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, 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
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 have 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 endemity (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 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 m$^{-2}$ 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, 485, 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 (K₂Cr₂O₇) and Sulfuric Acid (H₂SO₄), thereby titration against Ferrous Ammonium Sulfate (NH₄)₂Fe(SO₄)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) (Garcia 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 (NO₃⁻, NO₂⁻, NH₄⁺, PO₄³⁻, and SiO₄⁻), 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 NO₂⁻, NO₃⁻, NH₄⁺, PO₄³⁻, and SiO₄⁻, 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
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 v4.53 (ter Braak and Šmilauer, 2002). The study area map was constructed in QGIS v3.10 (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 oxygen varied widely along with the depth due to intense OMZ in the WICM.
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 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, and ammonium, and total phosphorus, while tophosphate, silicates, ammonium, nitrite, nitrate, and total phosphorus, while non-OMZ-S (1–5) was separated due to enrichment of fresh and phytolophatic 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.
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 at 111 m (non-OMZ-S) and lowest at 202 m within OMZ (Figure 4C). The mean meiofaunal biomass was highest (1198.84 ± 729.11 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, tanaids, turbellarians, insects, oligochaetes, gastrotrichs, sipunculids, cumaceams, isopods, crinarians, and holothurians. 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   | –                 | –         | –                | –     | –     | –     | –     |
| 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  | 0.38  | 0.14  | 0.19  |
| 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.
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 biomasses (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...
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
Abundance and diversity of meiofauna were significantly influenced by depth and OMZ conditions. The density was 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...
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 mollusks 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 Ölafsson, 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
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

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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