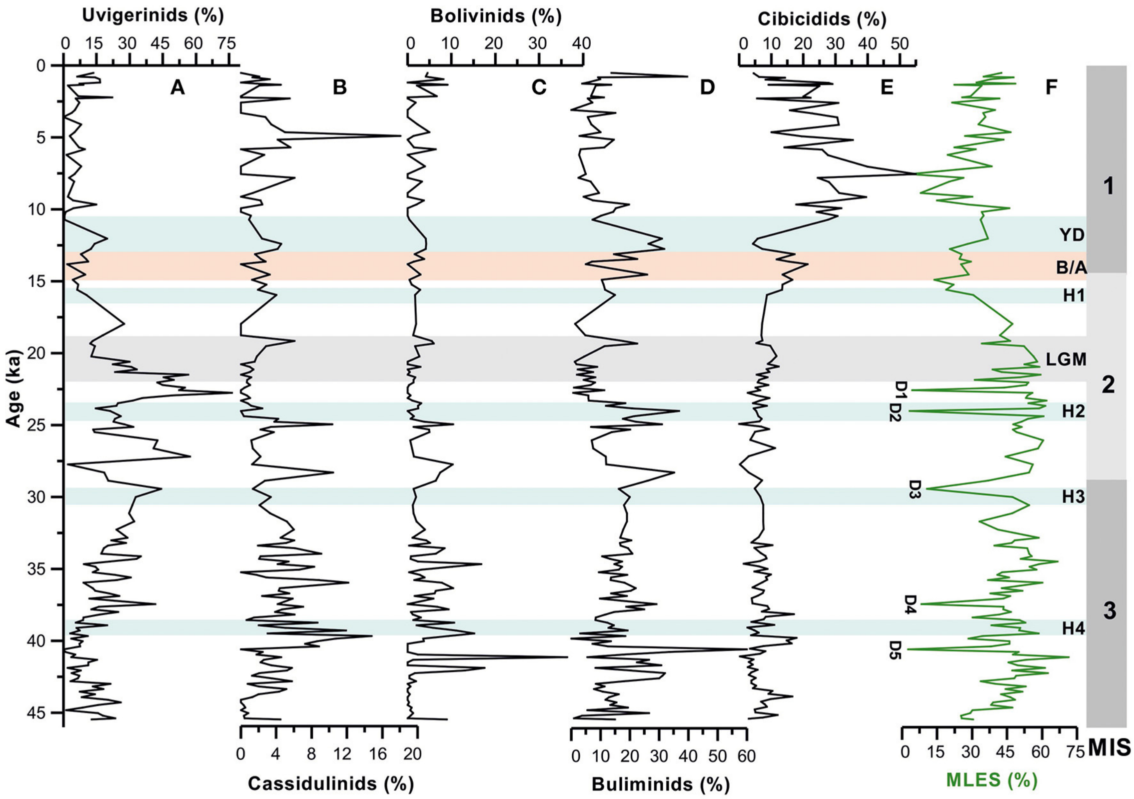

FIGURE 4 | Temporal variations in relative abundances of major benthic foraminiferal groups [**(A)** uvigerinids, **(B)** cassidulinids, **(C)** bolivinids, **(D)** buliminids, and **(E)** cibicidids] compared with **(F)** Mixed layer eutrophic species (MLES) abundance record (surface productivity proxy). D1–D5 represents possible dissolution points following Verma et al. (under revision)[1]. MIS 1–3 denotes the Marine Isotope Stages; H1–H4, Heinrich Events; YD, Younger Dryas; B/A, Bølling/Allerød; LGM, Last Glacial Maxima.

variation in sea bottom condition mainly organic matter flux and oxygen level.

The cassidulinids are known to prefer infaunal habitat, moderate to high organic matter flux, and low-oxygen environment (Kaiho, 1994; Almogi-Labin et al., 2000; den Dulk et al., 2000; Singh et al., 2015). The bolivinids being infaunal species are associated with low-oxygen condition and high organic matter content in the sediment. *Pullenia* prefers infaunal microhabitat in high productive regions (Gooday, 1994), suboxic condition and is less tolerant to oxic environment. Although the environmental preferences of *Oridorsalis* are not fully known, some studies have shown its association with the low productive condition (Kuhnt et al., 1999). Nevertheless, its abundant occurrence in high productivity areas has also been reported (Woodruff, 1985). *Gyroidinoides* species have a preference for shallow infaunal habitat and suboxic condition (Kaiho, 1994; Guichard, 1997). *Fursenkoina* and *Chilostomella oolina*, both are strikingly absent or rarely present in the Holocene sediment of the examined core. The abundance patterns of these taxa indicate their peak abundances during certain time intervals of the late glacial period (**Figure 3**). Earlier studies have shown these taxa to be associated with very low sea bottom oxygen condition (Kaiho, 1994, 1999).

Benthic Foraminiferal Morphotype and Microhabitat Categories

Benthic foraminifera depending upon their adaptation capabilities to variation in sea floor environment and microhabitat preferences develop various functional morphologies (e.g., Singh et al., 2015; Verma et al., 2018). Therefore, various morphotypes shown by benthic foraminifera and their association with specific microhabitats can be potentially used in paleoenvironmental reconstructions (e.g., Nigam et al., 2007; Singh et al., 2015). Epifaunal, shallow infaunal, and deep infaunal are the broad microhabitat categories of benthic foraminifera (e.g., Corliss and Fois, 1990; Jorissen et al., 1995). The epifauna are those living on the sediment surface, shallow infauna within sediment top 2 cm, and deep infauna below 2 cm (Buzas et al., 1993). As it is difficult to distinguish clearly the shallow infauna from epifauna, generally both together are classified as epifauna (Jorissen et al., 1995). We grouped quantitatively significant benthic foraminiferal taxa into two broad categories: epifauna and infauna based on the existing knowledge of their microhabitat preferences (**Figure 5**).

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[1] Verma, K., Singh, A. D., Singh, P., Singh, H., Satpathy, R. K., Uddandam, P. R., et al. (under revision). Monsoon-related changes in surface hydrography and productivity in the Bay of Bengal over the last 45 kyr. Palaeogeogr. Palaeoclimatol. Palaeoecol.

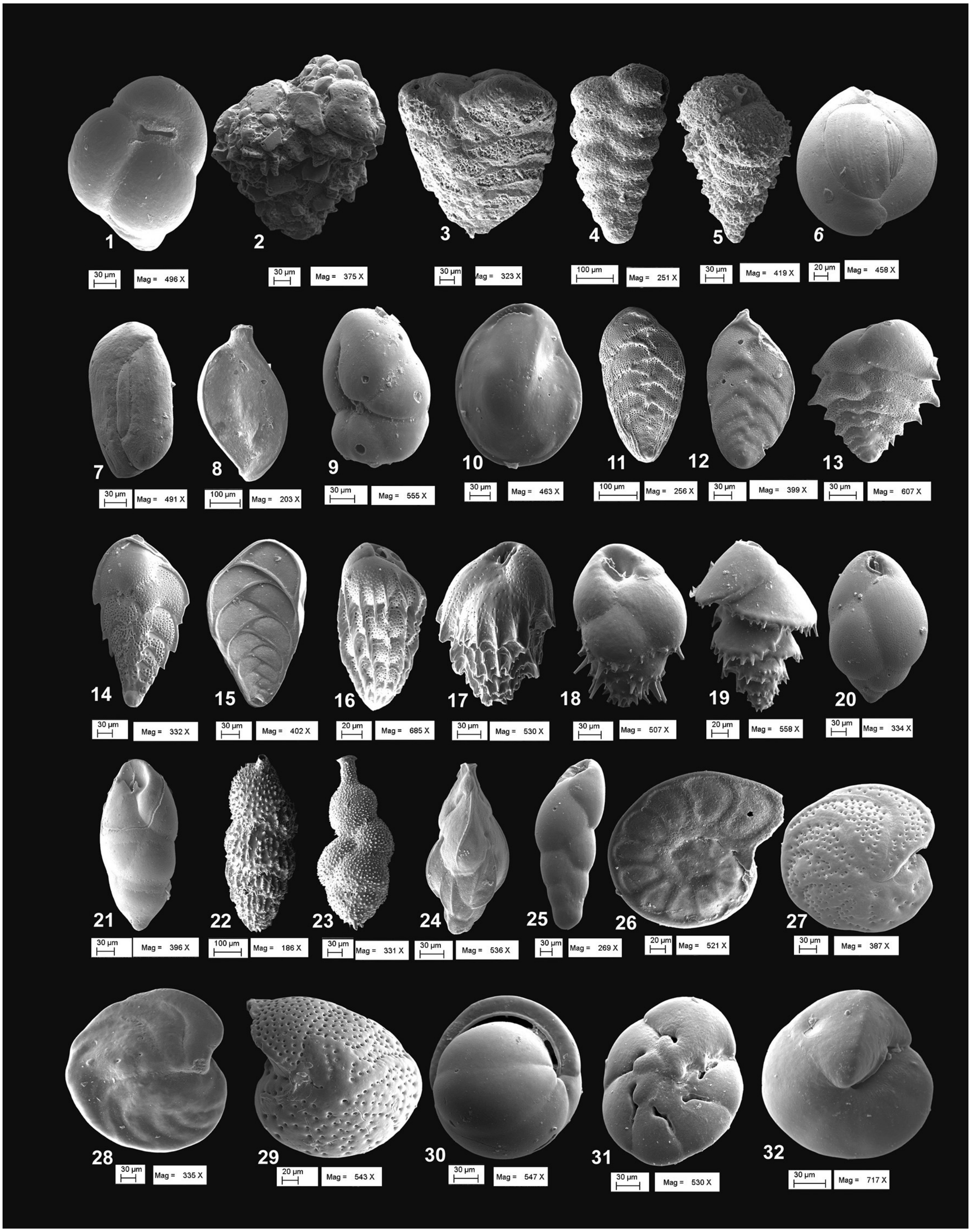

Plate 1 | The benthic foraminiferal species were recorded from the western Bay of Bengal (SK 218/1). 1. *Eggerella bradyi* (Cushman) Apertural view: 458–460 cm, 23.67 ka; 2. *Textularia lythostrota* (Schwager) Agglutinated form: 282–284 cm, 12.40 ka; 3. *Textularia laxata* (Schwager) Front view: 282–284 cm, 12.40 ka; 4. *Textularia agglutinans* d'Orbigny Agglutinated form: 290–292 cm, 13.11 ka; 5. *Siphotextularia bengalensis n. sp.* Oblique front view: 458–460 cm, 23.67 ka; 6. *Quinqueloculina seminulum* (Linné) Front view: 278–280 cm, 12.04 ka; 7. *Quinqueloculina oblonga* (Montagu) Front view: 262–264 cm, 10.71 ka; 8. *Quinqueloculina lamarckiana* d'Orbigny Front view: 144–146 cm, 3.09 ka; 9. *Ceratobulimina pacifica* Cushman and Harris Side view: 702–704 cm, 39.84 ka; 10. *Hoeglundina elegans* (d'Orbigny) Front view: 702–704 cm, 39.84 ka; 11. *Bolivina robusta* Brady Front view: 278–280 cm, 12.04 ka; 12. *Bolivina spathulata* (Williamson) Front view: 188–190 cm, 5.82 ka; 13. *Brizalina pygmaea* Brady Front view: 730–731 cm, 41.13 ka; 14. *Brizalina pseudobeyrichi* Cushman Front view: 514–516 cm, 27.74 ka; 15.

(Continued)

Plate 1 | *Bolivinita quadrilateral* (Schwager) Back view: 362–364 cm, 19.32 ka; 16. *Bulimina alazenensis* Cushman Front view: 518–520 cm, 28.31 ka; 17. *Bulimina striata* d'Orbigny Front view: 214–216 cm, 7.54 ka; 18. *Bulimina aculeata* d'Orbigny Front view: 278–280 cm, 12.04 ka; 19. *Bulimina marginata* d'Orbigny Side view: 118–120 cm, 2.14 ka; 20. *Protoglobobulimina pupoides* (d'Orbigny) Front view: 120–122 cm, 2.21 ka; 21. *Buliminella tenuata* Cushman Front view: 698–690 cm, 39.65 ka; 22. *Uvigerina peregrina* Cushman Front view: 390–392 cm, 20.58 ka; 23. *Neouvigerina proboscidea* Schwager Back view: 120–122 cm, 2.21 ka; 24. *Angulogerina carinata* Cushman Front view: 86–88 cm, 0.96 ka; 25. *Fursenkoina schreibersiana* (CŽjŽek) Side view: 514–516 cm, 27.74 ka; 26. *Hyalinea balthica* (Schröter) Spiral view: 282–284cm, 12.40 ka; 27. *Cibicides marialana gigas* Keijzer Umbilical view: 92–94 cm, 1.18 ka; 28. *Cibicides wuellerstorfi* (Schwager) Umbilical view: 99–100 cm, 1.40 ka; 29. *Cibicides lobatulus* (Walker and Jacob) Umbilical view: 170–172 cm, 4.63 ka; 30. *Pullenia bulloides* (d'Orbigny) Umbilical view: 170–172 cm, 4.63 ka; 31. *Alabaminatenui marginata* (Chapman, Parr, and Collins) Umbilical view: 298–300 cm, 13.82 ka; 32. *Oridorsalis tenara* (Brady) Umbilical view: 118–120 cm, 2.14 ka.

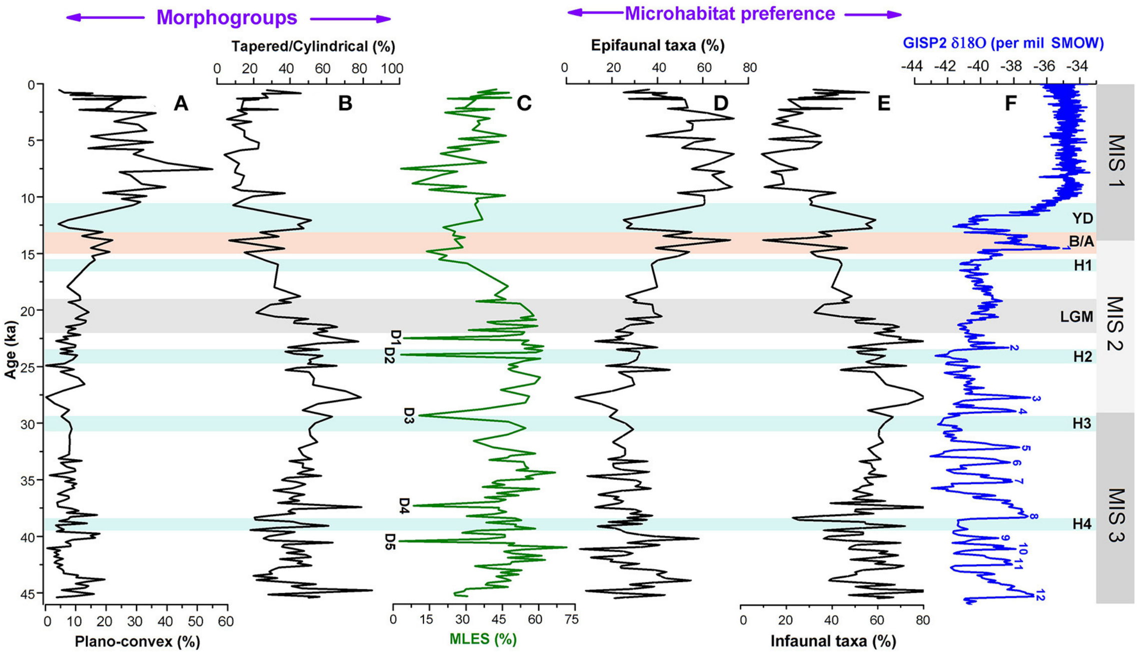

FIGURE 5 | Comparison of relative abundances of **(A,B)** major morphogroups (plano-convex and tapered/cylindrical), **(C)** mixed layer eutrophic species (MLES), and **(D,E)** microhabitat categories (epifaunal and infaunal taxa) of foraminiferal assemblages with **(F)** GISP2 $\delta^{18}O$ ice core record. D1–D5 represents possible dissolution points following Verma et al. (under revision). MIS 1–3 denotes the Marine Isotope Stages; H1–H4, Heinrich Events; YD, Younger Dryas; B/A, Bølling/Allerød; LGM, Last Glacial Maxima.

Down core variation in abundance patterns of these two groups reflects prominent changes on glacial/interglacial scale and also on the millennial scale. The Holocene period is characterized by a high abundance of epifaunal taxa and corresponding low abundances of infaunal taxa except for the late Holocene showing an opposite pattern since 3 ka. The abundance of infaunal taxa was generally high during the late glacial period between 21 and 45 ka. At the millennial timescale, the faunal record shows a conspicuous decline in infaunal taxa during 38–38.5, 28–29, 23.5–25, and 19–21 ka. During these time intervals, the abundances of epifaunal taxa increased. Additionally, there have been periods of a major increase in epifauna and corresponding decline in infauna between 13 and 15, 40 and 41, and 43 and 44 ka. The period between 10.5 and 13 ka is characterized by a conspicuous reduction of epifauna taxa and corresponding increased abundance of infauna (**Figure 5**).

Epifaunal taxa generally show varying morphologies such as plano-convex, biconvex, milioline, and rounded trochospiral. The infaunal species commonly prefer to have tapered/cylindrical, flattened ovoid, spherical, or rounded plani-spiral tests (Singh et al., 2015). Singh et al. (2015) in their recent study from the AS OMZ suggested benthic foraminifera with plano-convex tests (epifaunal) and tapered/cylindrical (infaunal) to be more sensitive to changes in bottom oxygen level coupled with organic matter flux. The relative abundance profiles of these two ecologically sensitive benthic morphotype categories in the examined core are shown in **Figure 5**. Abundance records of these morphogroups reveal that the pattern of variation in tapered/cylindrical category is broadly opposite to the plano-convex record. The variation pattern of tapered/cylindrical category mirrors to the pattern of infaunal abundance record both on glacial/interglacial and millennial scales. The abundance of tapered/ cylindrical forms was high during the late glacial, whereas, plano-convex tests were more abundant during the Holocene (**Figure 5**).

DISCUSSION

Impact of Surface Productivity Variation on Benthic Environment

The benthic foraminiferal distribution in deep sea is primarily controlled by primary productivity-related organic matter flux to the sea floor and dissolved oxygen level (Otto et al., 1995; den Dulk et al., 1998, 2000; von Rad et al., 1999; Schmiedl and Leuschner, 2005; Bharti and Singh, 2013; Singh et al., 2015). In this study, we evaluate the benthic foraminiferal response to the past changes in surface productivity in western BoB. We compared the abundance records of major benthic foraminiferal groups (uvigerinids, buliminids, bolivinids, and cassidulinids) with the record of mixed layer eutrophic planktic foraminiferal assemblage (relative abundances of *Globigerina bulloides, Globigerinita glutinata,* and *Globigerina falconensis*), which has been suggested to be linked to the surface primary productivity (Singh et al., 2011, 2018; Verma et al. under revision); **Figure 4**). From the faunal abundance records, it is evident that the intervals of increased abundances of these benthic groups broadly correspond to the peak abundances of eutrophic planktic species. It is to be noted that the abundance of eutrophic planktic species is high during the late glacial period as compared with the Holocene. The millennial-scale variations in both the planktic and benthic assemblage records broadly correspond to the Northern Hemisphere cold stadials and warm interstadials (**Figure 5**). However, the temporal variation in abundance of uvigerinid and buliminid groups appears to be governed by the surface primary productivity-driven organic carbon flux to the sea floor. The primary productivity in BoB is mainly modulated by the summer monsoon-induced precipitation and continental runoff. Earlier studies have shown low primary productivity and thus low export flux of organic carbon to the sea floor, during the periods of intensified summer monsoon when sea surface was more stratified due to increased fluvial discharge into the bay (e.g., Narvekar and Prasanna Kumar, 2006; Da Silva et al., 2017). In contrast, the surface productivity-induced organic flux enhanced during the periods of weakened summer monsoon resulting in less stratified surface waters coupled with winter monsoon intensification invoking vertical advection of nutrient-rich waters to the surface mixed layer.

Abundances of uvigerinids and buliminids are generally low during the Holocene and warm B/A periods when summer monsoon was intensified leading to the low primary production and reduced export flux of organic matter. Conversely, the group cibicidids show its maximum abundances during the periods of low primary productivity.

It is also noticed that the patterns of temporal variation in benthic foraminiferal groups individually vary and do not always match each other. These differences in the individual pattern may be related to their differential responses to the surface productivity-related organic fluxes. Additionally, it is plausible that changes in deep-water oxygenation/ventilation through externally sourced water masses might have influenced their distribution patterns.

Changes in Deep-Water Oxygenation

Benthic foraminifera are sensitive to changes in dissolved oxygen concentration over the sea floor. They show different microhabitat preferences in response to changes in ocean-bottom oxygen level and adapt distinct morphological features (Corliss, 1985; Corliss and Chen, 1988; Corliss and Emerson, 1990). Previous studies have indicated a good correlation between microhabitat preferences and morphological characteristics of benthic foraminifera and sea bottom oxygen condition (e.g., Corliss and Fois, 1990; Kaiho, 1994). Therefore, the abundance records of different microhabitat categories and morphogroups are the potential proxies to reconstruct the deep-sea oxygenation history (**Figure 5**). This approach has been applied to the late Quaternary benthic foraminiferal assemblages of the AS to decipher temporal changes of the OMZ intensity in the eastern AS (e.g., Nigam et al., 2007; Mazumder and Nigam, 2014; Singh et al., 2015; Verma et al., 2018). In this study, the relative abundance records of two broad groups of microhabitat categories (epifauna and infauna) in combination with the two predominant morphogroups (tapered/cylindrical and plano-convex) (**Tables 2**, **3**) show major changes on glacial/interglacial and millennial scales. Epifaunal taxa have a preference for high-oxygen condition over the sea floor, whereas infaunal taxa prefer a low-oxygen habitat associated with a decrease in dissolved oxygen content within the sediment (e.g., Corliss and Chen, 1988; Kaiho, 1994). High abundances of tapered/cylindrical benthic foraminiferal tests in sediment are suggestive of low bottom oxygen condition, whereas increased abundances of plano-convex tests indicate the presence of an oxygenated environment at the sea floor (Corliss and Fois, 1990; Gooday, 1994; Verma et al., 2018). The predominance of epifaunal taxa and benthic foraminifera with plano-convex tests during the Holocene suggests an oxygenated sea bottom environment compared with the late glacial period between 21 and 45 ka characterized by a general increase in abundances of infauna, tapered/cylindrical tests, and very low abundances of plano-convex tests. A rapid increase in epifaunal taxa corresponding to a significant decline of infaunal and tapered/cylindrical tests between 13 and 15 ka (equivalent to the warm B/A event) reflects a major shift in the benthic environment from a low-oxygen to the oxygenated condition. From the faunal record, it is clearly evident that the oxygenated benthic environment rapidly switched to a low-oxygen condition again during 10.5–13 ka, a period corresponding to the cold Younger Dryas (YD) event. Further, the relative abundance records of benthic microhabitat and morphotype categories for late glacial period depicts millennial-scale oscillations in the late glacial period, apparently in concert with the Northern Hemisphere Heinrich and Dansgaard–Oeschger (D-O) events (**Figure 5**). These short-term fluctuations in benthic records are obviously related to the changes in bottom water oxygen condition, which seems to be more pronounced between 40 and 45 ka.

In order to have a better reconstruction of past changes in bottom oxygen condition, we used oxygen-sensitive benthic species of assemblages and classified them into low-oxygen and high-oxygen groups based on their association with changing dissolved oxygen levels (e.g., Douglas, 1981; Hermelin and

TABLE 2 | Morphotype classification of benthic foraminifera from the examined core SK 218/1.

Plano-Convex	Tapered/cylindrical
Anomalinoides spp.[a,e]	*Angulogerina* sp.[c]
Anomalina colligera[e]	*Bulimina* spp.[a,d,e]
Cibicides spp.[b,c,d]	*Buliminella tenuata*[e]
Gavelinopsis lobatulus[e]	*Chilostomella oolina*[b,e]
	Dentalina spp.[e]
Milioline	*Ehrenbergina* sp.[b,e]
Biloculina murrhina[e]	*Fursenkoina* spp.[d,e]
Nummoloculina spp.[e]	*Lagenodosaria* spp.[e]
Quinqueloculina spp.[a,b,c,d,e]	*Marginulina* spp.[b,e]
Sigmoilina spp.[a,b,e]	*Nodosaria* spp.[b,e]
Sigmolopsis spp.[e]	*Reussella atlantica*[b]
Spiroloculina depressa[d,e]	*Trifarina bradyi*[b,e]
Triloculina spp.[c,d,e]	*Uvigerina* spp.[b,c,d,e]

[a]Corliss and Chen (1988), [b]Phleger (1951), Corliss and Fois (1990), [c] [d]Corliss (1985), [e]Singh et al. (2015).

TABLE 3 | Microhabitat preferences for quantitatively significant benthic foraminifera recorded from the core SK 218/1.

Epifauna	Infauna
Anomalina sp.[a]	*Angulogerina* sp.[o]
Anomalinoides colligera[b]	*Bolivina* spp.[b,d,e,f,g,q]
Ceratobulimina pacifica[b,d,e,q]	*Bulimina* spp.[b,d,e,f,o,p,q]
Cibicides spp.[a,b,d,e,f,g,q]	*Cassidulina* spp.[b,e,o,q]
Ehrenbergina pacifica[b,d,e,f]	*Cassidulinoides* spp.[c]
Gavelinopsis lobatulus [i,j,k]	*Chilostomella oolina*[a,b,c,n,o,q]
Globocassidulina spp.[b,e,l,m,q]	*Eggerella bradyi*[o]
Gyroidinoides spp.[a,q]	*Fursenkoina* spp.[a,d,e,f,q]
Hyalinea balthica [q]	*Melonis barleeanum*[a,n,o,q]
Hoeglundina elegans[a,b,n,q]	*Protoglobobulimina* spp.[a,d,e,f,q]
Miliolids[n,q]	*Pullenia* spp.[b,n,o,q]
Oridorsalis spp.[n,q]	*Rotaliatinopsis semiinvoluta*[k,q]
Osangularia bengalensis[a,d,e,f]	*Trifarina bradyi*[b]
Sphaeroidina bulloides[q]	*Uvigerina* spp.[a,d,e,f,i,n,o,q]

[a]Denne and Sengupta (1989), [b]Rathburn et al. (1996), [c]Jorissen (1999), [d]Corliss and Chen (1988), [e]Corliss and Fois (1990), [f]Corliss (1985, 1991), [g]Kaiho (1994, 1999), [i]Rathburn and Corliss (1994), [j]Guichard (1997), [k]Jorissen et al. (1998), [l]Gooday (1994), [m]Rathburn and Corliss, 1994, [n]Jorissen and Wittling (1999), [o]Schmiedl and Mackensen (1997), [p]Jannink et al. (1998), [q]Bharti (2008).

TABLE 4 | Constituent species of low O_2 (<0.5 ml/L O_2) and high O_2 (>0.5 ml/L O_2) benthic foraminiferal assemblages.

Low Oxic (O_2 < 0.5 ml/l)	High Oxic (O_2 > 0.5 ml/l)
Bolivinita quadrilatera	*Biloculina* spp.
Bolivina spp.	*Cibicides* spp.
Brizaina spp.	*Gavelinopsis lobatulus*
Bulimina spp.	*Quinqueloculina* spp.
Buliminella tenuata	*Triloculina* spp.
Cancris indicus	
Cassidulina spp.	
Cibicides refulgens	
Chilostomella spp.	
Dentalina spp.	
Ehrenbergina pacifica	
Fissurina spp.	
Fursenkoina spp.	
Globocassidulina spp.	
Gyroidinoides spp.	
Hoeglundina elegans	
Lagena spp.	
Lenticulina spp.	
Melonis barleeanum	
Neouvigerina proboscidea	
Nonion spp.	
Oridorsalis spp.	
Osangularia bengalensis	
Protoglobobulimina spp.	
Pullenia spp.	
Trifarina bradyi	
Uvigerina spp.	

