Distribution of Meiofauna in Bathyal Sediments Influenced by the Oxygen Minimum Zone Off Costa Rica

Carlos Neira[1]*, Jeroen Ingels[2]*, Guillermo Mendoza[1], Elvira Hernandez-Lopez[1] and Lisa A. Levin[1]

[1] Integrative Oceanography Division and Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, La Jolla, CA, United States, [2] Florida State University Coastal and Marine Laboratory, St. Teresa, FL, United States

Ocean deoxygenation has become a topic of increasing concern because of its potential impacts on marine ecosystems, including oxygen minimum zone (OMZ) expansion and subsequent benthic effects. We investigated the influence of oxygen concentration and organic matter (OM) availability on metazoan meiofauna within and below an OMZ in bathyal sediments off Costa Rica, testing the hypothesis that oxygen and OM levels are reflected in meiofaunal community structures and distribution. Mean total densities in our sampling cores (400–1800 m water depth) were highest with 3688 ind. 10 cm^{-2} at the OMZ core at 400 m water depth, decreasing rapidly downslope. Nematodes were overall dominant, with a maximum of 99.9% in the OMZ core, followed by copepods (13%), nauplii (4.8%), and polychaetes (3%). Relative copepod and nauplii abundance increased consistently with depth and increasing bottom-water O_2. Meiofaunal composition was significantly different among sites, with lower taxonomic diversity at OMZ sites relative to deeper, oxygenated sites. Vertical distribution patterns within sediments showed that in strongly oxygen-depleted sites less meiofauna was concentrated in the surface sediment than at deeper slope sites. Highest meiofaunal abundance and lowest diversity occurred under lowest oxygen and highest pigment levels, whereas highest diversity occurred under highest oxygen-concentrations and low pigments, as well as high quality of sedimentary pigment (chl a/phaeo) and organic carbon (C/N). The lower meiofaunal diversity, and lower structural and trophic complexity, at oxygen-depleted sites raises concerns about changes in the structure and function of benthic marine ecosystems in the face of OMZ expansions.

Keywords: meiofauna, oxygen minimum zone, eastern Pacific, bathyal, community structure, Costa Rica margin

INTRODUCTION

Large areas of the bathyal eastern Pacific continental margin harbor significant fisheries resources associated with upwelling, but are lined by oxygen-depleted waters (O_2 < 0.5 ml L^{-1} or <22 µmol kg^{-1}) known as oxygen minimum zones (OMZs) usually found between 100 and 1200 m water depth (Levin, 2003). OMZs are most prevalent in the eastern Pacific Ocean, the Arabian Sea, and off west Africa (Karstensen et al., 2008; Paulmier and Ruiz-Pino, 2009). The world's largest OMZ occurs along the eastern Pacific covering over 360,000 km^2 of seabed, and varying in intensity

and distribution with climate variability (Helly and Levin, 2004). Global warming resulting from climate change has exacerbated ocean deoxygenation in coastal and oceanic regions (Keeling et al., 2010; Schmidtko et al., 2017; Breitburg et al., 2018; Levin, 2018), leading to expansion of tropical OMZs in recent decades (Stramma et al., 2008; IPCC, 2014; Gobler and Baumann, 2016). Ocean deoxygenation has become a topic of increasing concern for scientists because of the damage that climate-driven oxygen loss will cause to ocean ecosystems (Stramma et al., 2010; Levin and Breitburg, 2015; Levin, 2018).

Oxygen minimum zones result from oxygen depletion and respiration often combined with sluggish circulation and oxygen-poor source waters. Where OMZs intercept the continental margins, strong oxygen and organic-matter gradients, often highly heterogeneous, are formed (Levin, 2003). These gradients influence the biogeochemical properties of sediments (Cowie and Levin, 2009), with consequences for the benthic ecosystem (Gooday et al., 2010; Stramma et al., 2010). Dissolved oxygen in the ocean is a key variable structuring communities because it modifies the energy flow in ecosystems (Wright et al., 2012), which can cause shifts in community structure and trophic transfer, as well as changes in productivity and biogeochemical cycling (Arntz et al., 2006). At OMZs, severe reductions of macro- and megafauna abundance and diversity occur (Levin, 2003; Gooday et al., 2009). Extended periods of hypoxia may negatively affect meiofaunal communities, reducing total densities and the most sensitive taxa and life stages (Murrell and Fleeger, 1989; Sergeeva and Zaika, 2013). However, there is evidence that metazoan meiofauna are much less negatively affected by low oxygen than the macrofauna (Cook et al., 2000; Neira et al., 2001b,c; Sellanes and Neira, 2006; Zeppilli et al., 2015).

Meiofauna are the most abundant metazoans in deep-sea sediments and play a critical role in trophic ecology and ecosystem functioning (Zeppilli et al., 2015; Schratzberger and Ingels, 2017). They have a short life cycle and respond quickly to disturbance and pollution, making them ideal subjects to study ecological change (Mahmoudi et al., 2005; Danovaro et al., 2008; Van Oevelen et al., 2011; Schratzberger and Ingels, 2017). There is consensus that metazoan meiofauna cope better with hypoxia than macrofauna and megafauna (Neira et al., 2001b). Thus, under oxygen decline (Schmidtko et al., 2017) and OMZ expansion (Stramma et al., 2008), an infaunal functional shift toward meiofauna may occur (Neira et al., 2013), with likely consequences for essential ecosystem functions. Although meiofauna represent the major metazoan component within the eastern Pacific OMZ, they remain poorly studied (Neira et al., 2001c,a, 2005, 2013; Neira and Decraemer, 2009; Veit-Köhler et al., 2009) and their community responses to oxygen depletion have not often been investigated.

In spite of considerable knowledge gained in recent decades on deep-sea meiobenthos in extreme marine ecosystems (Zeppilli et al., 2015, 2018), very little is known about them in OMZs. To our knowledge, there are no quantitative meiofauna studies in deep-sea areas associated with the OMZ in the geographic region off Costa Rica. The Pacific coast of Costa Rica, 1164 km in length, has a large diversity of coastal

habitats such as sandy, muddy and rocky beaches, mangroves, estuaries, islands, bays, and gulfs (Cortés and Jiménez, 2003; Quesada-Alpízar and Cortés, 2006), and a tropical fjord (Golfo Dulce), an anoxic basin that intermittently receives oxygen-enriched water (Nichols-Driscoll, 1976; León-Morales and Vargas, 1998).

Previous studies for Costa Rica where meiofauna have been considered are very scarce and are restricted to the Gulf of Nicoya, and focused on meiofauna community structure variations in soft bottom beaches (e.g., De la Cruz and Vargas, 1986, 1987; Vargas, 1988) and coral reefs around Isla del Caño (Guzmán et al., 1987). The OMZ depicts substantial habitat heterogeneity, e.g., step gradients in oxygen, variation in the OM quantity and quality, redox potential, pH, multiple water masses with different physical–chemical characteristics (Gooday et al., 2010; Levin et al., 2010), providing a natural scenario to address whether these changes are reflected in differing meiofauna assemblages and spatial distributions along the Costa Rica slope. The aim of the present work was to investigate the effects of the OMZ on meiofaunal communities in terms of abundance, composition, taxon diversity and spatial distribution in the sediment column, and identify environmental factors that most likely structure communities along a bathymetric transect (400–1800 m depth) on the Costa Rica margin. The overarching hypothesis guiding this study is that spatial habitat heterogeneity driven by bottom-water oxygen and OM availability within the OMZ selects for distinct meiofaunal community structure and spatial distribution relative to deeper, more oxygenated slope sites.

MATERIALS AND METHODS

Study Area and Sample Processing

Between February 21 and March 6, 2009 slope sediment samples were collected during a cruise on board of R/V Atlantis (Leg AT 15-44) off Costa Rica's Pacific margin. This was complementary to a larger study focused on macrofauna inhabiting methane seep carbonates. The area is characterized by an intense, well-developed, mid-water OMZ which impinges on the margin at depths between 300 and 700 m (Levin et al., 2015). Along the Costa Rica margin there is a high degree of local and regional heterogeneity caused by carbonates, submarine fluid venting sites, methane seeps, hydrothermal seeps, mud mounds, seamount subduction scars, and slope failures as well-strong vertical hydrographic gradients (Han et al., 2004; Mau et al., 2006; Sahling et al., 2008; Füri et al., 2010; Levin et al., 2012, 2015). Surface net primary production (NPP) is relatively high, as a result of macronutrient supply associated with thermocline shoaling, mixing and wind-driven upwelling, and exhibits intra-annual variability with highest primary production in September–October and lowest in January–February (Nielsen-Muñoz and Quesada-Alpízar, 2006; Pennington et al., 2006). Thus, the OMZ along with both topography and hydrography result in strong gradients in bottom-water oxygen concentration, temperature, and pH over a relatively short depth range (Levin et al., 2015).

