



Connectivity Between Coastal and Oceanic Zooplankton From Rio Grande do Norte in the Tropical Western Atlantic

Sigrid Neumann Leitão^{1*}, Mauro de Melo Junior², Fernando de Figueiredo Porto Neto³, Andréa Pinto Silva¹, Xiomara Franchesca Garcia Diaz⁴, Tamara de Almeida e Silva⁵, Dilma Aguiar do Nascimento Vieira¹, Lucas Guedes Pereira Figueiredo¹, Alejandro Esteweson Santos Faustino da Costa¹, Jana Ribeiro de Santana^{1,6}, Renata Polyana de Santana Campelo¹, Pedro Augusto Mendes de Castro Melo¹, Valdylene Tavares Pessoa¹, Simone Maria de Albuquerque Lira² and Ralf Schwaborn¹

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*Correspondence:

Sigrid Neumann Leitão
sigridnl@uol.com.br

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¹ Departamento de Oceanografia, Universidade Federal de Pernambuco, Recife, Brazil, ² Departamento de Biologia, Universidade Federal Rural de Pernambuco, Recife, Brazil, ³ Departamento de Zootecnia, Universidade Federal Rural de Pernambuco, Recife, Brazil, ⁴ Instituto Socioambiental e dos Recursos Hídricos (ISARH), Universidade Federal Rural de Amazônia, Belém, Brazil, ⁵ Departamento de Educação, Campus VIII, Universidade do Estado da Bahia, Paulo Afonso, Brazil, ⁶ Departamento de Ciências Humanas e Tecnologia, Campus XXIV, Universidade do Estado da Bahia, Xique-Xique, Brazil

The zooplankton off the coast of Rio Grande do Norte, Brazil was studied during four oceanographic campaigns from July 2002 to May 2004. A Bongo net (mesh sizes of 64, 120, and 300 μm) was used for sample collections. A total of 462 zooplankton samples was studied. These samples were classified in four areas (Coastal, Inner Shelf, Shelf Break, Slope) according to local depth and distance from coast. Most of the studied environment is oligotrophic, under the Tropical Water mass influence. We recorded 199 zooplankton taxa, and Copepoda was the most numerous with the highest number of species. There were 93 species of copepods, of which calanoids comprised 62%. The most frequent zooplankton taxa were *Undinula vulgaris*, *Nannocalanus minor*, *Oithona nana*, *Onychocorycaeus giesbrechti*, Crustacea nauplius, Bivalvia, and Gastropoda veligers. The species diversity varied from 0.87 ± 0.28 bits-ind⁻¹ (Coastal) to 3.96 ± 0.12 bits-ind⁻¹ (Slope). The minimum density was 11.5 ind·m⁻³ (macrozooplankton, Inner Shelf), and the maximum density was 161.6×10^6 ind·m⁻³ (microzooplankton, Coastal). The biomass decreased sharply between the microzooplankton to macrozooplankton fractions. The community presented a general trend in species composition that included coastal eutrophic indicators and oceanic oligotrophic indicators, with low numerical abundance of zooplanktonic organisms. A higher density occurs in the coastal area that is near the littoral area due to the continental flux and benthic regeneration. The seasonal effect was also highlighted as an important factor responsible for the dissimilarity of zooplankton communities. Cluster analysis of the samples based on Copepoda presented differences among the four campaigns corresponding to the rainy and dry seasons. The copepod's functional traits divided the community into three groups, and

the reproduction and the trophic strategies were the main factors in structuring the community. We found a pelagic gradient for the zooplankton community varying from a low diverse eutrophic coastal area to a high diverse oligotrophic oceanic area, located over a varied, high biomass benthic habitat, which is mostly covered by calcareous algae functioning on the shallow shelf as a large reef system.

Keywords: zooplankton, Copepoda, connectivity, functional traits, Southwestern Atlantic

INTRODUCTION

Studies on community ecology have emphasized the local processes influencing species composition and abundance. However, the effects of regional processes upon local dynamics have been shown by some researchers (Ricklefs and Schluter, 1993; Hubbell, 1997; Forbes and Chase, 2002), including those processes that connect communities. Physic-chemical processes can play an important role in the connectivity among habitats and in defining the community attributes at different size scales (Ricklefs, 1987; Cowen et al., 2006). For example, dispersal by currents in marine areas connects coastal communities to oceanic ones and *vice-versa*, thus forming species patches along interconnected environs (metacommunities) (Watson et al., 2011; Niebuhr et al., 2015).

Coastal ecosystems are of great human interest (both ecological and socioeconomic); in these ecosystems, biotic and abiotic factors vary continuously along scales that oscillate from short to long term (Walsh, 1988). In Northeastern Brazil, an arid climate, extensive beaches and high dunes characterize the littoral area in the northern region of the Rio Grande do Norte State. The continental shelf is approximately 30 km wide, and calcareous algae primarily cover the bottom; this represents the largest area covered by limestone sediments on the planet (Santos, 2010). This shelf functions as a huge “coral reef” that supports a high benthic diversity and biological production. The oligotrophic South Equatorial Current (SEC) dominates the pelagic inner shelf waters (Stramma et al., 1990); thus, like that of a coral reef area, the plankton productivity is very low, but it eventually increases due to localized enrichment events (Medeiros et al., 1999). In this “coral reef”-like area, regenerated production dominates (fueled by nutrients accumulated in the benthic realm biologically recycled). The continental slope starts at a depth of 80 m and extends until 1300–3600 m (Mabesoone and Coutinho, 1970; Gomes and Vital, 2010); further, the sea floor is far beneath the photic zone, so the influence of regenerating production can be ignored when budgeting for flow in the offshore oceanic pelagic ecosystem.

This variable scenario highly influences the lively populations flourishing in the littoral area, which can cause a misunderstanding of the annual biodiversity and abundance patterns. A cooperative research program was established between the Federal University of Pernambuco (Brazil) and the Brazilian Oil Company (PETROBRAS) to develop comprehensive biotic and abiotic characterizations of the north coast of Rio Grande do Norte State and to study the plankton community; this work took place from July 2002 to May 2004. In coastal ecosystems where local processes are linked to

anthropogenic impacts the biological community are threatened and can present large-scale changes (Guichard et al., 2004).

Plankton studies in this area are scarce. In relation to the zooplankton, previous investigations of tropical Southwestern Atlantic (SWA) were restricted to certain groups (Copepoda: Björnberg, 1963; Chaetognatha: Gusmão, 1986; Cnidaria: Gusmão et al., 2015) or to a few samples evaluated on a macro-scale level that were obtained by international expeditions. A zooplankton atlas (Boltovskoy, 1981, 1999) is an important reference of the SWA; however, data from the Rio Grande do Norte littoral area and the connectivity among habitats remains fragmented (e.g., Neumann-Leitão et al., 1999, 2008), and the main functional groups are still incipient (Campos et al., 2017; Neumann-Leitão et al., 2018).

Elucidation of the biotic community is important, particularly the zooplankton, and involves sampling methods capable of obtaining a representative population; as marine zooplankton comprise different size classes of organisms, they serve as a pivotal group in the transference of mass and energy from primary producers to higher trophic levels in the food web (Clark et al., 2001). The size of the zooplankton animals and their main functional traits are powerful forcing factors outlining marine systems. Also, few researches have been devoted to the comparison of the spatial-temporal variability of micro-, meso- and macrozooplankton densities in marine systems (Smeti et al., 2015).

Thus, the goal of the present study was to produce accurate and complete information on micro-, meso-, and macrozooplankton diversity, biomass, and density distribution in different seasons along a coastal-oceanic gradient.

MATERIALS AND METHODS

Study Area

The continental shelf at the North of Rio Grande do Norte State (**Figure 1**) is divided in three sedimentary environments: the first (coastal and inner shelf) is characterized by siliciclastic sediments and huge longitudinal sandbanks with a depth around 15 m. The second (mid shelf) has a mixture of siliciclastic and carbonate sediments, and transversal sandbanks approximately on 20 m. The third (outer shelf) dominated by carbonates sediments, with a narrow shelf and depths varying from 25 to 50 m. A beachrock line at the isobath of 25 m delimits the boundary from mid- and outer shelf. The shelf extends seawards into a steep slope that spreads until 2000 m at the basin plain (Gomes and Vital, 2010). This basin has a high economic status because of the daily

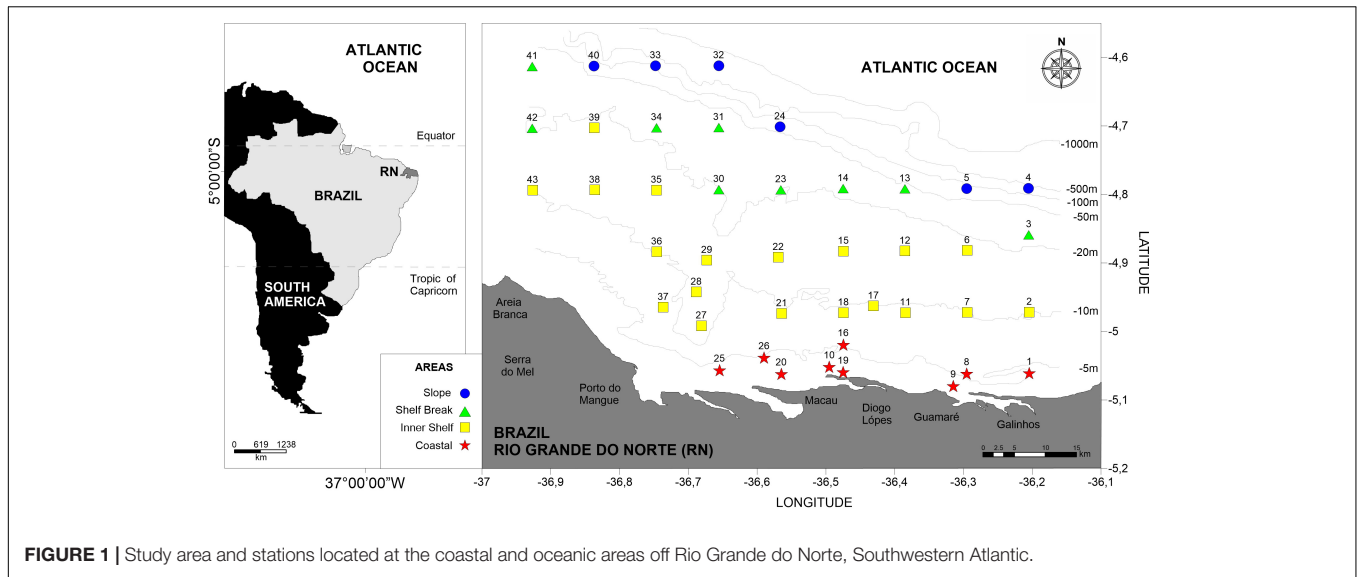


FIGURE 1 | Study area and stations located at the coastal and oceanic areas off Rio Grande do Norte, Southwestern Atlantic.

production of 80 thousand barrels of oil and 3 million·m³ of gas (2003 data, production on ocean and earth), and it is the second most productive oil basin offshore in Brazil (Soares et al., 2003).

The average monthly total rainfall of North of Rio Grande do Norte (data from 1962 to 2005¹) presents an annual average of 735.6 mm, with a higher rainfall from February to May, and a lower precipitation from September to November. The monthly average from 2001 to 2004 shows a warmer rainy season (January to May), and a dry season a bit cooler (July to November) (Figure 2)¹.