Oxygenation categories of species are based on: Harman (1964), Smith (1964), Douglas and Heitman (1979), Quinterno and Gardner (1987), Mackensen and Douglas (1989), Corliss and Fois (1990), Bernhard (1992), Kaiho (1994, 1999), Jannink et al. (1998), Jorissen et al. (2007), Ohkushi et al. (2013).

Shimmield, 1990; Kaiho, 1994; Jannink et al., 1998; Singh et al., 2015) (**Table 4**; **Figure 6**). Temporal changes in relative abundances of these oxygen-sensitive benthic foraminiferal groups exhibit major variations during 3–10.5 ka when low-oxygen taxa were significantly replaced by the benthic species associated with a high-oxygen environment. The faunal proxy record, however, further suggests a relatively low-oxygen condition between 3 and 5 ka (**Figure 6**).

Our study reveals that the sea bottom oxygen condition in the western BoB oscillated in concert with the Northern Hemisphere climate events. The bottom water was relatively oxygen-poor during the time intervals corresponding broadly to the North Atlantic Heinrich events H1, H2, H3, and H4 and D-O cold stadials as compared with the warm interstadials. Apparently, the change in bottom water oxygen condition during the H4 event was more pronounced than H1–H3. Furthermore, the benthic environment at the core site during the cold YD event is also characterized by low-oxygen condition. Prior to YD, the bottom water was oxygenated during the period corresponding to the warm B/A. It is also evident from the faunal record that the bottom water was relatively oxygen-poor during the LGM (19 - 22 ka). However, it appears that the bottom water during 19–21 ka was more oxygenated than during 21–22 ka suggesting two-step changes in sea floor environment within the LGM. The other most striking feature of major fluctuation in oxygen condition during MIS 3 is noticed between 35 and 45 ka. The faunal data reveal a high oxygenated environment at around 38, 40, and 42.5 ka which broadly corresponds to the D-O interstadials 8, 9, and 11, respectively (**Figure 6**).

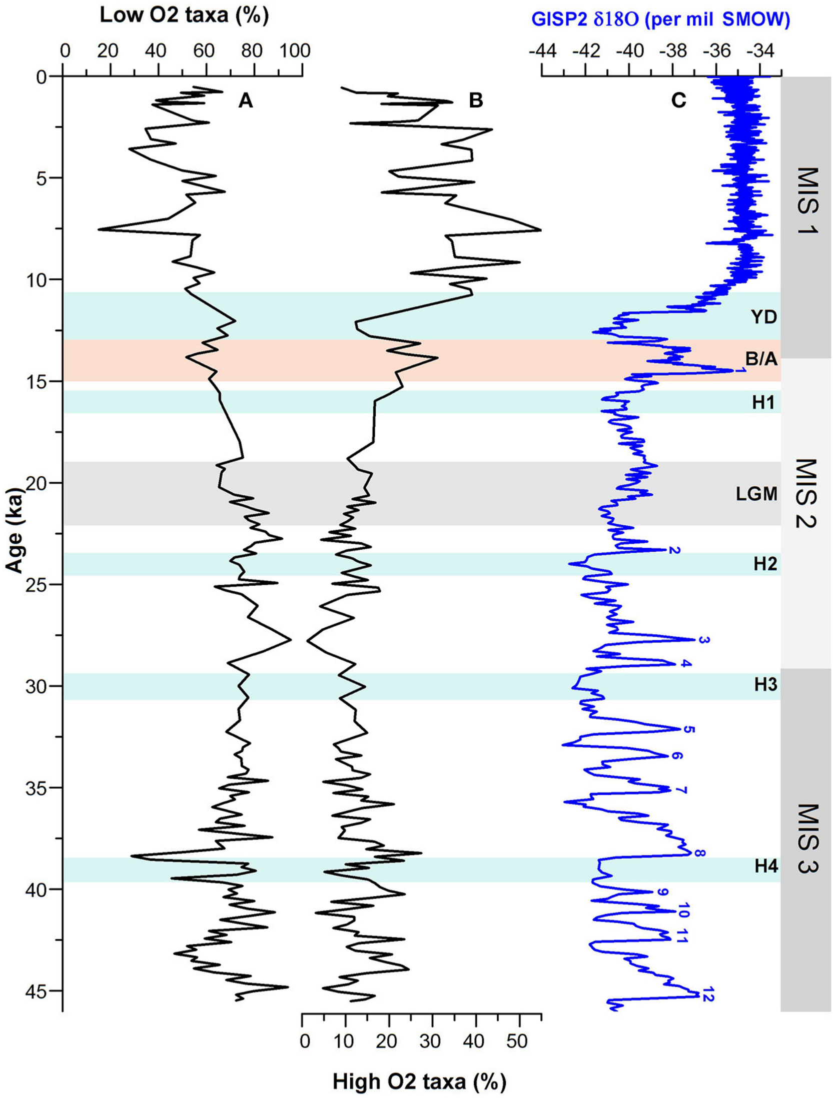

FIGURE 6 | Comparison of **(A)** % low-oxygen and **(B)** % high-oxygen taxa of benthic foraminiferal assemblages with **(C)** GISP2 $\delta^{18}O$ ice core record. MIS 1–3 denotes the Marine Isotope Stages; H1–H4, Heinrich Events; YD, Younger Dryas; B/A, Bølling/Allerød; LGM, Last Glacial Maxima.

The bottom water oxygen condition is driven mainly by two factors: (1) amount of organic matter to the sea floor and magnitude of its degradation and (2) deep-water circulation (Joos et al., 2003; Rathburn et al., 2018). By comparison of benthic foraminiferal record with the surface productivity record (mixed layer eutrophic planktic foraminifera abundance), it can be inferred that the bottom oxygen condition at the core site is governed primarily by the surface productivity-related export flux of organic carbon to the sea floor. The respiration of sinking organic matter and the release of CO_2 lead to a low-oxygen condition on the sea floor. The benthic environment was more oxygenated (as evident by high abundances of high-oxygen taxa) when surface productivity and export flux of organic carbon was low, a condition associated with the intensified SW summer monsoon precipitation resulting in high fluvial discharge and stratified surface waters in BoB. On the other hand, the export flux of organic carbon was enhanced during the intensified NE winter monsoon wind-induced vertical mixing, coupled with a weakened summer monsoon. Additionally, the deep-water circulation might have also influenced the oxygen level of bottom water mass at the core site. Previous studies have shown that the relative proportions of NADW and southern sourced AAIW and AABW modulated the bottom water oxygen condition in the northern Indian Ocean both on the glacial/interglacial and millennial scales (e.g., Ahmad and Labeyrie, 1994; Piotrowski et al., 2009; Ma et al., 2019 and references therein). A significant reduction in NADW export to the Indian Ocean during the cold North Atlantic events (Heinrich and YD events) has been suggested (Naqvi et al., 1994; Piotrowski et al., 2009). These studies provided ample evidences of increased propagation of

NADW to BoB during the Holocene (Piotrowski et al., 2009; Ma et al., 2019) compared with the late glacial period. It is plausible, therefore, that the deep water at the core site was more ventilated by NADW during the Holocene. We also suggest that the high-oxygen condition during the warm D-O interstadials of MIS 3 is most likely related to the effective propagation of NADW to the BoB. This is in line with the previous results indicating an enhanced influence of NADW during the warm B/A event (Piotrowski et al., 2009). However, more research on high-resolution timescale is required to better understand the relative contributions of NADW and AAIW/AABW flow in modulating the deep ocean oxygenation history in BoB in concert with the D-O oscillations.

CONCLUSION

A high-resolution deep-sea benthic foraminiferal assemblage record obtained from a sediment core in the western BoB reveals millennial-scale variations during the last 45 ka. Temporal variations in faunal proxy records suggest a strong influence of surface primary productivity-related organic matter flux on the bottom water oxygen condition at the core site. Our records indicate oxygenated sea bottom condition during the Holocene, when primary productivity was significantly low as compared with the late glacial period between 21 and 45 ka, due to intensified summer monsoon resulting in high fluvial discharge to BoB. In addition to the surface productivity factor, changes in deep-water circulation at the millennial timescale might have also strongly influenced the benthic environment.

The relative abundance records of two broad groups of microhabitat categories (epifauna and infauna) and morphogroups (tapered/cylindrical and plano-convex) show major changes on glacial/interglacial and millennial timescales. We also used oxygen-sensitive benthic foraminiferal groups (low-oxygen and high-oxygen taxa) to better understand past changes in bottom water oxygen conditions. Our records reveal that the sea bottom oxygen condition in the western BoB varied in concert with the Northern Hemisphere Heinrich and D-O events. The benthic environment was oxygen depleted during the North Atlantic cold events (YD and Heinrich events) and the LGM (19–22 ka). We suggest that the bottom water was more ventilated by NADW during the warm B/A event, D-O interstadials (8, 9, and 11) of MIS 3, and during the Holocene.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Materials**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

AS and PN conceptualized the study. KV carried out the sample analysis. AS supervised the study. AS and KV prepared the original draft of the manuscript with contributions from HS, PS, RS, and PN. All authors participated in reviewing, editing, and preparation of final draft of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.733365/full#supplementary-material

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Why Are Barnacles Common on Intertidal Rocks but Rare in Rock Pools? Effect of Water Temperature, Salinity, and Continuous Submergence on Barnacle Survival in Indian Ocean Rock Pools

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Barnacles are less common in rock pools of the rocky intertidal zone than on open rock surfaces adjacent to those pools. Rock pools on the Andaman coastlines of Thailand showed diurnal variations in water temperature, salinity, pH, and dissolved oxygen level, peaking in the afternoon. Multivariate analysis showed that water temperature and salinity (not pH and dissolved oxygen) can affect barnacle abundance in rock pools. The present study tests the hypothesis that a lack of recruitment or pool environmental conditions (continuous submergence, water temperature, and salinity extremes) affect the abundance of barnacles (*Chthamalus malayensis* and *Amphibalanus amphitrite*) in rock pools. During the recruitment season, recruits were found in a number of rock pools, but at significantly lower abundances than those in adjacent open rock surfaces. In a laboratory experiment, *C. malayensis* and *A. amphitrite* that were continuously submerged had a lower survival (80%) than the controls (simulated tide conditions; >90% survivals). Under different water temperature and salinities treatments, barnacles had low survival (<50%) in the low salinity ($0^{\circ}/_{oo}$) and high temperature treatment (40°C). The present study suggests that *C. malayensis* and *A. amphitrite* can recruit into rock pools, and the interplay of continuous submergence, high water temperature and low salinity in rock pools can bring about mortality in barnacles.

Keywords: acorn barnacles, intertidals, rock pools, salinity, submergence, Thailand, Andaman Sea

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INTRODUCTION

The factors affecting species distribution constitute an interesting topic in ecological studies. The rocky intertidal zone can comprise a variety of microhabitats, including vertical rocks, horizontal rocks, shaded and exposed surfaces, rock pools, and crevices (Williams and Morritt, 1995; Seabra et al., 2011). These microhabitats differ mainly in their levels of heat stress, which affect species distribution (Williams and Morritt, 1995; Wang et al., 2020). Rock pools are depressions on rocky shores that retain water during low tide. Rock pools are foraging habitats and refugia from predation and physical stresses for many intertidal species (Moran, 1985; Delany et al., 1998; Laure et al., 2009). The physico-chemical environment of rock pools, comprising water temperature, salinity, pH, and dissolved oxygen levels, is largely regulated by the tides (Metaxas and Scheibling, 1993; Chan, 2000; Legrand et al., 2018). This environment also varies with the volume, surface area, depth, and tidal position (intertidal vs. supratidal) of pools (Metaxas and Scheibling, 1993; Chan, 2000). When pools are disconnected from the sea, temperature, salinity, pH, and dissolved oxygen concentration can be affected by solar radiation from direct sunlight and bedrocks, water evaporation, and the pool fauna and flora (Morris and Taylor, 1983). Salinity in tropical rock pools can be as low as $0^\circ/_{oo}$ during heavy rain and as high as $40^\circ/_{oo}$ during hot days (Chan, 2000; Firth and Williams, 2009). Intertidal pools on the mid-low shores experience less variation in physico-chemical parameters compared to supratidal pools. They often have higher species richness and biodiversity than their supratidal counterparts (Moschella et al., 2005; Firth et al., 2013, 2014; Evans et al., 2016). Sponges, ascidians, hydroids, and gobies are often found in intertidal pools (Evans et al., 2016).

Barnacles (Suborder Balanomorpha) are common inhabitants of intertidal rocky shores in Thailand (Pochai et al., 2017; Sukparangsi et al., 2019; Chan et al., 2020). They are habitat modifiers and can regulate the abundance and distribution of other organisms (Branch, 1976; Amnuaypon and Wangkulangkul, 2018). In the temperate Atlantic, barnacles are rarer in rock pools than on open rock surfaces (Singletary and Shadlou, 1983; Firth et al., 2014; Evans et al., 2016; Hall et al., 2019). Two studies have been conducted in temperate regions of the Atlantic Ocean to examine factors affecting the distribution of barnacles in rock pools. Magre (1974) revealed that *Balanus* (*Semibalanus*) *balanoides* settle in rock pools, and its settlement density decreases with pool depth. Singletary and Shadlou (1983) qualitatively monitored physical and biological parameters in rock pools and found that *B. balanoides* can settle in pools at high volumes, but these settlers soon die from hypoxia. Chemicals released by pool algae can also affect the survival of barnacle spats (Singletary and Shadlou, 1983). Predation by snails, which are common in pools, might also cause mortality (Singletary and Shadlou, 1983).

Chthamalus malayensis Pilsbry, 1916 (Chthamalidae) (**Figure 1A**) and *Amphibalanus amphitrite* (Darwin, 1854) (Balanidae) (**Figure 1B**) are the most common acorn barnacles on intertidal rocky shores off the tropical Andaman coast of Thailand (latitude ∼6.4°-10°N) in the Indian Ocean (Tsang et al., 2012). *C. malayensis* is common on mid-high shores, while *A. amphitrite* occurs on low shores (Chen et al., 2014; Pochai et al., 2017). Rock pools are common in the intertidal zone of the Andaman coast. Barnacles (*C. malayensis* and *A. amphitrite*) are common on open intertidal rock surfaces, but rare inside rock pools (**Figure 1C**). Factors affecting the distribution of barnacles in tropical rock pools can be different from the results previously addressed in the temperate Atlantic Ocean. In the tropics, barnacles are rare in rock pools, which may be due to a lack of recruitment in pools. If barnacles can recruit in rock pools, then extreme variations in salinity and temperature inside the pool waters might affect barnacle survival. Marine invertebrates can tolerate a range of water temperatures (thermal windows) and salinities (Sherwood et al., 2012; Diaz et al., 2021). When barnacles experienced extremely high temperatures, heart beats increase, and they subsequently enter a coma state (opercular valves open without responses under stimulations). Barnacles will die if the coma condition persists for a long period (Chan et al., 2006). Gonads will also be impacted by high temperatures and result in a lower number of larvae produced (Fraser and Chan, 2019). Moreover, intertidal barnacles that live on rock surfaces experience tidal inundations, but those that live in pools experience continuous submergence. It is possible that continuous submergence is not the best living condition for intertidal barnacles.

The present study aims to investigate if and how recruitment and the pool physico-chemical environment determine barnacle distribution in rock pools. We tested the hypothesis that barnacles are not common in rock pools on the Andaman rocky shores due to (1) a lack of recruitment, (2) continuous submergence, and (3) the effects of extreme salinity and temperature on barnacle survivals in pools was tested.

MATERIALS AND METHODS

Study Shores

All rocky shores sampled were located in the Andaman Sea, Thailand (**Figures 1D,E**). The barnacle abundance and the physico-chemical environment of pools and the differences in barnacle abundance between pools and on rock, were examined on shores with a number of rock pools in Laem Panwa (7°47′57.7"N 98°24′30.1"E), Pleum Sook (7°53′13.7"N 98°26′31.7"E), Laem Sai (7°37′45.7"N 99°14′01.2"E), Whahin Island (6°47′14.0"N 99°45′38.3"E), and Tanyong Po (6°35′27.1"N 99°56′53.9"E). Lanta Island (7°35′23.2"N 99°01′50.2"E) was visited only to take diurnal measurements of the physico-chemical parameters of the rock pools. Lanta Island is suitable for such diurnal measurement because the accommodation site is very close to the field sites, which allows overnight monitoring possible. Recruitment surveys of barnacles on rocks and in pools were conducted in Tanyong Po and Had Sai Yao (6°37′13.5"N 99°57′10.2"E). All shores are wave-exposed or semi-exposed. Tide is semi-diurnal with a maximum tidal range of ∼2.5 m. Shale was the predominant type of rock in the study areas.

Physico-Chemical Environment of Rock Pools and Barnacle Abundance

In September 2019, 20 pools were selected in each of the five sampled shores and their physico-chemical environments were surveyed. Pools were selected based on the following criteria: (1) no more than 12-cm deep (to reduce the effect of heterogeneity within the habitat), (2) no cobbles (cobbles can be stirred by water currents and create unstable habitat within the rock pool), and (3) in the intertidal zone (mid-shore level), at the same, tidal level as the barnacle zone.

The pool depths were measured using a ruler (±10 mm). Each pool was photographed from the top of the rock

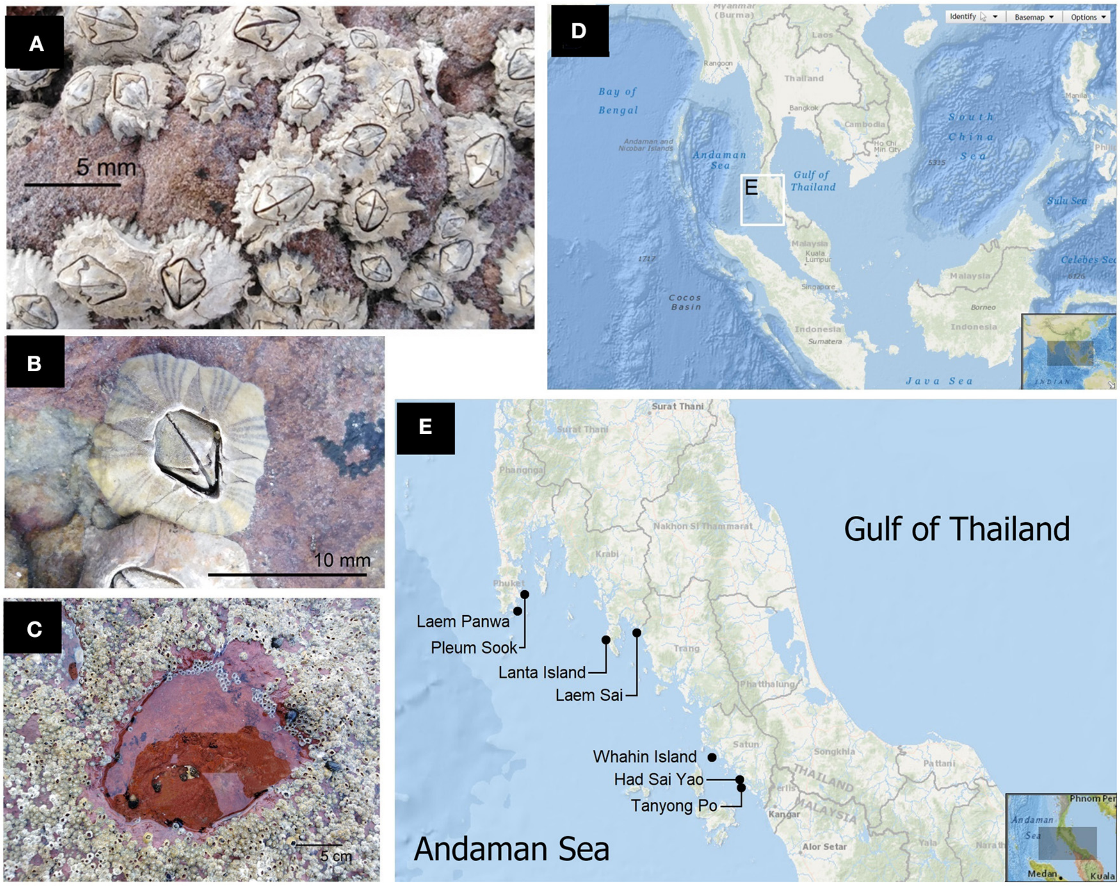

FIGURE 1 | (A) *Chthamalus malayensis* is a common barnacle on mid shores of the Andaman rocky shores. **(B)** *Amphibalanus amphitrite* are common on low shores of the Andaman intertidal zone. **(C)** On the Andaman Coast of Thailand, barnacles are common on open rock surfaces adjacent to rock pools, but relatively rare inside pools. **(D)** Study region on the Andaman coast of Thailand, magnified in **(E)**. **(E)** Seven study shores spanning from the northern to southern coasts on the Andaman coast of Thailand. **(D,E)** Courtesy of NOAA Bathymetric Data Viewer.

pools, then its surface area was calculated using the image analysis software ImageJ©. Temperature was measured using a glass thermometer (±0.1°C). Salinity was measured using a refractometer. pH was measured by a Portable Digital pH Meter (±0.1). Dissolved oxygen was measured by an OHAUS ST20 portable DO meter (±0.1 $\mathrm{mgl^{-1}}$). A quadrat (10 × 10 cm) was randomly placed inside each rock pool. The percentage cover of *C. malayensis* and *A. amphitrite* was scored for each quadrat.

The effect of physico-chemical parameters of rock pools (water temperature, salinity, pH, and dissolved oxygen) on the abundance of barnacles (*C. malayensis* and *A. amphitrite*) was analyzed using Multivariate Analysis (PRIMER 6.0 software). The relationship between barnacle abundance and physico-chemical parameters was assessed using the BEST routine in PRIMER (Clarke et al., 2008). The BIO-ENV function in the BEST routine was used to calculate the smallest subset of environmental variables that explained the greatest percentage of variation in the ordination patterns using the Spearman Rank Correlation method.

Diurnal Variation in Physico-Chemical Parameters in Rock Pools

To examine diurnal variation in the water temperature, salinity, dissolved oxygen, and pH of rock pools (methods for measuring physico-chemical parameters as in section Physico-Chemical Environment of Rock Pools and Barnacle Abundance), six rock pools (dimension criteria stated in section Physico-chemical Environment of Rock Pools and Barnacle Abundance) were selected from a rocky shore on Lanta Island on September 16–18, 2020 (late monsoon season). It rained during some periods of measurement. The water temperature, salinity, dissolved oxygen, and pH of pools were measured hourly during low tide (when pools were exposed to the air) and every 3 h during high tide (when pools were submerged).

Comparison of Barnacle Abundance Between Rock Pools and Adjacent Emergent Rocks

On each shore, whenever a rock pool within the selection criteria in section Physico-Chemical Environment of Rock Pools and Barnacle Abundance was found, a quadrat (10 × 10 cm) was randomly placed inside of that rock pools. A quadrat was established on the adjacent emergent rock surface (∼20 cm from the rock pool). One quadrat was established for each pool due to pool size limitations. Ten to 20 pools were sampled from each shore. In each quadrat, the percentage cover of *C. malayensis* and *A. amphitrite* was scored.

Barnacle Recruitment in Rock Pools and on Adjacent Rock Surfaces

A quadrat (5 × 5 cm) was established to monitor recruitment in rock pools and their adjacent rock surfaces (∼20 cm from the pools). Barnacle recruits (defined as having a rostral-carinal diameter of 0.5–1 mm) in each quadrat were scored. It is difficult to distinguish between recruits of *C. malayensis* and *A. amphitrite*, so recruits of both species were pooled. Recruitment monitoring was conducted monthly for 12 months, except from March to May 2020 because of logistical difficulties due to the COVID-19 lockdown.

Permutational Multivariate Analysis of Variance with 999 permutations was performed to test the effect of Habitat (two levels), Species (two levels), and Shore (five and three levels for *C. malayensis* and *A. amphitrite*, respectively) on the percentage cover of barnacles. As suggested by Anderson et al. (2008), Euclidean distance resemblance matrices (with a dummy variable added) were constructed from untransformed data for all univariate analyses. Data were pooled across the shores for the first analysis, and Habitat and Species were treated as fixed factors and crossed. For the second analysis, data from each species were analyzed separately and Habitat was crossed with Shore (random factor). *C. malayensis* was found on all shores, whereas *A. amphitrite* were not found in samples from Laem Panwa or Whahin Island. Hence, there was a difference in the number of shores between species. PERMANOVA was also performed to evaluate the effects of Habitats (fixed, two levels), Months

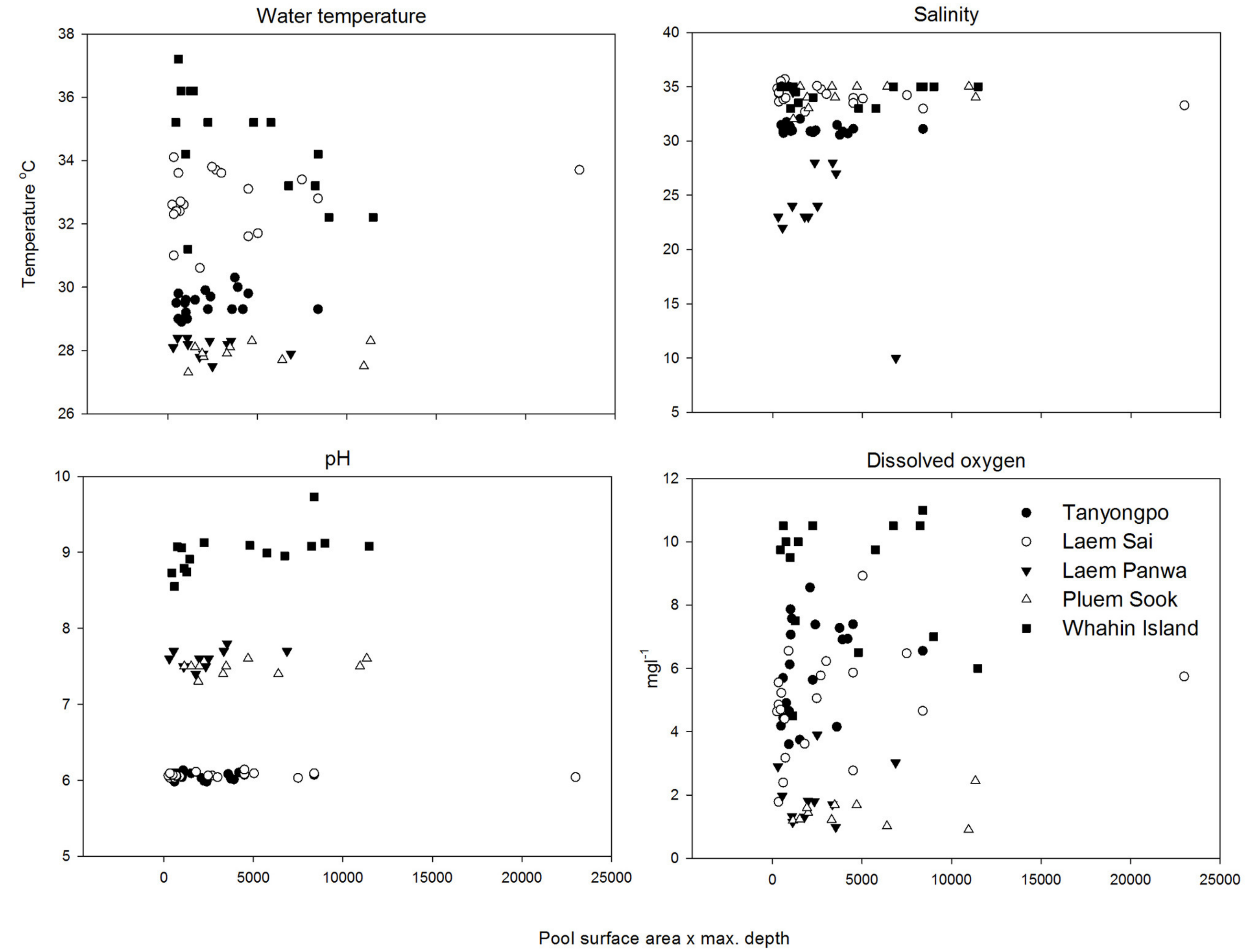

FIGURE 2 | Variation in water temperature, salinity, pH, and dissolved oxygen with pool size dimensions (depth × surface area) from five study shores. Note that none of the physico-chemical parameters were significantly correlated with pool size dimensions.