Sediment samples were collected with a multicorer (9.6 cm core liners i.d.) at six open slope sites (400, 620, 800, 1000, 1200, and 1800 m water depth; **Figure 1**). At each depth, three independent multicorer deployments were conducted (except the 1200 m site $n = 2$). Only undisturbed cores with clear overlying water were used. Subsamples were taken simultaneously from the same corer, for meiofauna and sediment properties, using Perspex tubes (3.6 cm inner diameter, 10 cm^{-2}). All sediment cores were sectioned vertically on board ship at 0–1, 1–2, 2–3, 3–5, and 5–10 cm. Sections were preserved in 4% buffered formalin (Pfannkuche and Thiel, 1988) for meiofauna analysis, while fractions for sediment properties were frozen until analysis. Water content (WC) was determined by weight loss after freeze-drying sediment aliquots. Sediment total organic carbon (TOC) and total nitrogen (TN) were determined from freeze-dried, homogenized sediment using a Costech CHN analyzer (Valencia, CA, United States) after removal of inorganic carbonates. Chl a and phaeopigments were determined spectrophotometrically from freeze-dried sediment (Hagerthey et al., 2006) after extraction with 90%

acetone (Danovaro, 2010). Chloroplastic pigment equivalent (CPE), i.e., the sum of chl a and phaeopigments was used as a measure of OM of phytodetrital origin. The ratio chl a to phaeopigments was used as a proxy of 'freshness' of the OM derived from primary production (García and Thomsen, 2008). The chl a to TOC ratio was used to indicate bioavailability of the bulk organic matter (OM; i.e., reflecting contribution of organic carbon of phytoplanktonic origin, Ramalho et al., 2014). Net primary production values for study sites were provided by M. Kahru (SIO) and were estimated from satellite data of chl-a concentration, photosynthetically active radiation and sea-surface temperature using an empirical algorithm (Kahru et al., 2012). Hydrographic data including temperature, salinity, dissolved oxygen, and pH were obtained from CTD casts.

Metazoan meiofauna were extracted from sediment by suspension-decantation (Pfannkuche and Thiel, 1988) using a 40 µm-sieve as the lower limit. The procedure was repeated at least five times for the 1-cm sections, 8–10 times for the larger fractions. Residual sediment was examined for extraction efficiency (>98%, Neira et al., 2013). All meiofaunal

FIGURE 1 | Location of meiofaunal sampling sites along the Costa Rica margin (Map data: 2009 Google Earth).

organisms were counted and classified to higher taxon level under a stereoscopic microscope after staining with Rose Bengal (0.5 g L^{-1}) (Pfannkuche and Thiel, 1988; Giere, 2009). Nauplii were counted separately given their ecological differences in size and diet compared to adults and copepodites (Decho and Fleeger, 1988).

Data Analysis

Meiofaunal density, taxon richness (number of higher taxa) and diversity indices [Pielou's evenness (J'), Shannon–Wiener (H' log10) and Rank 1 dominance (R1D, the proportion of the most abundant taxon, which is an inverse indicator of assemblage evenness)] were used to describe meiofauna assemblage structure. Taxon richness was also examined through rarefaction curves (number of taxa per number of individuals sampled – Hurlbert, 1971).

Meiofauna community composition (multivariate, square root transformed, Bray–Curtis Similarity) and total meiofauna abundance (univariate, square root transformed, Euclidean Distance) were analyzed with PERMANOVA tests (three-factor design: water depth, sediment depth, core). The random factor 'core 'was inserted as nested in water depth to account for the dependency of the sediment layers within each core; this approach has been used in several studies as a good solution to the sediment layer dependence issue (e.g., Ingels and Vanreusel, 2013; Rosli et al., 2016). This design allows us to investigate differences between water depths and sediment layers simultaneously. Additional PERMANOVA tests were performed on the meiofauna community matrix and the individual diversity indices (based on pooled 0–10 cm sediment data). Pairwise tests were performed for main factors and interactions when significant results were obtained. PERMDISPs were performed when PERMANOVA returned significant results, to investigate heterogeneity in dispersions. Monte Carlo tests were applied when the number of available permutations was <100. Non-parametric multidimensional scaling ordination (nMDS, square root transformation, Bray–Curtis Similarity) was used to visualize the dissimilarity in meiofaunal community structure among sites. Similarity percentage (SIMPER) analysis was used to determine which taxa were responsible for observed differences (Clarke, 1993).

Environmental data were subjected to univariate PERMANOVA analysis, testing differences between water depths for each variable separately (no transformation, Euclidean distance). Spearman-rank correlations were performed to examine collinearity between environmental variables, and possible relationships between environmental variables and meiofaunal taxa abundance. Redundancy analysis (RDA) was used to examine correlations between meiofaunal community composition and environmental variables (Ter Braak and Šmilauer, 2012) in order to assess the extent of the contribution of each variable to variance in community composition. Prior to RDA, a forward stepwise selection procedure was performed to minimize redundancy of variables (between-variable correlations) and select a set of explanatory environmental variables that account for the composition variation (Lepš and Šmilauer, 2003). This was followed by a Monte Carlo

permutation test to determine significant relationships between the taxa and environment.

All above analyses were performed with PRIMER v6 (Clarke and Gorley, 2006) and the PERMANOVA+ add-on (Anderson et al., 2008), except for the Spearman Rank correlations (JMP Pro 12.0.1., SAS Institute, Inc.) and the RDA ordination and gradient analysis [CANOCO for Windows 5 (Ter Braak and Šmilauer, 2012)].

RESULTS

Environmental Properties

Environmental and sediment properties are summarized in **Table 1**. Bottom-water temperature decreased progressively with depth along the entire transect, while bottom-water dissolved oxygen (DO) values progressively increased with depth, with a minimum of 0.05 ml L^{-1} at the 400 m site, and maximum of 1.61 ml L^{-1} at the 1800 m site. Bottom-water pH fluctuated between 7.68 and 7.77 along the transect. The OMZ 400 (core) and 620 m sites were enriched in TOC (∼2.5%DW) and CPE (147 µg g^{-1}) compared to the deepest oxygenated site (∼1.1%DW, 8.2 µg g^{-1}, respectively). The chl *a* value at the OMZ core site (400 m) was very high, as was the phaeopigment concentration, leading to a lower 'freshness' (chl *a*/phaeo) value than was observed at 800 m and deeper.

Quality of available OM was least refractory at the deepest site (1800 m), with lowest C/N (7.7) and highest chl *a*/phaeo (1.54). The vertical profile of chl *a*/phaeo values along the transect is shown in **Figure 2**. Sediment environmental variables were significantly different between study sites (PERMANOVA; **Supplementary Table S1**). Surface water chl *a* has been considered an indicator of the flux of phytodetrital OM to the seabed and thereby food availability to benthic animals (Rex and Etter, 2010). The relatively high and homogeneous NPP in surface waters for the study area (271–332 mg C m^{-2} d^{-1}) calculated for the sampling period (**Table 1**) was reflected in the partially degraded phytopigments found in sediments. Indeed, sediment C/N ratio compared with δ^{13}C signatures indicate that deposited sedimentary OM is predominantly of marine origin (**Figure 3**).

Several correlations between environmental variables were significant (**Supplementary Table S2**), but most prominent were the significant relations between DO, bottom-water temperature, and chl *a*. Bottom temperature was inversely related to DO ($r = -1.000$), and positively to chl *a* ($r = 1.000$). In general, variables related to food quantity, freshness, and availability correlated strongly with each other. As a result, DO correlated significantly, negatively with TOC, TN, TOC/TN, Phaeo, CPE, chl *a*/TOC and positively with chl *a*/Phaeo.

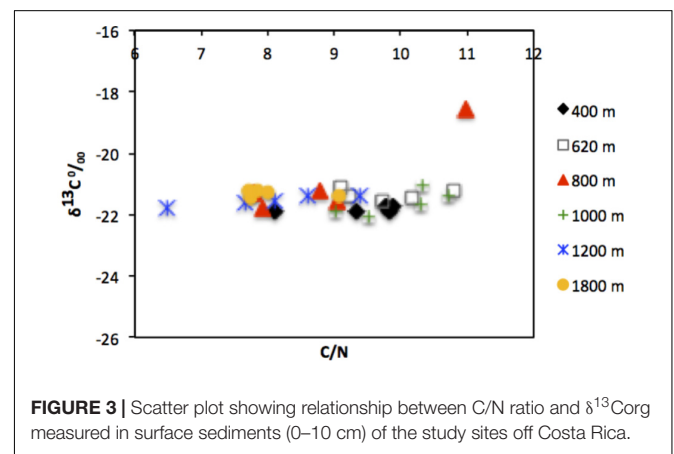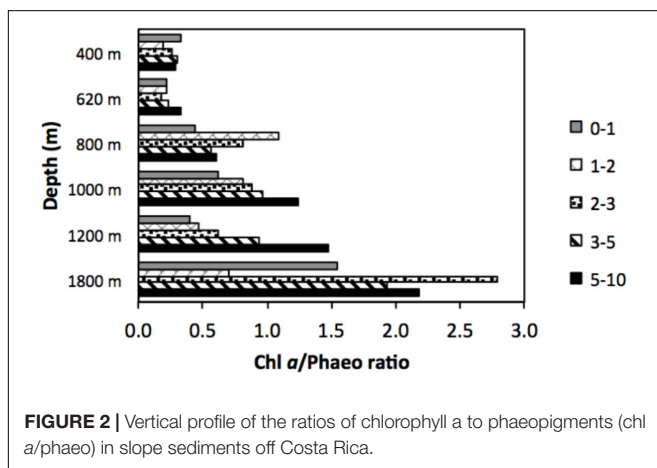### Meiofaunal Density, Composition, and Diversity

Density

Mean total meiofaunal densities (0–10 cm depth) were highest (3685 ± 1 SE 995 ind. 10 cm^{-2}) at the OMZ core site (400 m), decreased dramatically toward the 620 m site and the lower

TABLE 1 | Abiotic properties of benthic sites on the Costa Rica margin.