In the studied area the Tropical Water (TW: $\geq 20^{\circ}\text{C}$, ≥ 36.0) was present with relatively warm and salty waters, occurring from surface down to 70 m depth, and the South Atlantic Central Water (SACW: $\leq 18^{\circ}\text{C}$, ≤ 36.0) occurred below the TW and extended down to nearly 450 m. At depths between 70 and 150 m, there was also the Maximum Salinity Water (MSW), with temperatures varying from 18.0 to 26.0°C and salinity ≥ 37.0 (Schott et al., 1998).

The sea surface temperature average was $27.17 \pm 0.7^{\circ}\text{C}$ and ranged from 27.11°C (dry season, Slope) to 28.41°C (rainy season, Coastal). Salinity average was 36.2 ± 0.27 , with a minimum of 35.90 (rainy season, Slope) and a maximum of 36.77 (dry season, Inner Shelf). Chlorophyll-*a* average was $0.52 \pm 0.33 \text{ mg}\cdot\text{m}^{-3}$, fluctuating from 0.23 mg·m⁻³ (dry season, Slope) to 1.13 mg·m⁻³ (dry season, Coastal) (Figure 3, PETROBRAS, 2005).

Sampling Strategy

The survey was performed during four campaigns from July 21 to 30, 2002 (Campaign 1, dry season), May 12 to 30, 2003 (Campaign 2, rainy season), November 14 to 23, 2003 (Campaign 3, dry season), and May 17 to 31, 2004 (Campaign 4, rainy season). The zooplankton was sampled during daytime at 43 stations, along nine transects from the coast to the offshore

north of Rio Grande do Norte (latitude 4° to 5° S, longitude 36° to 37° W) (Figure 1). A total of 462 samples was collected; these samples were classified into four areas (Coastal: < 10 m, Inner Shelf: 10–20 m, Shelf Break: 20–50 m, and Slope: > 50 m) according to local depth and distance from coast.

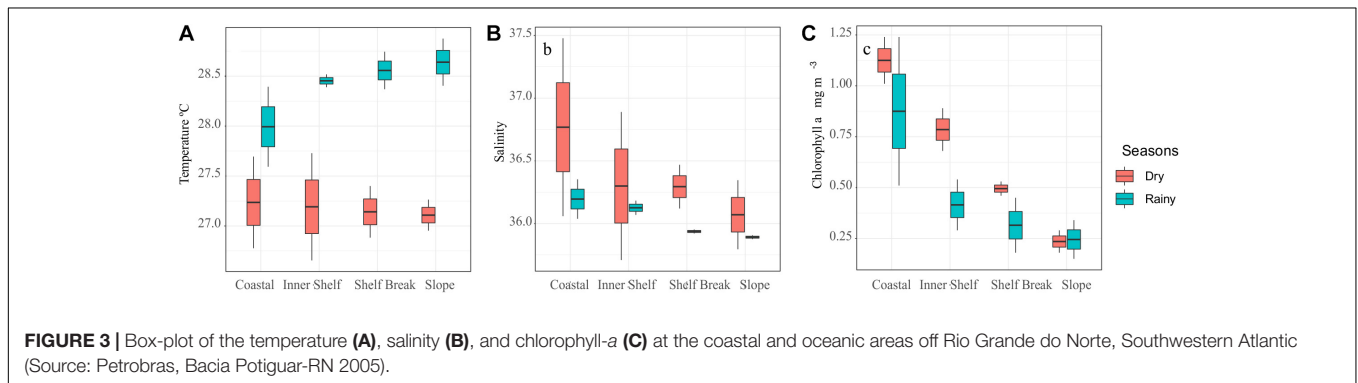
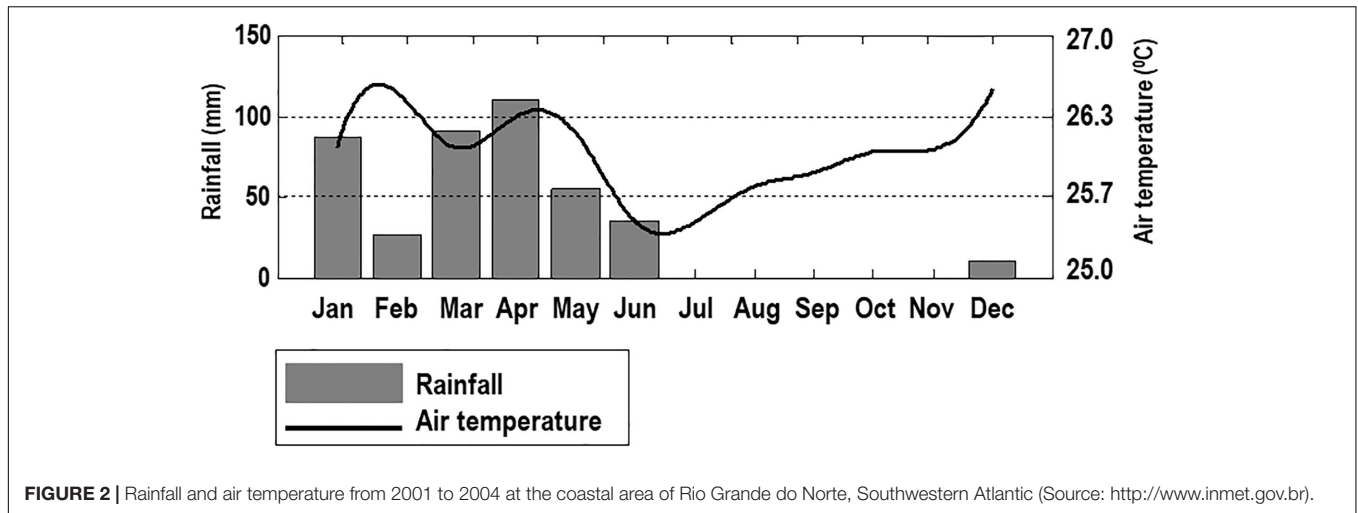
Field Sampling and Laboratory Analyses

The zooplankton sampling was carried out by bongo net hauls. The analyzed nets had the following mesh sizes and diameters: 64 μm/30 cm; 120 μm/30 cm; and 300 μm/60 cm. The terminology micro-, meso-, and macrozooplankton will be used throughout the text to refer to the net's mesh sizes, which were 64, 120, and 300 μm, respectively (although in the literature these sizes corresponded to micro- and mesozooplankton, see Omori and Ikeda, 1984). Oblique hauls were made at a speed of 2 to 2.5 knots from a depth of 14 m (nearshore) and 150 m (Shelf Break and Slope) to the surface. A flowmeter (Hydrobios, Kiel, Germany) was used to measure the water filtered volume. A 4% buffered formalin-seawater solution was used to preserve the samples. Seston biomass (mg·m⁻³) was assessed by using the Omori and Ikeda (1984) wet-weight method. To identify the species, we used the Trégouboff and Rose (1957) and Boltovskoy (1981, 1999) manuals, among others. Taxa enumeration and identification considered the lowest taxonomic unit of each phylum. Taxon density was calculated from subsamples of 1 mL (for microzooplankton using a Sedgwick-Rafter chamber) and 8 mL (meso- and macrozooplankton using a Bogorov plate) taken of the whole sample (standardized to 500 mL). For each sample, three subsamples (with at least of 300 individuals) were counted and the mean calculated for abundance valuation (ind·m⁻³).

Data Analysis

The Shannon diversity index H' was applied to Copepoda for the diversity evaluation (Shannon, 1948), as this was the most diverse

¹<http://www.inmet.gov.br>



taxon and the most identified species. Evenness was calculated according to Pielou (1977).

To investigate for trends in spatial distribution, total density (\log_{10} transformed), biomass and ecological indexes (diversity and evenness) of the micro-, meso- and macrozooplankton were compared among the coastal, inner shelf, shelf break and slope areas during both dry and rainy season. As even after data transformation, the assumptions of the ANOVA model could not be satisfied for total density and evenness, we applied Kruskal–Wallis tests to compare zooplankton total density and evenness among the areas in both seasons. When significant p values were found, the Dunn's Multiple Comparison test was applied. Diversity was compared by means of two-way ANOVA models, after checking the validity of the assumptions of normality in distribution of the errors and homoscedasticity by means of the Shapiro-Wilk and Bartlett tests, respectively.

A Permutational multivariate analysis of variance (PERMANOVA) was used to test the micro-, meso- and macrozooplankton community structure changes in response to the factors area, season, and to investigate possible interactions among these two factors. The calculation of pseudo- F and p values was based on 999 random permutations. *Pairwise* test between different levels of significant factor(s) was performed in case of significant differences identified by the PERMANOVA.

The non-metric multi-dimensional scaling (MDS) was used to represent the data in a bi-dimensional space. The PERMANOVA and the nMDS were performed with basis on a Bray–Curtis dissimilarity matrix constructed on the $\log(X + 1)$ transformed abundance of species with relative abundance $> 2\%$. The SIMPER (SIMilarity of PERcentages) routine was used to identify the taxa that contributed most to the Bray–Curtis dissimilarity of areas within the identified seasons. The SIMPER test was set at $\geq 50\%$ cumulative contribution.

A Redundancy Analysis (RDA) was applied to identify whether there were different size communities that could be explained by the temporal and spatial data variability. We used the total micro-, meso-, and macrozooplankton abundance and biomass data. Zooplankton groups were $\log(X + 1)$ transformed and compared with an abiotic factor matrix (Temperature, Salinity, Chlorophyll a). The spatio-temporal factors (Coastal, Inner Shelf, Shelf Break, Slope, Dry season and Rainy season) were transformed into dummy variables, represented by 1 and 0. Non-significant variables ($p > 0.05$) were excluded from the matrix of environmental data in a step by step procedure, using Monte Carlo permutation tests with 9999 permutations to remove collinearities between variables (Ter Braak and Smilauer, 2002). The analyses were performed using the CANOCO software (version 4.5; Ter Braak and Smilauer, 2002). All analyses were conducted considering $p < 0.05$ (Zar, 1996).

Hierarchical cluster analyses in Q mode using Ward's method (Legendre and Legendre, 1998) were performed with basis on a Bray–Curtis dissimilarity matrix calculated using Copepoda density data. The goodness of fit of the data was assessed by means of the cophenetic correlation coefficient (Rohlf and Fisher, 1968).

The functional trait matrix of copepods was built using the available literature (mainly Boltovskoy, 1999 and Benedetti et al., 2016). We included seven traits with 23 trait categories: (1) Average adult female body length (0.5–1.5, 1.5–2.5, 2.5–3.5, 3.5–4.5, >4.5 mm); (2) Trophic group (herbivore, carnivore, omnivore, detritivore); (3) Feeding type (active ambush, passive ambush, filter, cruise, mixed); (4) Mode of reproduction (broadcast-spawner, sac-spawner); (5) Vertical distribution preference (epipelagic, mesopelagic, bathypelagic); (6) Diel vertical migration behavior (Yes, No); and (7) Habitat type (estuarine, neritic, oceanic). These traits are functionally important, as they relate to the life history and ecology of species and are expected to be constant through time and space (Pomerleau et al., 2015). The Sorensen index was applied to a presence/absence species-by-trait matrix, and the cluster dendrogram was formed through the average linkage method. The Calinski and Harabasz (1974) criteria were used to establish the number of functional groups. This analysis was applied only to Copepoda at the species level (see **Supplementary Table S1**).