TABLE 1 | Range of variations in the physico-chemical environment of rock pools.

Shores	Range of water parameters in pools				
	Temperature (°C)	Salinity (°/$_{oo}$)	Dissolve oxygen (mg L^{-1})	pH	Rock temperature (°C)
Laem Panwa	27.5–28.4	10.0–34.5	1.0–3.9	7.4–7.8	27.7–28.4
Pleum Sook	27.3–28.3	32.0–35.0	0.9–2.4	7.3–7.6	26.8–28.3
Lanta Island	27.1–33.0	5.0–39.0	1.6–16.2	6.8–9.3	No data
Laem Sai	30.6–34.1	32.7–35.7	1.8–9.0	6.0–6.1	30.3–37.6
Whahin Island	31.2–37.2	33.0–35.0	4.5–11.0	8.6–9.7	32.1–41.4
Had Sai Yao	31.0–35.0	33.0–43.0	No data	No data	No data
Tanyong Po	28.9–37.5	30.6–46.0	3.6–8.6	6.0–6.1	27.2–30.9

Additional single measurements of salinity were conducted on 10 rock pools which has very high salinity in Tanyong pool, 6 rock pools in Had Sai Yao. Range recorded in these two sites were greater than the paired dataset in ***Figure 2****.*

(fixed, nine levels), and Shore (random, two levels) on the density of recruits. Pairwise comparisons were conducted on significant terms.

Effect of Continuous Submergence on Barnacle Survival

Small pieces of rock with barnacles attached were collected by a chisel and hammer. Sixty adult barnacles of each species with 4–6 mm (for *C. malayensis*) and 10–12 mm (for *A. amphitrite*) basal rostral-carinal diameter were collected from Tanyong Po. These sizes were determined to be small enough to represent young and vulnerable individuals but large enough to be handled in the experiment. Specimens were acclimated in aerated seawater for 48 h prior to the experiment. Each species of barnacle was maintained in two treatments: continuous submersion and control for 14 days. In the continuous submersion treatment, barnacles were continuously immersed in seawater. In the control treatment, barnacles were removed from the water for 4 h and immersed again in seawater for 8 h. This procedure was repeated two times a day to simulate the inundation period of the semidiurnal tide on the Andaman coast (a total of 8 h of emersion and 16 h of immersion per day). Each treatment had three replicates. For each replicate, 10 barnacles were kept in a 500 ml plastic container filled with continuously aerated 32°/$_{oo}$ seawater prepared from artificial seawater (Aquarise©). Barnacles were fed with an *ad libitum* diet of *Chaetoceros* sp. (concentration: 3×10^5 cell/ml) daily. Lamps (120 W Phillips Par 38 Flood) were suspended ∼30 cm above the containers and turned on for 12 h (06:00 to 18:00) per day. Heating from the lamps created an ambient temperature similar to the average shore temperature (∼30°C). Seawater was changed every 2 days and the number of surviving barnacles was scored daily. Surviving barnacles were checked by stimulating their operculum using a wooden stick (Fraser and Chan, 2019).

The percentages of barnacles that survived were compared between the continuous submersion and control treatments on different days by two-way ANOVA. Treatment (two levels) and Day (15 levels) were treated as fixed factors. Treatment was crossed with Day. Tukey's test was performed on significant terms for *post hoc* multiple comparisons.

TABLE 2 | Results of Bio-Env analysis in the BEST routine of PRIMER 6, showing the variation in the correlation coefficient with different subsets of physico-chemical variables.

Physico-chemical variables	Spearman correlation coefficients
Water temperature, salinity	0.30
Water temperature	0.28
Water temperature, salinity, dissolved oxygen	0.17
Water temperature, salinity, pH	0.16
Water temperature, salinity, dissolved oxygen, pH	0.16
Water temperature, dissolved oxygen,	0.15
Salinity, dissolved oxygen	0.15
Water temperature, dissolved oxygen, pH	0.14
Dissolved oxygen, salinity, pH	0.14

Effects of Temperature and Salinity on Barnacle Survival

Three hundred and sixty adult barnacles of *C. malayensis* and *A. amphitrite* were collected and acclimated as in section Effect of Continuous Submergence on Barnacle Survival. Barnacles were maintained in combinations of four different salinities (0, 33, 50, and 60°/$_{oo}$) and three temperature levels (30, 40, and 50°C), with three replications per treatment. For each replication, 10 barnacles were kept in a 500 ml plastic container filled with continuously aerated solution prepared from artificial seawater. Containers were placed in a thermostatic heating water bath and the solution was heated from 27°C (ambient) at ∼0.3°C min^{-1} until the target temperature was reached. Barnacles were exposed to the treatments for 5 h, after which the number of surviving barnacles was counted. Salinity was checked every 15 mins to ensure that the designated salinity levels were maintained. Distilled water was added in containers in which salinity had increased due to the heating. Barnacles were not fed.

Two-way ANOVA was performed to test the effect of temperature and salinity on the percentage of *C. malayensis* and *A. amphitrite* survival separately. Data was sqrt(x+1) transformed. Temperature (three levels) and salinity (four levels) were treated as fixed factors. Temperature was crossed with salinity. A Student–Newman–Keuls (SNK) test was performed on significant terms for *post hoc* multiple comparisons.

RESULTS

Physico-Chemical Environment of Rock Pools and Barnacle Abundance

A total of 76 rock pools was measured for surface area, depth, water temperature, salinity, pH and dissolved oxygen, and the

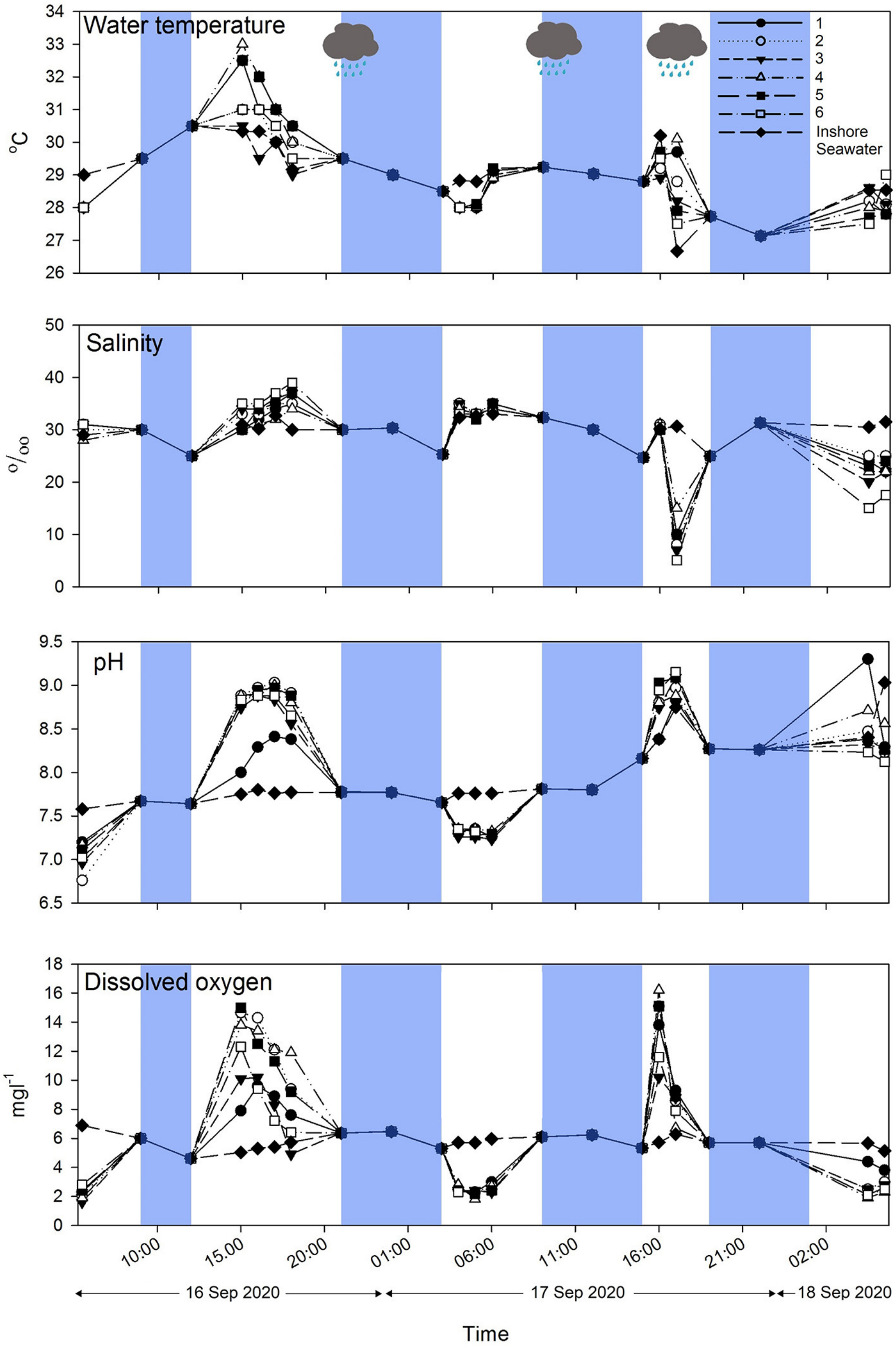

FIGURE 3 | Diurnal variation in water temperature, salinity, pH, and dissolved oxygen in six intertidal pools and inshore seawater. Blue regions indicate pools that were immersed in high tides. White regions indicate pools that were isolated from the sea during low tides. Raining clouds indicate that rain occurred during sampling.

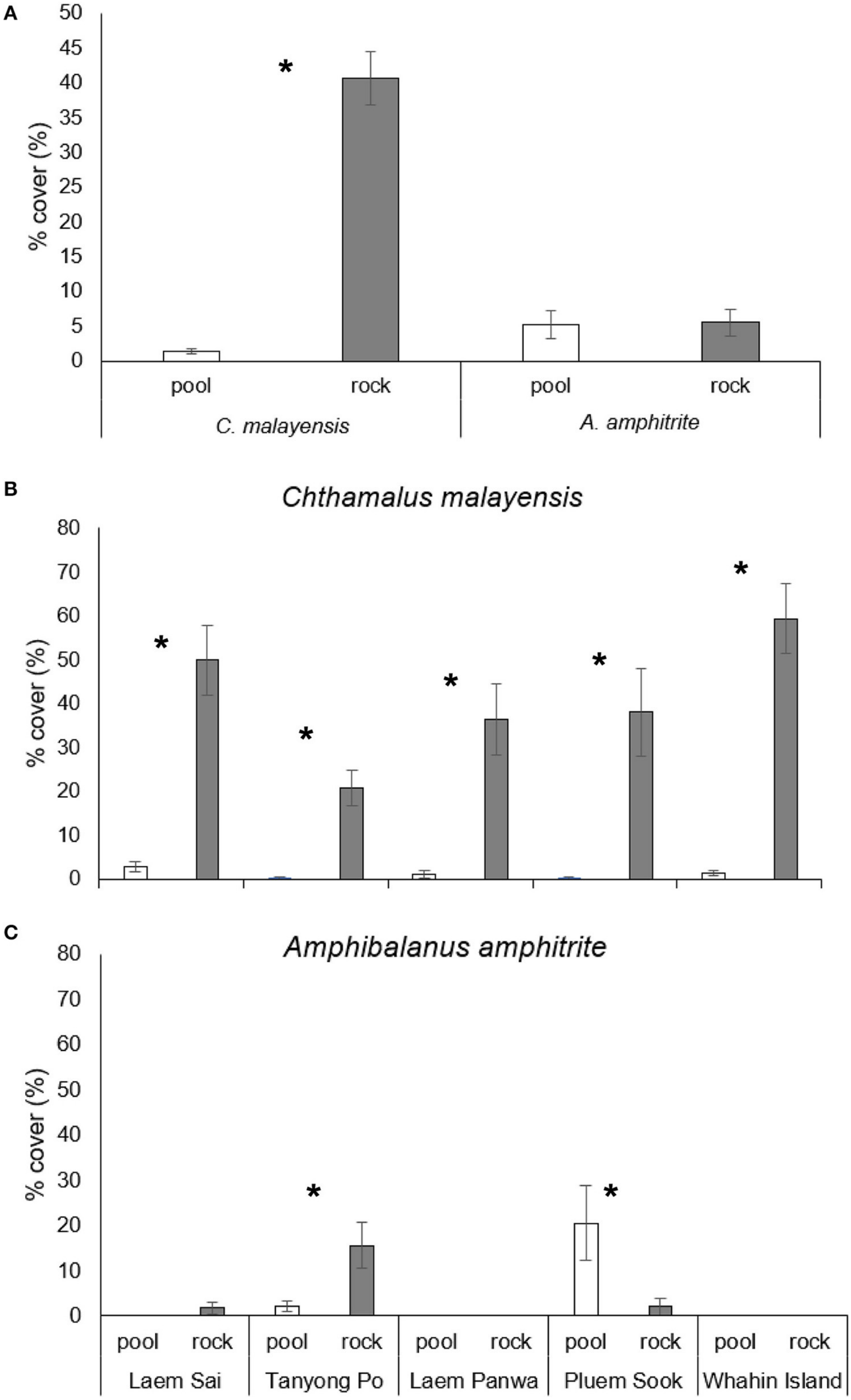

FIGURE 4 | Percentage cover of barnacles in rock pools and on open rock surfaces adjacent to pool. **(A)** Percentage cover of barnacles (mean ± SE) pooled from all shores. **(B,C)** Percentage cover on five shores of *C. malayensis* and *A. amphitrite,* respectively. Icon: * = significant differences between habitats suggested by pairwise tests.

corresponding abundances of *C. malayensis* and *A. amphitrite*. There was no significant correlation detected between the size dimension of pools (surface area × depth) and any physico-chemical parameters measured (**Figure 2**). Water temperature from all the pools measured ranged from an approximate temperature of 27–37°C. Salinity ranged from ∼5–46°/oo, pH ranged from ∼6–9.7 and dissolved oxygen concentration ranged from ∼0.9–11 mg L^{-1} (**Figure 2** and **Table 1**).

Based on the Bio-Env multivariate analysis in the BEST (Bio-Env) routine, the correlation coefficients from a combination of different subsets of physico-chemical parameters to the barnacle abundance ranged from 0.14 to 0.30 (**Table 2**). The subset, including water temperature and salinity, yielded the highest correlation coefficient (0.30) to the barnacle abundance (**Table 2**). Having all the physico-chemical parameters in the analysis yielded a correlation coefficient of 0.16, lower than the subset containing water temperature and salinity (**Table 2**).

Diurnal Variation in Physico-Chemical Parameters in Rock Pools

Water temperature, salinity, pH, and dissolved oxygen followed a diurnal pattern of variation. Pools were emersed and immersed two times daily. When the pools were immersed in seawater during high tides, all their physico-chemical parameters were similar to those of inshore seawater. When the pools were isolated during the daytime low tide, water temperature, salinity, pH, and dissolved oxygen started to increase gradually, peaking (water temperature at 33°C, salinity at 38°/oo, pH at 9.0 and dissolved oxygen at 15 mg L^{-1}) in the late afternoon (at ∼ 15:00) and then decreasing. When the pools were immersed again after the first low tide, the physico-chemical parameters became similar to those of inshore seawater again. The second low tides happened in the very early morning (03:00 to 07:00). During this period, when the pools were isolated, the water temperature, dissolved oxygen, and pH decreased and reached its lowest values (water temperature at ∼27–28°C, pH at ∼7.2 and dissolved oxygen at ∼2 mg L^{-1}) at around 05:00–06:00. In contrast to other physio-chemical parameters, salinity continued to increase during the early morning low tide. On the second conservative day of measurement, it rained during the afternoon low tides when the pools were emersed. Water temperature dropped (∼27°C) and salinity plummeted to as low as 5°/oo, compared with 33°/oo for the inshore seawater (**Figure 3**). The pH and dissolved oxygen followed previous trends of increase, peaking at around 17:00 and dropping again during high tides (**Figure 3**).

Abundance of Barnacles in Rock Pools and on Emergent Rock

Chthamalus malayensis had a higher abundance on the adjacent open rock surfaces than in pools on all shores (**Figures 4A,B** and **Table 3**). The abundance of *A. amphitrite* on adjacent open rock surfaces and in pools varied among shores (**Figure 4C** and **Table 3**). In Tanyong Po, *A. amphitrite* was more abundant on open rock surfaces than in pools, and this pattern was reversed in Pleum Sook (**Figure 4C**). Based on the pooled data from across all shores, there were no significant differences in *A. amphitrite* between the open rock surfaces and pools (**Table 3**). In general, *A. amphitrite* had a lower abundance than *C. malayensis* on open rock surfaces (**Figure 4** and **Table 3**).

TABLE 3 | Permutational multivariate ANOVA (PERMANOVA) for the effects of habitat (rock pools and adjacent open rock surfaces), species and shore on barnacle abundance.

Source of variation	df	MS	Pseudo-F	*p* (perm)
Pooled across shores				
Habitat (Ha)	1	29674	86.67	**<0.05***
Species (Sp)	1	23284	68.01	**<0.05***
Ha × Sp	1	29085	84.96	**<0.05***
Residual	300	342.37		
Total	303			
C. malayensis				
Habitat (Ha)	1	55229	33.71	**<0.05***
Shore (Sh)	4	1983.10	4.12	**<0.05***
Ha × Sh	4	1714.50	3.56	**<0.05***
Residual	142	480.97		
Total	151			
A. amphitrite				
Habitat (Ha)	1	180.63	0.16	0.77
Shore (Sh)	2	801.15	5.15	**<0.05***
Ha × Sh	2	1213.40	7.81	**<0.05***
Residual	94	155.46		
Total	99			

Bold values and asterisks indicate significant effects.

Barnacle Recruitment in Rock Pools and on Emergent Rock

Barnacle recruitment was observed in October 2019 and from June to September 2020, when recruits could be seen on open rock surfaces (**Figure 5**). There was a significant difference in the density of recruits between the rock pools and adjacent open rock surfaces (**Figure 5A** and **Table 4**). Recruits were only recorded in pools at Had Sai Yao in June 2020 and at Tanyong Po in August 2020. No recruitment was found in pools in any other month on either shore (**Figure 5**). In Tanyong Po, the density of recruits was more than three times higher on adjacent open rock surfaces than inside pools (**Figure 5A**).

Submersion Experiment

Survivorship for *C. malayensis* differed between treatments (**Figure 6A** and **Table 5**). After 2 weeks, all *C. malayensis* survived well in the control treatment (> 90% survival) but had a survival of 80% under continuous submersion (**Figure 6A**). Survival of *A. amphitrite* was not different between the treatments (**Figure 6B**, **Table 5**).

Effect of Temperature and Salinity on Barnacle Survival

The *C. malayensis* and *A. amphitrite* had similar survival patterns at different temperatures and salinities (**Figure 7**). Based on the two-way ANOVA, the interaction between temperature × salinity in barnacle survivals was significant. At 50°C, none of the

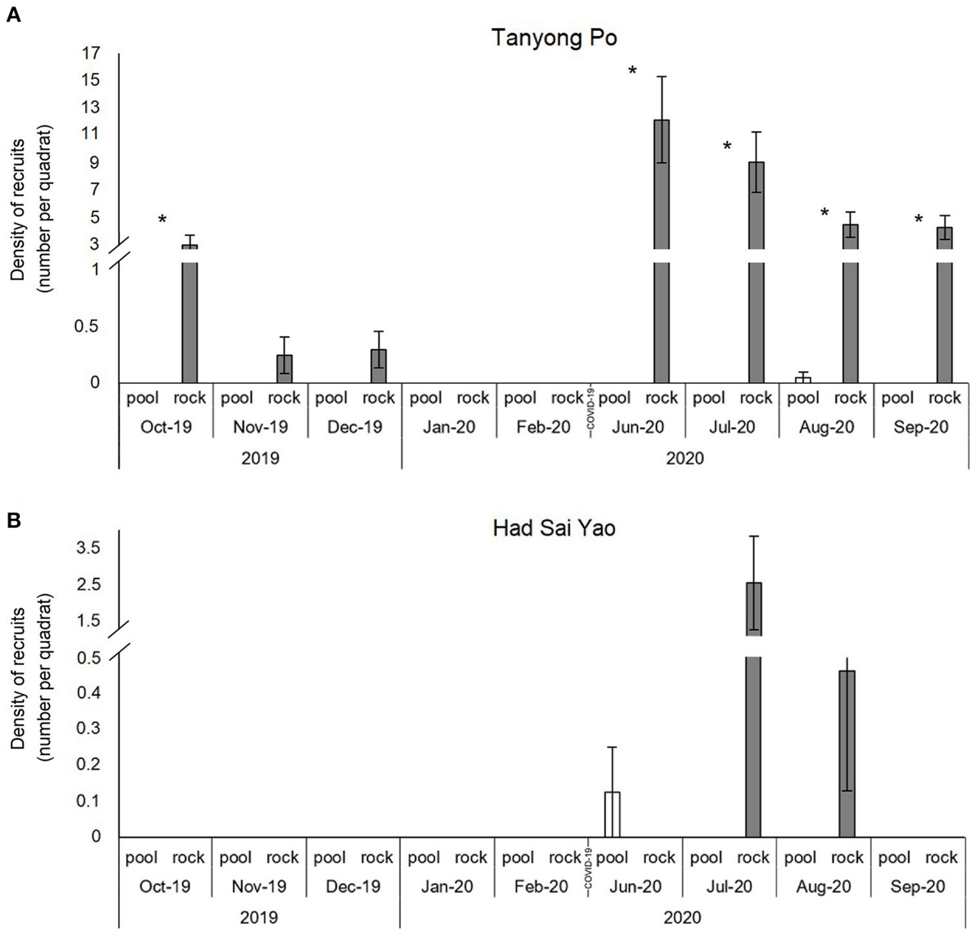

FIGURE 5 | Density of recruits (mean ± SE) in rock pools and on emergent rock from October 2019 to September 2020. Samplings were not carried out from March 2020 to May 2020 due to logistical difficulties during COVID-19 lockdown. **(A)** and **(B)** Tanyong Po and Had Sai Yao, respectively. Icon: *significant differences between habitats as suggested by pairwise tests.

barnacles survived (0% survival), regardless of the salinity level. When barnacles were maintained at 40°C, ∼40–50% survived at 0°/oo, whereas survival was up to 90% under 33, 50 and 60°/oo salinities, with no significant difference among these top three salinities (SNK test; $p < 0.05$). At 30°C, there was no significant difference in survival among salinity treatments, and >90% of all barnacles survived (**Figure 7** and **Table 6**).

DISCUSSION

Physico-Chemical Environment in Indian Ocean Rock Pools

The present study is the first to describe the physico-chemical environment of rock pools and its diurnal variation in the Indian Ocean. Water temperature, salinity, pH, and dissolved oxygen levels fluctuate across diurnal cycles, with one maximum and minimum period per day during the two low tides periods. The diurnal pattern of variations in physico-chemical parameters in the rock pools of the present study is similar to the patterns addressed in the subtropical Hong Kong, in the South China Sea of the Pacific region (Chan, 2000). Both regions have two periods of pool isolations from low tides, and the physico-chemical parameters of both peaked in the later afternoon. The range

TABLE 4 | PERMANOVA on the effects of habitat, shore, and month on the recruitment of barnacles.

Source of variation	df	MS	Pseudo-F	*p* (perm)
Habitat (Ha)	1	456.19	1.42	**<0.05***
Shore (Sh)	1	318.16	24.16	**<0.05***
Month (Mo)	8	72.67	1.49	0.20
Ha × Sh	1	321.34	24.40	**<0.05***
Ha × Mo	8	71.10	1.42	0.21
Sh × Mo	8	48.63	3.69	**<0.05***
Ha × Sh × Mo	8	50.15	3.81	**<0.05***
Residual	508	13.17		
Total	543			

**indicate p <0.05.*
Bold values and asterisks indicate significant effects.

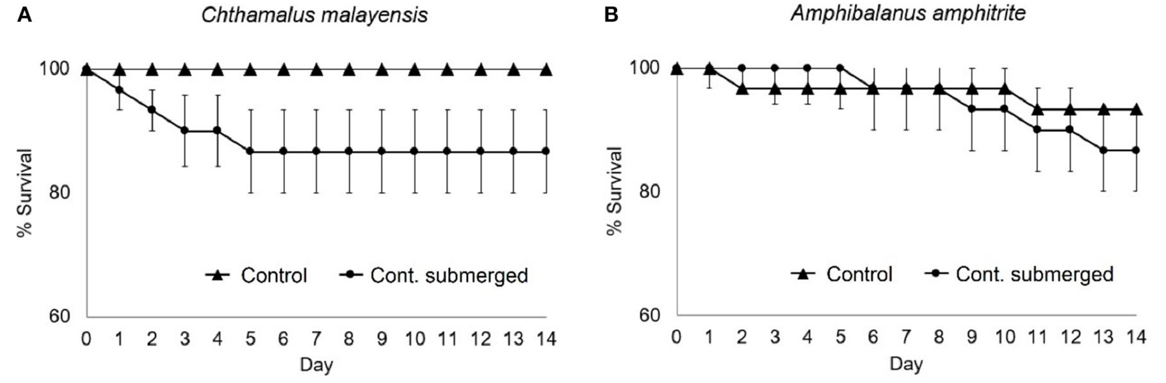

FIGURE 6 | Percentage of survival (mean ± SE) of barnacles in submersion experiment. **(A)** *C. malayensis* and **(B)** *A. amphitrite*.

TABLE 5 | Two-way ANOVA on the effects of treatment and day on the percentage of surviving barnacles in the submergence experiment.

Source of variation	df	MS	*F*	*P*
C. malayensis				
Day (D)	14	27.30	0.51	0.92
Treatment (T)	1	2667.78	50.02	**<0.001***
D × T	14	27.30	0.51	0.92
Residual	60	53.33		
Total	89			
A. amphitrite				
Day (D)	14	71.11	1.68	0.08
Treatment (T)	1	17.78	0.42	0.52
D × T	14	17.78	0.42	0.96
Residual	60	42.22		
Total	89			

**indicate $p < 0.05$.*
Bold values and asterisks indicate significant effects.

of variations in water temperature, salinity, pH, and dissolved oxygen is similar between Thailand and Hong Kong (Chan, 2000). Similar to the present study, the water temperature, salinity, pH and dissolved oxygen concentration in the NW coast of Brittany in the temperate region of the Atlantic had one maximum (later afternoon) and one minimum (early morning). However, rock pools in the Atlantic coast of France have a single low tide isolation per day. This isolation can last up to 10 h, much longer than the 6- to 7-h low tide isolation in the present study. Water temperature in the present study is higher than the summer water temperature in the Britany rock pools, but the range of salinity variation is similar between the present study and the Atlantic rock pools.

Distribution of Barnacles in Rock Pools and Adjacent Open Rock Surfaces

In the present study, it was found that *Chthamalus malayensis* was more abundant (>40%) on the adjacent rock surfaces than inside rock pools (<5%). This pattern is similar to the pattern addressed in *Balanus balanoides* in the temperate Atlantic (Singletary and Shadlou, 1983) that barnacles were more intense on rock surfaces than inside rock pools. High shore intertidal species often inhabit open rock surfaces instead of inside rock pools. The high shore limpet, *Cellana grata*, for example, are common on open rock surfaces and at rock pool interface (adjacent surface to pools) but never get submerged in rock pools. The limpets at pool interface had relatively lower heat stress when compared to open rock surfaces. The lower shore barnacle, *Amphibalanus amphitrite*, in contrast, had overall similar abundances (5–10%) in pools and also on the rock surfaces. The vertical distribution of *A. amphitrite* extends from lower intertidal to subtidal region. *A. amphitrite* often has intense settlement on shores and subtidal man-made objects (Desai and Anil, 2005). *A. amphitrite* is also one of the marine fouling species due to its intense settlement and high tolerance to environmental stresses (Desai and Anil, 2005). *A. amphitrite* had higher abundance in rock pools when compared with *C. malayensis* indicates this barnacle survives well inside the rock pools environment.