	OMZ			Beneath OMZ		
Sites	400 m	620 m	800 m	1000 m	1200 m	1800 m
Depth (m)	400	620	800	1000	1200	1800
BT (°C)	9.06	7.11	5.8	4.65	4.295	2.66
DO (ml L^{-1})	0.05	0.16	0.38	0.57	0.83	1.61
pH	7.68	7.74	7.68	7.68	7.73	7.77
TOC (%)	2.50	2.58	1.95	2.15	1.62	1.12
TN (%)	0.31	0.31	0.25	0.26	0.23	0.17
C/N ratio (molar)	9.33	9.74	9.06	9.52	8.10	7.73
WC (%)	81.0	82.9	71.6	80.2	77.5	79.1
Chl a (µg g^{-1})	36.28	19.47	9.31	7.94	6.37	4.98
Phaeo (µg g^{-1})	110.51	68.51	21.31	12.90	15.91	3.24
CPE (µg g^{-1})	146.79	87.98	30.62	20.84	22.28	8.22
Chl a/phaeo ratio	0.33	0.28	0.44	0.62	0.40	1.54
Chl a/TOC ratio	14.54	7.54	4.77	3.69	3.93	4.44
δ^{13}C (^{o}/$_{oo}$)	−21.878	−21.583	−21.546	−22.094	−21.529	−21.453
δ^{15}N (^{o}/$_{oo}$)	4.827	7.061	5.387	5.931	3.076	5.164
*NPP (mg C m^{-2} d^{-1})	279.20	308.30	277.30	265.20	276.10	341.70

*Sedimentary parameters are given for the top 0–1 cm layer. BT, bottom water temperature; DO, bottom-water dissolved oxygen; TOC, total organic carbon; TN, total nitrogen; C/N, molar carbon/nitrogen ratio; WC, water content; Chl a, chlorophyll a; Phaeo, phaeopigments; CPE, chloroplastic pigment equivalents. *Surface Net Primary Production data (courtesy of M. Kahru, SIO).*


FIGURE 2 | Vertical profile of the ratios of chlorophyll a to phaeopigments (chl a/phaeo) in slope sediments off Costa Rica.

FIGURE 3 | Scatter plot showing relationship between C/N ratio and δ^{13}Corg measured in surface sediments (0–10 cm) of the study sites off Costa Rica.

OMZ boundary site (800 m) (250 ± 1 SE 100 ind. 10 cm^{-2}), and increased slightly at the deeper, more oxygenated sites (but still < 500 ind. 10 cm^{-2}; **Figure 4**). Nematodes were dominant at all sites with an overall mean relative abundance of 79.7%; with a maximum at the OMZ core (99.9%), followed by copepods (13.0%), nauplii (4.8%), and polychaetes (3.0%) (**Table 2**).

Other taxa present included kinorhynchs, ostracods, turbellarians, bivalves, gastrotrichs, nemerteans, oligochaetes, isopods, tanaids, priapulids, aplacophorans, amphipods, cnidarians, gastropods, and cumaceans (listed in decreasing order of relative abundance) and together represented ∼2.3% of total abundance (**Figure 5** and **Table 2**). The PERMANOVA test on meiofauna density showed significant effects on the level of water depth (p = 0.002) and sediment layers (p = 0.001), with significant interaction effects (**Supplementary Table S3**).

Pairwise comparisons showed that water depth differences were mainly caused by the contrasting density differences between 400 m and the other stations, and this mainly for the top sediment layers (0–1, 1–2, 2–3 cm). Sediment depth layer differences were significant in all pairwise comparisons, but when separated per station, it became clear that differences between the surface 0–1 cm layer and the deeper layers were more prominent outside the OMZ influence (**Supplementary Table S3**). PERMDISP results indicated that the 400 m station exhibited significant dispersion heterogeneity compared to the other stations, which is not surprising given the large density differences and the fact that density is a univariate measure.

Composition
The PERMANOVA result (not considering sediment layers separately; i.e., based on 0–10 cm) indicated significant
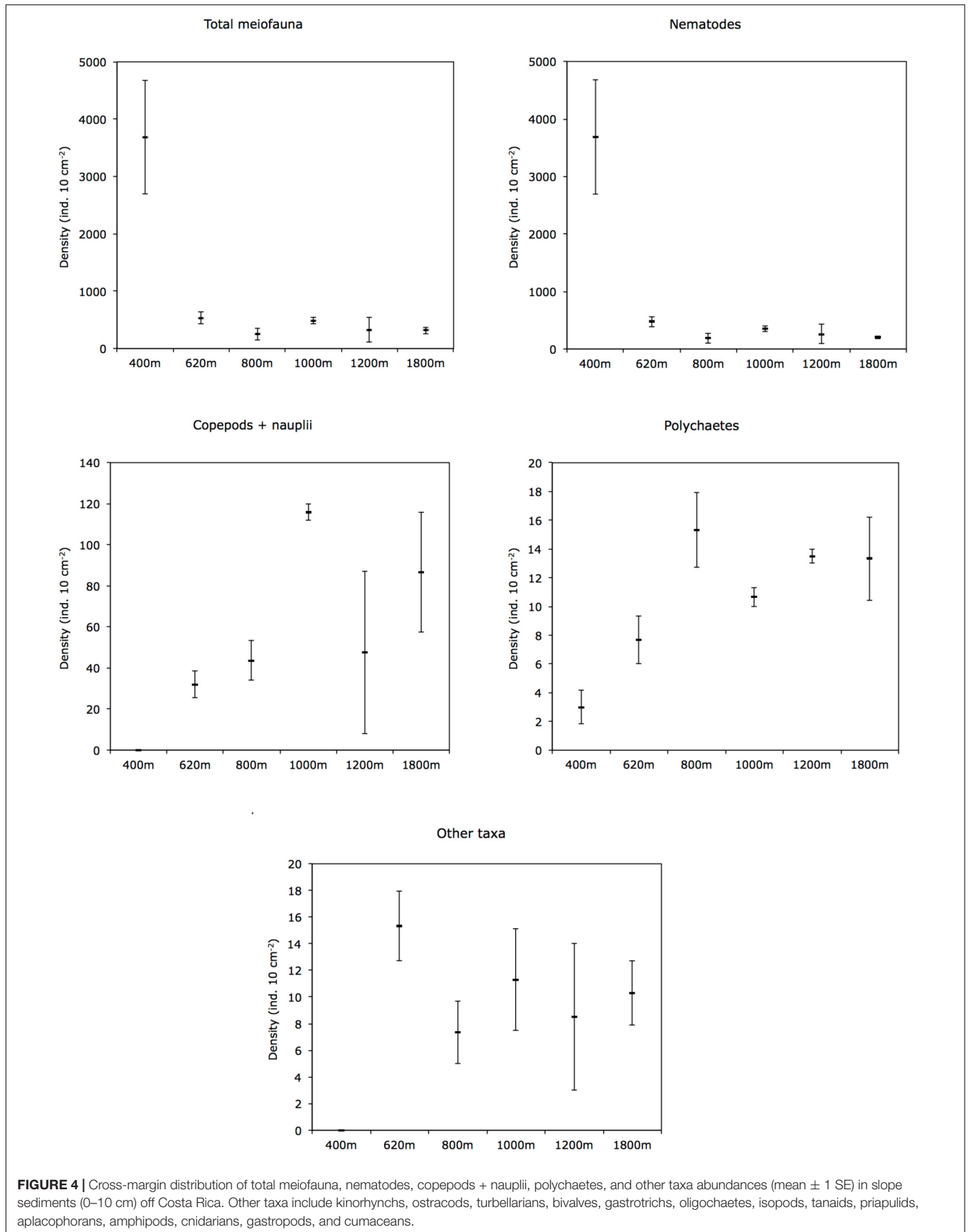
FIGURE 4 | Cross-margin distribution of total meiofauna, nematodes, copepods + nauplii, polychaetes, and other taxa abundances (mean ± 1 SE) in slope sediments (0–10 cm) off Costa Rica. Other taxa include kinorhynchs, ostracods, turbellarians, bivalves, gastrotrichs, oligochaetes, isopods, tanaids, priapulids, aplacophorans, amphipods, cnidarians, gastropods, and cumaceans.