RESULTS

Species Composition

We identified 199 taxa in the three zooplankton size fractions composed of Foraminifera, Ciliophora, Radiozoa, Cnidaria, Aschelminthes, Mollusca, Annelida, Arthropoda, Echinodermata, Chaetognatha, Bryozoa, Cephalochordata, and Chordata (**Tables 1, 2**). A total of 88 taxa occurred in the microzooplankton fraction, 115 taxa in the mesozooplankton fraction, and 102 taxa in the macrozooplankton fraction. In the three fractions, 69 taxa cooccurred and consisted mostly of juveniles in the microzooplankton fraction and adults in the meso- and macrozooplankton fractions. Holoplankton comprised 87, 67, and 61% in the micro-, meso-, and macrozooplankton fractions, respectively. Most zooplankton species (91) were oceanic indicators and were obtained mainly from the North Brazil Current. Several neritic taxa were larval stages of benthic organisms that normally occur in the continental shelf.

The most important group was Copepoda, both in richness and abundance. There were 93 copepod species, of which 62% were calanoids. In total, 54 species occurred in the microzooplankton fraction, 69 species in the mesozooplankton fraction, and 68 species in the macrozooplankton fraction. An important group found in the Coastal area was the estuarine plume indicators, which consisted of *Acartia (Odontacartia) lilljeborgi*, *Parvocalanus crassirostris*, *Oithona hebes*, *Oithona oswaldocruzi* and *Euterpina acutifrons*.

In the microzooplankton fraction, there was a high frequency of occurrence of Crustacea nauplius (94%), Bivalvia veliger

(92%), Gastropoda veliger (82%), and *Oithona nana* (76%); furthermore, nearly 51% of the species occurred at frequencies of less than 10%. Tintinnina was observed only in the microzooplankton fraction with 18 species. The higher frequency of occurrence recorded in the mesozooplankton fraction were of Bivalvia larvae (90%), *O. nana*, and *Undinula vulgaris* (81%), as well as *Nannocalanus minor* (74%); nearly 50% of the taxa occurred at frequencies of less than 10%. In the macrozooplankton fraction, the most frequent group was composed of *Onychocorycaeus giesbrechti* (80%) and *U. vulgaris* (79%), and nearly 68% of the community occurred at a frequency of occurrence of less than 10%.

Total Density (ind·m⁻³)

At the dry season, the total microzooplankton density varied from 904 ind·m⁻³ (Slope, Campaign 3) to 161.6 × 10⁶ ind·m⁻³ (Coastal, Campaign 1). At the rainy season, total microzooplankton densities ranged from 2,985 ind·m⁻³ (Inner Shelf, Campaign 2) to 34 × 10⁵ ind·m⁻³ (Inner Shelf, Campaign 4). During both the dry and rainy seasons significant differences among the areas were found (Kruskal–Wallis, $p > 0.05$). During the dry season, the coastal area was different from all the other, and the inner shelf was different from the slope area (Dunn, $p < 0.05$). A decreasing pattern in total density was observed during this season. During the rainy season the coastal area was different from all other areas, presenting higher total density values, and no further differences were detected (Dunn, $p < 0.05$) (**Figure 4**).

The total mesozooplankton density varied from 275 ind·m⁻³ (Shelf Break, Campaign 1) to 39.2 × 10⁴ ind·m⁻³ (Coastal, Campaign 1) during the dry season, and from 183 ind·m⁻³ (Inner shelf, Campaign 2) to 50.9 × 10³ ind·m⁻³ (Coastal, Campaign 4) during the rainy season. During the rainy season no difference among the areas was found (Kruskal–Wallis, $p > 0.05$), but during the dry season a gradient in the distribution of the total density was detected in which the Coastal area presented densities significantly higher than all the other areas, and the Inner Shelf presented higher densities than the Shelf break and Slope (Dunn, $p < 0.05$). No difference between the Shelf break and Slope was detected (Dunn, $p > 0.05$) (**Figure 4**).

The total macrozooplankton density varied from 11.5 ind·m⁻³ (Inner shelf, Campaign 3) to 1,251 ind·m⁻³ (Coastal, Campaign 3) during the dry season, and from 14 ind·m⁻³ (Inner shelf, Campaign 4) to 613 ind·m⁻³ (Inner shelf, Campaign 4) during the rainy season. During the dry season no evidence for differences among the areas was detected (Kruskal–Wallis, $p > 0.05$). During the rainy season differences were detected (Kruskal–Wallis, $p < 0.05$), and the Slope area was different from all the other areas (Dunn, $p < 0.05$), with higher density values (**Figure 4**).

Total Copepoda density varied from 3 ind·m⁻³ (Inner Shelf, Campaign 3) to 480 ind·m⁻³ (Inner Shelf, Campaign 1) during the dry season, and from 4 ind·m⁻³ (Shelf Break, Campaign 2) to 582 ind·m⁻³ (Inner Shelf, Campaign 4) during the rainy season. The statistical results were the same as for the total macrozooplankton density, since Copepods constituted most of the organisms within the macrozooplankton size class.

TABLE 1 | List of zooplankton taxa (without Copepoda) from coastal and oceanic areas of Rio Grande do Norte, Northeastern Brazil.

RADIOZOA	Gastropoda other (veliger/adult)
Spumellaria (others)	Bivalvia (veliger/juvenile)
<i>Dictyocoryne profunda</i> Ehrenberg, 1872	Cephalopoda (paralarvae)
<i>Rhopalastrium malleus</i> Haeckel, 1887	POLYCHAETA
FORAMINIFERA	Alciopidae (larvae)
<i>Globigerinoides rubra</i> (d'Orbigny, 1839)	<i>Tomopteris</i> sp.
<i>Trilobatus trilobus</i> (Reuss, 1850)	Polychaeta other larvae (different stages)
<i>Globigerinoides sacculifer</i> (Brady, 1879)	CRUSTACEA
<i>Globigerinoides conglobatus</i> (Brady, 1879)	Cladocera
<i>Globigerinoides</i> sp.	<i>Penilia avirostris</i> Dana, 1849
<i>Globorotalia menardii</i> (Jones and Brady, 1865)	<i>Pseudevadne tergestina</i> Claus, 1877
<i>Globorotalia</i> sp.	Ostracoda
<i>Orbulina universa</i> d'Orbigny, 1839	<i>Euconchoecia chierchiae</i> Muller, 1890
<i>Tretomphalus bulloides</i> d'Orbigny, 1826	Cirripedia
<i>Amphistegina</i> sp.*	<i>Lepas</i> sp. (nauplius)
<i>Triloculina</i> sp.*	<i>Balanus balanoides</i> (Linnaeus, 1767) (nauplius and cypris)
<i>Textullaria</i> sp. *	Stomatopoda (larvae erichthus and alima)
<i>Quinqueloculina</i> sp *	Euphausiacea
<i>Remaneica</i> sp. *	<i>Euphasia</i> sp. (adults and furcilia, calyptopis)
<i>Spirillina</i> sp. *	Cumacea
<i>Planispirillina</i> sp.*	Decapoda
CILIOPHORA	<i>Belzebub typus</i> H. Milne-Edwards, 1837
<i>Tintinnopsis radix</i> (Imhof, 1886)	<i>Belzebub faxoni</i> (Borradaile, 1915)
<i>Tintinnopsis aperta</i> Brandt, 1906	Luciferidae (larvae)
<i>Tintinnopsis tocantinensis</i> Kofoid and Campbell, 1929	<i>Acetes americanus</i> Ortmann, 1893
<i>Tintinnopsis nordqvisti</i> Brandt, 1906	Penaeidae (larvae)
<i>Tintinnopsis campanula</i> Ehrenberg, 1840	Paguridae larvae (<i>Parapagurus</i> sp.)
<i>Tintinnopsis</i> sp.	Carideae (larvae)
<i>Codonellopsis morchella</i> (Cleve, 1900)	Brachyura (zoeae and megalopa)
<i>Codonellopsis</i> sp.	Palinuridae (phyllosoma)
<i>Favella ehrenbergii</i> (Clapadere and Laachmann, 1858)	Porcellanideo (larvae)
<i>Epiplocyliis acuminata</i> (Daday, 1887)	Mysida
<i>Epiplocyliis</i> sp.	Isopoda (Epicaridea - larvae)
<i>Rhabdonella spiralis</i> (Fol, 1881)	Amphipoda
<i>Rhabdonella</i> sp.	Gammaridea
<i>Undella hyalina</i> Daday, 1887	Hyperidae
<i>Undella claparedei</i> (Entz Sr., 1885)	BRYOZOA (cyphonauta of <i>Membranipora</i> sp.)
<i>Eutintinnus lusus-undae</i> (Entz Sr., 1885)	CHAETOGNATHA
<i>Amphorellopsis</i> sp.	<i>Ferrosagitta hispida</i> (Conant, 1895)
<i>Xystonellopsis</i> sp.	<i>Flaccisagitta enflata</i> (Grassi, 1881)
CNIDARIA	<i>Flaccisagitta hexaptera</i> (d'Orbigny, 1834)
Hydrozoa	<i>Serratosagitta serratodentata</i> (Krohn, 1853)
<i>Zanclaea costata</i> Gegenbaur, 1856	<i>Sagitta bipunctata</i> Quoy and Gaimard, 1827
<i>Liriope tetraphylla</i> (Chamisso and Eysenhardt, 1821)	<i>Parasagitta tenuis</i> (Conant, 1896)
<i>Aglaura hemistoma</i> Péron and Lesueur, 1809	<i>Pterosagitta draco</i> (Krohn, 1853)
<i>Bougainvillia</i> sp.	<i>Krohnitta subtilis</i> (Grassi, 1881)
<i>Obelia</i> sp.	<i>Krohnitta pacifica</i> (Aida, 1897)
Siphonophora	ECHINODERMATA (pluteus, bipinaria, brachiolaria)
<i>Lensia</i> sp.	ENTEROPNEUSTA (tornaria)
<i>Bassia bassensis</i> (Quoy and Gaimard, 1834)	LARVACEA
NEMATODA (<i>Oncholaymus</i> sp.)	<i>Oikopleura (Vexillaria) dioica</i> Fol, 1872
MOLLUSCA	<i>Oikopleura (Coecaria) longicauda</i> (Vogt, 1854)
<i>Atlanta</i> sp.	<i>Oikopleura</i> spp.
<i>Limacina (Limacina) retroversa</i> (Fleming, 1823)	<i>Fritilaria</i> sp.

(Continued)

TABLE 1 | Continued

<i>Limacina (Munthea) bulimoides</i> (d'Orbigny, 1836)	THALIACEA
<i>Limacina (Munthea) trochiformis</i> (d'Orbigny, 1836)	<i>Thalia democratica</i> (Forskal, 1775)
<i>Heliconoides inflatus</i> (d'Orbigny, 1835)	<i>Doliolum</i> sp.
<i>Limacina</i> sp.	ASCIDIACEA (larvae)
<i>Cavolinia inflexa</i> (Lesueur, 1813)	CEPHALOCHORDATA
<i>Creseis clava</i> (Rang, 1828)	<i>Branchiostoma</i> sp. (larvae)
<i>Creseis virgula</i> (Rang, 1828)	VERTEBRATA
<i>Creseis</i> sp.	Teleostei (egg and larvae)
Gastropoda other (veliger/adult)	

* = tycho planktonic = benthic and other non-planktonic organisms that are carried into the plankton.

Fish eggs varied from 0 (several samples) to 53 eggs·m⁻³ (Coastal, Campaign 1) during the dry season, and from 0 (several samples) to 13 larvae·m⁻³ (Inner Shelf, Campaign 4) during the rainy season. During the dry season, a decreasing pattern in total density of fish eggs m⁻³ was detected (Kruskal–Wallis, $p < 0.05$), with higher values at the coastal area, and lower values at the slope (Dunn, $p < 0.05$). No evidence for differences in fish larvae total density was detected across the areas during the dry season (Kruskal–Wallis, $p > 0.05$). During the rainy season, no difference in fish eggs density m⁻³ was observed (Kruskal–Wallis, $p > 0.05$). However, fish larvae density m⁻³ was higher at the Slope when compared to all other areas (Dunn, $p < 0.05$).