Factors Affecting Barnacle Survival in Rock Pools

In the present study, sparse recruitment of barnacles was recorded in some of the rock pools, suggesting that barnacle larvae can settle in the rock pools and grow into recruits. This does not support the first hypothesis, that barnacles are rare in pools because of a lack of recruitment. However, the density of recruits is much lower in pools than on adjacent open rock surfaces. This suggests that some factors may affect the post-settlement and post-recruitment mortality of barnacles recruited inside of rock pools. Rock pools in the Andaman Sea of Thailand are often inhabited by various species of gastropods including the *Monodonta* and *Nerita* snails (Sanpanich and Duangdee, 2013). Bulldozing effect of the settled cyprids by these mobile molluscan grazers can affect the success of the settlement (Chan and Williams, 2003). In the temperate Atlantic, the occurrence of some algae and biofilms might affect the settlement and post-settlement mortality of barnacles (Singletary and Shadlou, 1983).

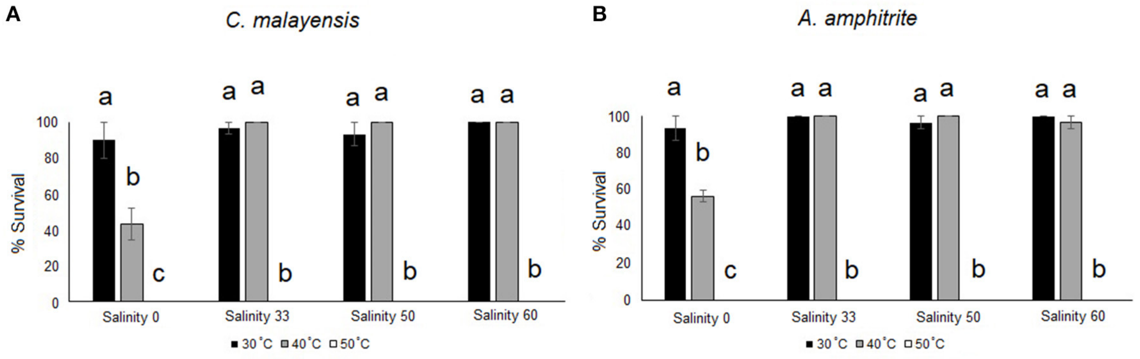

FIGURE 7 | Percentage of barnacles, namely, **(A)** *C. malayensis* and **(B)** *A. amphitrite* (mean ± SE), that survived under different temperature and salinity treatments. Different small letters = significant difference between temperature within each salinity treatment. Note survival of barnacles is 0 in 50°C.

TABLE 6 | Two-way ANOVA on the effects of Temperature and Salinity on the percentage of survival of two species of barnacles.

Source of variation	Df	MS	*F*	*P*
C. malayensis				
Temperature (T)	2	289.67	325.23	**<0.001***
Salinity (Sa)	3	3.68	16.85	**<0.001***
T × Sa	6	2.72	12.48	**<0.001***
Residual	24	0.22		
Total	35			
A. amphitrite				
Temperature (T)	2	300.53	224.66	**<0.001***
Salinity (Sa)	3	1.83	31.77	**<0.001***
T × Sa	6	1.31	22.74	**<0.001***
Residual	24	0.06		
Total	35			

**indicate $p < 0.05$.*
Bold values and asterisks indicate significant effects.

Algae are more abundant in rock pools than on open rock (Nylund and Pavia, 2003; Othmani et al., 2016).

Submergence experiments indicated that both *C. malayensis* and *A. amphitrite* can have at least 80% lower survival under submergence conditions compared to simulated tidal conditions (control) although barnacles suffer slight mortality under submerged conditions. Continuously submerged conditions in pools do not appear to be the major cause of barnacle mortality in rock pools. Compared to the high shore intertidal limpets, *Cellana grata*, which are common on rock surfaces but not found in rock pools, continuous submergence under laboratory conditions can result in 70% mortality after 96 h (Gray, 2010). This may explain continuous submergence can be a factor for the absences of *C. grata* inside rockpools.

Based on the multivariate analysis of rock pool physico-chemical environment and barnacle abundance, water temperature and salinity are the main factors controlling barnacle distribution. In the laboratory temperature and salinity experiment, barnacles did not survive in the high water temperature (50°C) environment. At 40°C, barnacles had greater mortality (∼40–50%) only in the low salinity treatment (0°/$_{oo}$), but not in the high salinity treatments. For the 30°C treatment, both barnacle species had high survivals in all salinity treatments. When barnacles were exposed to low salinity water, their opercular valves were closed to stop external water from getting inside the shell. As a result, mantle water and haemolymph can have higher osmolality than the external environment (Chan et al., 2001). However, at high temperatures, barnacles can enter a coma state and lose the ability to close their opercular valves. As a result, low salinity water can enter the mantle and affect the osmolality of the hemolymph, reducing survival. This suggests that the combination of high water temperature and low salinity (after rain) can lead to high barnacle mortality in rock pools. In natural rock pools, salinity can be as low as almost 0°/$_{oo}$ during the heavy rain monsoon season on the Andaman coast (May to October), and intense solar radiation shortly after rains can heat up pool water. This condition can cause mortality in barnacles inside pools. This is probably a common phenomenon on tropical shores. During the wet season in Hong Kong, the limpet *Cellana grata* experienced heavy rainfall and subsequently, heat stresses had faster heart beat rates and lower haemolymph and mantle osmolalities when compared with limpets that were not stressed. Such patterns suggest that heat and raining can both impose different levels of stress and protein responses, but their combination had an interactive effect on the limpets' metabolism and survival (Williams et al., 2011). The brittle star, *Ophiopholis mirabilis*, is common in the temperate intertidal region of the West Pacific. The combination of temperature and salinity can affect its metabolism, ammonia excretion, and tissue moisture. Reduced salinity conditions in combination with temperature variations can result in mortality due to the tissue moisture beyond their regulatory capacity (Fang et al., 2015). In the cold Baltic Sea, the barnacle *Balanus improvisus* had increased mortality in low salinity (5 psu) and low temperature (12°C) because low water temperature narrowed the barnacle's tolerance toward low salinity (Nasrolahi et al., 2013). Salinity and water temperature can thus interplay together and impose interactive stress toward intertidal species and affect their mortality.

However, the present study has not tested the effect of dissolved oxygen on barnacle survival. On the Atlantic coast of the USA, pools may not be able to support high densities of settlers because such a condition would decrease the dissolved oxygen needed to support such densities of barnacles, thus resulting in hypoxia and high barnacle mortality (Singletary and Shadlou, 1983). In the present study, some of the rock pools had very low dissolved oxygen (1–3 mg. L^{-1}). In such an environment, barnacles, if recruited in those pools, probably would not survive.

In conclusion, barnacles are rare in tropical Indian Ocean rock pools. This is a result of the interplay of continuous submergence, high water temperature, and low salinity causing barnacle mortality. Future research should investigate biological factors like predation (density of whelks in rock pools) or the grazing of molluscs, which bulldoze settlers (Chan and Williams, 2003).

DATA AVAILABILITY STATEMENT

The original contributions generated for the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

KW conceived the idea and designed the study. NB analyzed the data and wrote the first draft of the manuscript. BC involved in experiment design, manuscript writing and provided advice. All authors read and commented on the manuscript.

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Differences in the Structural Components Influence the Pumping Capacity of Marine Sponges

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Marine sponges are important sessile, benthic filter feeders with a body plan designed to pump water efficiently. The sponge body plan generally consists of mineral spicules, gelatinous mesohyl, and the pores and canals of the aquiferous system. These structural components have stark differences in compressibility, mass, and volume; therefore, their proportion and distribution are likely to affect sponge morphology, anatomy, contraction, and finally the pumping capacity. We examined seven demosponge species (from high spicule skeleton contents to no spicules) commonly found along the central west coast of India for structural components, such as total inorganic contents (spicule skeleton and foreign inclusions), body density, porosity, and mesohyl TEM for the high microbial abundance/low microbial abundance status. Additionally, we estimated the sponge pumping rate by measuring the excurrent velocity, the abundance of individual pumping units and cells, i.e., choanocyte chambers and choanocytes, and also carried out a morphometric analysis of aquiferous structures. The excurrent velocity and the oscular flow rates showed a positive relationship with the oscular crosssectional area for all the study species. The inorganic spicule contents by their weight as well as volume formed a major component of tissue density and higher proportions of spicules were associated with reduced aquiferous structures and lower pumping rate. The ash mass% and the ash free dry weight (AFDW %) in the sponge dry mass showed separate and distinct associations with aquiferous system variables. For example, the number of choanocytes per chamber showed a wide difference between the studied species ranging from 35.02 ± 2.44 (*C.* cf. *cavernosa*) to 120.35 ± 8.98 (*I. fusca*) and had a significant positive relationship with AFDW% and a negative relationship with ash mass%. This study indicates that the differences in the proportions of structural components are closely related to sponge gross morphology, anatomy, and probably body contractions, factors that influence the sponge pumping capacity.

Keywords: pumping, spicules, sponge (porifera), mesohyl, choanocyte chamber, aquiferous module, canal

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INTRODUCTION

Poriferans (sponges) are found in almost all benthic habitats and are capable of processing the volume of water several times their body volume per hour (Reiswig, 1971, 1981; Riisgaard and Larsen, 1995). Filter feeding sponges play an important role in recycling nutrients and coupling pelagic food supply with benthic communities (Gili J M Coma, 1998; Maldonado et al., 2012; Pawlik and McMurray, 2020). Although, being filter feeders, a major portion of sponge diet is composed of the dissolved organic carbon (DOC) (Yahel et al., 2003; McMurray et al., 2016) and it is suggested that sponge assimilated DOC facilitates its bioavailability to other tropic levels in form of detritus (De Goeij et al., 2013) and biomass that feeds various sponge predators (McMurray et al., 2018).

Considering the wide distribution range and exposure to different environmental regimes, different morphological adaptations are observed in sponges. These morphological differences can manifest on macro as well as microlevels i.e., gross morphology and spicule morphology, respectively (Bell et al., 2002). Sponges are sessile metazoans lacking muscular, nervous, and digestive systems. Instead, they have a body full of pores and canals with a body plan designed to efficiently pump water. The sponge body plan generally consists of three major structural features, the aquiferous system, gelatinous mesohyl, and the spicule skeleton. The aquiferous system constitutes the pores, canals, and hollow spaces that conduct a unidirectional flow of water to filter and absorb the nutrients, exchange gases, and expel the waste products. The mesohyl is a gelatinous matrix with a free-floating population of different cell types and is bound between choanoderm and pinacoderm made of flagellated choanocytes and flattened pinacocytes, respectively. The pinacoderm covering the outer surface of the sponge is referred to as an exopinacoderm and the layer of pinacocytes lining the canals inside the sponge is referred to as endopinacoderm (Leys and Hill, 2012). The spicule skeleton consists of microscopic inorganic spicules. The mesohyl and the spicule skeleton support the pores and the canals of the aquiferous system by forming a three-dimensional scaffold structure.

Scaffold design is an important aspect of tissue engineering, and studies show that successful designs require a fine balance between mechanical function and interconnected pore network for flow transport of nutrients and metabolic waste (Hollister et al., 2000; Hutmacher, 2000; Hollister, 2005). This balance is often achieved by a trade-off mechanism between a denser scaffold for better mechanical function and a more porous scaffold for better flow transport (Hollister, 2005). Such mechanisms are evident in sponges. The proportion and distribution of scaffold materials (spicule skeleton and mesohyl), and the pore network (aquiferous system) have variations within and between species as a function of ecology and natural history. For instance, sponges have narrower canals when the proportion of spicules is higher in high disturbance environments (Palumbi, 1986) or when the mesohyl is densely packed with high biomass of associated microbes (Vacelet and Donadey, 1977; Wilkinson, 1978, 1983). Sponges have evolved strong symbiotic association with microorganisms (Taylor et al., 2007) and are characterized into two distinct categories of high microbial abundance (HMA) sponges and low microbial abundance (LMA) sponges based on the abundance of microbes within the mesohyl (Hentsshel et al., 2003). Both HMA and LMA sponges show a high degree of host specificity and temporal stability of the microbial symbionts with low seasonal and interannual variation (Taylor et al., 2007; Gloeckner et al., 2014; Erwin et al., 2015). In HMA sponges, the mesohyl with the microbial biomass can comprise up to one-third of the total sponge biomass (Vacelet and Donadey, 1977). When compared with LMA sponges, the disproportionate increase in the mesohyl of HMA sponges is associated with an increase in tissue density (Weisz et al., 2008), a decrease in the abundance of choanocyte chambers (CC; Poppell et al., 2014), and the narrowing of canal (Vacelet and Donadey, 1977) features that are related to the aquiferous system.

Although sponges have high anatomical and morphological variation, the aquiferous system follows specific design principles to control the water velocity at specific regions within the sponge (LaBarbera and Vogel, 1982; LaBarbera, 1990; Labarbera, 1995; Vogel, 1996). This has a functional significance and is evident in the morphometric models which show that the canal systems of sponges with different morphologies reduce water velocities at the filtering structures to enable nutrition absorption and food capture (Leys et al., 2011; Ludeman et al., 2016). The water flow in the aquiferous system starts at the numerous microscopic inhalant pores called ostia, present on the external body surface. Beneath the ostia are subdermal lacunar spaces connected to the incurrent canals that successively branch into fine, narrower canals and open into the CC *via* a pore called a porospyle. The CC is lined with cells that have an apical flagellum, surrounded by a microvillar collar. Here, the incurrent water spreads and slows down due to the increased surface area of the numerous narrow canals and the microvillar collar. This helps to filter and absorb the particles and exchange the gases. The filtered water flows out of the CC into the excurrent canals *via* a pore called apopyle. The increasing diameter and the reducing surface area of the converging excurrent canals expel the water out of the osculum, the excurrent opening, with a high velocity so that same water is not refiltered (Riisgård et al., 1993; Riisgaard and Larsen, 1995; Leys et al., 2011; Ludeman et al., 2016).

The efficacy of the aquiferous system would depend on the canal architecture with optimum branching pattern. However, high-resolution 3D reconstructions of the aquiferous system of sponge *Tethya wilhelma* show that the aquiferous system architecture diverges from the theoretical optimum and the branching topology follows a non-hierarchical and a non-uniform pattern (Hammel et al., 2012). This deviation could be attributed to the interdependent development of the canal structures, skeletal structures, and sponge tissue (Hammel et al., 2012). For example, morphologically similar sponges *Haliclona permollis* and *Halicondria panacea* vary in the cross sectional area of ostia due to differences in the spicule arrangement (Reiswig, 1975). Additionally, the erect tree-like growth forms of sponge *Haliclona oculata* and *Haliclona simulans* display radiate-accretive growth, with a regular anisotropic reticulate type of skeleton (de Weerdt, 1986; Kaandorp, 1991), but the aquiferous system of *H. oculata* is poorly developed, and the canals are only present in proximity to the oscula, whereas in *H. simulans* the aquiferous system is more complex and is visible as an extensive system of canals (de Weerdt, 1986; Kaandorp, 1991). These observations indicate that morphologically similar sponges can differ in their spicule skeleton and show major differences in the architecture of their aquiferous system. These structural components have stark differences in compressibility, mass, and volume; therefore, their proportion and distribution are likely to affect sponge morphology, anatomy, contraction, and pumping capacity.

In the present study, we compare the abundance of the filtration apparatus, dimensions of the aquifereous components, and the pumping parameters in sponges with different proportions of the structural components. To do this, we measured the body density, total inorganic contents (spicule skeleton and foreign inclusions), porosity, and examined the TEM of mesohyl for HMA/LMA status of seven demosponge species (*Cinachyrella* cf. *cavernosa*, *Suberites carnosus*, *Ircinia fusca*, *Amorphinopsis foetida*, *Haliclona* sp., *Calyspongia* sp., and *Biemna fortis*) from the rocky intertidal regions on the west coast of India. We selected sponge species from different sponge taxa representing different characteristics such as psammobiotic species with buried growth form (*B. fortis*) having high inorganic contents and keratose sponges (*Ircinia fusca*) with massive morphology and no mineral spicule skeleton. The species also represented morphological shapes such as tetillid sponge *Cinachyrella* cf. *Cavernosa* having a characteristic spherical morphology with circular depressions called porocalices (Szitenberg et al., 2013) and mineral skeleton of spicule bundles radiating from the sponge center. Other morphological shapes included in the study were the tubular shaped *Haliclona* sp., *Calyspongia* sp., and the thick encrusting form of *A. foetida.* The goal of the present study was to examine the influence of the structural components on sponge pumping by (1) assessing anatomical variations in the sponges with a different morphology from the central west coast of India (2) and determining if structural differences in sponge anatomy influence their function.

MATERIALS AND METHODS

Measurement of Excurrent Velocity and Pumping Rate

The fieldwork was conducted at two intertidal zones, Anjuna (15°33′57.51″N 73° 44′30.39″E) and Kunkeshwar (15°55′28. 16″N 73°33′26.69″E) along the Central West Coast of India (**Figure 1**). A total of seven sponge species were included in the present study. The representative specimens of the studied sponges have been deposited at the CSIR–NIO Repository and Taxonomic Center under the following reference code–*A. foetida* (NIO1012/21), *B. fortis* (NIO1011/21), *Calyspongia* sp. (NIO1009/21), *Cinachyrella* cf. *cavernosa* (NIO-41), *Haliclona* sp. (NIO1010/21), *Ircinia fusca* (NIO1007/21), and *Suberites carnosus* (NIO1008/21) (**Figure 1**). Sponge pumping rate was measured using an *in situ* dye technique, as described by Weisz et al. (2008). The volume of water passing through the osculum per second was calculated as a product of excurrent velocity and the osculum crosssectional area. A small volume (2–3 ml) of a concentrated fluorescein dye solution was released near the sponge osculum. The excurrent velocity was determined by video recording the movement of dye fronts. Video recordings were analyzed by monitoring the dye movement frame-by-frame (30 frames per second) with reference to a laminated graph paper held in the background behind the osculum. The travel time of 5–10 dye fronts across the first 3–5 cm was averaged together to obtain the mean excurrent velocity. This mean value was multiplied by the osculum cross sectional area (OSA). Sponge oscula were photographed *in situ*, with an underwater camera and the OSA was measured using functions in ImageJ software. For sponges with more than one osculum, the pumping rate of the whole sponge was obtained by adding the pumping rate measured for each osculum present on that individual. Some of the oscula on multiosculated individuals of *I. fusca* ($n = 6$) and *S. carnosus* ($n = 5$) were not accessible for measurements. In such situations, an average pumping rate (obtained by measuring a minimum of three oscula for each specimen) was used for the osculum that could not be measured. Following the velocity measurements, the whole sponge was collected to measure the sponge biovolume by the water displacement method. It was difficult to determine the individual specimen for *Haliclona* sp., *Calyspongia* sp., and *A. foetida* as the sponges converged and covered large patches of rock ledges or extended inside rock crevices. Therefore, for these sponges, we measured the excurrent velocity on the osculum adjacent to each other and collected that portion of the sponge, and the biovolume was divided by the number of oscula to obtain the biovolume specific pumping rate per osculum. The ratio of volume to dry weight of 3–4 pieces from the collected sponge individuals was calculated to standardize the volume flow rate to dry weight. Before and during all excurrent velocity measurements, no physical contact was made with the sponges.

Structural Components

To measure the body density, tissue composition (organic and inorganic material), and porosity a whole individual (three to nine individuals per species) or a portion of the sponge was fixed in 7% formalin immediately after collection in the field. Sponges were washed in seawater to remove sand and debris from the surface. Sponge volume was determined by measuring the water displacement using the immersion method. The sponge density was measured as the mass (dry weight)/volume ratio. Dry weight (DW) was obtained by drying the samples in an oven at 60°C for more than 48 h (Weisz et al., 2008). To determine the proportion of the spicule skeleton in the body composition, dry sponge samples were combusted in a muffle furnace at 450°C for 8 h (Chanas and Pawlik, 1995). The ash remains i.e., the ash weight (AW) constitute the total inorganic contents (spicule skeleton + foreign inclusion) within the sponge tissue. The proportion of the organic material in the dry bodyweight could be

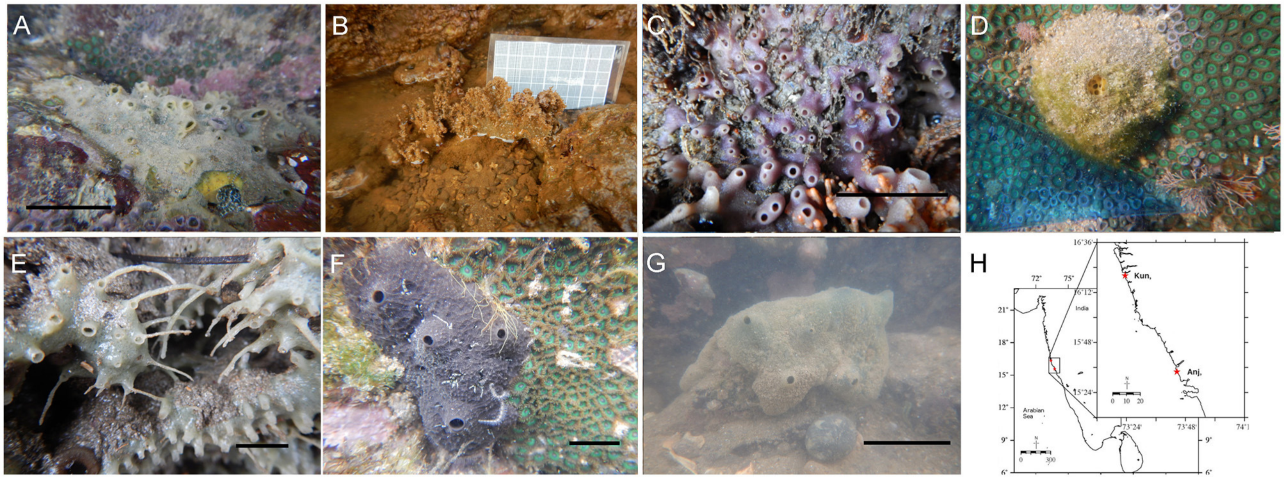

FIGURE 1 | The study species **(A)** *Amorphinopsis foetida,* **(B)** *Biemna fortis,* **(C)** *Calyspongia* sp., **(D)** *Cinachyrella* cf. *cavernosa,* **(E)** *Haliclona* sp., **(F)** *Ircinia fusca,* **(G)** *Suberites carnosus,* **(H)**. The study area showing the location of Anjuna (Anj) and Kunkeshwar (Kun). [Scale **(A)** = 5 cm, **(C)** = 3 cm, **(E)** = 2 cm, **(F)** = 5 cm, **(G)** = 5 cm].

estimated by calculating the ash-free dry weight (AFDW) using the following equation.

$$DW - AW = (AFDW) \tag{1}$$

Since spicules are non-compressible, their volume remains unaltered during body contraction events. Therefore, we also calculated the volumetric proportions of the spicule skeleton and inorganic contents within the sample by dividing the weight data by the material density of substances having comparable density with siliceous spicules (Fang et al., 2013). The material density of opal (2.09 g cm^3) is similar to the siliceous spicules of hexactinellid and demosponge species (Sandford, 2003) and thus was used to calculate the volume proportion of the spicule skeleton within the samples.

The porosity measurements were carried out according to the methods described by Miron-Mendoza et al. (2010). SEM images were subjected to threshold adjustment to convert the pores/canals and collagen/mesohyl matrix to black and white images. The pixel density was adjusted to eliminate the obviously deep collagen fibrils. The 2D black and white representation of the matrix was evaluated using the Analyze Particle Function of ImageJ (particles = black pores).

Morphometric Analysis: Histology and Scanning Electron Microscopy

For morphometric analysis, the dimensions of the aquiferous structures were measured from both histological sections and scanning electron microscopy (SEM) images using ImageJ. For histology, sponge pieces from four to six specimens per species were processed. Samples were fixed in 7% formalin for at least 48 h, rinsed twice in filtered seawater, and then treated with hydrofluoric acid (HF) for 8–10 h to dissolve the spicules. Sponge spicules are frequently dissolved in 5% HF (Langenbruch and Jones, 1990). However, this concentration did not dissolve the spicules completely, so we used 20% HF (Gerasimova and Ereskovsky, 2007) to dissolve the spicules in large sponge pieces, particularly the thick spicule bundles in *C.* cf. *Cavernosa* and the sand grains in the buried growth form of *B. fortis.* The sponge pieces were dehydrated through a graded series of ethanol, embedded in paraffin, sectioned to 5 µm, and stained using Harris's Haematoxylin, and Young's Eosin Erythrosin.

For SEM, two to three sponge pieces (~10×5 mm) from each species were fixed in a fixative consisting of 2% OsO_4, 2.5% glutaraldehyde in filtered seawater. Some sponge pieces were desilicified in 4% HF then and rinsed with distilled water. Sponge pieces used for porosity measurements were not treated with HF. The samples were dehydrated through a graded series to 100% ethanol, critical point dried (Leica EM CPD300), and then mounted on stubs with double-sided carbon tape. Specimens were then sputter coated in gold: palladium mixture and viewed in a scanning electron microscope. Some pieces of *Ircinia fusca* were embedded in paraffin wax sectioned at 20–30 µm, treated with xylene for 15–20 min to remove the wax, and then processed the same way as other samples.

Mesohyl Examination: Transmission Electron Microscopy

Transmission electron microscopy (TEM) was used to visually assess the bacterial symbionts density in the mesohyl matrix. Freshly collected sponge material of 7–8 mm^3 in size was fixed in 2.5% glutaraldehyde/phosphate-buffered saline for a minimum of 24 h. The samples were rinsed three times for 20 min each in PBS and post-fixed in 2% osmium tetroxide/PBS for 1 h. After fixation, the samples were treated with 5% HF for 2 h to dissolve the spicules followed by three washes in PBS, 20 min each. Samples were dehydrated in ethanol series (30, 50, 70, 90, 3 × 100%), at room temperature and impregnated in the resin. Thin sections were cut with a diamond knife mounted on an

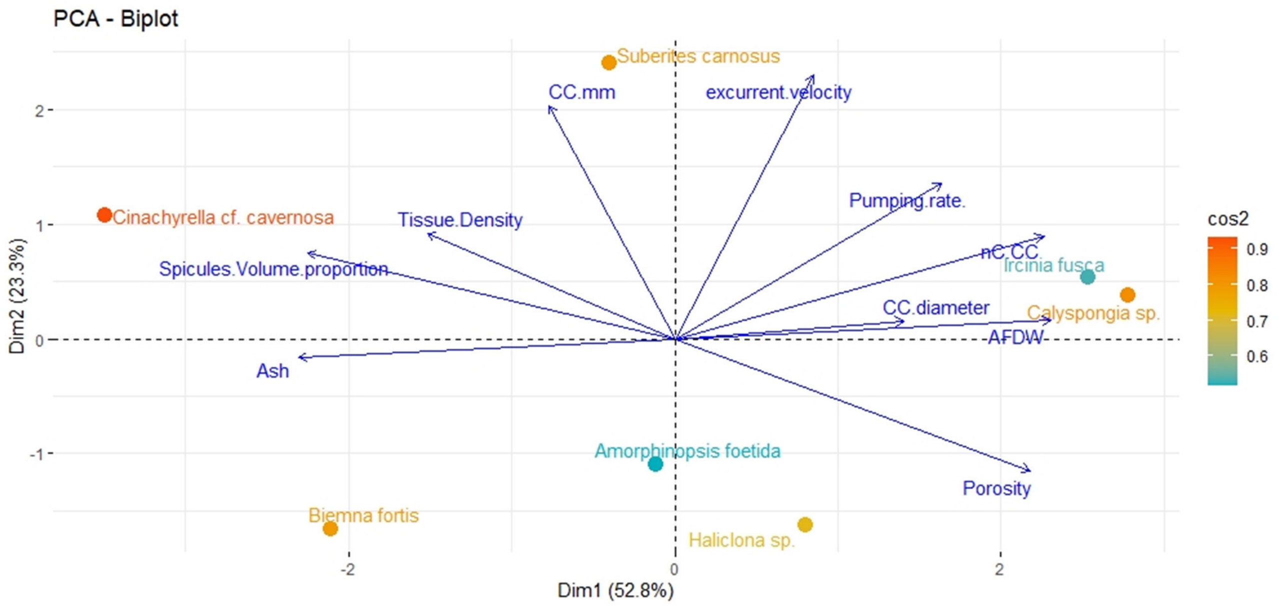

FIGURE 2 | Principal components analysis Dim1 (PCA1) and Dim2 (PCA2) of the combination of structural, filtration, and pumping variables indicating the position of the studied sponge species on a plane defined by the first two axes. Arrows indicate the direction of factor loadings on axes 1 and 2.