TABLE 2 | Relative abundance (%) of meiofaunal taxa at six sites sampled along the slope off Costa Rica.

	OMZ			Beneath OMZ		
	400 m	620 m	800 m	1000 m	1200 m	1800 m
Nematoda	99.92	89.62	73.50	71.49	78.78	64.97
Copepoda	–	5.47	13.85	14.05	9.47	22.22
Nauplii	–	0.57	3.60	9.92	5.04	5.29
Polychaeta	0.08	1.45	6.13	2.20	4.12	4.23
Kinorhyncha	–	1.45	0.80	0.69	1.37	0.11
Ostracoda	–	0.19	0.27	0.55	–	0.95
Gastrotricha	–	0.13	–	0.07	–	1.06
Oligochaeta	–	0.63	–	–	–	–
Platyhelminthes	–	–	0.27	0.21	0.61	0.21
Nemertina	–	0.06	0.40	0.14	–	0.11
Tanaidacea	–	0.19	–	0.07	0.15	0.11
Bivalvia	–	–	0.67	0.55	–	0.11
Cnidaria	–	–	0.13	–	–	–
Gastropoda	–	0.13	–	–	–	–
Amphipoda	–	–	–	–	0.15	0.11
Cumacea	–	–	–	–	–	0.11
Isopoda	–	0.06	0.27	–	0.15	0.11
Priapulida	–	–	–	0.07	0.15	0.21
Aplacophora	–	0.06	0.13	–	–	0.11

differences between mainly the 400 and 620 m OMZ stations, and the deeper sites (**Table 3**). These water depth distinctions are clearly visible on the accompanying nMDS (**Figure 6**). Based on integrated 0–10 cm community data, similarity (SIMPER) within sites ranged from 53% at the 1200-m site to 87% in the OMZ core. Assemblage dissimilarities were highest between the OMZ-core site and all other sites (53.5–68.8%, SIMPER) (**Table 3**), driven by the high abundance of nematodes at the OMZ core. The lowest dissimilarity occurred between the 1000 and 1800-m sites (23.1%, SIMPER) and the 800 and 1800-m sites (26.7%) (**Table 3**), driven by an increased relative abundance contribution of copepods, nauplii, and other taxa such as gastrotrichs, kinorhynchs, and ostracods. The PERMANOVA test on community data is remarkably similar to that performed on total density, with significant differences between water depths ($p = 0.003$), sediment layers ($p = 0.001$), and their interaction ($p = 0.001$) (**Supplementary Table S4**). None of the PERMDISP analyses came out significant. Pairwise comparisons indicated that water depth differences were caused by contrasting meiofauna composition between the OMZ core 400 m station and the other sites and mainly for the top 3 cm of the sediment. Sediment layer differences occurred between all layers, but these differences changed depending on the water depth considered, with for instance significant composition differences between 0–1 and 1–2 cm at 1800 m, but not at 400 m (**Supplementary Table S4**).

Diversity

Taxon richness, H′ diversity, and J′ evenness were highest and rank 1 dominance (an inverse indicator of assemblage evenness) was lowest at the deepest site (1800 m), while the opposite was

observed at the OMZ core site (400 m) (**Table 4**). In addition, comparative rarefaction curves of OMZ sites pooled together (i.e., 400, 620, and 800 m) vs. non-OMZ sites (i.e., 1000, 1200, and 1800 m), clearly reflecting the higher community diversity at the oxygenated sites (**Figure 7** and **Table 4**). All diversity indices differed significantly between stations, with pairwise comparisons showing that the 400- and 620-m stations were the contrasting sites, setting them apart from the other stations (**Supplementary Table S5**).
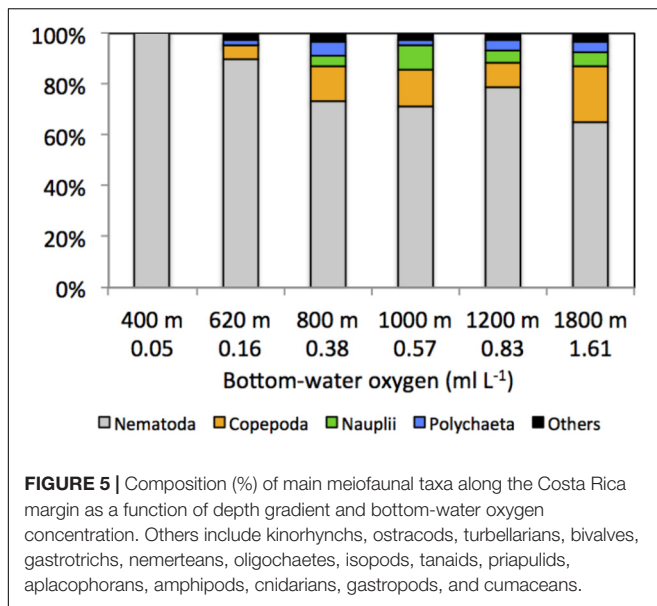
Vertical Distribution of Meiofauna

In the OMZ core (400 m), most meiofauna was concentrated in the upper 2 cm, almost divided equally between the 0–1 and 1–2-cm horizons, while densities at the adjacent OMZ site (620 m) peaked in the 1–2 cm layer, but with relatively high numbers at the surface (0–1 cm) (**Figure 8**). At the deeper, more oxygenated sites, however, meiofauna are mostly concentrated in the top 1 cm, declining consistently with depth in the sediment (**Figure 8**). In strongly oxygen-depleted sites (∼0.05–0.16 ml L^{-1}) about 20–40% of meiofauna abundance is concentrated in the uppermost 1 cm, while at deeper slope sites (>800–1800 m water depth), 55–70% of meiofauna were found in the top 1 cm sediment layer (**Figure 9A**). The relative importance of copepods and nauplii increased (and nematodes decreased) toward the deeper (620 to 1800 m), more oxygenated sites (**Figures 4**, **9B**). The PERMANOVA results on density and community composition reported above support these observations statistically, with sediment layer differences being more evident at the OMZ core and adjacent sites (620 and 800 m) where abundances do not significantly change in the upper fraction (∼0–3 cm). In contrast, the more oxygenated sites (1000 and 1800 m) show significant differences between the 0–1 cm fraction and deeper layers, reflecting the higher abundances concentrated at the sediment surface (**Supplementary Tables S3**, **S4**).

Meiofauna in Relation to the Environment

Spearman's correlation coefficients are shown in **Supplementary Table S6**. Copepod and nauplii densities were positively correlated with DO ($p < 0.05$) and freshness of the OM (chl a/phaeo) ($p < 0.05$) (**Figure 9B**). At the same time, their densities were negatively correlated with chl a and phaeo ($p < 0.05$) and bioavailability of the OM (chl a/TOC) ($p < 0.001$). Polychaetes and other taxa showed no significant relationships with the measured environmental variables. Nematodes on the other hand correlated significantly and positively with sediment TOC ($p < 0.05$).

The forward stepwise selection procedure identified a suite of environmental variables that in combination offer the best explanatory value for meiofauna community structure (cf. RDA ordination model visualized for meiofauna community in **Figure 10**). Those environmental variables that were selected are shown in **Supplementary Table S7** and include chl a/TOC, phaeopigments, chl a, water depth, and DO. The RDA analysis yielded four axes that explained 98.02% of the variance between

FIGURE 5 | Composition (%) of main meiofaunal taxa along the Costa Rica margin as a function of depth gradient and bottom-water oxygen concentration. Others include kinorhynchs, ostracods, turbellarians, bivalves, gastrotrichs, nemerteans, oligochaetes, isopods, tanaids, priapulids, aplacophorans, amphipods, cnidarians, gastropods, and cumaceans.

TABLE 3 | PERMANOVA comparisons of meiofaunal assemblages (0–10 cm) along the Costa Rica margin.

Sites (m)	400 m	620 m	800 m	1000 m	1200 m	1800 m
400	86.79	**0.0009**	**0.0029**	**0.0003**	**0.0203**	**0.0013**
620	53.47	81.16	0.1157	**0.045**	0.309	**0.053**
800	68.83	32.12	69.44	0.364	0.4403	0.294
1000	61.25	26.69	27.94	85.88	0.3365	0.204
1200	64.74	32.85	31.92	30.12	53.1	0.259
1800	67.41	31.97	26.65	23.06	33.42	78.63

Significance probabilities P(MC) from pair-wise tests (PERMANOVA) are given above the diagonal. Average similarities within-station are given on the diagonal (gray boxes, based on SIMPER analysis), and percent dissimilarity between sites are given below the diagonal. Significant values are indicated in bold.

meiofaunal community structure and environmental variables, which were significant ($p = 0.002$) for all canonical axes. The direction of vectors indicates that OM related descriptors (chl *a*, phaeo, chl *a*/TOC) increased along the first axis, and are associated with presence of nematodes, which are markedly dominant at the OMZ core site. Copepods, nauplii as well as other crustaceans such as amphipods, ostracods and cumaceans, mostly occur in the uppermost sediment layer, where they are likely associated with increased DO availability. Other taxa such as kinorhynchs, tanaids, and oligochaetes do not appear to be associated with these environmental variables over the range tested (**Figure 10**).