Copepods Diversity

The Shannon diversity index for copepods ranged from 0.155 bits·ind⁻¹ (Coastal, Rainy season, macrozooplankton) to 4.12 bits·ind⁻¹ (Shelf break, Dry season, mesozooplankton) (Figure 4). Although an increasing trend from coastal to offshore stations in Copepoda diversity was observed, this pattern was not statistically confirmed, nor any interaction effect among seasons and spatial areas was detected (two-way ANOVA, $p > 0.05$). The minimum evenness was 0.064 (Slope, Rainy season, macrozooplankton), and the maximum evenness was 0.953 (Inner shelf, Rainy season, mesozooplankton) (Figure 4). No spatial gradient was detected on evenness in any season (Kruskal–Wallis test, $p > 0.05$).

Seston Biomass (mg·m⁻³)

The total seston biomass decreased sharply from the microzooplankton to macrozooplankton fractions (Figure 5). Mesozooplankton biomass was significantly lower than the microzooplankton biomass (Kruskal–Wallis, $p < 0.05$), with values lower than 300 mg·m⁻³. This pattern occurred during all campaigns, except in Campaign 2, when the macrozooplankton fraction had a higher biomass than the mesozooplankton. The biomass spatial distribution pattern varied over time, which demonstrated the importance of collecting different size classes of zooplankton. In all campaigns, microzooplankton biomass peaks were registered near coastal areas, and significant differences (Kruskal–Wallis, $p < 0.05$) were found between the Coastal and other areas. Higher macrozooplankton biomass occurred at the stations over

the slope; however, the biomass was low in comparison to other fractions.

The minimum and maximum values of seston biomass for the microzooplankton community occurred in the campaign 1, varying from 16.35 mg·m⁻³ in the Shelf Break to 34,798.30 mg·m⁻³ in the Coastal region. The minimum recorded for the mesozooplankton community occurred in the Slope in the campaign 3 (18.67 mg·m⁻³) and the maximum (17,285.5 mg·m⁻³) in the Shelf Break in the campaign 4. The minimum and maximum biomass for the macrozooplankton community varied between 0.06 mg·m⁻³ in the Inner Shelf (Campaign 3) to 2434 mg·m⁻³ in the Slope in the campaign 2.

The spatial effect over the seston biomass of the microzooplankton community was verified in both sampled seasons (ANOVA Kruskal–Wallis, $p < 0.05$) (Figure 5). A decreasing trend from Coastal to Slope occurred for the microzooplankton in the dry season (Figure 5). From the *post hoc* test we found that the average biomass recorded during the dry season in the Coastal region (4666.9 ± 9498.9 mg·m⁻³) was significantly higher than those recorded in the Inner Shelf (347.3 ± 776.9 mg·m⁻³), Shelf Break (121.2 ± 98.8 mg·m⁻³) and Slope (92.9 ± 68.4 mg·m⁻³) (Dunn, $p < 0.05$). In the rainy season, the same pattern was observed. The coastal region (2929.5 ± 3274.5 mg·m⁻³) recorded a significantly higher biomass than the Inner Shelf (617.1 ± 938.5 mg·m⁻³), Shelf Break (728.2 ± 898.7 mg·m⁻³) and the Slope (560 ± 695.2 mg·m⁻³) (Dunn, $p < 0.05$).

The seston biomass of mesozooplankton differed among the marine areas only during the dry season (ANOVA Kruskal–Wallis, $p < 0.05$) (Figure 5). The Coastal area presented a biomass of 871.5 ± 1,734.6 mg·m⁻³ and this value was significantly higher than the Inner Shelf (84.3 ± 55.4 mg·m⁻³), Shelf Break (63.3 ± 42.1 mg·m⁻³) and Slope (67.2 ± 41.6 mg·m⁻³) (Dunn, $p < 0.05$). During the rainy season the average values were 637.3 ± 456.6 mg·m⁻³, 464.8 ± 728.6 mg·m⁻³, 1,221.2 ± 3,813 mg·m⁻³ and 407 ± 411.4 mg·m⁻³, respectively recorded to the Coastal, Inner Shelf, Shelf Break and Slope areas.

The seston biomass of the macrozooplankton community differed significantly only in the rainy season (ANOVA Kruskal–Wallis, $p < 0.05$) (Figure 5). During this season, an increase in biomass toward the Slope was recorded (Figure 5), with values in the Coastal (28.6 ± 33.3 mg·m⁻³) significantly lower than that

TABLE 2 | List of Copepoda species from coastal and oceanic areas of Rio Grande do Norte, Northeastern Brazil.

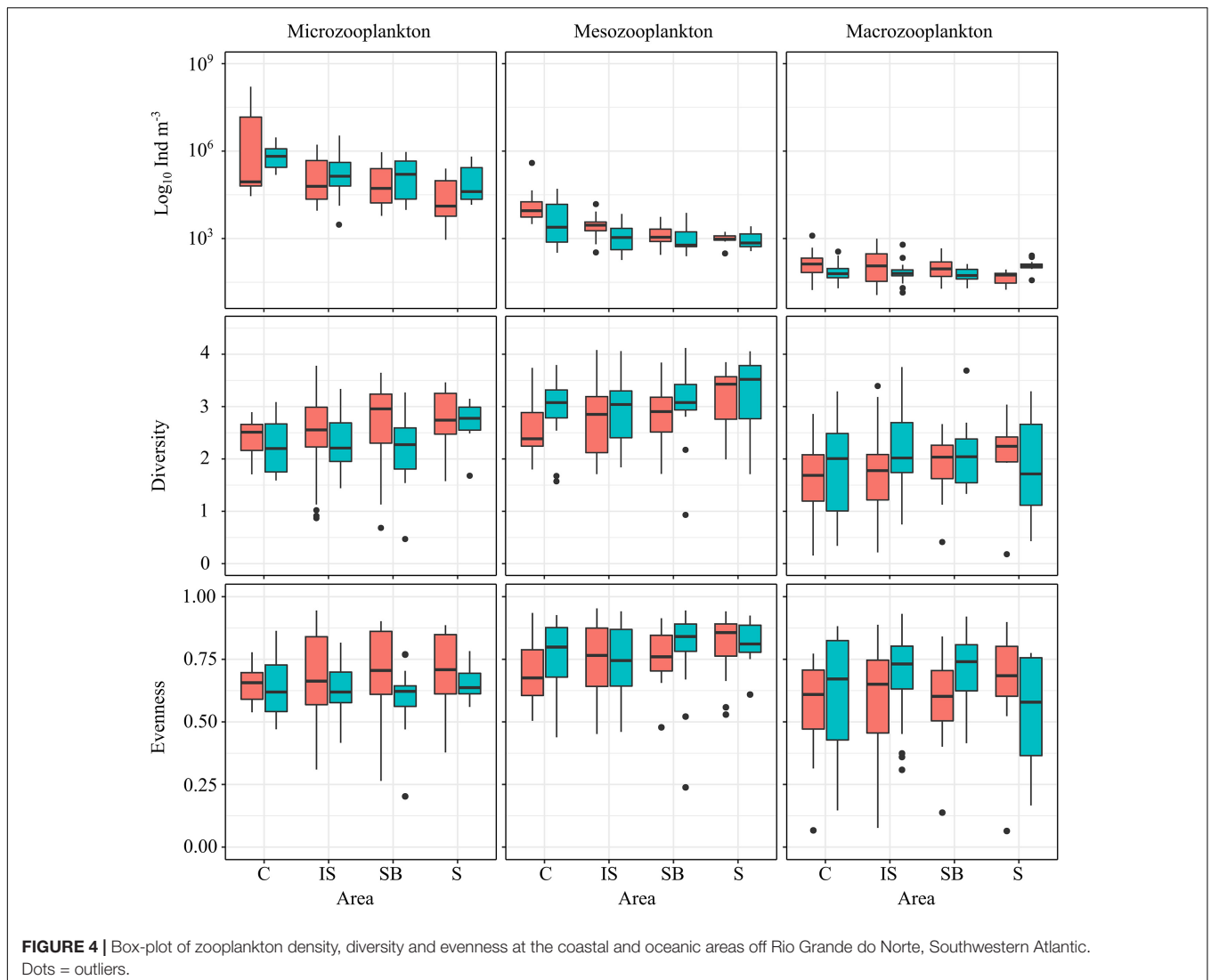
<i>Nannocalanus minor</i> (Claus, 1863) ^O	<i>Labidocera acutifrons</i> (Dana, 1849) ^O
<i>Nannocalanus</i> sp.	<i>Labidocera fluviatilis</i> F. Dahl, 1894 ^N
<i>Neocalanus robustior</i> (Giesbrecht, 1888) ^O	<i>Labidocera nerii</i> (Kroyer, 1849) ^O
<i>Undinula vulgaris</i> (Dana, 1849) ^N	<i>Labidocera</i> sp.
<i>Subeucalanus pileatus</i> (Giesbrecht, 1888) ^O	<i>Pontellina plumata</i> (Dana, 1849) ^O
<i>Subeucalanus</i> sp.	<i>Pontellopsis</i> sp.
<i>Rhincalanus cornutus</i> (Dana, 1849) ^O	<i>Calanopia americana</i> F. Dahl, 1894 ^N
<i>Paracalanus aculeatus</i> Giesbrecht, 1888 ^O	<i>Acartia</i> (<i>Odontacartia</i>) <i>lilljeborgi</i> Giesbrecht, 1889 ^{NE}
<i>Paracalanus quasimodo</i> Bowman, 1971 ^N	<i>Acartia</i> (<i>Acartia</i>) <i>danae</i> Giesbrecht, 1889 ^O
<i>Paracalanus indicus</i> Wolfenden, 1905 ^N	<i>Acartia</i> sp.
<i>Paracalanus</i> spp.	<i>Oithona atlantica</i> Farran, 1908 ^O
<i>Parvocalanus crassirostris</i> (Dahl, 1894) ^N	<i>Oithona nana</i> Giesbrecht, 1892 ^{NE}
<i>Acrocalanus longicornis</i> Giesbrecht, 1888 ^O	<i>Oithona plumifera</i> Baird, 1843 ^{ON}
<i>Acrocalanus</i> sp.	<i>Oithona setigera</i> (Dana, 1849) ^{ON}
<i>Calocalanus pavo</i> (Dana, 1849) ^O	<i>Oithona hebes</i> Giesbrecht, 1881 ^{NE}
<i>Calocalanus pavoninus</i> Farran, 1936 ^O	<i>Oithona oswaldocruzi</i> Oliveira, 1945 ^{NE}
<i>Delibus sewelli</i> (Björnberg T.K.S., 1982) ^O	<i>Oithona</i> sp.
<i>Mecynocera clausi</i> Thompson, 1888 ^O	<i>Oncaea media</i> Giesbrecht, 1891 ^O
<i>Clausocalanus furcatus</i> (Brady, 1883) ^O	<i>Oncaea venusta</i> Philippi, 1843 ^{ON}
<i>Clausocalanus</i> sp.	<i>Oncaea</i> sp.
<i>Ctenocalanus</i> sp.	<i>Lubbockia aculeata</i> Giesbrecht, 1891 ^O
<i>Euchaeta marina</i> (Prestandrea, 1833) ^O	<i>Sapphirina nigromaculata</i> Claus, 1863 ^O
<i>Euchaeta pubera</i> Sars, 1907 ^O	<i>Sapphirina angusta</i> Dana, 1849 ^O
<i>Phaenna spinifera</i> Claus, 1863 ^O	<i>Sapphirina</i> sp.
<i>Scolecithrix bradyi</i> Giesbrecht, 1888 ^O	<i>Copilia mirabilis</i> Dana, 1849 ^O
<i>Scolecithrix danae</i> (Lubbock, 1856) ^O	<i>Copilia quadrata</i> Dana, 1849 ^O
<i>Scolecithrix</i> sp.	<i>Copilia</i> sp.
<i>Haloptilus acutifrons</i> (Giesbrecht, 1892) ^O	<i>Agetus limbatus</i> (Brady, 1883) ^O
<i>Temora stylifera</i> (Dana, 1849) ^{ON}	<i>Corycaeus clausi</i> F. Dahl, 1894 ^O
<i>Temora turbinata</i> (Dana, 1849) ^{ON}	<i>Corycaeus speciosus</i> Dana, 1849 ^O
<i>Temora</i> sp.	<i>Ditrichocorycaeus amazonicus</i> (F. Dahl, 1894) ^N
<i>Pleuromamma xiphias</i> (Giesbrecht, 1889) ^O	<i>Onychocorycaeus giesbrechti</i> (F. Dahl, 1894) ^O
<i>Pleuromamma</i> sp.	<i>Onychocorycaeus latus</i> (Dana, 1849) ^O
<i>Centropages violaceus</i> (Claus, 1863) ^O	<i>Corycaeus</i> sp.
<i>Centropages gracilis</i> (Dana, 1849) ^{ON}	<i>Farranulla gracilis</i> (Dana, 1849) ^O
<i>Centropages vellicatus</i> (Dana, 1849) ^{ON}	<i>Farranulla rostrata</i> (Claus, 1863) ^O
<i>Pseudodiaptomus acutus</i> (F. Dahl, 1894) ^E	<i>Farranulla</i> sp.
<i>Pseudodiaptomus richardi</i> (F. Dahl, 1894) ^E	<i>Microsetella rosea</i> (Dana, 1847) ^O
<i>Lucicutia flavicornis</i> (Claus, 1863) ^O	<i>Microsetella norvegica</i> (Boeck, 1864) ^{ON}
<i>Lucicutia</i> sp.	<i>Miracia efferata</i> Dana, 1849 ^O
<i>Metridia princeps</i> Giesbrecht, 1889 ^O	<i>Macrosetella gracilis</i> (Dana, 1847) ^O
<i>Candacia pachydactyla</i> (Dana, 1848) ^O	<i>Euterpina acutifrons</i> Dana, 1847 ^O
<i>Candacia cheirura</i> (Cleve, 1904) ^O	<i>Hemicyclops thalassius</i> Vervoort and Ramirez, 1966 ^N
<i>Candacia varicans</i> (Giesbrecht, 1892) ^O	<i>Tigriopus</i> sp.*
<i>Candacia</i> sp.	<i>Caligus</i> sp. ^P
<i>Pontella atlantica</i> (Milne-Edwards, 1840) ^O	<i>Longipedia</i> sp. ^P
<i>Pontella securifer</i> Brady, 1883 ^O	