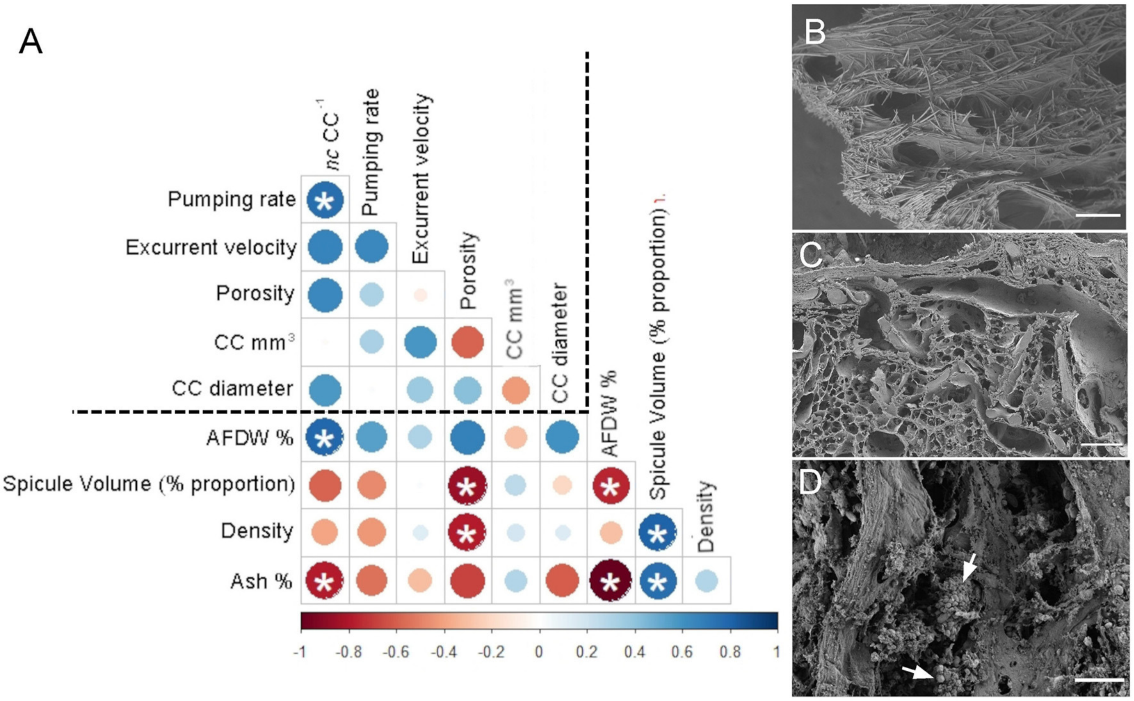

FIGURE 3 | (A) Correlation matrix summarizing all pairwise comparisons between structural components, filtration apparatus, and pumping parameters. The intensity of the color and the size of the circle indicate the strength of the correlation, with red being negative and blue being positive. The dashed line separates the variables related to structural components from the filtration apparatus and pumping parameters. Significant relationships ($p < 0.05$) are marked with an asterix **(B)** *Amorphinopsis feotida* tissue with spicules **(C)** *Ircinia fusca* tissue without any spicules **(D)** *Calyspongia* sp. with the empty spaces around the choanocyte chambers. White arrows point to choanocyte chambers. [scale **(A)** = 500 μm, **(B)** = 100 μm, **(C)** = 20 μm].

ultramicrotome (Cryo-ultra-Microtome, RMC) and stretched on copper grids. The sections were post-stained with uranyl acetate and lead citrate. Micrographs were taken using a Tecnai T12 G2 spirit (FEI) transmission electron microscope.

Data Analysis

An Abundance of Filtration Apparatus (Choanocyte and Choanocyte Chambers)

Six to eight sections per sponge species were photographed at 10X magnification, 10 images per sponge were examined to quantify the number of choanocyte chambers. Repeat count of the CC extending into the adjacent sections was avoided by selecting sections at least 100 μm apart from each other. The number of CC per mm^3 sponge tissue (N) was calculated with the formula used by Abercrombie (1946) with a modification used by Elvin (1976) and Ereskovsky (2000).

$$N = N\,(\frac{t}{D+t})\,K \qquad (2)$$

where N is the average number of CC in the histological section; t is the thickness of the histological section (0.005 mm); D is the diameter of the choanocyte chamber, and K is the constant (200) for converting the number of CC in one square millimeter to the number in a cubic millimeter.

The number of cells along the CC circumference was counted from the SEM images and histological sections to estimate the number of choanocytes per CC with the following formula.

$$ncc = \frac{4\,nc^2}{\pi^2} \qquad (3)$$

where ncc is the number of choanocytes per CC, nc is the count of the choanocytes along the CC circumference.

Multivariate analyses were used to visualize the studied sponge species in multivariate space with respect to the variables related to the structural components, filtration apparatus, and pumping parameters. Multivariate patterns were examined with the principal component analysis (PCA) computed using similarity matrixes based on Euclidean distance on normalized data set as a method of ordination. The loading plots of the PCA analysis indicated potential correlations between the variables (structural components, filtration apparatus, and pumping parameters). Therefore, to examine how the proportions of the structural components affect the variables related to the filtration apparatus and the pumping parameters, we conducted Pearson's correlations. The results were visualized as a correlation matrix using the corrplot package in R (Watson et al., 2017). *B. fortis* did not have excurrent velocity and pumping rate, therefore the data had missing values. To calculate the correlation for every pair of variables without losing information because of missing values, we set the argument to use = "pairwise." To compare the pumping parameters of different sponge species, we explored the relationship of the OSA with the excurrent velocity and the oscular flow rates using ordinary least squares regression. The data were tested for the assumptions of normal distribution, homoscedasticity, and independence of residuals. A multivariate ANOVA (MANOVA) was conducted to compare the variables related to filtration apparatus (CC mm^3, ncc CC^{-1}, CC diameter) and structural components (Ash%, AFDW%, porosity%, density, and spicule volume%) as the dependent variables and the sponge species as the independent variables.

RESULTS

Multivariate Analysis and the Relationship Between Structural Components, Filtration Apparatus, and Pumping Parameters

Principal component analysis revealed two significant components (eigenvalue < 1) explaining 76.1% of the total variation (**Figure 2**). The first principal component showed strong associations with the number of choanocytes per chamber (nc CC^{-1}), choanocyte chamber size (CC diameter), AFDW, and porosity. The vectors representing these variables were close to each other indicating a positive relationship with each other. Additionally, the vectors were oriented toward sponge species with high scores on these variables (example–*Callyspongia* sp. and *I. fusca*). Variables related to the structural components such as tissue density, spicule volume, and inorganic contents (ash%) were positioned along with the second component and their vectors were oriented toward species scoring high on these variables (*C.* cf. *cavernosa* and *B. fortis*).

The angles between the vectors on the PCA loading plot indicated a potential relationship between the variables and were further examined on Pearson's correlation matrix (**Figure 3A**). In general, the variables related to the filtration apparatus (CC mm^3, CC diameter, and the number of choanocytes per chamber (ncc) CC^{-1}, and porosity%) showed a positive correlation with the pumping parameters (excurrent velocity mm s^{-1} and pumping rate ml s^{-1} ml^{-1}) and a negative correlation with structural components (density, ash mass%, and spicule volume proportion%). Particularly, the number of choanocytes per chamber (ncc CC^{-1}) showed a significant positive correlation with the pumping rate ($r = 0.77$, $n = 7$, $p < 0.05$). Note that within the structural components, the density–porosity, the ash mass%, AFDW% have a naturally inverse association. Interestingly, this was reflected in their relationship with the variables related to the pumping parameters and the filtration apparatus. For instance, ncc CC^{-1} had a significant positive correlation with AFDW%, but a significant negative correlation with Ash%. Similarly, spicule volume which had a significant positive correlation with tissue density had a significant negative correlation with porosity ($r = -0.93$, $n = 7$, $p < 0.001$). This indicated that spicules can form notable intrusions in the water passages and pores of the sponge aquiferous system (**Figure 3B**). For example, *Calyspongia* sp. showed distinctive lacunar spaces around CC, and *I. fusca* had the largest CC and both the sponges had high porosity and low spicule contents (**Figures 3C,D**).

Sponge Pumping Parameters

Mean excurrent velocity and pumping rate with respect to the sponge biovolume and dry mass of the studied species is given in **Table 1**. Both excurrent velocity and the oscular flow rates showed a positive relationship with the OSA

TABLE 1 | Mean excurrent velocity and pumping parameters of the studied species.

Species	Number of specimens (n)	Excurrent velocity (mm s^{-1})	Pumping rate (ml s^{-1} ml^{-1} sponge)	Pumping rate (ml s^{-1} g^{-1} DWsponge)
Amorphinopsis foetida	3	13.44± 0.83	0.04 ± 0.01	0.54 ± 0.09
Beimna fortis	5	–	–	–
Calyspongia sp.	5	28.83± 1.38	0.33 ± 0.05	1.85 ± 0.43
Cinachyrella cf. *cavernosa*	9	27.59 ± 1.46	0.05 ± 0.005	0.07 ± 0.01
Haliclona sp.	5	11.03 ± 0.34	0.11 ± 0.01	0.65 ± 0.09
Ircinia fusca	7	33.46 ± 1.06	0.12 ± 0.02	0.41 ± 0.06
Suberites carnosus	5	35.54 ± 0.75	0.23 ± 0.01	1.68 ± 0.03

Data are means ± SE pumping rate is standardized by sponge volume (per ml sponge) and sponge weight [per gram dry weight (DW)].

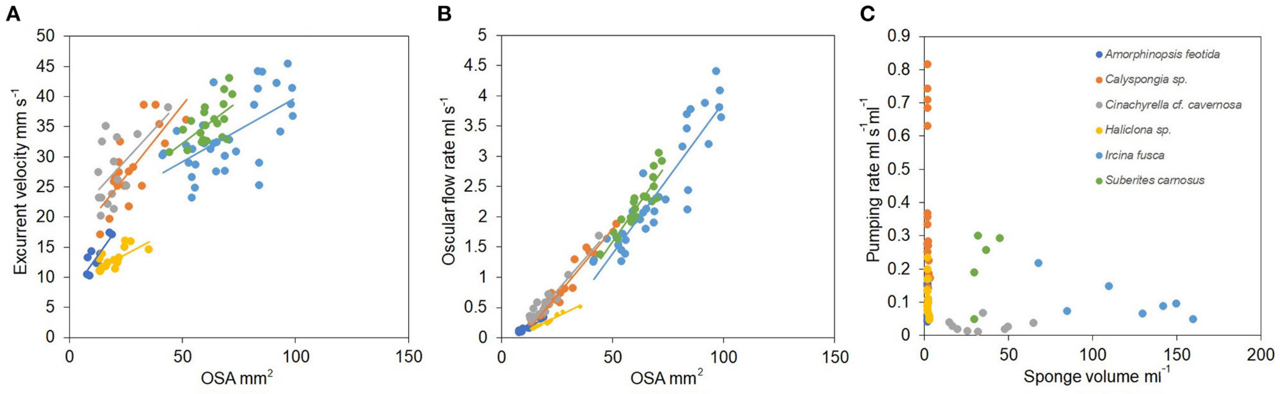

FIGURE 4 | (A) Relationship between the excurrent velocity (mm s^{-1}) and the osculum cross sectional area (mm^2). **(B)** Relationship between the oscular flow rate (ml s^{-1}) and the oscular cross sectional area (mm^2). **(C)** Pumping rate (ml s^{-1} ml^{-1}) vs. sponge volume (ml).

TABLE 2 | The relationship of excurrent velocity and oscular flow rate with the oscular cross sectional area of the studied sponges assessed with linear regression.

Species	Excurrent velocity						Oscular flow rate					
	n	***F***	**Constant**	***B***	***R*²**	***p***	***N***	***F***	**Constant**	***B***	***R*²**	***p***
Amorphinopsis feotida	9	17.25	6.97	0.52	0.71	0.004	9	163.50	−0.092	0.02	0.95	<0.001
Calyspongia sp.	19	22.10	15.03	0.47	0.56	<0.001	19	242.83	−0.40	0.04	0.93	<0.001
Cinachyrella cf. cavernosa	15	6.61	19.37	0.40	0.33	0.023	15	166.60	−0.27	0.04	0.92	<0.001
Haliclona sp.	20	19.75	8.92	0.19	0.52	<0.001	20	349.45	−0.08	0.01	0.95	<0.001
Ircinia fusca	33	17.82	18.47	0.21	0.36	<0.001	33	160.52	−1.10	0.05	0.83	<0.001
Suberites carnosus	20	11.62	17.95	0.28	0.39	0.003	20	87.84	−1.03	0.05	0.83	<0.001

n is the number of oscula.

(**Figures 4A,B** and **Table 2**). Note that species that clustered tightly around the regression line, such as *Haliclona* sp. had small, non-contractile, and consistent oscular size within and between different individuals of different sizes, whereas species with high deviations from the regression line such as *I. fusca*, *C.* cf. *cavernosa* had contractile oscula with variable size within and between individuals. The volume of water processed per ml of sponge, i.e., the size-specific pumping rate, decreased with sponge volume for all the studied species (**Figure 4C**).

Sponge Body Composition

Mean values for the filtration apparatus [CC mm^3, CC diameter, and the number of choanocytes per chamber (*ncc*) CC^{-1}, and porosity %] and the structural components (density, ash mass%, AFDW%, and spicule volume proportion%) of the studied species is given in **Table 3**. For most of the species, the ash% was more than 50% of the dry weight. The proportion of the total volume occupied by spicules/inorganic material ranged from 3 to 9% (**Figure 5A**) and also showed a significant positive relationship with the tissue density (DW/volume) (*r*

TABLE 3 | Mean values of the structural components and the filtration apparatus of the studied species.

Species	Density (Dry W/vol)	Ash% dry weight	Porosity %	Spicules% (Volume proportion)	AFDW %	CC diameter (um)	CC mm^3	*ncc* CC^{-1}
Amorphinopsis foetida	0.16 ± 0.01	53.14 ± 7.07	52 ± 2.83	4.23 ± 0.45	46.85 ± 7.69	17.46± 0.13	3690.67± 87.49	84.11 ± 3.02
Biemna fortis	0.26 ± 0.01	52.41 ± 6.22	38.5 ± 2.75	6.73± 1.04	47.58± 6.22	17.18±0.42	2781.85± 242.20	35.02 ± 2.44
Calyspongia sp.	0.13 ± 0.01	42.20 ± 4.38	56 ± 2.39	2.80 ± 0.19	57.79 ± 2.74	19.35±0.2	3452.09±113.17	121.11 ± 4.33
Cinachyrella cf. *cavernosa*	0.28. ± 0.01	65.71 ± 1.27	30 ± 2.09	8.73 ± 0.67	34.28 ± 4.82	18.62±0.21	4482.82 ±81.48	51.87 ± 3.77
Haliclona sp.	0.11 ± 0.008	50.00 ± 1.56	54.51 ± 2.08	2.80 ± 0.18	49.99 ± 1.56	19.69±0.23	3301.86 ±118.31	68.83 ± 2.82
Ircinia fusca	0.25 ± 0.01	36.97 ± 2.93	52.45 ± 0.96	4.32 ± 0.39	63.02± 2.93	30.68±0.29	3052.59 ±92.39	120.35± 8.98
Suberites carnosus	0.23 ± 0.01	47.96 ± 7.61	35 ± 2.02	5.60 ± 1.27	52.03 ± 7.61	16.21±0.23	5736.16 ±51.82	84.21 ± 3.82

Data are means ± SE.

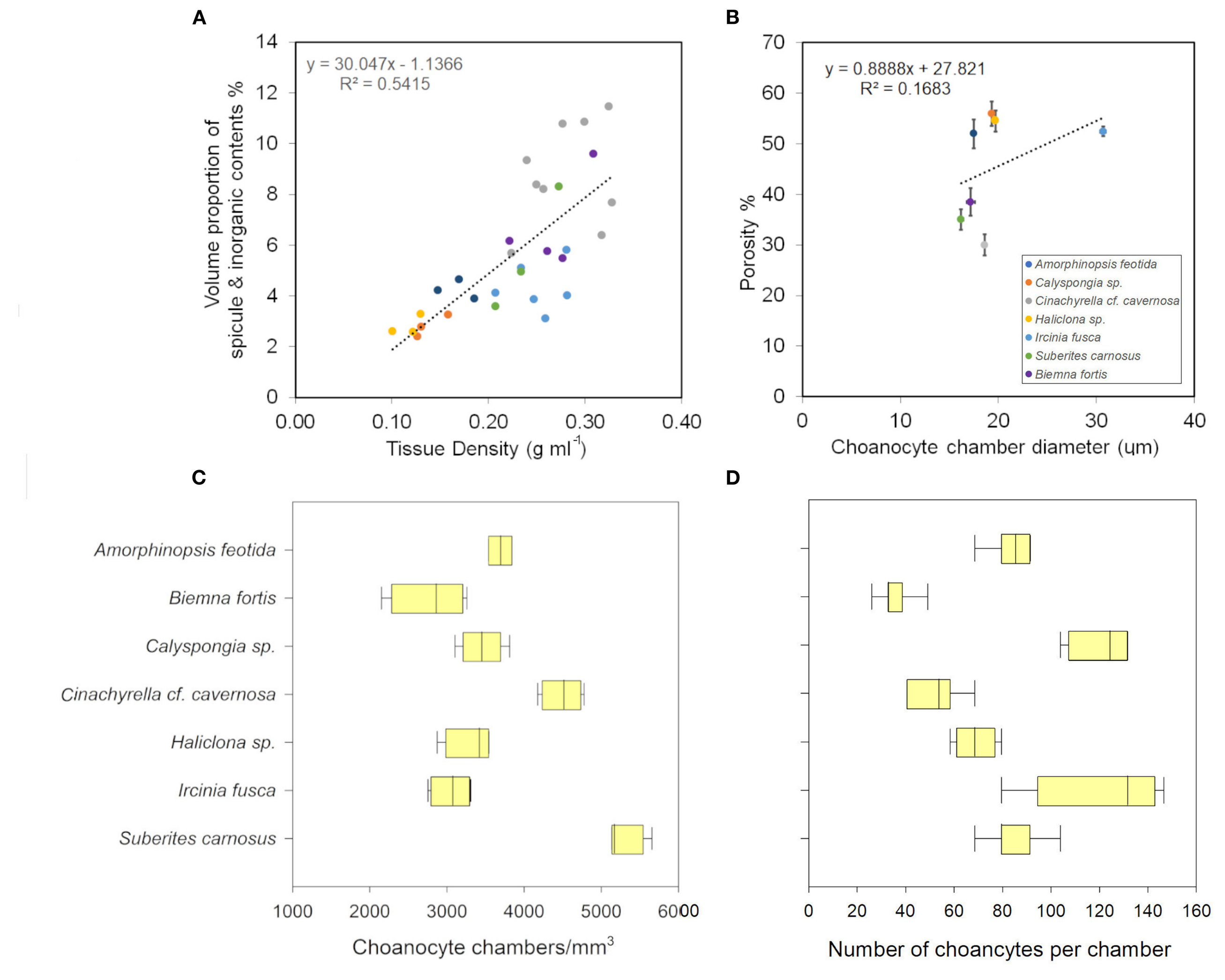

FIGURE 5 | (A) Volume of sponge tissue occupied by spicules (%) increases as the tissue density increases. **(B)** Porosity and the choanocyte chamber diameter show a positive relationship. **(C)** The choanocyte chamber abundance in different sponges. **(D)** The number of choanocytes per chamber in different sponges.

$= 0.73$, $n = 31$, $p < 0.001$). This suggests that the spicules constitute a major portion of sponge dry weight and also sponge volume. Porosity in the form of canals and pores between the collagen fibers, cells, and mesohyl matrix ranged from 30 to 55 % for the studied sponges and showed a positive relationship with the choanocyte diameter (**Figure 5B**), although

TABLE 4 | A pairwise comparison (Tukey test) of the mean differences between the sponge species with respect to the dependent variables: filtration apparatus (CC mm^3, *ncc* CC^{-1}, CC diameter) and structural components (ash%, AFDW%, porosity%, density, and spicule volume%).

	Amorphinopsis feotida	***Biemna fortis***	***Calyspongia* sp.**	***Cinachyrella* cf. *cavernosa***	***Haliclona* sp.**	***Ircinia fusca***	***Suberites carnosus***
CC mm^3							
Amorphinopsisfeotida	–	**908.82**	238.57	**758.95**	388.80	**638.08**	**1590.98**
Biemna fortis		–	**670.24**	**1667.77**	520.01	270.73	**2499.80**
Calyspongia sp.			–	**997.53**	150.22	399.50	**1829.56**
Cinachyrella cf. *cavernosa*				–	**1147.75**	**1397.03**	**832.03**
Haliclona sp.					–	249.27	**1979.79**
Irciniafusca						–	**2229.06**
Suberites carnosus							–
*ncc*CC^{-1}							
Amorphinopsisfeotida	–	**42.70**	**42.36**	27.98	10.96	**36.74**	6.02
Biemna fortis		–	**85.07**	14.72	**31.74**	**79.44**	**48.73**
Calyspongia sp.			–	**70.35**	**53.33**	5.62	**36.34**
*Cinachyrella*cf. *cavernosa*				–	17.02	**64.72**	**34.01**
Haliclona sp.					–	**47.70**	16.98
Irciniafusca						–	**30.71**
Suberites carnosus							–
CC diameter							
Amorphinopsisfeotida	–	2.26	2.56	2.30	3.43	**12.50**	0.69
Biemna fortis		–	0.29	0.04	1.17	**10.24**	1.56
Calyspongia sp.			–	0.25	0.87	**9.94**	1.86
*Cinachyrella*cf. *cavernosa*				–	1.12	**10.19**	1.61
Haliclona sp.					–	**9.07**	2.73
Irciniafusca						–	**11.81**
Suberites carnosus							–
Ash							
Amorphinopsisfeotida	–	0.86	11.11	**20.93**	3.22	16.35	5.40
Biemna fortis		–	**10.25**	**21.79**	2.36	15.48	4.45
Calyspongia sp.			–	**32.04**	7.88	5.23	5.70
*Cinachyrella*cf. *cavernosa*				–	**24.1**	**37.28**	**26.33**
Haliclona sp.					–	13.12	2.17
Irciniafusca						–	10.94
Suberites carnosus							–
AFDW							
Amorphinopsisfeotida	–	5.6	15.87	16.17	7.98	**21.10**	10.16
Biemna fortis		–	10.25	**21.79**	2.36	15.48	4.54
Calyspongia sp.			–	**32.04**	7.88	5.23	5.70
Cinachyrella cf. *cavernosa*				–	**24.15**	**37.28**	**26.33**
Haliclona sp.					–	13.12	2.17
Irciniafusca						–	10.94
Suberites carnosus							–
Porosity							
Amorphinopsisfeotida	–	**13.50**	3.33	**21.25**	**2**	0.33	**17**
Biemna fortis		–	**16.83**	7.75	**15.50**	**13.83**	3.50
Calyspongia sp.			–	**24.58**	1.33	3	**20.33**
Cinachyrella cf. *cavernosa*				–	**23.35**	**21.58**	4.28
Haliclona sp.					–	1.66	**19**
Irciniafusca						–	**17.33**
Suberites carnosus							–

(Continued)

TABLE 4 | Continued

	Amorphinopsis feotida	*Biemna fortis*	*Calyspongia* sp.	*Cinachyrella*cf. *cavernosa*	*Haliclona* sp.	*Ircinia fusca*	*Suberites carnosus*
Density							
Amorphinopsisfeotida	–	**0.09**	0.02	**0.12**	0.05	**0.08**	0.07
Biemna fortis		–	**0.12**	0.02	**0.14**	**0.01**	0.02
Calyspongia sp.			–	**0.15**	**0.02**	**0.11**	**0.09**
Cinachyrella cf. *cavernosa*				–	**0.17**	0.03	0.05
Haliclona sp.					–	**0.13**	**0.12**
Irciniafusca						–	0.01
Suberites carnosus							–
Spicule volume							
Amorphinopsisfeotida	–	2.49	1.43	6.07	1.42	0.08	1.36
Biemna fortis		–	**3.92**	**3.57**	**3.92**	**2.41**	1.13
Calyspongia sp.			–	**7.50**	0.00	1.51	2.79
*Cinachyrella*cf. *cavernosa*				–	**7.50**	**5.98**	**4.70**
Haliclona sp.					–	1.51	2.79
Irciniafusca						–	1.27
Suberites carnosus							–

Significant differences ($p < 0.05$) are in bold.

the relationship was not significant. The abundance of the CC and the number of the choanocytes per chamber showed high variation between the studied species (**Figures 5C,D**). The multivariate analysis indicated a significant difference between examined species with respect to the variables related to filtration apparatus (CC mm^3, *ncc* CC^{-1}, CC diameter) and structural components (ash%, AFDW%, porosity%, density, and spicule volume%) (MANOVA, Wilks test 0.00, $F = 9.08$, $p < 0.001$). *Post-hoc* Tukeys HSD test was performed to examine individual mean difference comparisons across all studied sponge species. Statistically significant ($p < 0.05$) mean differences between the species are presented in **Table 4**. Several factors influenced the abundance of choanocyte chambers. The least number of CC were found in *B. fortis*. The buried growth form of the sponge showed very sparse cellular tissue after the dissolution of the spicules and sand grain inclusions (**Figure 6**). *I. fusca* and *A. foetida* showed several spermatic cysts in different stages of development, which may have affected the abundance of CC (**Figure 6**). The histological sections of *Calyspongia* sp. showed a loose organization of cells and CC along with the elements of the collagen skeletal framework (**Figure 6**).

Morphometric Analysis

Dimensions of the aquiferous structures for the sponges included in the present investigation are given in **Table 5**. Sponge morphology and growth form affected the distribution and abundance of the components of the aquiferous system. For example, for the buried growth form of *B. fortis*, the surface in current pores, ostia, were observed on the fistules growing above the ground, and for *C.* cf. *cavernosa* the ostia were restricted to the rounded depression/pits called porocalices present on the lateral surfaces around the base of the sponge (**Figures 7A,B**). Ostia was observed to be in varying states of contraction (**Figures 7C,D**). The CC in *C.* cf. cavernosa was set in densely packed mesohyl, which was interspersed with several large spherulous cells (**Figure 8A**). The CC opened into the excurrent canals *via* the apopyle (**Figures 8B–D**). A glycocalyx mesh and flat gasket like structure around the choanocyte microvilli are likely to be a common occurrence in the demosponges; however, these structures are usually very difficult to preserve (Ludeman et al., 2016) and could not be observed clearly due to poor preservation. The largest CC was observed in *I. fusca* (**Figure 8E**).