DISCUSSION

Environmental Properties
Sediment TOC levels were not significantly different within the different OMZ sites (400-m core, 620-m adjacent site, and 800-m lower boundary site) but they were higher in the OMZ compared to those at the deeper, more oxygenated

sites (**Supplementary Table S1**). The strong inverse correlation between TOC (and other food-related variables) and DO follows a similar trend to those observed previously in other OMZs, such as off Peru (Neira et al., 2001b), off central Chile both shelf (Sellanes and Neira, 2006) and slope (Veit-Köhler et al., 2009; Neira et al., 2013), and in the Arabian Sea (Gooday et al., 2000; Levin et al., 2000). This strong correlation suggests that DO may play a primary role in controlling TOC distribution on the Costa Rica margin, potentially through regulation of biological activity resulting in variable consumption and degradation of TOC. Also, very high levels of sinking OM may lead to rapid consumption and aerobic degradation (Stukel et al., 2016), quickly consuming the available oxygen in low-ventilation waters and leaving relatively large amounts of OM in the sediment under hypoxic conditions where anaerobic degradation by microbial organisms takes over (McKew et al., 2013). In such a scenario other factors such as bioturbation, burial, sediment sorption, as well as sediment transport, sedimentation rates and local topography may additionally influence margin TOC distributions (Cowie and Levin, 2009; Cowie et al., 2009).

The TOC levels (~2–2.5%DW) of the OMZ sediments were comparable to those reported for the Golfo Dulce (Costa Rica), a nearshore oxygen-depleted basin (~100–200 m depth) located southeast of the present study region (Nichols-Driscoll, 1976; Thamdrup et al., 1996) and Panama Basin (3900 m) (Aller et al., 1998), but lower than in other eastern Pacific OMZs such as off Chile (~122–309 m) (Neira et al., 2001c, 2013; Veit-Köhler et al., 2009). However, at the Costa Rica margin, C/N (molar) ratios were much lower (7.7–9.7; **Table 1**) and similar to more oceanic waters with OM of phytoplanktonic origin, compared to the nearshore Golfo Dulce (6.1–12.9), where terrestrial OM input with enhanced content of N-poor detritus occurs (Thamdrup et al., 1996). Higher C/N ratios can be indicative of preferential use of nitrogen during the remineralization of OM of phytoplanktonic origin (Sánchez and Carriquiry, 2007). The relatively high chl *a*/phaeo values at deeper sites suggest that material deposited is more fresh relative to that of OMZ sites (400 and 620 m). Furthermore, C/N ratios and carbon isotopic composition shows little spatial variability between sites (**Figure 3**). This suggests that little degradation of OM or at least only partial degradation occurs in the overlying water column (Cowie et al., 2009), and that the deposited OM is of marine origin, with $\delta^{13}C$ signatures typically between -18 and $-22^o/_{oo}$ and C/N ratios of 6–11. Spatial variability of C/N ratios among sites reflects the diagenetic state, reactivity and the quality of the particulate OM as well as bioturbation and bio-irrigation by fauna (Cowie, 2005; Cowie et al., 2009; Lessin et al., 2018).

Meiofaunal Density and Diversity
Metazoan densities along the outer shelf-slope margin generally decrease with water depth and surface primary productivity (Rex et al., 2006). **Table 5** summarizes information on mean total meiofauna abundances, number of taxa, and relative abundance of nematodes for the Costa Rica margin and compares it with studies conducted in other regions along the eastern Pacific. The mean densities registered at the OMZ core site (400 m) off Costa
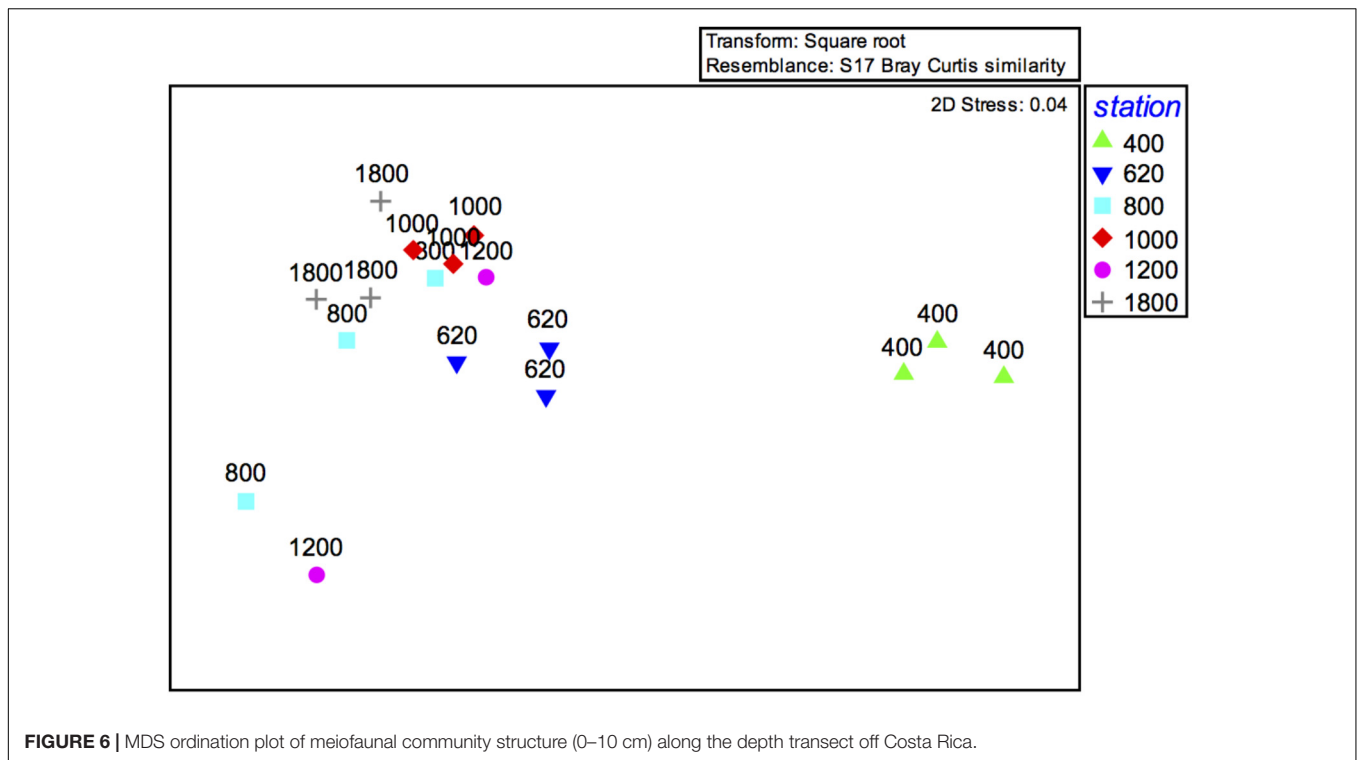
FIGURE 6 | MDS ordination plot of meiofaunal community structure (0–10 cm) along the depth transect off Costa Rica.

TABLE 4 | Mean density, taxon richness, Pielou's evenness (J'), Shannon–Wiener (H') and rank 1 dominance (R1D) for meiofauna (0–10 cm).