O – oceanic, N – neritic and E – estuarine (according to Björnberg, 1963, 1981; Bradford-Grieve et al., 1999), * – tycho planktonic, P – parasite.

observed in the Inner Shelf ($259.1 \pm 242.7 \text{ mg}\cdot\text{m}^{-3}$), Shelf Break ($307.1 \pm 242.8 \text{ mg}\cdot\text{m}^{-3}$) and Slope ($876.8 \pm 745.7 \text{ mg}\cdot\text{m}^{-3}$) (Dunn, $p < 0.05$). For the dry season, the averages recorded in the Coastal, Inner Shelf, Shelf Break and Slope areas were, respectively $37.6 \pm 42.5 \text{ mg}\cdot\text{m}^{-3}$, $42.6 \pm 40.6 \text{ mg}\cdot\text{m}^{-3}$, $59.1 \pm 55.2 \text{ mg}\cdot\text{m}^{-3}$ and $46 \pm 46 \text{ mg}\cdot\text{m}^{-3}$.

Zooplankton Community Structure

The nMDS analyses indicated differences in the structure of micro- (Figure 6A), meso- (Figure 6B) and macrozooplankton (Figure 6C) community between areas, as well as marked differences among the seasonal periods sampled (Figures 6D–F). The micro-, meso- and macrozooplankton community



differences across a coastal-oceanic gradient was verified through the PERMANOVA test (Table 3). The seasonal effect was also highlighted as an important factor responsible for the dissimilarity of zooplankton investigated communities (Table 3). We recorded a significant interaction between the tested factors (area and season) only for the macrozooplankton community (Table 3C).

Results of *pairwise t* tests indicate that the coastal area differs from the Inner Shelf, Shelf Break and Slope in terms of the taxonomic composition of micro-, meso- and macrozooplankton community (Table 4). However, the greatest difference was recorded between the coastal area and the slope for the micro- (Table 4A) and mesozooplankton (Table 4B). The significant interaction between the area and season for the macrozooplankton showed that in the dry season the greatest dissimilarity in the taxonomic composition occurred between the Coastal area and the Shelf Break (Table 4C), while in the rainy season occurred between Coastal area and the Slope (Table 4D).

The SIMPER analysis reinforced the greatest dissimilarity of the taxonomic composition of the microzooplankton occurring between the Coastal and the Slope areas (Average dissimilarity = 46.01), whose cumulative contribution of the taxa, *O. hebes*, *E. acutifrons*, *P. crassirostris*, *Oikopleura dioica*, *Oithona* (copepodite) and *Oithona* sp. corresponded to 51.86% of the dissimilarity (Table 5A). For the mesozooplankton the greatest dissimilarity (64.49) was also recorded between the Coastal area and the Slope (Table 5B). The taxa, *O. nana*, *N. minor*, *Temora turbinata*, *O. hebes*, *P. crassirostris* and *Clausocalanus furcatus* corresponded to 52.26% of the differences recorded between these areas (Table 5B).

For the macrozooplankton, the greatest dissimilarity (average dissimilarity = 75) of the taxonomic composition observed in the dry season between the coastal area and the Shelf Break occurred as a response of the highest contribution of the taxa, *T. turbinata*, *U. vulgaris*, *Lucifer* sp. (mysis), *Lucifer* sp. (protozoa), *Centropages furcatus*, *Oikopleura longicauda* and *Flaccisagitta enflata*. These showed a cumulative contribution of 50.94%.

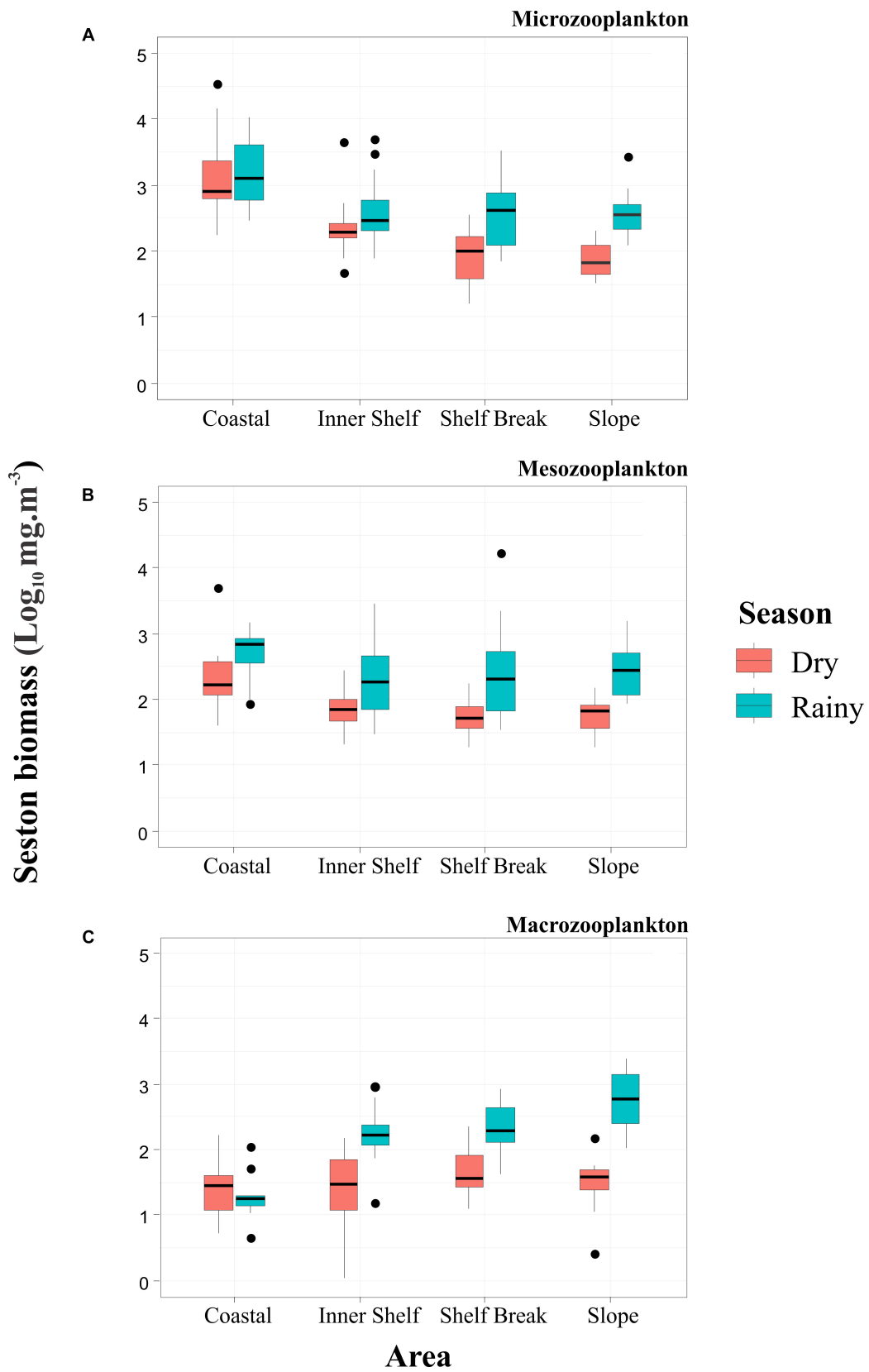


FIGURE 5 | Box-plot of seston biomass (Log₁₀ mg.m⁻³) of microzooplankton (A), mesozooplankton (B), and macrozooplankton (C) at the coastal and oceanic areas off Rio Grande do Norte, Southwestern Atlantic. Dots = outliers.