Transmission Electron Microscopy

No microbial cells were detected in the TEM micrographs of *Halicona* sp., *Calyspongia* sp., *A. foetida,* and *S. carnosus* (**Figures 9A–D**). In contrast, a high number of bacterial cells was detected in TEM micrographs of *I. fusca* (**Figure 9E**). The bacterial cells had diverse morphotypes and were located extracellularly in the sponge mesohyl. *B. fortis* and *C.* cf. *cavernosa* showed moderate to few bacterial cells in the mesohyl, respectively (**Figures 9F,G**). Additionally, various cell types were observed in the TEM micrographs. Choanocytes in the *Halicona* sp. were spherical or oval in shape and measured 3.2–4 µm in size. Several larger cells with a nucleolated nucleus, almost double the size of the choanocytes, were also detected. *Calyspongia* sp. showed large cells 10–11 µm in size and with a high number of oval-shaped inclusions (**Figure 9B**), suggesting the possibility of mucus-secreting cells. Oval-shaped archeocytes having a nucleus with the distinct nucleolus and a well-developed endoplasmic reticulum could be seen in the *A. foetida* (**Figure 9C**). Large irregularly shaped cells with several spherical

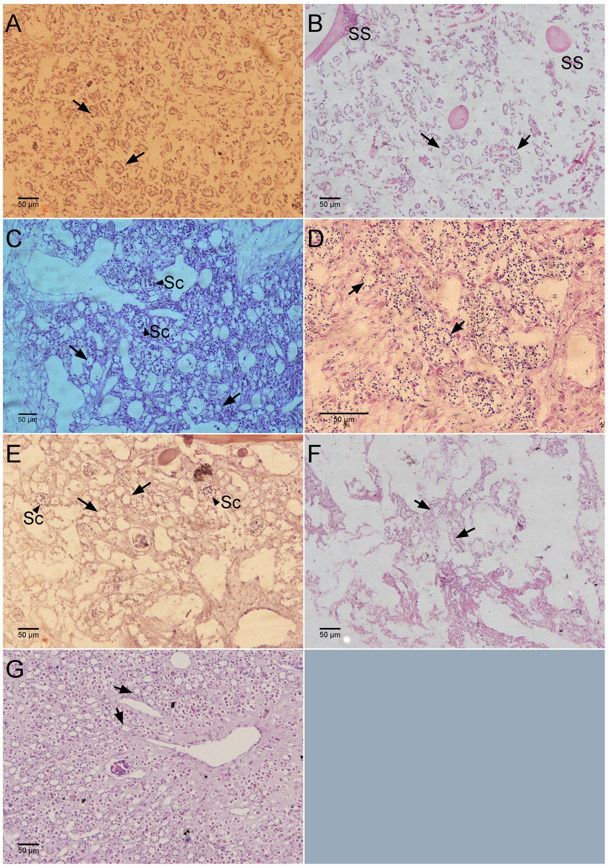

FIGURE 6 | Histological sections showing the number of chaonocyte chambers per view field. **(A)** *Haliclona* sp., **(B)** *Calyspongia* sp., **(C)** *Amorphinopsis foetida,* **(D)** *Suberites carnosus,* **(E)** *Ircinia fusca,* **(F)** *Biemna fortis,* **(G)** *Cinachyrella* cf. *cavernosa.* Black arrows point toward the choanocyte chambers. The black arrow head indicates the sperm cysts (Sc). SS, Spongin skeleton.

shaped and electron-dense inclusions were seen in *S. carnosus* (**Figure 9D**).

DISCUSSION

Sponge Species and the Variations in the Proportions of the Structural Components

Several intrinsic factors such as microbial abundance (Weisz et al., 2008), sponge shape (McMurray et al., 2014), osculum contraction (Hadas et al., 2008; Strehlow et al., 2016; Kumala et al., 2017; Goldstein et al., 2019), canal system (Reiswig, 1975), and the number of CC (Massaro et al., 2012) are known to influence sponge pumping rate. However, recent studies show sponge volume as the major factor to influence the size-specific pumping rate, i.e., the pumping rate normalized to the sponge volume (Morganti et al., 2019, 2021). The differences in the size-specific pumping rates of different sized individuals within and between species can transcend the effects of some of the distinctions such as HMA–LMA dichotomy on sponge pumping. Although HMA sponges are generally large and fleshy (Gloeckner et al., 2014) and have higher volume compared with LMA sponges (Morganti et al., 2019, 2021), the increase in the structural component of the mesohyl and tissue density results in the reduction of the hollow structures of the aquiferous system. In the present study, we examined the structural and functional variation in the anatomical and morphological characteristics of seven sponge species. PCA analysis of the variables related to the structural components, filtration apparatus, and pumping parameters revealed a scatter plot of the sponge species driven by the relationships between these variables (**Figure 2**). The structure and the efficiency of the filtration system show huge interspecific variation in sponges and are related to biological strategies in response to environmental conditions (Turon et al., 1997). The sponge species selected in the present study involve diverse modifications in terms of morphological growth forms (buried, globular, massive) and anatomical variations in terms of quantity of spicule skeleton, mesohyl proportion, and dimensions of the aquiferous structures.

Dimensions of the Aquiferous Structures in the HMA and LMA Sponges Vary With Respect to the Proportion of Spicules

In the present study, TEM images of *I. fusca*, *B. fortis,* and *C.* cf. *cavernosa* showed a high to a moderate abundance of microbes in the mesohyl, respectively. Although the high abundance of microbes in the *I. fusca* indicates a higher proportion of mesohyl and cellular mass, as represented by the high AFDW%, the tissue density remained moderate (**Table 3**). Histological sections and SEM images showed that *I. fusca* had the largest CC compared with other species studied in the present investigation. In demosponges, the size and volume of the choanocyte chamber vary between species, and keratose sponges are known to have large choanocyte chamber volumes (Vacelet et al., 1989). These sponges also lack mineral spicule skeletons (Bergquist, 1978; Maldonado, 2009; Erpenbeck et al., 2012). The absence of spicules along with large CC counterbalance the higher proportion of mesohyl and maintain a high pumping rate of *I. fusca* compared with other sponges, which were mainly LMA (**Figure 4**).

Sponges acquire the mesohyl microsymbionts *via* vertical transmission as well as horizontal/environmental transmission (Schmitt et al., 2007; Webster et al., 2010; Turon et al., 2018). Vertical transmission of microbes indicates that the mesohyl densely packed with microbes, characteristic of HMA sponges, is present from larval stages. The microbial communities are temporally stable in both HMA/LMA sponges (Taylor et al., 2007; Gloeckner et al., 2014; Erwin et al., 2015), suggesting that the mesohyl characteristics are preserved. Additionally, studies show that HMA sponge *Geodia barreti* phagocytose symbiont microbes in a controlled manner (Leys et al., 2018), indicating the microbial abundance in the mesohyl is maintained. However, the proportion of spicules and the filtration components vary with the sponge growth and reproductive seasons. For instance, the

TABLE 5 | Dimensions of the components of the aquiferous system calculated from the SEM and histological images of the study species.

Aquiferous structures	***Amorphinopsis foetida***	***Biemna fortis***	***Calyspongia* sp.**	***Cinachyrella* cf. *cavernosa***	***Haliclona* sp.**	***Ircinia fusca***	***Suberites carnosus***
Ostia (area μm^2)	138.99	707.7508	730.38	647.45	430.67	239.56	38.05
Subdermal spaces (diameter μm^2)	25084.58	15689.93	13891.48	65354.63	4908.92	78282.41	45791.22
Large incurrent canals (diameter μm)	10688.02	22338.30	2840.24	1800.18	3685.68	39268.21	1257.98
Medium incurrent canals (diameter μm)	2849.97	5291.09	7304.40	985.09	1407.26	6856.69	892.56
Small incurrent canals (diameter μm)	1863.25	176.74	1708.22	293.25	758.35	820.94	741.22
Choanocyte chambers (area μm^2)	245.86	232.19	301.23	272.97	303.28	665.28	220.93
Apopyle (area μm^2)	124.11	–	168.54	–	113.21	211.25	–
Small excurrent canals (diameter μm)	2174.32	454.89	1355.85	371.38	879.42	783.41	691.75
Medium excurrent canals (diameter μm)	3485.21	1207.65	5864.75	1571.24	1562.34	7644.56	834.15
Large excurrent canals (diameter μm)	8662.71	11968.58	6142.35	20781.25	4235.71	26218.21	2784.68
Osculum (area mm^2)	21.24	56.34	18.01	31.59	7.32	73.31	19.65

distribution and the proportions of tissue (mesohyl), spicules, and the aquiferous system vary between different stages of development, as observed in the developing buds of sponge *Tehya wilhelma* (Hammel et al., 2009). Thus, the proportion of spicule content and the aquiferous system is more likely to vary in different sized individuals within the species than the microbial abundance in the mesohyl. These considerations seem compatible with the wide range of size-specific pumping rates observed in the different sized individuals of HMA and LMA sponges (Morganti et al., 2019, 2021).

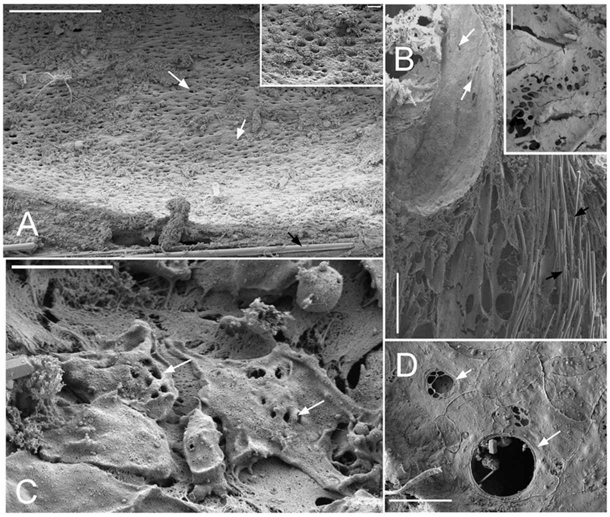

FIGURE 7 | SEM images showing the ostia **(A)** *Cinachyrella* cf. *cavernosa* the incurrent pores, ostia, are present in rounded depression/pits of the porocalices on the lateral surfaces along the base of the sponge. Inset magnified view of the ostia. **(B)** For the buried growth form of *Biemna fortis,* the ostia present on the fistules/finger-like projection growing above the ground. Inset magnified view of ostia **(C)** *Suberites carnosus* porocytes with ostia **(D)** *Amorphinopsis foetida* ostia. The white arrows point to the ostia. Scale bars: **(A)** 500 µm, inset = 50 µm; **(B)** 500 µm, inset 50 µm; **(C)** 20 µm; **(D)** 5 µm.

Recent studies evaluated a large number of sponge species for their HMA/LMA status (Gloeckner et al., 2014; Moitinho-Silva et al., 2017). Moreover, new methods and techniques like machine learning algorithms are being developed and employed to cover a large number of sponge species to predict their HMA-LMA status (Moitinho-Silva et al., 2017). Sponge species along the Indian coast have not been evaluated for their HMA-LMA status. TEM analysis showed low microbial abundance for the sponges *Haliclona* sp., *Calyspongia* sp., *A. foetida*, and *S. carnosus*. Bacterial cells were found to have moderate to high abundance in sponges *Cinachyrella* cf. *cavernosa*, *B. fortis,* and *I. fusca*. The microbial abundance in sponge mesohyl represented by the HMA–LMA dichotomy is best described as a continuum with a highly bimodal distribution, where most species are found at the extreme ends, and few species show an intermediate microbial load (Gloeckner et al., 2014). However, for sponges with intermediate bacterial abundance, TEM analysis alone is not sufficient to determine if the species is HMA or LMA (Gloeckner et al., 2014). Therefore, the HMA and LMA status of the sponge species in the present investigation need to be further determined by additional techniques such as 16 s rRNA gene sequence data.

Spicule (Weight and Volume) Form a Major Component of Tissue Density and Have an Inverse Relationship With Porosity

Spicules form important support structures assembled into large pole-and-beam formations with a variety of morphologies (Uriz, 2006). In the sponge *Ephydatia muelleri* the spicules are secreted and carried by specialized cells to the distant assembly locations and held up along their long axis (Nakayama et al., 2015). Such spicule tracts support the apical pinacoderm, which is raised and lowered during the contraction events, like a diaphragm, reducing the volume of the subdermal space (Elliott and Leys, 2007). Such mechanisms indicate that spicules have an important role in sponge body contractions. Although spicules themselves form a non-contractile component of the sponge

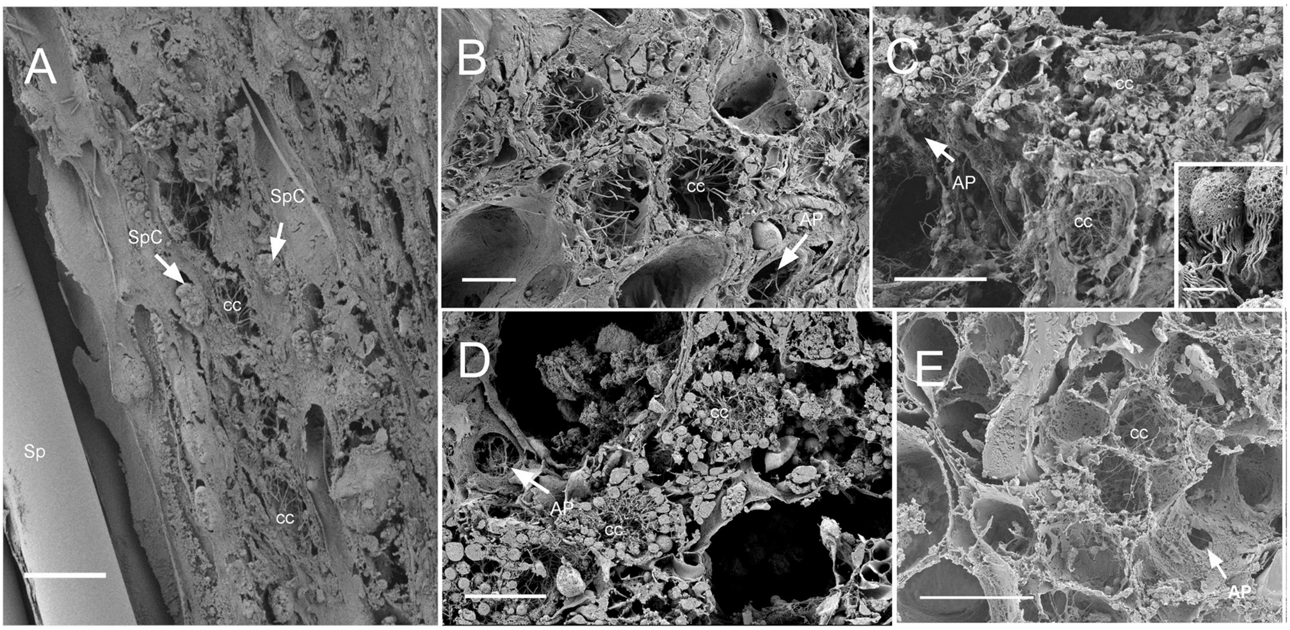

FIGURE 8 | SEM of chaonocyte chambers. **(A)** The choanocyte chambers (CC) and the spherulous cells (SpC) are present in the sponge *Cinachyrella* cf. *cavernosa*, spicules are indicated with sp. **(B)** The CC in *Amorphinopsis foetida*. The apopyle (AP) is indicated with a white arrow. **(C)** *Calyspongia* sp. with the choanocyte chamber (cc) and the apopyle (AP) indicated with a white arrow. The inset shows a closeup of the choanocytes with the flagella and microvillar collar, individual microvilli can be seen connected with glycocalyx mesh. **(D)** *Haliclona* sp. CC and the flagella of another choanocyte chamber seen through Apopyle (AP) indicated with white arrow. **(E)** *Ircinia fusca* CC and the apopyle (AP). Scale bar: **(A)** 20 µm; **(B)** 10 µm; **(C)** 20 µm, inset 2 µm; **(D)** 20 µm; **(E)** 50 µm.

body, their weight and position likely help to collapse the hollow spaces within the sponge during contraction. In fluid transport systems, architectural characteristics like porosity, pore size, and permeability of the biological scaffold, play a significant role in flow transport (Hollister, 2005). The increase in the spicule skeleton weight was a major contributor to the tissue density (and decrease porosity) as represented by the ash mass% (**Table 3** and **Figure 5**). Also, the volume proportion of the spicules within the tissue showed a significant positive correlation with the density (**Figure 5**) and a significant negative correlation with porosity%. The high porosity observed in *Haliclona* sp. and *Calyspongia* sp. could be attributed to the combination of low spicule contents and the presence of several lacunar spaces, which contained the choanocyte chambers, canals, and the loose organization of the cells. Porosity is a measure of the void fraction in material, and these voids can either be "closed" or "open" and connected to other voids and thence to the exterior of the material (Lawrence and Jiang, 2017). The internal and external surfaces of sponges are covered by pinacoderm which is made of flat cells called pinacocytes. Sponges are known to actively close and open the oscula and ostia present on the pinacoderm, thus effectively regulating the water flow (Nickel, 2004, 2010; Ellwanger and Nickel, 2006; Elliott and Leys, 2007; Ludeman et al., 2014; Goldstein et al., 2020). Some species show a flow-regulating cell type "reticuloapopylocyte" at the apopylar opening of the CC, suggesting a possibility of flow control mechanism at the level of individual CC and their connecting canals (Hammel and Nickel, 2014; Ludeman et al., 2016). Several sponge species are capable of coordinated contractions (Nickel, 2010), and pinacoderm acts as a major conductive pathway during contraction processes which lead to the collapse of the internal void spaces in the form of in and excurrent canals and the subdermal cavities (Hammel et al., 2012; Goldstein et al., 2020). Thus, sponges control the surface pores, as well as the internal porosity, and effectively manage the volume of water pumped and filtered.

Actively pumping sponges generate a water current by the beating action of the choanocyte flagella in the choanocyte chambers. It has been suggested that the pumping rate could be correlated to the abundance of CC (Riisgård et al., 1993). However, CC is a dynamic structure with a high proliferation activity and cell shedding of choanocytes (De Goeij et al., 2009; Luter et al., 2012; Alexander et al., 2014). Additionally, gametogenesis in some sponges involves the conversion of choanocytes into reproductive cells (Shore, 1971; Simpson, 1984; Tanaka-Ichihara and Watanabe, 1990; Tsurumi and Reiswig, 1997; Ereskovsky and Gonobobleva, 2000). Several sperm cysts were observed in the histological sections of *A. foetida* and *I. fusca* (**Figure 6**), and such mechanisms are likely to affect the abundance of chaonocyte chambers within the tissue and also the number of choanocytes within the chambers. In the present investigation, the formula used for calculating the number of choanocytes within the chamber (*ncc* CC^{-1}) does not consider the apopyle and the porospyle. Therefore, the formula

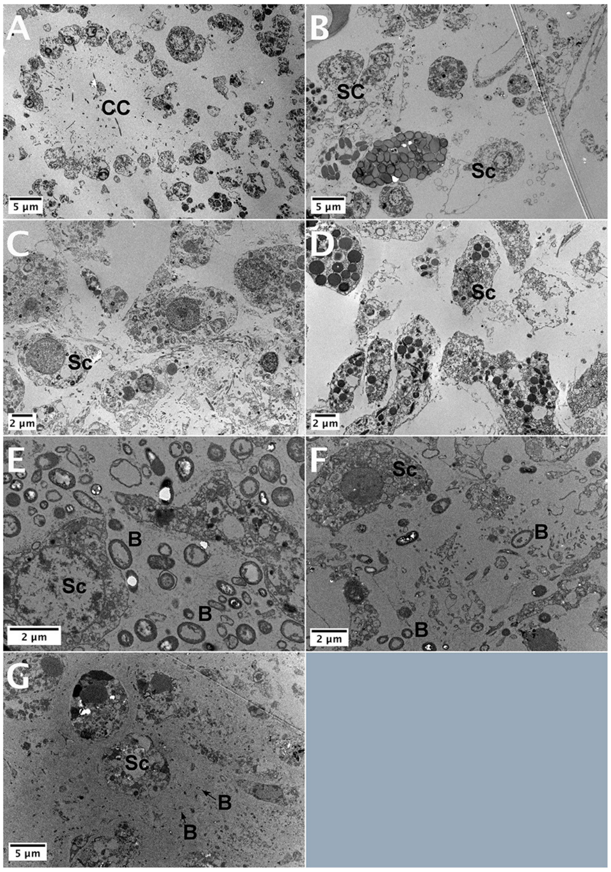

FIGURE 9 | TEM images of the study sponges **(A)** *Haliclona* sp., **(B)** *Calyspongia* sp., **(C)** *Amorphinopsis foetida,* **(D)** *Suberites carnosus,* **(E)** High abundance of bacterial cells present in the *Ircinia fusca* mesohyl, **(F)** *Biemna fortis,* and **(G)** *Cinachyrella* cf. *cavernosa* showing a moderate abundance of bacterial cells in the mesohyl. CC, choanocyte chamber; Sc, sponge cell; B, bacterial cell.

estimates the maximum number of choanocytes present within the chamber and showed large differences between the species ranging from 35.02 ± 2.44 (*C.* cf. *cavernosa*) to 121.11 ± 4.33 (*Calyspongia* sp.), majorly due to the different sized chambers between the species (**Table 3** and **Figure 3**). Interestingly, the *ncc* CC^{-1} showed a significant positive correlation with the AFDW%, indicating that the number of choanocytes within the chamber increased with the percentage of the organic/cellular material in the dry weight of the sponge sample (AFDW). Choanocytes are one of the most common and prominent cell types in sponges (Funayama et al., 2005; Riisgård et al., 2016) and most of the species in the present study showed a low or total absence of microbes in the mesohyl (except *I. fusca*) (**Figure 9**), implying that the AFDW% in the dry sponge samples represented the sponge cellular material. Theoretical estimates and experimental studies on small sponge explants suggest that the CC has a uniform distribution within the sponge tissue and has similar individual pumping rates (Reiswig, 1975; Riisgård et al., 2016; Goldstein et al., 2019). The distribution of the CC within the sponge and abundance of the chambers in different-sized individuals is likely to depend on the proportion of the structural and aquiferous components. The modularity of sponges is defined by the aquiferous modules which are described as a system of CC and aquiferous canals associated with a single osculum (Fry, 1970, 1979; Ereskovskii, 2003) (**Figure 10A**). However, the aquiferous structures and the proportion of the structural components (mesohyl and spicule skeleton) between different aquiferous modules may differ between different parts of the sponge and between different-sized individuals.

The Distribution of the Aquiferous Structures Is Influenced by the Sponge Morphology

The distribution of the aquiferous structures was governed by the morphological characteristics of the sponge (**Figures 10A,B**). For instance, the ostia restricted to the porefields porocalices situated laterally along the base of the spherical shaped sponge *C.* cf. *cavernosa* indicates the components of the aquiferous system do not have a homogenous distribution pattern (**Figure 10C**). Similarly, *B. fortis* had a buried growth form and high proportions of inclusions of inorganic debris in the buried portion with elongated, finger-like apical extensions or fistules visible above ground, which did not show any pumping activity. Sediment dwelling sponge species often show physiological and morphological adaptations to their environment (Ilan and Abelson, 1995; Schönberg, 2016). A previous study on sponge *Biemna ehrenbergi* reported the presence of ostia mostly on the buried surface of sponge, and it was also observed that the dye injected into the sediment was pumped and expelled through the oscula present on the chimney like siphons that protrude from the sediment surface (Ilan and Abelson, 1995). However, it is also suggested that sponges that inhabit soft sediments may have a reverse mechanism in which water flow is directed from the fistules into the sediments (Schönberg, 2016). Studies on sediment dwelling in *Oceanap iaoleracea* and *Oceanap iapeltata* report that both these species possess inhalant siphons, which draw water from above the sediment surface and conduct it to the central body, buried in the sediments (Werding and Sanchez, 1991). In the present study, for *B. fortis*, the ostiawere observed on the surface of the siphons exposed above the sediments, which suggests that the water enters the sponge *via* the fistules and siphons exposed above the ground and is pumped into the sediments by the buried portion of the sponge body.

CONCLUSION

In sponges, the proportion between the weight of tissues and the distribution and arrangement of the components of the aquiferous system leads to the optimization of some physiological factors (Ereskovskii, 2003). The sponge body has a characteristic of a composite material with a flexible matrix

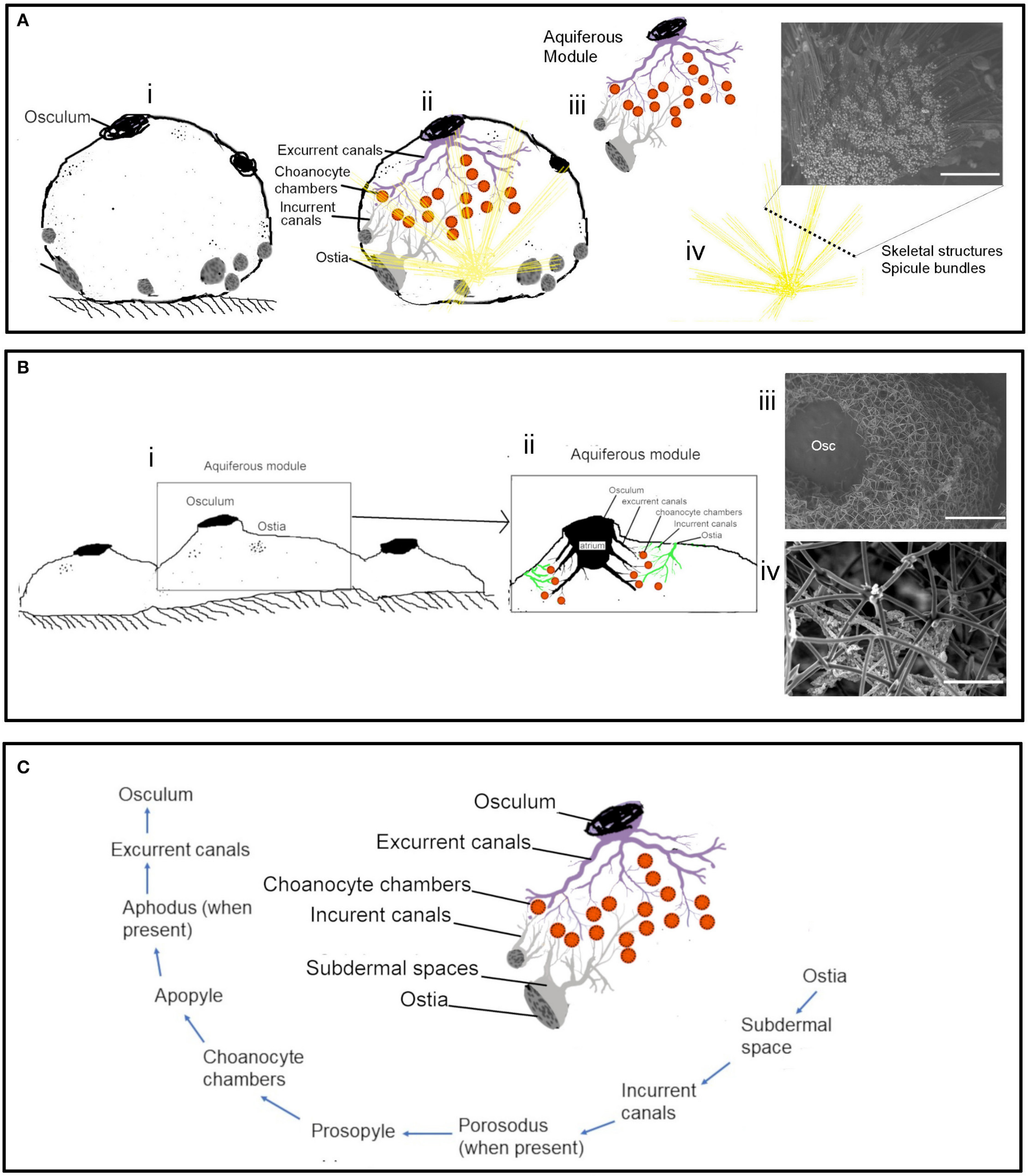

FIGURE 10 | The aquiferous system and the skeletal system in different morphologies: **(A)** Schematic representation of the spherical-shaped sponge *Cinachyrella* cf. *cavernosa* (i) the aquiferous system associated with a single osculum and the skeletal structures with the radiating spicule bundles (ii). the functional unit of the aquifeorus system-aquiferous module (iii). The skeleton of radiating spicule bundles, the dotted line represents a transverse section of the spicule bundles as seen in an SEM (iv). **(B)** Encrusting morphology of sponge (i). Aquiferous module (ii) with the SEM of the skeleton structure of *Calyspongia* sp. (iii) and *Haliclona* sp. **(C)** The components of an aquiferous module and the path of the water through the aquiferous system of sponge.

of tissue, organic (spongin) with inclusions of an inorganic skeleton (spicules or incorporated foreign material) (Palumbi, 1986). Shifting proportions of these materials change the properties of a sponge body to being more elastic with an increase in spongin, whereas an increase of inorganic skeleton makes the sponge harder and more resistant to physical forces (Palumbi, 1984, 1986; Sim and Lee, 2002; Uriz et al., 2003). Sponges with higher tissue density are known to have a reduced aquiferous system in form of narrower canals, fewer chaonaocyte chambers, and lower pumping rates. In the present study, we hypothesized that the structural differences in sponge anatomy influence their function, particularly the effect of spicules on the sponge pumping, and found that the inorganic spicule contents by their weight as well as volume form a major component of tissue density and sponge volume. Higher proportions of spicules were associated with reduced aquiferous structures and a lower pumping rate. Additionally, the inverse relationship of the proportion of the ash mass% and the AFDW in the sponge dry weight showed separate and distinct associations with aquiferous system variables such as porosity and the number of choanocytes per chamber. Wider surveys of proportions of the structural components in different-sized individuals of both HMA and LMA sponges will be useful for a greater understanding of the pumping physiology of sponges.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary materials, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Radular Morphology and Relationship Between Shell Size and Radula Size of Few Dominating Intertidal Gastropod Mollusks of Veraval Coast, Gujarat

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The radula is the main feeding organ and also very significant to the majority of the mollusks (especially gastropod) taxonomy. With shell morphology, radular morphology is the key characteristic for the identification of gastropod species. The shape and structure of the radular teeth are unique from family to species level. In this study, five basic types of radula (i.e., docoglossan, rhipidoglossan, taenioglossan, stenoglossan, and toxoglossan), which were observed from a total of 23 different species belonging to 12 families, were examined. Collection of the voucher intertidal gastropod specimen for the study had initiated during May–October 2019 in the rocky intertidal area near Veraval of the south Saurashtra coastline. Direct handpicking methods were used for the collection of the specimen for experiments.