Sites	N	Taxon richness	Pielou J'	H'(log$_{10}$)	R1D (%)
400 m	3688 (995)	2	0.177	0.053	99.92
620 m	530 (103)	9	0.706	0.673	88.99
800 m	250 (100)	8	0.809	0.733	68.71
1000 m	484 (57)	8	0.785	0.719	70.99
1200 m	328 (217)	7	0.784	0.658	78.62
1800 m	315 (57)	10	0.809	0.777	66.46
OMZ	1483 (645)	6	0.06	0.073	97.22
Non-OMZ	381 (68)	9	0.36	0.424	71.03

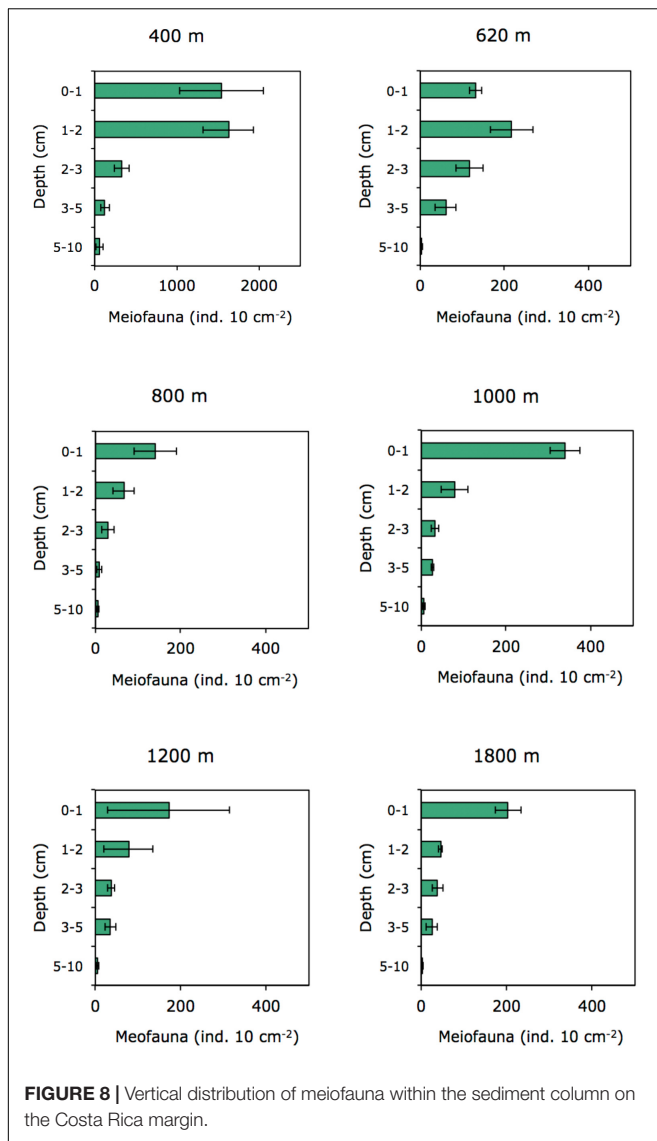*OMZ comprises sites 400, 620, and 800 m; Non-OMZ sites 1000, 1200, and 1800 m (N = ind. 10 cm^{-2} ± 1 SE).*

Rica (∼3688 ind. 10 cm^{-2}) are one the highest compared to other OMZ core sites (independent of water depth) along the eastern Pacific, such as off Concepción (< 2000 ind. 10 cm^{-2}) (Neira et al., 2001c, 2013; Sellanes et al., 2003; Sellanes and Neira, 2006), off Callao, Peru (∼1500 ind. 10 cm^{-2}), and almost double that reported for an OMZ off Antofagasta (Veit-Köhler et al., 2009). The drastic decline in total abundance of meiofauna from the OMZ core toward the adjacent site (620 m) with increasing oxygen, but still within the OMZ, was a pattern similar to that observed at the Peru margin (Neira et al., 2001b).

Marine benthic diversity usually increases with increasing water depth along the upper continental slope (Menot et al., 2010; Rex and Etter, 2010). In this study, a total of 19 meiofaunal taxa were found, but at the OMZ core site, only two taxa
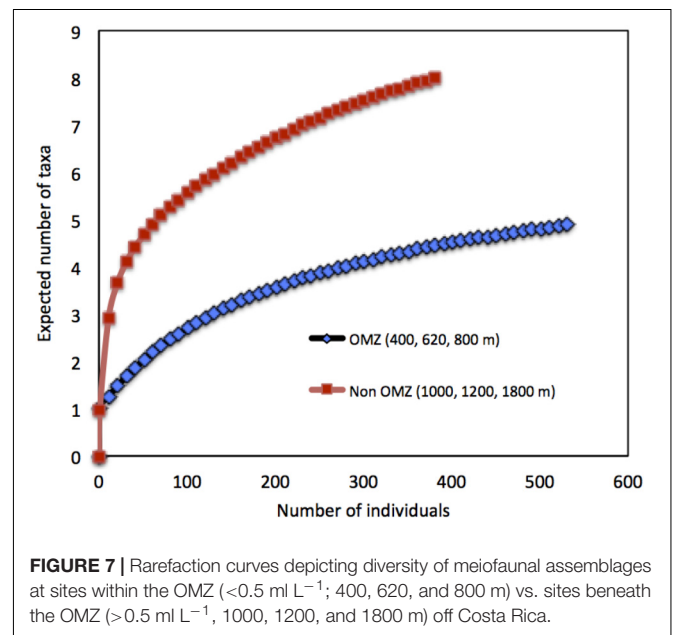

FIGURE 7 | Rarefaction curves depicting diversity of meiofaunal assemblages at sites within the OMZ (<0.5 ml L^{-1}; 400, 620, and 800 m) vs. sites beneath the OMZ (>0.5 ml L^{-1}, 1000, 1200, and 1800 m) off Costa Rica.
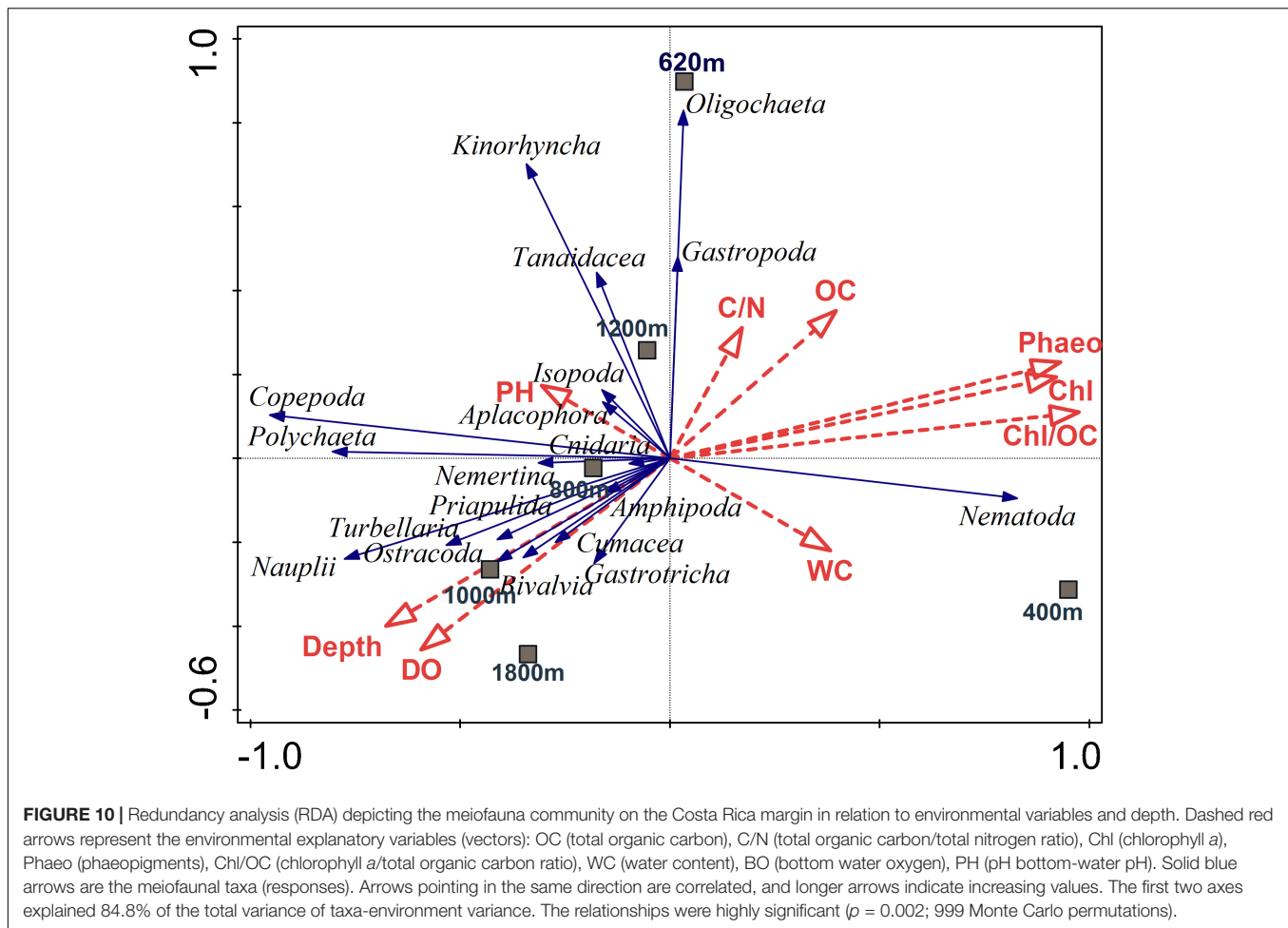
were collected (Nematoda and Polychaeta), with nematodes completely dominating meiofaunal composition (99.9% at the 400 m site, **Table 2**). This low number was even lower than reported for other Pacific OMZ sites such as off Antofagasta (4 taxa, Veit-Köhler et al., 2009), central Chile (4–8 taxa, Neira et al., 2001c; Sellanes and Neira, 2006) and, off Peru (7 taxa, Neira et al., 2001b) (**Table 5**). Differing diversity between OMZ vs. non-OMZ sites was also clearly reflected in diversity indices

FIGURE 8 | Vertical distribution of meiofauna within the sediment column on the Costa Rica margin.