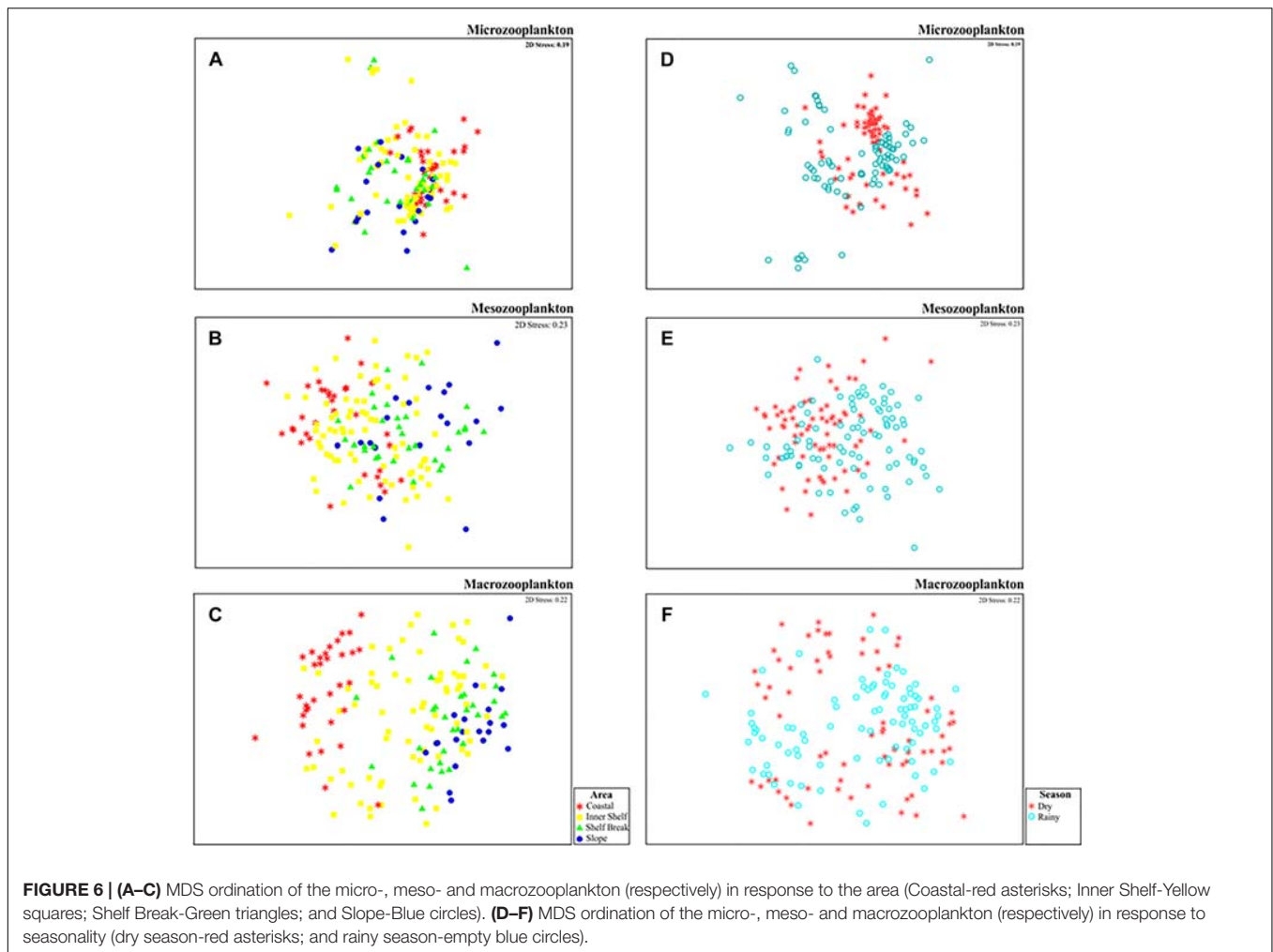


FIGURE 6 | (A–C) MDS ordination of the micro-, meso- and macrozooplankton (respectively) in response to the area (Coastal-red asterisks; Inner Shelf-Yellow squares; Shelf Break-Green triangles; and Slope-Blue circles). **(D–F)** MDS ordination of the micro-, meso- and macrozooplankton (respectively) in response to seasonality (dry season-red asterisks; and rainy season-empty blue circles).

TABLE 3 | Summary: PERMANOVA, this analysis tests differences in quantitative taxonomic composition of the micro- meso- and macrozooplankton community considering area and season as factors.

PERMANOVA												
Source	(A) Microzooplankton				(B) Mesozooplankton				(C) Macrozooplankton			
	Df	MS	Pseudo-F	P(perm)	Df	MS	Pseudo-F	P(perm)	Df	MS	Pseudo-F	P(perm)
Area	3	3789.2	3.7047	0.001	3	10088	9.4294	0.001	3	20505	14.331	0.001
Season	1	6060	5.9249	0.001	1	15228	14.233	0.001	1	10134	7.0828	0.001
Area vs. Season	3	1183.9	1.1575	0.32	3	2484.3	2.322	0.004	3	2713.4	1.8964	0.01
Residual	146	1022.8			148	1069.9			148	1430.8		
Total	153				155				155			

Differences are considered significant if $P(perm) = 0.01$ (in bold). df = degrees of freedom; MS = average squares; P = probability associated with the Pseudo F statistic.

(Table 5C). In the rainy season, the high difference between the Coastal area and the Slope (Average dissimilarity = 79.66) occurred due to the greater cumulative contribution of 50.85% of the taxa *U. vulgaris*, *T. turbinata*, *Lucifer* sp. (mysis), *F. enflata*, *Luciferidae* (protozoa) and *C. furcatus* (Table 5D).

The RDA explained 68% of the variance in the zooplankton community (Figure 7). Two vectors with significant values (RDA,

$p < 0.05$) were highlighted for the community. One vector separated the coastal from the other areas (Figure 7) and other associated the zooplankton to temperature. The groups most associated with the coastal area were mainly the organisms of the microzooplankton (both sestonic biomass and abundance); however, the other zooplanktonic size fractions were also associated with the coastal area. The only group associated with

TABLE 4 | Results of *pairwise t* test of the micro- meso- and macrozooplankton community structure considering area and season as factors.

Pairwise t test					
(A) Microzooplankton			(C) Macrozooplankton/Dry		
Areas	t	P(perm)	Areas	t	P(perm)
Coastal vs. Inner Shelf	2.3447	0.001	Coastal vs. Inner Shelf	2.7176	0.001
Coastal vs. Shelf Break	2.6599	0.001	Coastal vs. Shelf Break	3.4473	0.001
Coastal vs. Slope	2.9971	0.001	Coastal vs. Slope	3.3509	0.001
Inner Shelf vs. Shelf Break	0.90931	0.559	Inner Shelf vs. Shelf Break	1.8362	0.011
Inner Shelf vs. Slope	1.5759	0.041	Inner Shelf vs. Slope	2.1845	0.004
Shelf Break vs. Slope	1.0186	0.407	Shelf Break vs. Slope	1.5406	0.031
(B) Mesozooplankton			(D) Macrozooplankton/Rainy		
Areas	t	P(perm)	Areas	t	P(perm)
Coastal vs. Inner Shelf	2.3447	0.001	Coastal vs. Inner Shelf	3.9052	0.001
Coastal vs. Shelf Break	2.6599	0.001	Coastal vs. Shelf Break	4.5206	0.001
Coastal vs. Slope	2.9971	0.001	Coastal vs. Slope	5.1289	0.001
Inner Shelf vs. Shelf Break	0.90931	0.559	Inner Shelf vs. Shelf Break	1.5656	0.009
Inner Shelf vs. Slope	1.5759	0.041	Inner Shelf vs. Slope	2.224	0.001
Shelf Break vs. Slope	1.0186	0.407	Shelf Break vs. Slope	1.4468	0.03

In bold the main differences identified for the zooplankton community from Rio Grande do Norte in the Tropical Western Atlantic. Perm = PERMANOVA.

temperature was the macrozooplankton biomass. Coastal and temperature vectors explained together 33% of the variability.

A cluster analysis of the samples based on Copepoda presented four groups (Cophenetic $r = 0.89$), which corresponded to the four campaigns (Figure 8). In the groups corresponding to Campaigns 1 and 2, two subgroups were formed and consisted of Coastal and Inner Shelf samples at one subgroup, and Shelf Break and Slope samples at the other. In Campaigns 3 and 4, the Coastal stations were separated from the subgroups formed by Inner Shelf, Shelf Break, and Slope.

Functional Traits

The major functional traits dividing the Copepoda community was the reproductive and trophic attributes, which formed three main groups: herbivorous and broadcaster (Group 1), omnivorous-detritivorous, omnivorous-herbivorous, carnivorous and sac-spawner (Group 2), and carnivorous-omnivorous and sac-spawner (Group 3) (Figure 9). These groups each included different lengths, costal distances and vertical migration.

Group 1 comprised mostly species with broadcaster reproduction, with epipelagic offshore distribution, herbivorous and filter feeding, non-migrant behavior and smaller sizes varying from 500 to 1500 μm . This group contained mainly calanoids of the genera *Acartia*, *Calocalanus*, *Temora*, *Paracalanus*, *Calanopia*, *Undinula* and *Centropages*. Group 2 consisted mostly of sac-spawner species, neritic or neritic-oceanic, epimeso-bathipelagic and presented three sub-groups, sub-group 1: carnivorous, sub-group 2: omnivorous-herbivorous and sub-group 3: omnivorous-detritivorous. All *Oithona* spp., which exhibit active ambush behavior belonged to sub-group 2. Group 3 also consisted of sac-spawners and included the

large (2,500–6,500 μm) oceanic calanoids *Euchaeta*, *Candacia*, *Labidocera* and *Haloptilus*, and cyclopoids *Saphirina* and *Copilia* which exhibit omnivorous or carnivorous feeding habits, cruising or active ambush behavior types, and vertical diel migration that varies from weak to strong.

DISCUSSION

The study of the zooplankton community structure and function between coastal and oceanic regions from Rio Grande do Norte in the Tropical Western Atlantic showed the great spatial diversity, seasonal variations and the productive potential, chiefly of the coastal region (<10 m depth), possibly caused by continental influence. The coastal zone is extremely complex and is affected by a variety of oceanographic processes (Walsh, 1976; Sousa et al., 2016) that are influenced by diverse anthropic impacts related to continental sources (Mee, 2012). In general, the seasonal distribution presented higher densities for the communities in the rainy season, when fertilization and discharge of nutrients from the continent are more intense.

Our study revealed a high number of taxa occurring in the mesozooplankton community and a greater numerical importance of the microzooplankton community. These results show that net mesh selectivity is an important factor to be considered in studies of the zooplankton community structure. The mesh size effect has already been investigated on the copepod assemblage in the South China Sea (Tseng et al., 2011) and on planktonic cnidarians from neritic and oceanic habitats in the equatorial Atlantic Ocean (Tosetto et al., 2019). The results of the mentioned studies demonstrate that the mesh size directly affects important descriptors (abundance and diversity) which

TABLE 5 | Results of SIMPER analysis for micro-, meso- and macrozooplankton and the zooplankton taxa that contributed to the composition and their values in %, off Rio Grande do Norte, Southwestern Atlantic.