Keywords: intertidal, *Gastropoda*, radular morphology, shell morphology, Veraval coast

INTRODUCTION

The radula, a unique taxonomical characteristic and feeding organ of mollusks, is found in every class except the class Bivalvia (Arularasan et al., 2011). This ribbon-like structure is found and used to slide on odontophore (another supportive part to radula) in the mouth and supports a variety of different feeding mechanisms. This odontophore is embedded with rows of many tiny denticles or teeth. From the front side, new fragments of denticles will be produced constantly when old ones are worn out by abrasion. The radula has attached at both ends, and it grows continuously during the life of the gastropod. With the help of this cumulative mechanism, food particles or pieces of food and debris go into the esophagus of the animal. The outline and the radular arrangement are the significant tools for species identification (Mutlu, 2004). Researchers currently understood that modifications of the radular arrangements have long been recognized as a key feature for the diversity of molluscans which is related to the important process of gaining energy from the surrounding environment (Cruz et al., 1998; Guralnick and Smith, 1999). In the case of molluscan taxonomy, marine intertidal gastropods, in particular, were identified on the basis of diverse morphological characteristics such as shape, size, color, and band pattern, which were not sufficient for an individual to be identified up to species level. Shell pattern and its coloration pattern vary due to several reasons such as coastal environment (wave action, light, humidity, salinity, and temperature), geographical distribution, and age-related variations, which may inhibit proper identification up to species level (Vakani et al., 2020). Other than the shell pattern, characteristics are needed for species identification. The radula can be a useful potential source of such characteristics. After a long research, we understood that radula is important not only for nutrition but also for classification and phylogenetic studies, which is responsible for the differences in intraspecific classification better than the morphology of foot and shell (Mutlu, 2004; Andrade and Solferini, 2006; Mutaf and Aksit, 2009). Generally, it indicates similarities up to family level and compatibility differences up to species level. The shapes and structures of molluscan radular teeth are often unique to a species or a genus, and these structures have traditionally been one of the most widely used sources of data for studies on molluscan systematics. Some features of the radula have also been used to study higher-level molluscan taxonomic relationships (Roberts, 2000; Kruta et al., 2013, 2014).

Gastropoda is represented by species with tremendous adaptative success, specifically regarding the strategies of food search and food capture (Taylor et al., 1980; Hughes, 1986), which can be well understood by the example of the toxoglossan radular structure. This radula is totally different from the radula of the other gastropod. The teeth are usually arrow-shaped and not fixed to a base plate. Central (rachidian) teeth are fully destroyed from the base plate. These teeth are long and linked to the toxin channel. Each tooth can be individually moved to the snout similar to a spear that is ready to be thrown to hunt (Kantor, 1990).

As molluscan is the second most diverse group in the animal kingdom, they are existing in all kinds of habitats available worldwide (Mutlu, 2004). Habitat-wise, every molluscan family has different kinds of feeding organ radula (Padilla, 1989). Few examples are discussed in this study for a better understanding of the radular pattern of the group: the very first example is the single-shelled mollusks true limpets possess radula covered with denticles, which enables the animal to scrape tiny vegetation from the rocky surface (Guralnick and Smith, 1999). Whelks have a stalk radula that can be extended outside to the shell and be helped to bore toxicant digestive juice into the shells of other gastropods or other animals and suck out the flesh that was digested and became jelly or semifluid of the prey. Similarly, the cone radula is modified into a poisoned harpoon-like structure with which they throw like a spear to paralyze their prey. In still more active carnivores, the heavy shell is reduced in size and may even be lost as has occurred in the sea slugs that have an upper surface covered with tentacles. One species of sea slugs actively hunts jellyfish and ingests the stinging cells of these animals, which it then concentrates in the tentacles and uses them for protection.

In this study, we have tried to find different types of radulae and their basic structure and relationship between radular size and shell size for a particular family of the selected abundant gastropods of the intertidal area of the south Saurashtra coast of India. The radula of different gastropods was analyzed by compound stereomicroscope.

MATERIALS AND METHODS

Study Area

For this study, the sample was collected from Veraval, south Saurashtra coast of Gujarat, India. Veraval is one of the largest fish landing sites in India.

Selected Study Species

The molluscan species selected for radular analysis were selected based on their occurrence during all seasons of the study period. For a long-term study on the same aspect, we also ensured that all these species were moreover reported as Inter-coast species (non-migrant). We have also used few previous research reports such as Vaghela (2010) and Vakani (2013) as references for selecting the species. Few species that were also used to compare species-level differentiation were from the previous collections of the Museum of the Department of Biosciences.

Collection of a Voucher Specimen

Samples are collected from the intertidal zone of the Veraval coastal area during the low tide. Before the sample was collected for the laboratory experiment, it was identified by using different field manuals and available literature such as Apte (1998). The sample was preserved in 10% formalin or 70% alcohol for the laboratory experiment and identification.

Method for Radular Analysis

For radular analysis, an individual sample of gastropod mollusk was separated from the shell, and a small cut was made on the dorsal surface of the head until radula was not exposed. Then, dissection was performed until the end of the snout, and the tongue-like odontophore was detached from the muscle fibers attached to it. The separated radula was washed or cleaned in dilute sodium hypochlorite, and a soft brush was used to remove the adhering tissue (Vakani et al., 2020). In this study, we have observed the pattern of teeth and the variation of shape, size, and formation of radular teeth in different species. The full amylaceous radular strip was detached from the buccal mass of each species, and the radular structure was examined under a dissecting microscope (Vakani and Kundu, 2021). Scanning electron microscopy (SEM) was also performed on the radular teeth of the observed species.

The teeth of radular (except in toxoglossan) are always found to attach with the odontophore in transverse rows consisting of two or more teeth that are mirror images about the midpoint, and for that, all gastropods have been found with bilateral symmetry in radular ribbon. Each transverse row is identical to the adjacent rows, producing columns of identical teeth (Smith, 1988; Shaw et al., 2008). The teeth are mostly odd in number when rachidian or central or middle teeth are present. In case of no rachidian (or central or middle) teeth, radula has an even number of teeth. The common formula of radula is $M + L + R + L + M$. Each row in the radula has one central or rachidian tooth (R): on each side, a few lateral teeth (L), and then beyond that, a few marginal teeth (M). Different species could have different lateral teeth, and then, numerous marginal teeth may be uncountable. All studied animals are described in **Table 1**. In this study, we have posted only half a row (only left side) of the counting of teeth of ribbon (R + L + M) of radular pattern to avoid repetition and to save space (**Table 1**).

Method of Tree Generation for Systematics

Cytochrome oxidase I (*COI*) gene sequence of gastropods was retrieved from the NCBI database. The phylogenetic tree for gastropods was constructed by unweighted pair group method with arithmetic mean (UPGMA) using Jones-Taylor-Thornton (JTT) estimate models of amino acid replacement with 1,000 bootstrap replicates in Molecular Evolutionary Genetics Analysis (MEGA11) software.

RESULTS

The communication was deal with the study of the radular morphology of the selected dominating intertidal gastropod mollusks and found the radular pattern that was made by the combination of different kinds of denticles (teeth). This report creates baseline data about the radular patterns and radular types of dominating intertidal gastropod mollusks of the Saurashtra region. In total, 23 different species belonging to 12 different gastropod families were analyzed for the undersetting of the radula and its pattern into the different families as well as species. The results showed that all selected gastropods were followed by all five basic different types of radular patterns, namely, docoglossan, rhipidoglossan, taenioglossan, stenoglossan, and toxoglossan. A graphical representation of species and family number against radula types showed that among the 23 species, 8 from 3 families represent rhipidoglossan radula while among the 12 families, 4 families represent taenioglossan radula. Both docoglossan and toxoglossan radulae were represented by the very least species as well as family (**Figure 1**).

SEM Analysis

Different families of the gastropod showed obvious different types of radula among five known types. Individuals from the same family were observed with more or less differentiation in the same types of radula (**Table 1**). To be more precise, it can be said that, interfamily variation was observed but no intrafamily variation was observed in the case of radular type. With the same types of radulae, different species showed variation in radular pattern for the same family (**Figures 2–5**).

Docoglossan Radula

The docoglossan radula observed in family Nacellidae with only one representative species has a dwarf rachidian tooth with one lateral and one marginal tooth on each side of the radular ribbon.

Almost concealed or dwarf and narrow unicuspid rachidian tooth, one unicuspid pointed lateral tooth, and one bicuspid marginal tooth were observed on each side of the radular ribbon of *Cellana karachiensis* (**Figure 2A**).

Rhipidoglossan Radula

The rhipidoglossan radula was represented by three different families of the gastropod, namely, Trochidae with one species, Turbinidae with four species, and Neritidae with three species. In this study, the types of radula were found similar in these three families with quite spectacular modifications of the denticles. All individuals of these three families have a single central/rachidian tooth. Among these three families, two families such as Trochidae and Turbinidae were observed with 5 or [4 + D] lateral teeth (**Figure 2B–F**). Marginal teeth were observed with quite different shapes and very numerous to count. In *Nerita*, a narrow and blunt unicuspid central/rachidian tooth was present with plate-like lateral teeth and many narrow pointed marginal teeth (**Figures 3A–C**).

Monodonta australis has a broad unicuspid central/rachidian tooth that has multiple serrations at the broad anterior part. The rachidian tooth is followed by a unicuspid bent finger such as five lateral teeth having multiple serrations at the sideward part of each cusp. These lateral teeth have a broader basal part and are sharp at the squared anterior edge. There are numerous narrow bases and multilayered feathery marginal teeth on both sides of lateral teeth (**Figure 2B**).

Lunella coronata has a broad-based unicuspid rachidian tooth, narrow unicuspid five adjacent lateral teeth and marginals looks narrow, triangular blunt at a tip on each side of the radular ribbon. The size of the marginal teeth decreases in descending array as to outer marginal teeth (**Figure 2C**).

Turbo bruneus has a flat, ellipsoid shape, unicuspid rachidian teeth. The size of inner marginal teeth is in the descending array while outer marginals are similar in size. Inner marginal teeth are tricuspid with a central larger cusp enclosed by two similar-shaped cusps. The multilayered feathery outer marginal teeth are multicuspid (**Figure 2D**).

Turbo intercostalis has a single, vase-shaped rachidian teeth followed by four rhomboid lateral teeth on each side and an immediate one pointed dominant lateral tooth at each side. Among the marginal teeth, four inner marginals are tricuspid with middle larger pointed triangular cusp surrounded by two blunt triangular cusps. These are followed by feathery multicuspid outer marginal teeth on each side (**Figure 2E**).

Astralium semicostatum has a single saucer-shaped rachidian tooth followed by five falcate-shaped lateral teeth. This is also followed by the bifurcated leaflet-shaped, multiple feathery marginal teeth (**Figure 2F**).

Nerita albicilla has one central mortar or hyoid bone-shaped rachidian teeth, which is followed by the footstep of shoe-shaped lateral teeth. The single lateral teeth are followed by an inverted saucer-shaped second lateral plate and many feather-like marginal teeth (**Figure 3A**). The central/rachidian tooth of *Nerita costata* are slightly concave shaped at both the sides, i.e., up and down (**Figure 3B**). The rachidian teeth of *Nerita undata* are urn-shaped. The shapes of lateral teeth, plates, and marginal teeth of *N. costata* and *N. undata* are similar to those of the *N. albicilla* with bit modifications, which can be observed in **Figures 3A–C**.

Taenioglossan Radula

The taenioglossan radulae were observed in a diverse range of families. Nearly 4 representative families, namely, Cypraeidae with 1 species, Cerithiidae with 3 species, Littoridae with 1 species, and Onchidiidea with 1 species from 12 families, were

TABLE 1 | Radular pattern of selected species.

Type of radula	No.	Family	Fig.	Species	Diet	Pattern of radula (Half Row Left side)
Docoglossan	1	Nacellidae	2A	*Cellana karachiensis*	Herbivore	R 1 + L 1 + M 1
Rhipidoglossan	2	Trochidae	2B	*Monodonta australis*	Herbivore	R 1 + L 5 + M ∞
	3	Turbinidae	2C	*Lunella coronata*	Herbivore	R 1 + L 5 + M ∞
			2D	*Turbo bruneus*	Herbivore	R 1 + L4 + D1 + M ∞
			2E	*Turbo intercostalis*	Herbivore	R 1 + L 4 + D1 + M ∞
			2F	*Astralium semicostatum*	Herbivore	R 1 + L 5 + M ∞
	4	Neritidae	3A	*Nerita albicilla*	Herbivore	R 1 + L 1 + plate + M ∞
			3B	*Nerita costata*	Herbivore	R 1 + L 1 + plate + M∞
			3C	*Nerita undata*	Herbivore	R 1 + L 1 + plate + M∞
Taenioglossan	5	Cypraeidae	3D	*Naria* sp.	Carnivore	R 1 + L 1 + M 2
	6	Cerithiidae	3E	*Cerithium coralium*	Detritivore	R 1 + L 1 + M 2
			3F	*Rhinoclavis sinensis*	Detritivore	R 1 + L 1 + M 2
			4A	*Clypeomorus bifasciata*	Detritivore	R 1 + L 1 + M 2
	7	Littorinidae	4B	*Echinolittorina pascua*	Herbivore	R 1 + L 2 + M 1
	8	Onchidiidae	4C	*Peronia verruculata*	Herbivore	R 1 + L ∞ + M 0
Stenoglossan	9	Mitridae	4D	*Scabricola guttata*	Carnivore	R 1 + L 1 + M 0
			4E	*Strigatella scutulata*	Carnivore	R 1 + L 1 + M 0
	10	Muricidae	4F	*Murex* sp.	Carnivore	R 1 + L 1 + M 0
			5A	*Thais* sp.	Carnivore	R 1 + L 1 + M 0
			5B	*Tylothais savignyi*	Carnivore	R 1 + L 1 + M 0
	11	Pisaniidae	5C	*Pollia undosa*	Carnivore	R 1 + L 3 + M 0
Toxoglossan	12	Conidae	5D	*Conus figulinus*	Carnivore	R 0 + L 0 + M 1
			5E	*Conus achatinus*	Carnivore	R 0 + L 0 + M 1

R, central or median tooth; L, lateral teeth of each side; M, marginal teeth; each number indicating the count of the denticles of respective teeth; D, represented dominated one. ∞ represents a symbol for non-countable teeth.

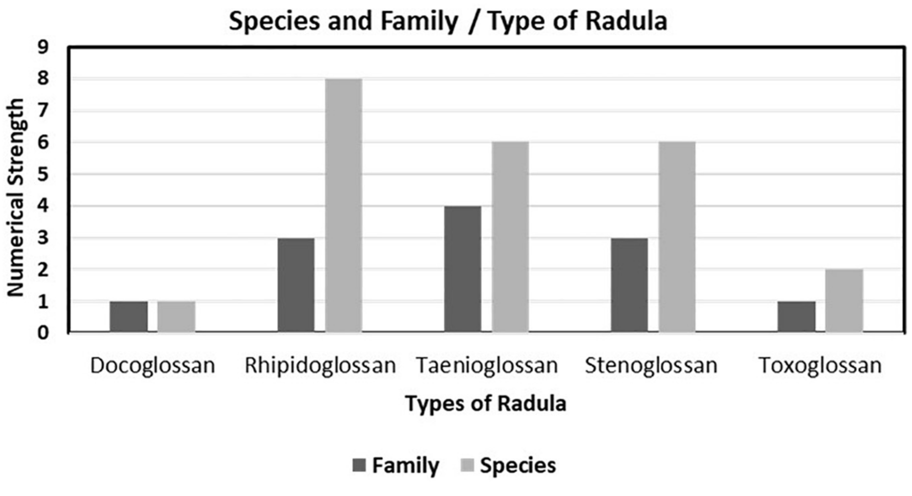

FIGURE 1 | Species and family ratio of different types of radula observed in selected coast.

identified. They all have a single functional and primarily analogous (interfamily level) central tooth. Most of the individuals have one lateral tooth while very few consist of more than one lateral tooth. In the case of marginal teeth, most have been observed with a gradient change in the pattern of tooth, and the first lateral tooth is, in most cases, dominated or bigger than others (**Table 1**).

In Cypraeidae, radula, the rachidian tooth observed with a moderately broad base which is curved and less pointed from the front, also has one lateral and two marginal teeth (**Table 1**). In *Naria* sp., a single rachidian tooth looks similar to Serpentes hood shape followed by one lateral tooth, where marginal teeth are observed bifurcated anteriorly into two sharp pointed structure (**Figure 3D**) (*Naria sp.*).

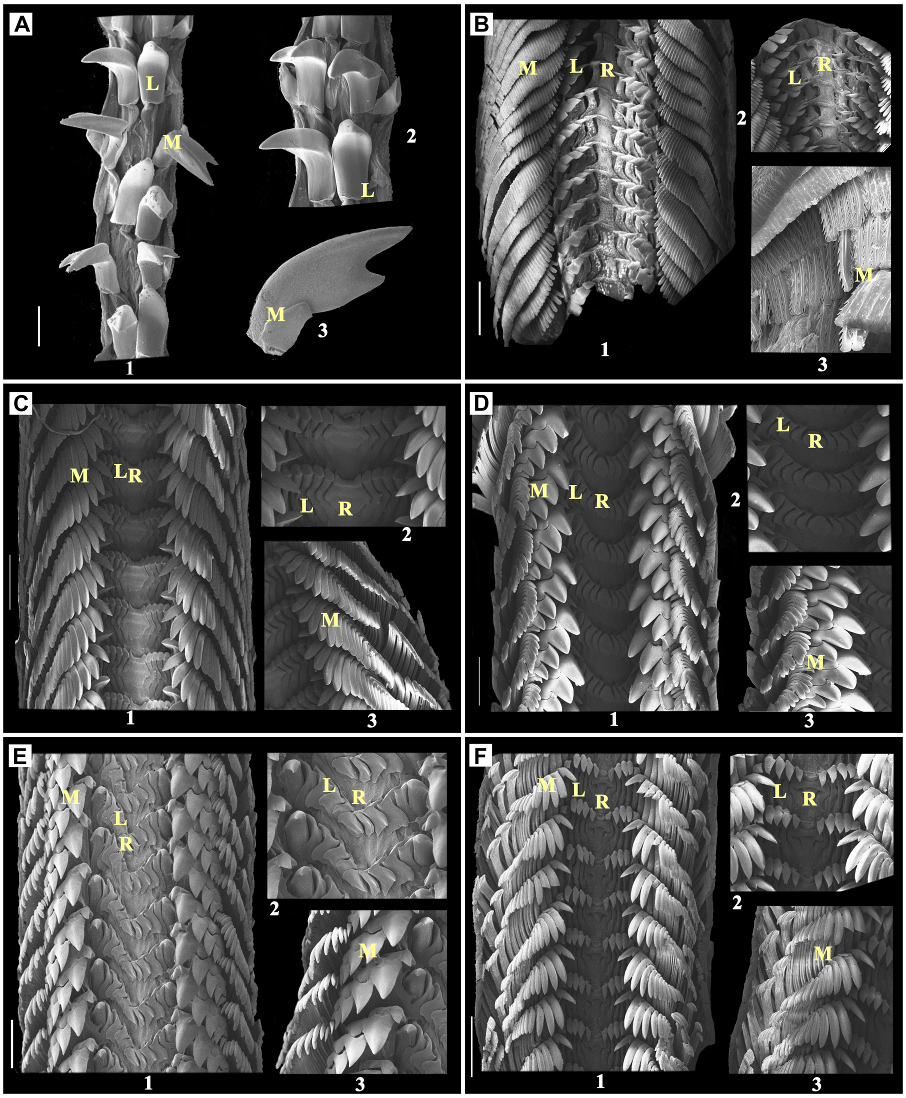

FIGURE 2 | (A) *Cellana karachiensis*, Scale bar:100 μm; **(B)** *Monodonta australis*, Scale bar: 200 μm; **(C)** *Lunella coronata*, Scale bar: 300 μm; **(D)** *Turbo bruneus*, Scale bar: 200 μm; **(E)** *Turbo intercostalis*, Scale bar: 300 μm; **(F)** *Astralium semicostatum*, Scale bar: 300 μm; 1: radula; 2 and 3: enlarged part of radula; R, rachidian teeth; L, lateral teeth; M, marginal teeth.

Cerithiidae has a broad-based rake-like multicuspid rachidian tooth with one lateral and two marginal teeth in each row of the radular ribbon.

Cerithium coralium has a single but pentafurcated rachidian tooth, in which the middle is a larger round pointed tip with two comparatively smaller similar-shaped teeth found sideways to the middle one. The single lateral teeth with rake like (mostly 5) in which the second one was found to be dominated and larger than the other. In this study, it was followed by two boomerang-shaped marginals that are also unequally bifurcated from the top (**Figure 3E**).

Rhinoclavis sinensis has a radula that looks exactly similar to *C. coralium*. When observed carefully, the radular arrangement was found to be highly overlapped, and the structure appears tightly packed as compared to C. *coralium* (**Figure 3F**).

Clypeomorus bifasciata has a pentafurcated rachidian tooth, which has a central serpent hood-shaped furcation with a broad-based curved blunt cusp with two smaller than central cusps at each side. This structure is followed by a single pentacuspid lateral tooth on each side having a larger broader blunt end. From the rachidian tooth, the inner second cusp was found broadly larger than the remaining cusps with a broader rounded tip. Then, two marginal multicuspid teeth were observed at each side, followed by these lateral teeth (**Figure 4A**).

Echinolittorina pascua has a maple leaf-shaped rachidian tooth with a very broader end, two lateral teeth with four cusps, i.e., outer cusps of rectangular chisel-shaped, the second one from outside cusp larger and pointed, and last one with a dwarf growth, bent, fork-shaped marginal tooth with many pointed cusps and narrow neck on each side (**Figure 4B**).

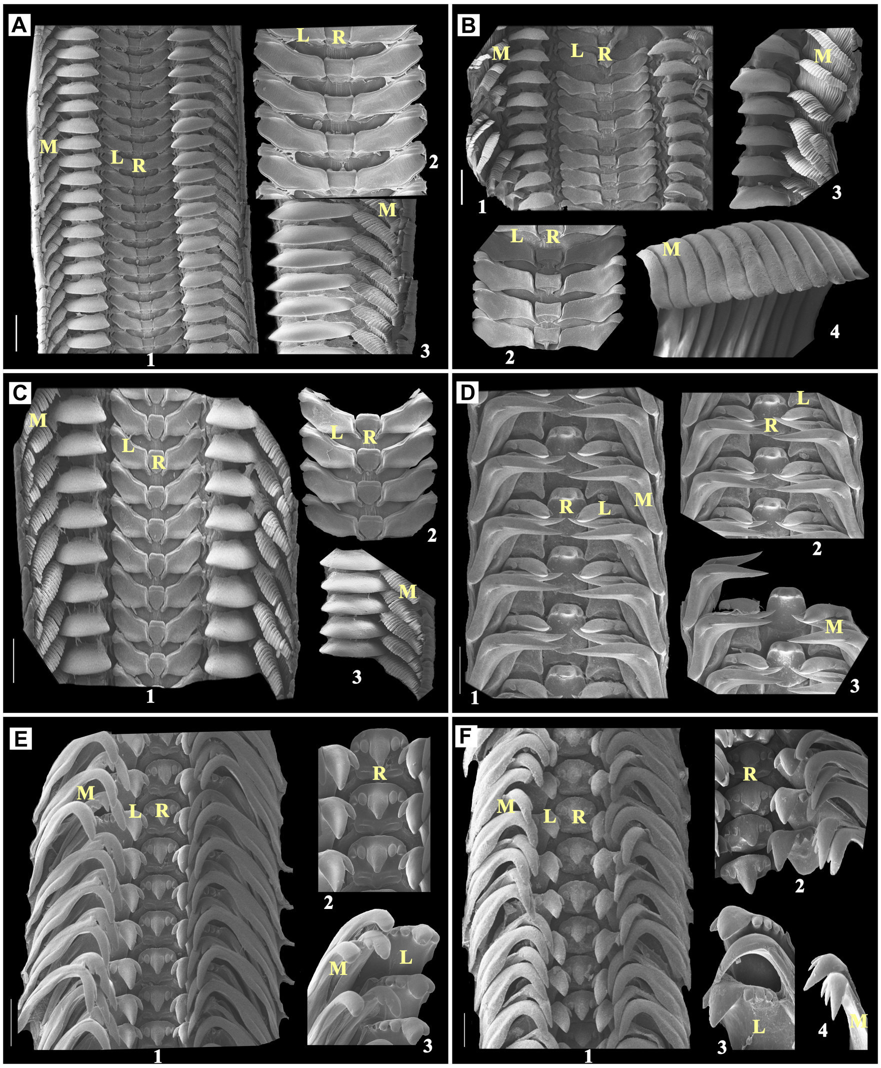

FIGURE 3 | (A) *Nerita albicilla*, Scale bar: 300 µm; **(B)** *Nerita costata*, Scale bar: 300 µm; **(C)** *Nerita undata*, Scale bar: 200 µm; **(D)** *Naria* sp., Scale bar: 200 µm; **(E)** *Cerithium coralium*, Scale bar: 100 µm; **(F)** *Rhinoclavis sinensis*, Scale bar: 100 µm; 1: radula; 2 and 3: enlarged part of radula; R, rachidian teeth; L, lateral teeth; M, marginal teeth.