FIGURE 9 | (A) Relative abundance (%) of meiofauna per sediment layer at each study site. (B) Relative abundances (%) distribution of nematode and copepods + nauplii for the upper 1 cm sediment along the bottom-water oxygen gradient.

(Table 4 and Supplementary Table S5). Studies off Peru suggest that beyond the OMZ habitat, sediment heterogeneity has more relevance in shaping metazoan meiofaunal diversity compared to within the OMZ core, where oxygen is the main limiting factor (Neira et al., 2001b; Gooday et al., 2010; Sellanes et al., 2010). Oxygen availability in sediments plays a key role in controlling meiofaunal diversity (Gooday et al., 2010; Zeppilli et al., 2015). Reduced conditions may negatively impact meiofaunal diversity (e.g., Neira and Rackemann, 1996), and nematode community structure and trophic diversity (Ingels et al., 2011; Neira et al., 2013). Interestingly, this is illustrated by the changing diversity of Foraminifera from a site off Pakistan, showing consistently higher diversity during the inter-monsoon season (when the study site was outside the OMZ) compared to during the monsoon season (when the site was within the OMZ) (Larkin and Gooday, 2009; Gooday et al., 2010). Similarly, off Pakistan macrofaunal ($>300\,\mu$m) and megafaunal diversity was strongly reduced where DO was lowest, but diversity recovered rapidly at slightly higher
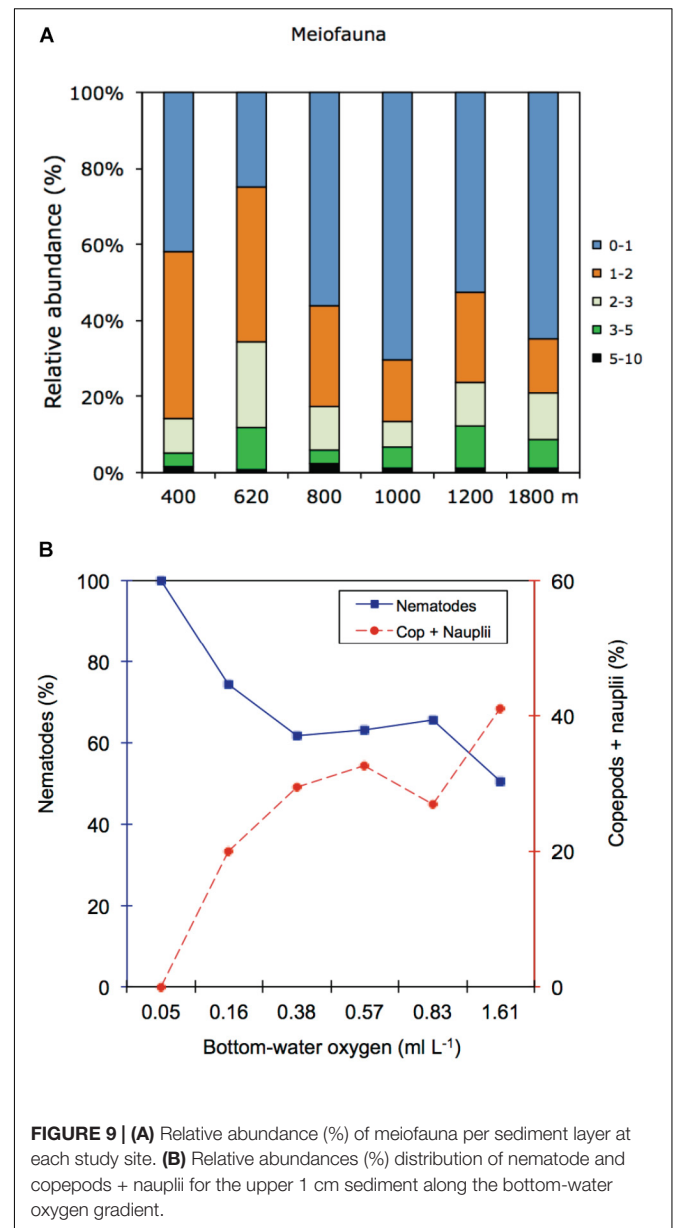
oxygen levels (Gooday et al., 2009; Levin et al., 2009). These observations are likely attributable to an 'edge effect' where a release from oxygen stress combined with an abundant food supply occurs (Murty et al., 2009; Gooday et al., 2010). Veit-Köhler et al. (2009) reported 10 taxa at an OMZ site off Chile that had slightly elevated oxygen levels (0.79 ml L^{-1}) compared to 4 taxa from the lower-oxygen sites, suggesting comparable processes may be taking place in that area. For the Costa Rica margin, this is reflected by the increase in the number of meiofauna taxa from 2 (400 m) to 9 (620 m) within a gradient of DO from 0.05 to 0.16 ml L^{-1} (Table 5), and likely related to the relatively low C/N values and higher food quality (resulting from fresher OM, i.e., higher chl a/phaeo) toward the more oxygenated sites (Figure 2 and Table 1).

FIGURE 10 | Redundancy analysis (RDA) depicting the meiofauna community on the Costa Rica margin in relation to environmental variables and depth. Dashed red arrows represent the environmental explanatory variables (vectors): OC (total organic carbon), C/N (total organic carbon/total nitrogen ratio), Chl (chlorophyll a), Phaeo (phaeopigments), Chl/OC (chlorophyll a/total organic carbon ratio), WC (water content), BO (bottom water oxygen), PH (pH bottom-water pH). Solid blue arrows are the meiofaunal taxa (responses). Arrows pointing in the same direction are correlated, and longer arrows indicate increasing values. The first two axes explained 84.8% of the total variance of taxa-environment variance. The relationships were highly significant (p = 0.002; 999 Monte Carlo permutations).

Factors Influencing Meiofauna Community Structure

Meiofaunal community distribution is influenced by numerous factors such as physical sediment properties (Giere, 2009), interactions with macrofauna (Pfannkuche and Thiel, 1987; Lambshead et al., 1994; Van Colen et al., 2009) or microbiota (Danovaro et al., 1995, 2000), habitat heterogeneity (Van Gaever et al., 2009), and oxygen availability (Levin et al., 2002; Sellanes and Neira, 2006). The potential role of oxygen is reflected in the RDA plot (**Figure 10**) where oxygen is positively correlated with a number of taxa. In fact, there are distinctly divergent meiofaunal responses across OMZ-influenced settings compared to deeper, more oxygenated ones (**Figures 6**, **7**). The most oxygen-depleted sites were characterized by lower meiofaunal taxon richness, lower diversity (H′) and lower taxonomic evenness (J′), but higher rank 1 dominance (R₁D) (**Table 4**). The more similar evenness (J′) and diversity (H′) exhibited at deeper, better-oxygenated sites suggests a more equitable distribution of meiofaunal assemblages relative to the OMZ core site (400 m) (**Figure 6** and **Table 4**). Nematode densities at our Costa Rica sites were enhanced at low-oxygen sites, consistent with other OMZs studies (e.g., Levin et al., 1991; Cook et al., 2000; Neira et al., 2001b,c, 2013;

Sellanes and Neira, 2006). The very high densities and total numerical dominance of nematodes at the site with lowest oxygen concentration, and the proportional decline of nematode abundance with increasing oxygen (**Figure 9B**) supports previous observations of a potential positive effect of low-oxygen levels on nematode abundance (e.g., Neira et al., 2001b), including the indirect effect of decreasing hypoxia-intolerant predators and competitors (Neira et al., 2001b; Levin et al., 2002; Levin, 2003). Time series data at a shelf site (98 m) off Callao, Peru has shown fluctuations in nematode density and a community 100% dominated by nematodes. Such extreme dominance, termed a "nematode state" was suggested to take place during extreme La Niña conditions, when bottom-water oxygen concentrations are at their lowest and macrofaunal densities are strongly reduced (Gutiérrez et al., 2008). This is likely reflected by the consistent decline in abundance of meiofaunal-size (and larger) polychaetes toward the most oxygen-depleted sites (**Figure 4**). Also crustaceans, such as copepods and nauplii, isopods, amphipods and ostracods are sensitive to low-oxygen conditions (Josefson and Widbom, 1988; Wetzel et al., 2001; De Troch et al., 2013) and compete with nematodes for space and resources, so their absolute and relative decline with decreasing oxygen levels likely allows nematodes to dominate the sediment

TABLE 5 | Comparison of meiofaunal densities, number of meiofaunal taxa present, relative abundance of nematodes in and outside the OMZ along the eastern Pacific margin (range depths: 120–1800 m) in relation to bottom-water DO and CPE as food availability.