Taxa	Coastal	Slope	Cumulative contribution (%)
	Average abundance	Average abundance	
(A) Coastal vs. Slope (Average dissimilarity = 46.01) – Microzooplankton			
<i>Oithona hebes</i>	10.07	5.04	9.82
<i>Euterpina acutifrons</i>	7.35	1.72	18.91
<i>Parvocalanus crassirostris</i>	8.51	4.4	27.86
<i>Oikopleura dioica</i>	6.83	3.52	36.03
<i>Oithona</i> (Copepodito)	6.24	2.29	43.97
<i>Oithona</i> sp.	7.07	3.43	51.86
Foraminifera	6.11	2.16	59.54
Gastropoda (veliger)	8.48	6.05	66.4
<i>Oikopleura</i> sp.	4.83	2.23	73.14
<i>Oithona nana</i>	5.85	6.31	79.45
Bivalvia (veliger)	8.75	6.58	85.58
<i>Tintinnopsis</i> sp.	3.51	1.5	90.64
(B) Coastal vs. Slope (Average dissimilarity = 64.49) – Mesozooplankton			
<i>Oithona nana</i>	6.06	1.49	10.91
<i>Nannocalanus minor</i>	6.11	2.08	20.55
<i>Temora turbinata</i>	4.44	0.11	30.05
<i>Oithona hebes</i>	3.85	0.74	37.97
<i>Parvocalanus crassirostris</i>	3.45	0.4	45.3
<i>Clausocalanus furcatus</i>	3.26	3.14	52.26
<i>Undinula vulgaris</i>	2.56	4.09	59.18
Bivalvia (veliger)	5.72	3.29	65.64
<i>Euterpina acutifrons</i>	3.19	1.38	71.99
Gastropoda (others)	2.8	1.66	77.78
<i>Oikopleura</i> sp.	2.98	1.46	83.4
<i>Oithona plumifera</i>	0.7	2.32	89.01
<i>Oithona oswaldocruzi</i>	1.72	1.46	94.09
(C) Coastal vs. Shelf Break (Average dissimilarity = 75) – Macrozooplankton/Dry			
<i>Temora turbinata</i>	2.74	0.29	11.68
<i>Undinula vulgaris</i>	0.48	2.6	22.12
Luciferidae (mysis)	1.78	0.08	29.48
Luciferidae (protozoa)	1.42	0.21	35.23
<i>Centropages furcatus</i>	1.23	0.23	40.59
<i>Oikopleura longicauda</i>	1.18	0.77	45.81
<i>Flaccisagitta enflata</i>	0.23	1.15	50.94
Brachyura (zoeae)	1.01	0.66	55.81
<i>Parasagitta tenuis</i>	1.26	0.55	60.68
Brachyura (zoeae)	0.79	0.81	65.33
Teleostei (egg)	0.7	1.06	69.89
<i>Calanopia americana</i>	0.96	0.42	74.41
<i>Onychocorycaeus giesbrechti</i>	0.75	1	78.35
Gastropoda (veliger)	0.73	0.51	81.92
<i>Temora stylifera</i>	0.27	0.78	85.41
<i>Oikopleura</i> sp.	0.46	0.46	88.56
<i>Subeucalanus pileatus</i>	0.28	0.69	91.61

(Continued)

TABLE 5 | Continued

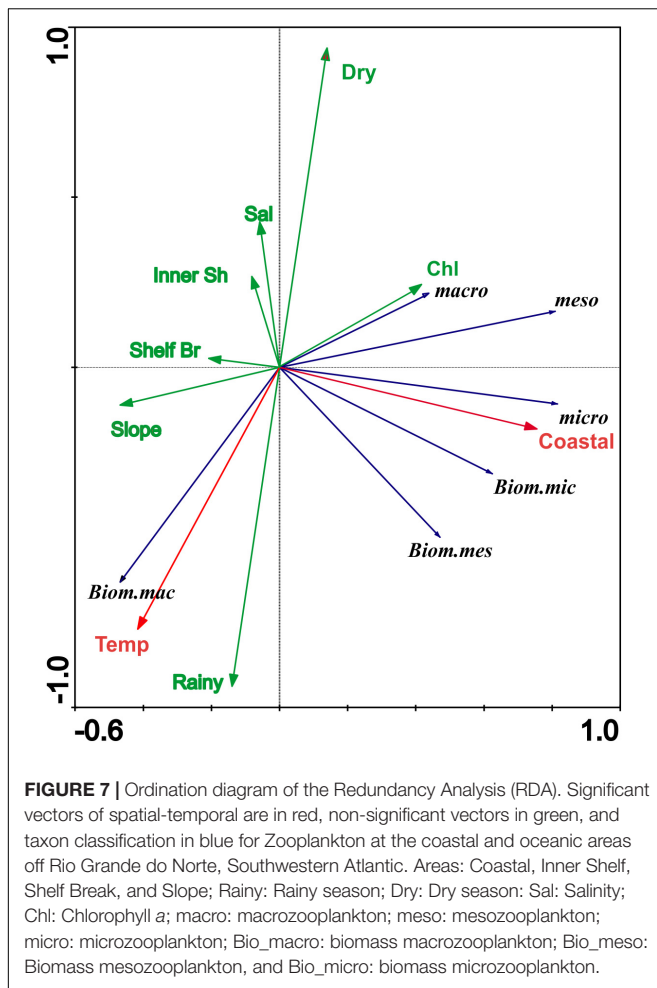
Taxa	Coastal	Slope	Cumulative contribution (%)
	Average abundance	Average abundance	
(D) Coastal vs. Shelf Break (Average dissimilarity = 79.66) – Macrozooplankton/Rainy			
<i>Undinula vulgaris</i>	0.48	3.1	12.61
<i>Temora turbinata</i>	2.74	0.01	25.11
Luciferidae (mysis)	1.78	0.01	32.71
<i>Sagitta enflata</i>	0.23	1.53	39.47
Luciferidae (protozoa)	1.42	0.07	45.33
<i>Centropages furcatus</i>	1.23	0.02	50.85
<i>Oikopleura longicauda</i>	1.18	0.57	55.83
<i>Parasagitta tenuis</i>	1.26	0.54	60.37
Brachyura (zoeae)	1.01	0.26	64.68
<i>Calanopia americana</i>	0.96	0.35	68.75
Brachyura (zoeae)	0.79	0.34	72.76
<i>Temora stylifera</i>	0.27	0.85	76.72
<i>Onychocorycaeus giesbrechti</i>	0.75	0.8	80.15
<i>Membranipora</i> sp.	0.58	0.38	83.5
<i>Subeucalanus pileatus</i>	0.28	0.64	86.83
Gastropoda (veliger)	0.73	0.36	90.13

In bold the main taxa, whose cumulative contribution corresponds to $\geq 50\%$.

are particularly useful for the management of marine resources, mostly of the marine regions studied (Coastal, Inner Shelf, Shelf Break and Slope).

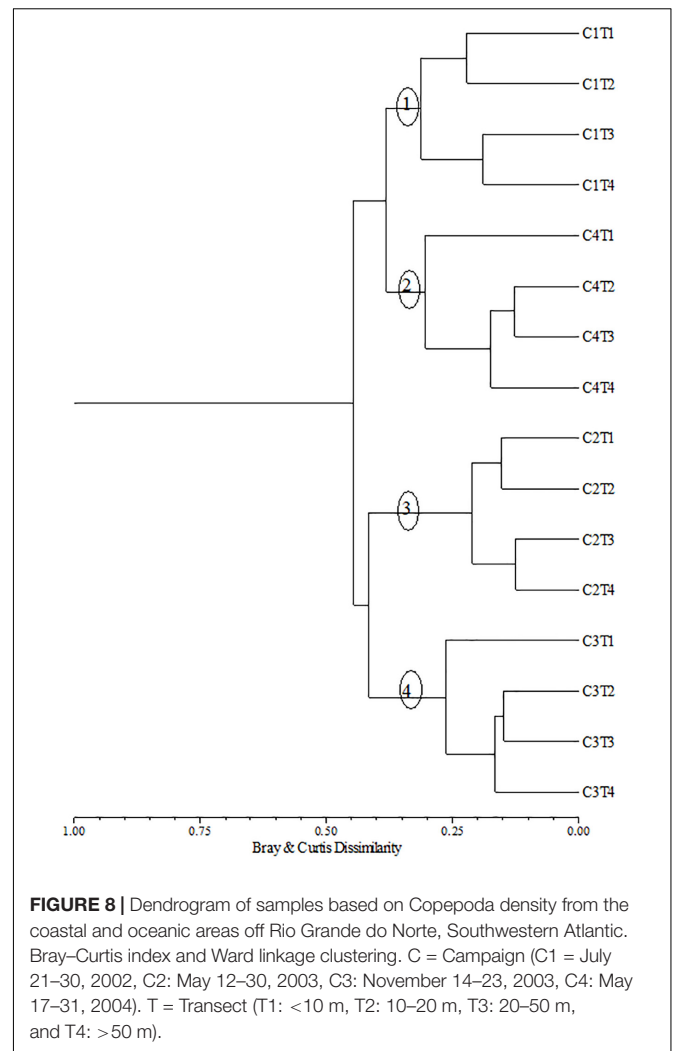
Spatial differences were observed for the zooplanktonic communities among the marine regions investigated with a Coastal and Inner Shelf group (related to higher chlorophyll-*a*, shallow area and higher meroplanktonic forms) and Shelf Break and Slope group (linked to lower chlorophyll-*a*, deeper areas and higher percentage of holoplanktonics). However, greater dissimilarity was registered between the Coastal and the Slope areas (e.g., microzooplankton extremely high density was associated with the shallower coastal area). This Coastal region is enriched by rivers discharges from the continent (including outflow from the intensive shrimp culture ponds), delivering nutrients to the marine system. These nutrients stimulate the phytoplankton growth, favoring most zooplankton species, which are characteristically herbivores or omnivores (Johnson and Allen, 2005). This pattern is commonly found in Continental shelves (Neumann-Leitão et al., 1999, 2008; Dias et al., 2015; Bueno et al., 2017) and oceanic islands (Campelo et al., 2018; Santana et al., 2018) in Brazil and reflect the typical coast-ocean gradient.

An increase in macrozooplankton density was observed near the Shelf Break, caused by local topographic upwellings (Stramma et al., 1990). However, the condition of each location may strongly affect the distribution of the zooplankton, such as reefs currents, canyons, ravines, eddies and vortices (Regner, 1985), and alter the general pattern of the studied area. For instance, the Rio Grande do Norte coast has a narrow continental shelf; therefore, the zooplankton community has a high degree of



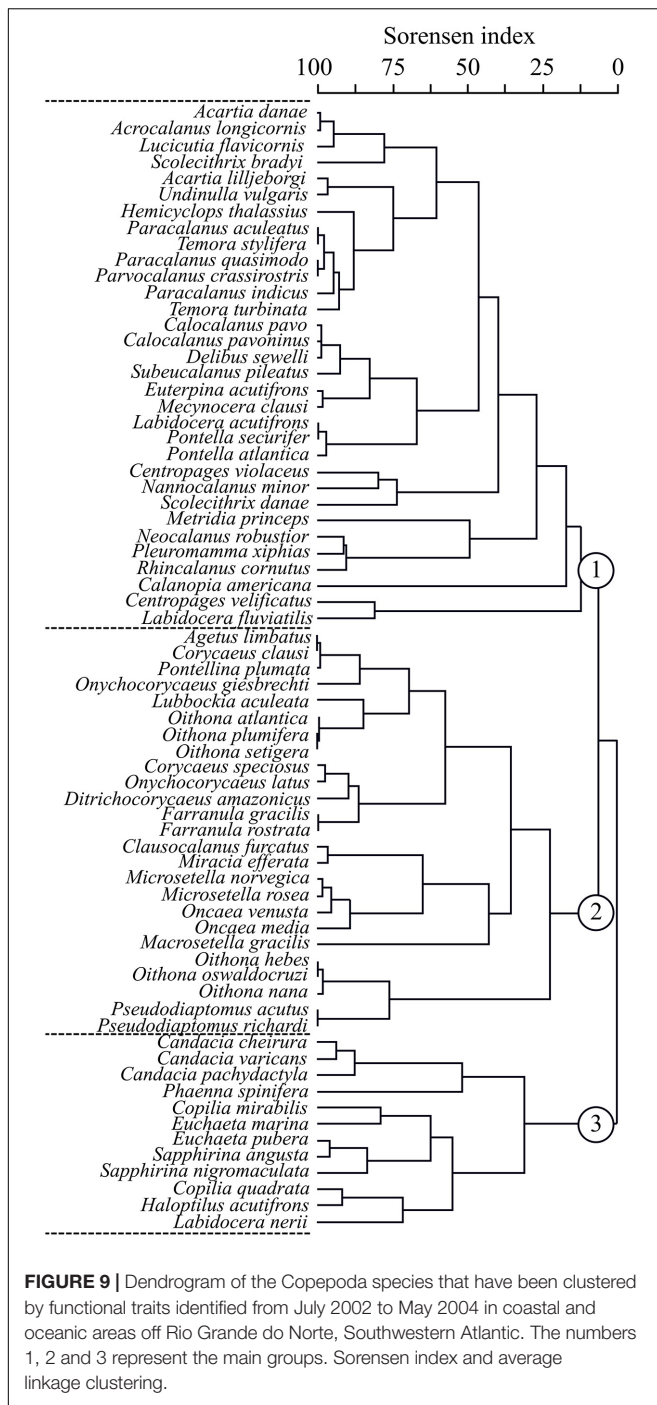
influence from oceanic intrusions. Thus, a mixture of oceanic and neritic micro-, meso-, and macrozooplankton was observed, which resulted in difficulties separating the communities. As expected, diversity increased from inshore to offshore. This pattern is usual for SWA (Boltovskoy, 1981; Neumann-Leitão et al., 1999, 2008; Dias and Bonecker, 2009; Dias et al., 2015); however, due to the reproductive requirements, some species prefer shallow waters.