Each radular row of *Peronia verruculata* contains a tricuspid rachidian tooth. The middle cusp of the rachidian tooth is rounded and blunt at the tip. Many unicuspidal lateral teeth at each side of the rachidian tooth look similar to chisel shape, except few inner- and outermost lateral teeth that look similar to blunt triangular. Radula of *P. verruculata* is broader than other selected species. This kind of radular arrangement is commonly found in Siphonariids (**Figure 4C**).

Stenoglossan Radula

It was observed in three different families, namely, Mitridae with two species, Muricidae with three species, and Pisaniidae with one species. In stenoglossan radula, a central tooth was found extremely variable than the other observed radular types (**Figures 4D–5C**) and looked similar to the bunch of small furcated pieces of a central tooth (5–8 furcation), but those together originated from a same or single broad base. A vast range of variation is observed in the pattern of lateral teeth in different families that have this type of radula. No marginal teeth were observed here.

In the representative of Mitridae family, such as *Scabricola guttata* has a triseriated radula, each radular row contains broad-based multicuspid rachidian tooth which has seven very short and looks similar to robust cusps. Lateral multicuspid about ten short and robust cusps situated proximally with their distal halves has smooth and wavy plate-like formation on each side of the rachidian tooth (**Figure 4D**).

Strigatella scutulata have been observed with similar radular structure as *S. guttata*. In this study, the difference was found with the rachidian tooth that has six rather than seven, which is also the same as *S. guttata*, very short and robust cusps (**Figure 4E**).

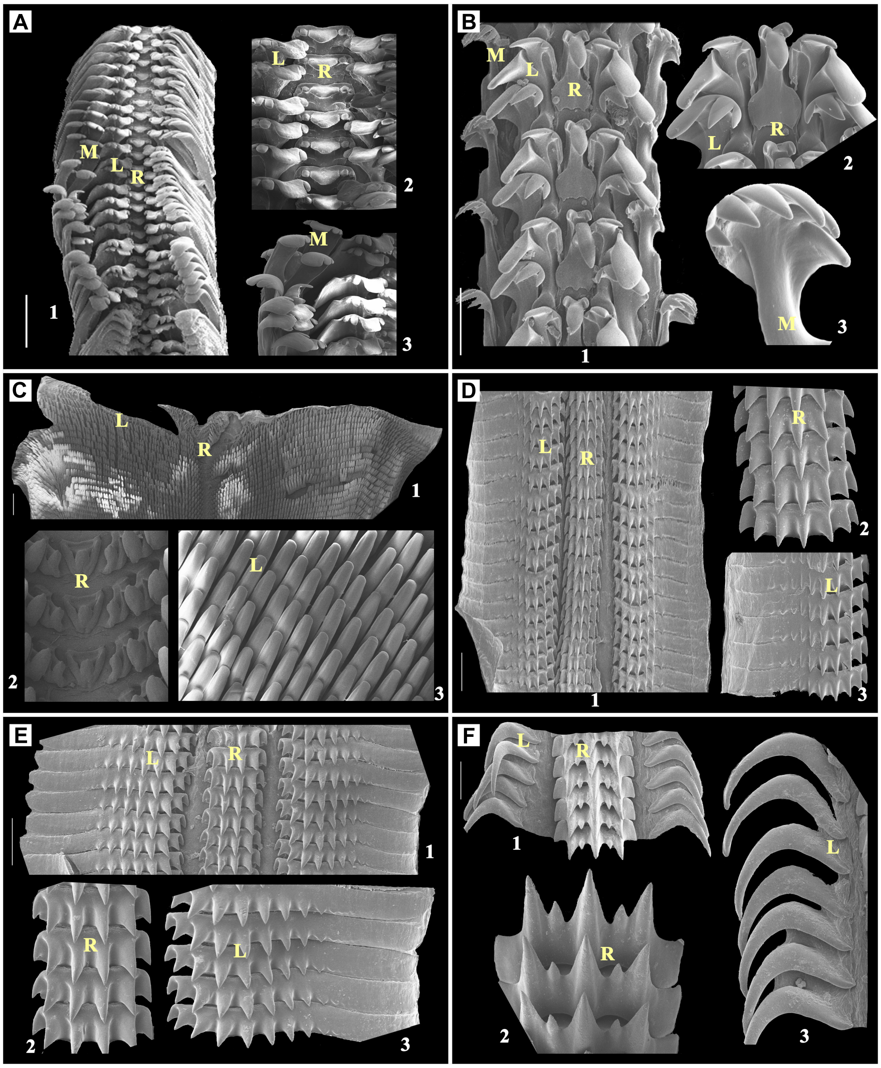

FIGURE 4 | (A) *Clypeomorus bifasciata*, Scale bar: 200 μm; **(B)** *Echinolittorina pascua*, Scale bar: 50 μm; **(C)** *Peronia verruculata*, Scale bar: 500 μm; **(D)** *Scabricola guttata*, Scale bar: 50 μm; **(E)** *Strigatella scutulata*, Scale bar: 100 μm; **(F)** *Murex* sp., Scale bar: 50 μm; 1: radula; 2 and 3: enlarged part of radula; R, rachidian teeth; L, lateral teeth; M, marginal teeth.

Muricidae family has three representatives. In this study, the rachidian tooth was observed with uneven multicusps with boomerang- or sickle-like distal lateral teeth.

Murex sp. contains broad-based multicuspid (seven) rachidian teeth, including a central, a consecutive cusp that is sharp and pointed, and the outermost two cuspids that look undeveloped. There are single long boomerang-shaped lateral teeth pointed at the basal end on each side of the rachidian teeth (**Figure 4F**).

Thais sp. was observed with a multicuspid broad-based rachidian tooth that had central bezel-shaped; this was followed by maple leaf-like trifurcated cusps at each side. These cusps are followed by multiple narrow similar-sized denticles that are single sickle-shaped lateral teeth with a blunt-ended base on each side of the rachidian teeth (**Figure 5A**).

Tylothais savignyi also has a multicuspid broad-based rachidian tooth similar to *Thais* sp. In this study, the arrangement was found to be quite loosely attached as compared to *Thais* sp., in which central longer sharp and pointed cusp, and small and narrower cusp on each side of the central longer cusp are followed by broad-tipped cusp and two rounded blunts and look similar to undeveloped denticles at each side. There are single falcated lateral teeth with a pointed tip with a broader base on each side of the rachidian teeth (**Figure 5B**).

There was only one representative of the family Pisaniidae observed during the field survey, i.e., *Pollia undosa*.

The rachidian tooth of *P. undosa* was observed with a broad base and multicuspid. It has a central triangular pointed cusp and one instant outward pointed similar-sized cusp on each side of the central cusp, which are followed by one smaller denticle that has a blunt tip. There is one lateral tooth on each side of the rachidian teeth, which has a tricuspid shape that looks similar to three attached bezels. From that, the innermost cusp is larger than

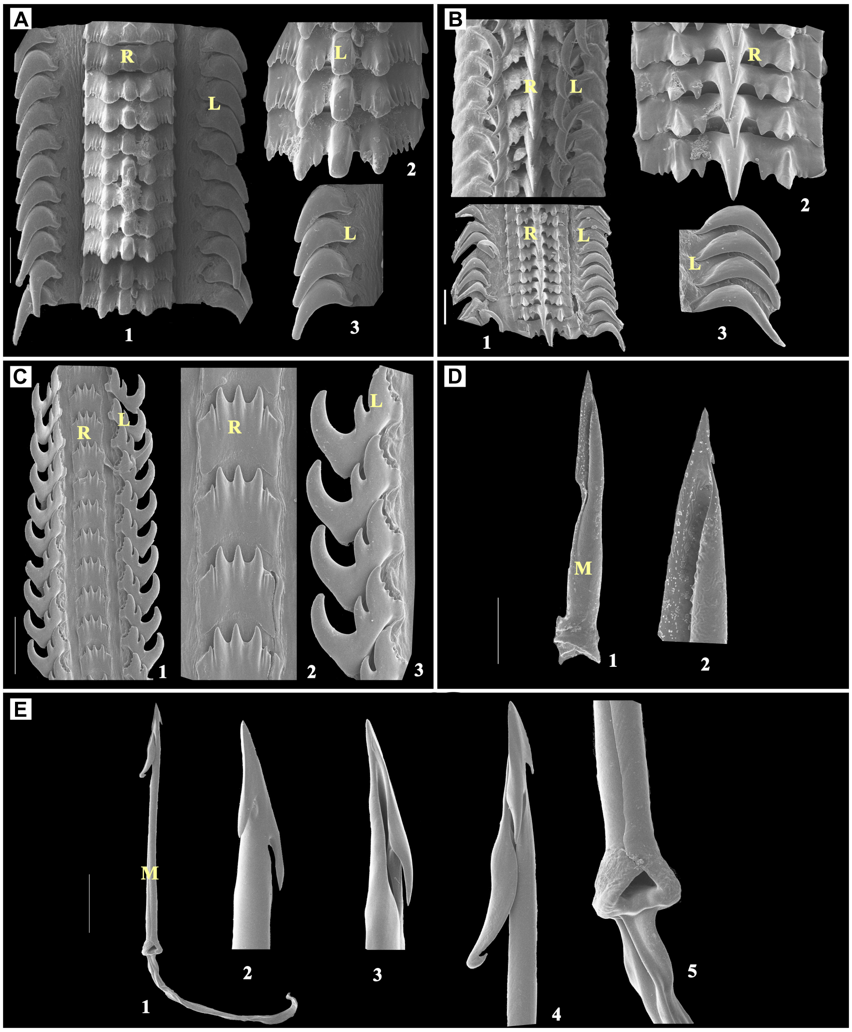

FIGURE 5 | **(A)** *Thais* sp., Scale bar: 100 µm; **(B)** *Tylothais savignyi*, Scale bar: 50 µm; **(C)** *Pollia undosa*, Scale bar: 100 µm; **(D)** *Conus figulinus*, Scale bar: 100 µm; **(E)** *Conus achatinus*, Scale bar: 100 µm; 1: radula; 2–5: enlarged part of radula; R, rachidian teeth; L, lateral teeth; M, marginal teeth.

the other two cusps and also has small denticles (approximately 3–4). The middle one cusp is short and sharp with a pointed tip (**Figure 5C**).

Toxoglossan Radula

The toxoglossan radula has neither a central tooth nor a lateral tooth, and the structure has only marginal harpoon-like teeth observed on each side.

Conus figulinus has only single lateral harpoon-shaped tooth with a single barb at the apex and a blade on its opposite side. The longer serration opposite to the blade terminates to the waist region. The knob at the terminal end has a single prominent spur at the side opposite to the barb (**Figure 5D**).

In this study, in *Conus achatinus*, the harpoon has three barbs at the tooth apex; among them, two are short and a third is long with a recurved tip. The long shaft lacks serration and cusp. The shaft ends in an enlarged terminal knob without a spur (**Figure 5E**).

In this research perspective, all 23 species belonging to 12 families were observed for their shell length measurement and radular length (**Figure 6**). Among these families, the Nacellidae family persists in the docoglossan type of radula which can be represented in *C. karachiensis* in which radula is almost about five times longer than the shell length. In genus *Turbo* of the family Turbinidae, the radular length is found to be half of the shell length. Individuals of the family Neritidae reported almost the same ratio of shell length to the radular length. In the Cerithiidae family, shell length was noted with approximately five times larger than the radular length. Shell length of *E. pascua* representative of family Littorinidae was found to be very less as compared to radula, which is a very distinctive feature. In *P. verruculata*, the radular ribbon was very small and broad in contrary to body size as it was a shell-less organism. Individuals of the Mitridae family were observed with a small radular ribbon than the shell length, most probably either half or less than half of the shell length. Most of the individuals of

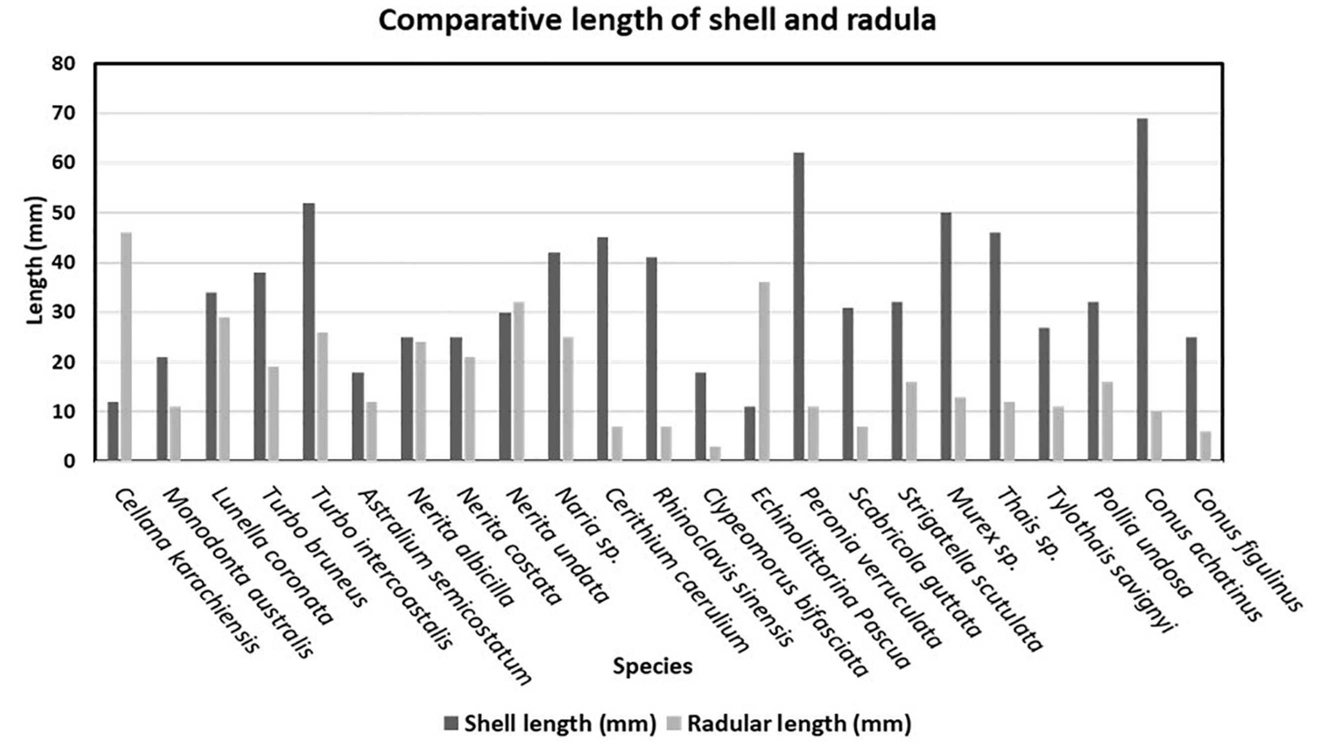

FIGURE 6 | Comparative study of shell length and radular length.

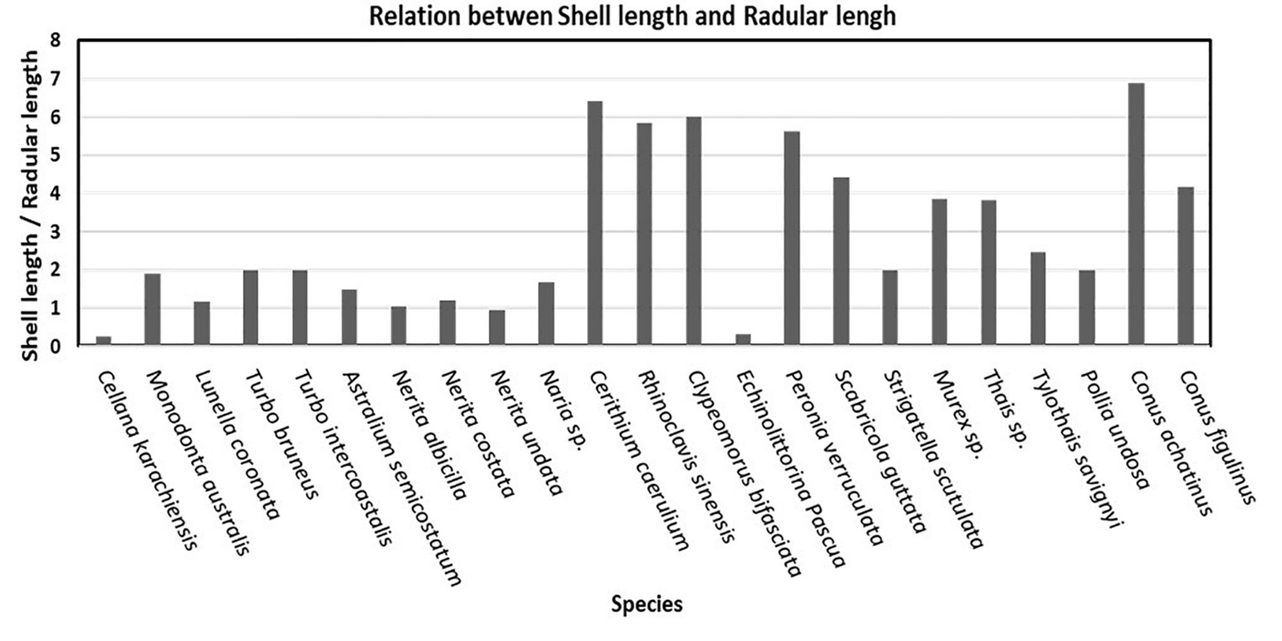

FIGURE 7 | Relationship between shell length and radular length of selected species.

the family Muricidae were observed with three times smaller radula than the shell length. In the Conidae family, the harpoon-like structure was observed differently in every species. For an instance, in *Conus achatinus* and in *Conus figulinus*, shell size was found to be very high as compared to the harpoon length (**Figure 7**).

The ratio of shell length and radular length is low in the animals possessing rhipidoglossan and docoglossan types

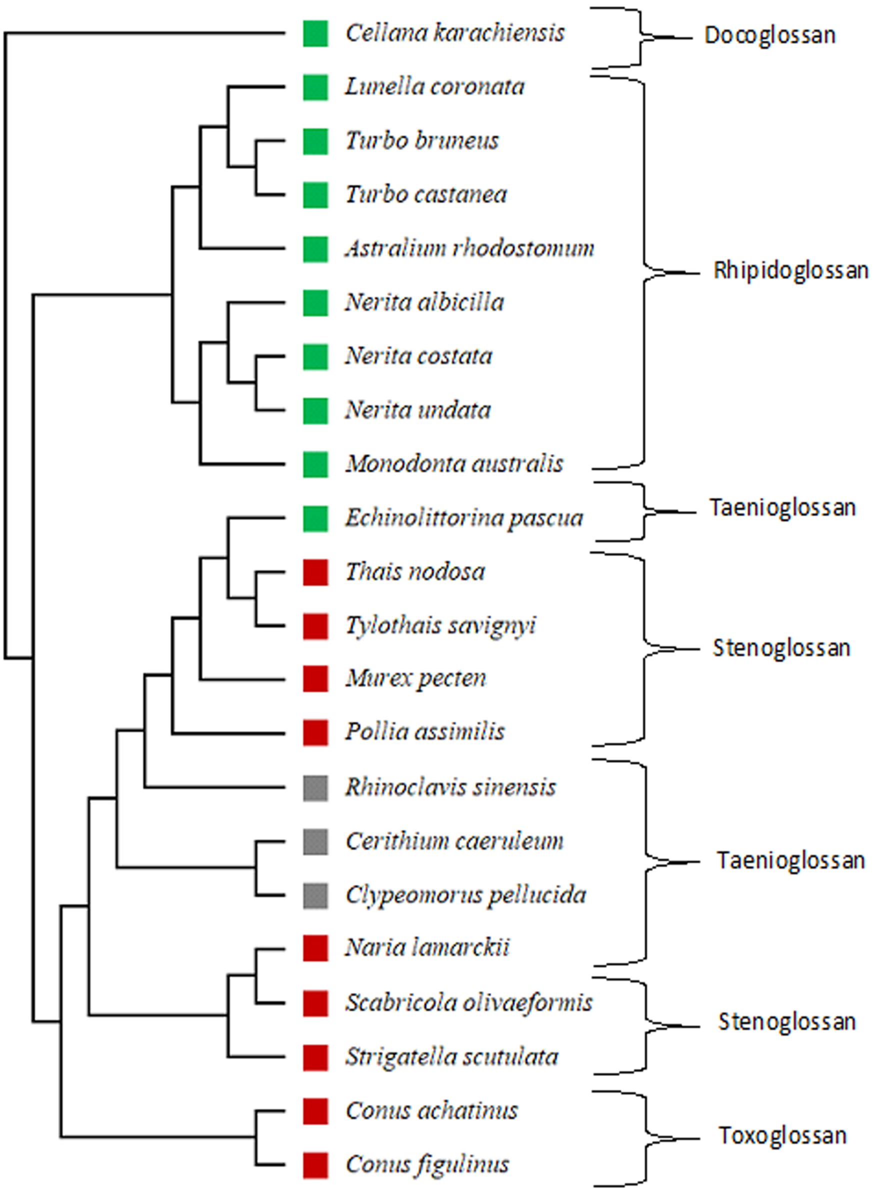

FIGURE 8 | Phylogenetic tree based on cytochrome oxidase I (*COI*) gene for gastropod analyzed using UPGMA (without out-group) with Jones-Taylor-Thornton (JTT) estimate models of amino acid replacement with 1,000 bootstrap replicates in Molecular Evolutionary Genetics Analysis (MEGA11) software. Green color square: herbivore; gray color square: detritus feeder; red color square: carnivore.

of radula as compared to taenioglossan types of radula. The gastropods that contain taenioglossan types of radula were observed with a comparatively high ratio of up to 6 excluding *E. pascua* and *Naria* sp. which showed very low ratios of about 0.3 and 1.6, respectively. Individuals of stenoglossan type bearing radula have a moderate ratio. A harpoon-like radula observed in *Conus* sp. was identified as toxoglossan radula in which ratio is dependent on the shell size of the individuals (**Figure 7**).

Results of Phylogenetic Tree

Cellana karachiensis is the most primitive species and is shown in **Figure 8**, which shows a distinct clade in the phylogenetic tree. This species represents the docoglossan type of radula. In our study, rhipidoglossan types of radula are the most representative radula in the group of herbivores. The families such as Turbinidae and Neritidae show a clear difference in the phylogenetic tree, and the cladistic representation also supports our description on the radular arrangements of those families (**Figure 8**). In other cases, representative families in the phylogenic tree support our observed results (**Figure 8**). Out of 22 species, 10 are herbivores (**Figure 8**, green color square), 9 are carnivores (**Figure 8**, red color square), and 3 are detritus feeders (**Figure 8**, gray color square). *Naria* sp. is a carnivore, but its radular formula is similar to cerithiids.

The results of the phylogenetic tree with the JTT estimation model revealed that *Patellogastropoda* may be a primitive group and more ancient lineage among the studied gastropods. The docoglossan type of radula is a primitive and simple herbivore radula compared to the rhipidoglossan and taenioglossan. While the radula types of the carnivore indicated a gradual evolution through taenioglossan to stenoglossan and toxoglossan. Thus, the toxoglossan radula is a modern radula among all radular types. During this gradual evolution, the changes in radula from herbivores to carnivores was observed in teeth morphology and revealed from simple arrangements to complex ones. This study also revealed the evolution of radular arrangements which shows the conversation of chitinous ribbon in limpets to harpoon shape in *Conus*. Thus, we can conclude that the development of the radular morphology is passing through the evolutionary processes and is strongly dependent on the feeding guilds of the organisms.

DISCUSSION

In this study, the radular morphology of 23 species from 12 different families were analyzed. The collected samples from the south Saurashtra coastline were fixed and analyzed. This feeding organ is very significant in molluscan, especially in the taxonomy of the gastropod. As they are limited to a species or genus, it is useful to identify the feeding habitat of the animal (Vakani et al., 2020). Radula reveals the variances in intraspecific level better than the morphology of shell, foot, and other significant characteristics (Mutlu, 2004; Mutaf and Aksit, 2009; Vakani et al., 2020). Only through radular morphology, we could point out similarities in the family level as well as in the species level.

The docoglossan is known as the very earliest radula, which is commonly found in *Patellogastropoda*. The habitation of this group has been found in the initial rocky intertidal area, which itself is harsh to survive due to less algal growth and tearing wave actions of the intertidal zone. Toxoglossan radula that has the harpoon shape of denticles has been found in carnivorous species such as *Conus*. Thus, harpoons can be useful to sting prey and paralyze it (Kantor, 1990). The structure of radula is dependent on their size, form, the material of teeth, and the reactions between teeth and nutrition material on which they feed. This condition creates few specifications in radula which can lead to species-specific radular ribbon (Eisapour et al., 2015). A number of each type of radula, specific arrangement and structure of teeth, different functions of teeth, different diets, and different nutritional methods indicate different ecological conditions of an animal. The habitat of various species or families directly concerns with the diet, which can lead to understand the interactions and competitions between the species or family.

The docoglossan and rhipidoglossan types of radula were found in herbivore organisms. According to this study, carnivorous animals have smaller radula than herbivorous ones. In this study, *C. karachiensis* inhabits in spray and upper littoral zone and feeds on microalgal film from rock that represents the docoglossan type of radula in which the radular size was found to be very large as compared to shell length. The families of Turbinidae (Foster et al., 1999), Trochidae (Wakefield and Murray, 1998), and Neritidae (Aliakrinskaia, 2003) have rhipidoglossan type of radula. The enlargement of the radula in gastropods with rhipidoglossan radula type made a possible use of a larger area of substratum during the food scraping (Fretter and Graham, 1994), and they have broad radula with many narrow marginal teeth. Animals from the family Cerithiidae are mostly detritivores which consist of long marginal teeth, well adapted for capturing particles from the substratum (Morton, 1968). Cerithiids were observed with very small radula as compared to the shell size, and hence, the length of marginal teeth seems to be efficient for capturing food. *E. Pascua* and *P. verruculata* have taenioglossan type of radula and both of them are herbivores. *E. Pascua* lives in the upper portions of the upper littoral zone, feeds on microfilm of algae from the rock, and has a very long radular ribbon that helps to scrape microalgae and nutrients from the rock surface. *P. verruculata* has a very shorter radular length as compared to body length. A very broad radular ribbon was observed as compared to other gastropods with many lateral teeth that made possible use of the larger area of substratum during food scraping. Muricidae and Conidae families in the *Neogastropoda* group are carnivorous, but the mechanism of capturing prey is different (Watanabe and Young, 2006). Muricids have access to the soft parts of the prey which is typically obtained by boring a hole through the shell by means of a softening secretion and the scraping action of the radula. The Conidae family has a special type of toxoglossan radula, and compared to other gastropods, they use a completely different way of capturing prey. They have a movable harpoon-like structure in the radular pouch and a separate poisonous gland that is used for paralyzing their prey.

According to the study by Guralnick and De Maintenon (1997), the radula type or diet affects not only the morphological characteristics of each individual from each species but also the prey-capturing strategies and the food processing mechanism (how the whole radula teeth are used and time taken for being reconstructed), the environmental pressures (phenotypic plasticity and food competition), and the species ontogeny.

CONCLUSION

Different kinds of radula also vary in structure and arrangement of denticles of radular teeth. The carnivore animals (toxoglossan radula) required less teeth, and herbivores (rhipidoglossan radula) need more teeth than carnivores; this feature can be used to study the evolution of gastropods. A total of 23 studied species belong to 12 different families of gastropods. These types of enlisting data can be used for further experimental purposes in future. Basic knowledge about the dentition details will be useful for true inter-anticipation of taxonomy and ecology of gastropods.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

RK was a guiding faculty for this work. All authors contributed to the article and approved the submitted version.

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