Region	Depth (m)	DO (ml L^{-1})	Nr taxa	Total Meiofauna		Food availability	
				(Ind. 10 cm^{-2})	% Nematodes	(CPE μg g^{-1})	Reference
Chile Margin							
Off Concepcion							
OMZ	122-205	0.10-0.13	4-7	1964-1672	99.4-95.6	321.4-68.9	Neira et al., 2013
OMZ	120	0.19-1.39	5-8	757-1319	97.1-99.3	54.4-90.7	Neira et al., 2001c; Sellanes et al., 2003; Sellanes and Neira, 2006
Non-OMZ	364-827-972	0.52-2.89-3.50	9-13-16	2076-874-1285	96.6-77.5-83.8	146.6-75.5-90.7	Neira et al., 2013
Off Antofagasta							
OMZ	310	0.06	4	1829	96.9	38.3	Veit-Köhler et al., 2009
Off Concepcion							
OMZ	126	0.45	4	2071	98	85.3	"
Non-OMZ	367	0.79	10	7713	96.8	29.9	"
Off Chiloe							
Non-OMZ	296	1.52	16	1428	82.6	14.1	"
Peru Margin							
OMZ	305–562	0.013-0.23	7-14	1517-456	99.3-88.9	99.4-11.2	Neira et al., 2001b
Non-OMZ	830–1210	0.75-1.62	15-14	440-1210	85.3-79.9	23.3-10.5	"
Costa Rica Margin							
OMZ	400	0.05	2	3688	99.9	146.8	This study
OMZ	620	0.16	9	530	88.9	87.9	"
OMZ	800	0.38	8	250	68.7	30.6	"
Non-OMZ	1000	0.57	8	484	70.9	20.8	"
Non-OMZ	1200	0.83	7	328	78.6	22.3	"
Non-OMZ	1800	1.61	10	315	66.5	8.2	"

system. Copepods are active swimmers and their metabolism requires more oxygen than other meiofaunal groups (Moodley et al., 1997; Modig and Olafsson, 1998; Giere, 2009). Summer hypoxic conditions (1985/86) on the Louisiana shelf resulted in the loss of copepods for a month, with moderate loss of nematode and kinorhynch densities. After the habitat returned to normal oxygen conditions, the copepods recovered slowly (Murrell and Fleeger, 1989). Oxygen depletion may lead to a feeding stop and unsuccessful reproduction in adult copepods (Veit-Köhler et al., 2009, 2018; De Troch et al., 2013) and hence absence of nauplii and adult copepods at the OMZ core. Recovery, speed and extent of colonization of meiofauna after hypoxic events are variable. For instance, the high mobility of copepods and ostracods promotes a rapid recolonization of azoic sediments, compared to nematodes which require more time to cover similar distances (Chandler and Fleeger, 1983). Experiments in the Wadden Sea reduced sediments ("black spots") showed that meiofauna recolonized sediments only after redevelopment of an oxidized sediment layer (Neira and Rackemann, 1996). Van Colen et al. (2009) found strong changes in nematode community composition after exposing them to experimentally-induced hypoxia, but this did not result in complete nematode mortality. For instance, under El Niño conditions, which cause enhanced bottom-water oxygen concentrations, there was an increased representation of copepods and nauplii by one order of magnitude at sites influenced by the OMZ (Neira et al., 2001c). We suspect that the most important driver of meiofaunal communities is bottom-water oxygen, but that the co-occurrence of low oxygen and chl *a*/phaeo, and high chl *a*, phaeo, and chl *a*/TOC (and hence food quality and availability) lie behind some of the causality of the correlations.

The quality of food resources, in addition to oxygen, can play an important role in structuring faunal communities. For meiofauna, the role of food availability has been highlighted in many studies as one of the most important factors structuring communities and spatial biodiversity patterns (Danovaro et al., 1995; Neira et al., 2001b; Giere, 2009; Pusceddu et al., 2009). The importance of food quantity and availability on nematode abundance and diversity in OMZs has also been suggested by Cook et al. (2000) for the Arabian Sea. Food availability is a regulating factor along the vertical sediment profile (Ingels et al., 2009, 2011; Ingels and Vanreusel, 2013). At the Costa Rica margin, meiofauna densities declined with increasing depth in the sediment, a recurrent gradient observed in marine sediments (Levin et al., 2002; Soltwedel et al., 2005). However, at the lowest oxygen sites of Costa Rica (400 and 620 m), meiofauna, dominated by nematodes, were concentrated in subsurface sediments (~41–45% in the 1–2 cm layer); whereas

toward deeper sites, the surface 1-cm layer harbors most of the meiobenthos (**Figure 9A**). The vertical distribution of meiofauna was similar to that observed at the OMZ off Callao (transect 305–1210 m, Neira et al., 2001b), where densities declined consistently with depth in the sediment only at the oxygenated sites (**Figure 8**). The high meiofaunal densities as well as the high dominance of nematodes at the OMZ sites, and their high subsurface densities, are most likely attributable to the extensive availability of food, and relatively fresh phytodetritus (**Figure 2**) even in the deeper sediment layers (e.g., CPE ranging from 147 $\mu g\ g^{-1}$ at 0–1 cm to 88 $\mu g\ g^{-1}$ at 5–10 cm depth at site 400 m), as well as the relative tolerance of nematodes to low-oxygen levels (Neira et al., 2001a, 2005; Neira and Decraemer, 2009; Sajan et al., 2010), and reduced competition for food by exclusion of the more oxygen-sensitive macro- and meiofauna (Neira et al., 2001b; Levin et al., 2002; Sajan et al., 2010; Jeffreys et al., 2012). Macrofaunal activity may also influence vertical meiofauna patterns in the sediment through bioturbation. For instance, tuna crab (*Pleuroncodes* sp.), common on the Central American margin (Pineda et al., 2016), can sift out the food material present in the substrate and extract small animals such as nematodes, and other invertebrates (Boyd, 1962, 1967; Lovrich and Thiel, 2011). During Alvin dives in 2017, large masses of galatheid crabs were observed apparently feeding on the sediment bottom of Quepos slide, an active seep area (bacterial mats) influenced by the OMZ and nearby our 400 m site (L. A. Levin personal observation). Galatheid crabs such as *Pleuroncodes* spp. have often been seen associated with oxygen-depleted waters (Sellanes et al., 2007; Lovrich and Thiel, 2011; Gallardo et al., 2017) and can form dense aggregations swarming the seafloor (Thiel and Lovrich, 2011; Pineda et al., 2016). Bioturbating macrofauna, mainly annelids tolerant to hypoxic conditions found at OMZs, including at very low oxygen sites (e.g., Levin et al., 2000, 2002; Smith et al., 2000; Sellanes et al., 2007), may induce mixing downward, advecting "fresh" and nutritional material deep into the sediment (Levin et al., 1997; Gutiérrez et al., 2000), which, in turn, may support higher nematode survival rates in subsurface and deeper sediments (Braeckman et al., 2010).

CONCLUSION

To our knowledge, this is the first quantitative study of OMZ influence on meiofauna conducted along the Costa Rica margin. Results indicate that lowest oxygen levels along with highest CPE yielded the highest meiofaunal abundances and lowest diversity, whereas the inverse occurred under highest oxygen and lowest CPE and TOC conditions (even though food quality was higher as deduced from lower C/N and higher chl *a*/phaeo ratios).

High abundance of nematodes in bathyal sediments is enhanced in low oxygen settings where food is plentiful, although not necessarily fresh. In addition, low-oxygen conditions may have an additional indirect positive effect on nematode abundances by reducing potential predators and competitors. Low-oxygen conditions at the OMZ core site seem unfavorable for copepods, nauplii, and other meiobenthos. Increasing

meiofaunal diversity and presence of animals such as copepods and nauplii downslope – mostly concentrated in the surface sediment – are most likely promoted by enhanced bottom-water oxygen and freshness of available food outside the OMZ. The abrupt transition in meiofaunal abundance and diversity from the OMZ core (400 m) to the adjacent within OMZ site (620 m) and deeper sites suggests a strong response to oxygen thresholds (Levin et al., 2009) interacting with OM availability and quality. The overall presence and dominance of nematodes across the vertical profile of the sediment in association with gradients in food quantity, quality, and oxygen, even in the deeper sediment layers, reflect the well-developed nutritional selectivity, wide range of diets, and different oxygen and food requirements attributed to meiofauna (Giere, 2009; Neira and Decraemer, 2009; Ingels et al., 2011; Neira et al., 2013; Schratzberger and Ingels, 2017).

More local and regional information on meiofaunal community structure and biodiversity, as well as understanding their responses to current environmental conditions will contribute to elucidating the role of food sources and oxygen and hypoxia thresholds (Vaquer-Sunyer and Duarte, 2008, 2011; Levin et al., 2009) in structuring meiobenthic fauna and will help to make predictions about future responses to ocean deoxygenation and OMZ expansion.

AUTHOR CONTRIBUTIONS

LL designed and funded hydrographic measurements and field sampling. The original manuscript was written by CN. GM, CN, and JI conducted statistical analyses, and prepared the figures and tables. All authors contributed equally to the reworking and editing of the original manuscript toward the submitted version.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2018. 00448/full#supplementary-material

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