The high biomass of micro- and mesozooplankton was mainly recorded in the Coastal area in both studied seasonal periods, being able to consider that these fractions of the community are key elements in the planktonic food chain of this region. In addition, it is important to consider the large amount of particulate matter from the estuaries and bays (Lopes, 2007). These particulates matter (plankton, marine snows and detritus) are important components of the pelagic system because they are a food source for the zooplankton, being sampled more efficiently by smaller mesh sizes (Silva et al., 2019). In general, the lowest values of biomass observed for the macrozooplankton community occurred in the coastal area and the largest on the slope. This is a result of a coast-ocean size gradient (Marcolin et al., 2013), implying a change in the taxonomic composition of the organisms, with a greater contribution of siphonophores



and fish larvae in the slope, considered organisms of larger body size, better sampled with the a net of 300 μm mesh size. A maximum of zooplankton biomass occurs in neritic waters of SWA (Boltovskoy, 1981; Dias et al., 2015), with 100 $\text{mg}\cdot\text{m}^{-3}$ in the top layer (200 m).

Copepoda were the most diverse group in all fractions, accounting for 93 species. This result is expected for the SWA tropical waters (Boltovskoy, 1981, 1999; Neumann-Leitão et al., 1999, 2008; Lopes et al., 1999; Bueno et al., 2017). Highest Copepoda diversity were registered in the mesozooplankton fraction during this study and most of them were of small size. In oligotrophic areas, species occur with smaller sizes and in developmental stages that are important in planktonic communities and these areas are dominated by microbial components (Calbet et al., 2001; Turner, 2004; Calbet, 2008). Small-sized copepods are a pivotal link between the classical and microbial food webs (Nakamura and Turner, 1997; Melo et al., 2014); they present a much higher growth rate (Peterson et al., 1991; Hopcroft et al., 1998) and influence the effectiveness of the trophic connection between primary



producers/protozooplankton and larger species (Zervoudaki et al., 2007). One of the most oligotrophic oceans in the world is the Southwest Atlantic Ocean (Andrade et al., 2007); and, Dias et al. (2015) mention that oligotrophic areas present higher production than formerly supposed and have an extraordinary amount of biotic complexity, encompassing nearly 75% of marine surfaces.

Young forms (copepodites) of *N. minor*, *Temora stylifera*, *C. furcatus*, *Centropages velificatus*, and *O. giesbrechti* and

adults of *Microsetella norvegica* and *Macrosetella gracilis* predominated the microzooplankton fraction. The species *M. norvegica* and *M. gracilis* were generally associated with the cyanobacterium *Trichodesmium eritheum*. Pelagic harpacticoids can also be found in close association with floating substrates, such as *Trichodesmium* (Calef and Grice, 1966; O'Neil and Roman, 1994; O'Neil, 1998; Uye et al., 2002). These blue-green colonies offer both a firm substratum and food for the accompanying plankton in tropical and subtropical oligotrophic oceans, thus supporting multifaceted microenvironments (Sheridan et al., 2002; Bergman et al., 2013).

The copepod *P. crassirostris* is very important to the microzooplankton community of the Coastal stations; *P. crassirostris* commonly occurs in nearly all Brazilian estuaries and the estuarine plume (Björnberg, 1981; Eskinazi-Sant'Anna and Björnberg, 2006), including those that are severely anthropically impacted (Schwamborn et al., 2004; Silva et al., 2004). This species forages mainly on pico- and nanoplankton fractions, behaving as an *r*-strategist (opportunistic) particle feeder and revealing high ingestion rates of the most profuse cells (2–5 μm nanoplankton) (Calbet et al., 2000). *P. crassirostris* is dominant in eutrophic systems, evidencing the estuarine effect in the coastal studied area. In the offshore direction, a characteristic zooplanktonic community is commonly found in reef areas. The high abundance of the Oithonidae and Paracalanidae families is typical of the coastal waters of Brazil (Björnberg, 1981; Dias and Bonecker, 2009).

Epipelagic, oceanic, and widespread species were the dominant groups in this region, and they occur in tropical and subtropical oceans (Atlantic, Pacific, and Indian), except for *U. vulgaris* and *O. nana*, which demonstrate neritic occurrence (Björnberg, 1981; Bradford-Grieve et al., 1999). There is a reported relation between *U. vulgaris* and coastal areas due to its occurrence in neritic environs; *U. vulgaris* exhibits a high abundance in many inshore plankton hauls in the surface layer (Razouls et al., 2005). However, *U. vulgaris* dominated among copepods in samples from oceanic provinces in the economic exclusive zone (EEZ) of Northeastern Brazil (Cavalcanti and Larrazábal, 2004; Melo et al., 2014; Campelo et al., 2018). In our study, *U. vulgaris* was also abundant at young stages under oceanic influence, which suggested that it also inhabits oceanic regions with an epi-mesopelagic distribution.

The wide distribution of numerous Copepoda species in our study is due their passive transportation by currents (*Calocalanus pavo*, *U. vulgaris*, *Oithona plumifera*, *Oncaea venusta*, *M. gracilis*, *Microsetella rosea*, and *Corycaeus speciosus*), Chaetognatha (*F. enflata* and *Serratogitta serratodentata*), and Appendicularia (*Oikopleura* spp.) results in circumglobal distribution patterns. This occurs much more commonly than endemism for pelagial plankton (Boltovskoy et al., 2002; Pierrot-Bults and Angel, 2012). Species with high proportions of neritic organisms and benthopelagic forms are excluded from this pattern (Angel, 1993).

Chaetognatha predominated in the macrozooplankton fraction and comprised species from coastal and oceanic provinces; oceanic origin was predominantly represented. *F. enflata*, *S. serratodentata*, *Flaccisagitta hexaptera*,

Sagitta bipunctata, and *Krohnitta subtilis* are indicators of the Tropical Water, and *Parasagitta tenuis* a coastal-water indicator. *Pterosagitta draco* have a wide distribution recorded in both oceanic and coastal water masses (Boltovskoy, 1981). High densities of *F. enflata* are common to this area (Boltovskoy, 1981, 1999; Gusmão, 1986; Neumann-Leitão et al., 1999, 2008).

The zooplankton species indicator classified by Björnberg (1963, 1981) and Bradford-Grieve et al. (1999) showed that the most relevant Copepoda group in our analysis included a mixture of neritic and oceanic species from the North Brazil Current, which is under the Shelf Break influence that presents the general scenario of a huge reef system. Campos et al. (2017) found a similar result to a coastal area north of the present studied area. Also, holoplanktonic organisms, mainly the oceanic Copepoda, predominated the entire studied region, including the inshore area. This pattern is a consequence of the weak continental freshwater runoff over the shelf due to arid climate and geomorphology. Thus, freshwater flux fertilizes the very coastal area under 10 m depth. Other authors for Northeastern Brazil (e.g., Gusmão et al., 1998; Neumann-Leitão et al., 1999, 2008; Campos et al., 2017) registered this same pattern. The constant northeast tradewinds and arid climate in this area permits for the establishment of widespread beaches and dunes, which are in continuous movement due to the absence of anchoring vegetation (Mabesoone and Coutinho, 1970). These dunes prevent the free flux of rivers to the sea during dry season, and many freshwater lakes form behind the dunes. The changes recorded along the shelf seem to be chiefly driven by the rain and periodic blooms of benthic invertebrate larvae.

The role of zooplankton through functional groups involves information that precisely capture their complex dynamics (Everett et al., 2017). The zooplankton are represented by many functional groups, that oscillate in size from small ($>0.002 \mu\text{m}$) to large ($>5000 \mu\text{m}$) organisms. Zooplankton also presents vast trophic malleability that can modify considerably along a time interval as the community structure changes. Many external factors (e.g., nutrients, temperature, phytoplankton, competition, predation) regulate the growth of an organism and/or of a population, that by its turn is strongly connected to life cycles, such as reproduction with generations fluctuating (from days to years) (Williams and Conway, 1982). Zooplankton species modify its diet preferences throughout different periods or life stages, or substitute a food item behavior (Stibor et al., 2004; Sommer and Sommer, 2006). To complicate the dynamics of the zooplankton community, several species of microzooplankton are mixotrophic (Caron, 2016), the phytoplankton succession is seasonal (Pingree et al., 1976; O'Boyle and Silke, 2010) and many meroplanktonic species emerge in the shelf (Williams and Collins, 1986). Thus, zooplankton within a specified size class (e.g., microzooplankton, mesozooplankton, macrozooplankton) are thus unlikely to behave reliably over a spatial-temporal scale.

The main traits separating the Copepoda groups were the reproductive and trophic strategies, and a very similar outcome was found by Campos et al. (2017) to a shelf area located North of the present studied area; and, by Neumann-Leitão et al. (2018) for the reef system in the Amazonas coastal area. Trophic strategies

and reproduction are normally controlled by female weight, ecosystem temperature, and diet (Blaxter et al., 1998; Bunker and Hirst, 2004; Brun et al., 2017). In terms of feeding, Kiørboe and Sabatini (1995) presented three strategies in copepods: filtering, active ambushing and cruising; and, Kiørboe (2011) presented the following not necessarily exclusive feeding strategies: Passive (Ambush feeding, particle feeding) Active (Feeding currents, cruise feeding) Mixed (Combination of active and passive modes) and Other (Parasitic).

In conclusion, the study area presents spatial heterogeneity, with low diversity limited to Coastal stations; high diversity and low abundance occur along the Inner Shelf, Shelf Break, and Slope. This is a pelagic oligotrophic habitat located off the coast of tropical Brazil over a diverse, high biomass benthic habitat, which is mostly covered by calcareous algae functioning on the shelf as a large reef system. The narrow and shallow shelf is responsible for the strong connectivity between nearshore enriched coastal water and the oceanic oligotrophic Tropical Water mass, which results in a complex mixed system that is critical to the food web structure and forms a peculiar pattern of zooplankton diversity and distribution.

AUTHOR CONTRIBUTIONS

SNL and RS coordinated the project. SNL, RS, AS, PM, and VP designed and coordinated the fieldwork. SNL, FPN, MMJ, RS, AS, and LF wrote and reviewed the manuscript. SNL, RS, MMJ, FPN, TS, DNV, PM, XD, AS, VP, LF, AC, RC, JS, and SL contributed with data and data analyses.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00287/full#supplementary-material>

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