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Research paper

Ecological indicators and functional groups of copepod assemblages

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A R T I C L E I N F O

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A B S T R A C T

Copepods are important ecological indicators of ecosystem functioning. In this study, we analyzed the structure of copepod assemblages and cross-shelf patterns based on functional traits and indicator value analysis. Copepod samples were collected from 54 stations distributed along the inner, middle, and outer continental shelves covering a wide geographical area (20,100 km^2). Overall, 38 species were identified: 20 Calanoida, 14 Cyclopoida, and 4 Harpacticoida. Copepod density was the highest in the inner shelf profile, with richness and diversity being higher on the outer shelf close to the shelf break. The results suggest that there is a gradient of zooplankton distribution even on narrow (< 50 km) continental shelves. The cluster analysis of the stations showed a tendency to form three groups largely corresponding to physical location. Two major functional groups were identified, sorted by spawning strategy. These were subdivided according to the trophic regime and feeding strategy. *Temora turbinata* (alien species), *Clausocalanus furcatus*, and *Ditrichocorycaeus amazonicus* (native species) were found to be ecological indicators. These species have different functional traits and distinct cross-shelf distributions, where the alien species dominates the turbid coastal waters, and *C. furcatus* is an indicator of outer-shelf waters. Thus, these species can be considered ecological indicators of the different continental shelf waters. The results indicate that it is necessary to understand the functional diversity and ecological indicators of copepods, considering their importance for the basis of marine food webs.

1. Introduction

Taxonomic diversity and spatiotemporal variations over different scales in relation to environmental or anthropogenic factors offer information on how modifications in biodiversity affect ecosystem function (Pomerleau et al., 2015). Interest in specific ecological roles and the relations of diversity and ecosystem functioning lately was expressed by researchers recently (Barton et al., 2013) because these parameters characterize the diversity of species traits (Díaz and Cabido, 2001). Functional traits are phenotypic features of organisms that affect their fitness (Violle et al., 2007) and can be categorized according to ecological functions (Benedetti et al., 2016; Litchman et al., 2013). Describing the patterns in taxonomic diversity and functional traits indicate variation in ecological functioning and may be as good indicators of functioning of marine systems.

The value of zooplankton as an indicator of ecological conditions comes from its position in the food web, as a link between bottom-up (phytoplankton) and top-down (e.g., fishes) energy transfer components (Kiørboe, 2008), thus providing information about the ecological implications for fish production and for the regional and overall biogeochemical cycles (Miyashita et al., 2009). In most tropical and subtropical marine waters, the copepod assemblage dominates the zooplankton community and it is usually characterized by small individuals, many of which are rare or absent in the open sea (McKinnon et al., 2008; McKinnon et al., 2005).

Copepods form a part of the diet of innumerable animals (Miyashita et al., 2009) and they are considered a key group in the marine pelagic environment (Gismervik, 2006). In the South Atlantic, there are more than 500 species, with a little more than 70 being endemic (Bradford-Grieve et al., 1999). There are no studies of copepod distribution and ecological indicators along the continental shelf of the Tropical Southwestern Atlantic (TSA) (Spalding et al., 2007), from the inner shelf to the shelf break. Worldwide, studies of this type are normally carried out on wide continental shelves (> 50 km) of subtropical and temperate zones and with clear differentiation of water masses. There are few studies of the occurrence and distribution of copepods in neritic and/or oceanic zones or on their role as ecological indicators in neritic waters (Benedetti et al., 2016; Costa et al., 2016a; Costa et al., 2016b;

Abbreviations: IndVal, indicator value; TSA, Tropical Southwestern Atlantic; ind., individuals; UPGMA, unweighted pair group method with arithmetic mean; SIMPROF, similarity profile analysis

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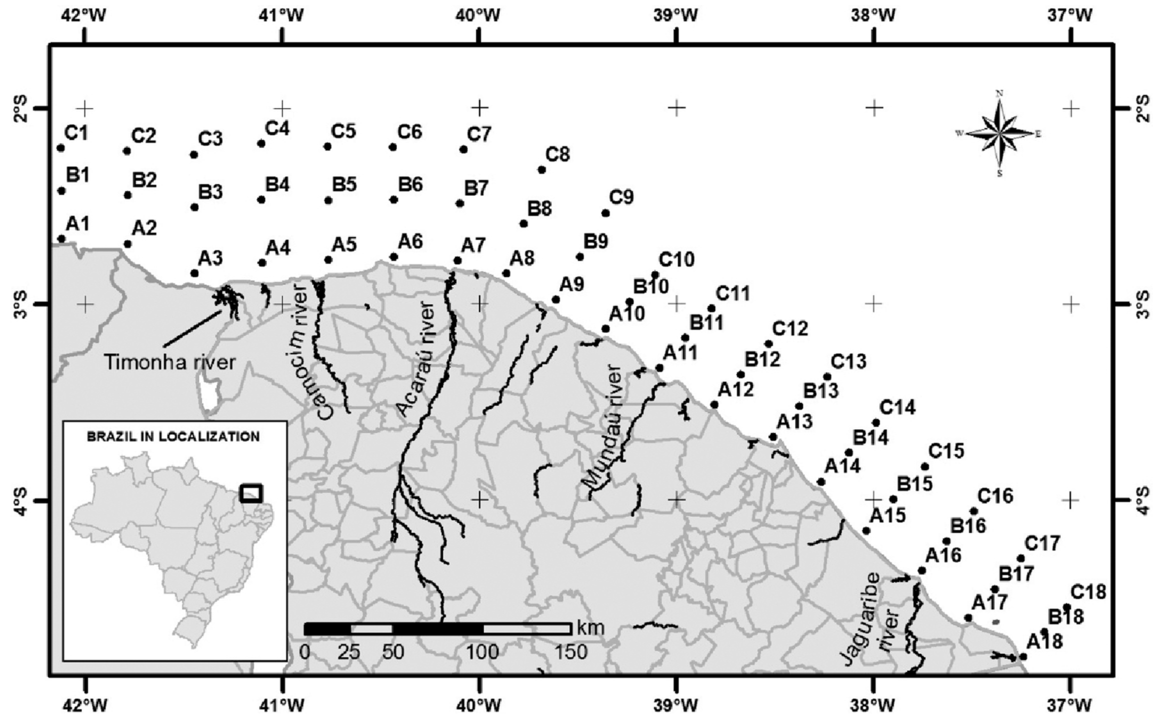


Fig. 1. Sampling stations along the continental shelf (inner A1–A18, middle B1–B18, and outer C1–C18) in the Tropical Southwestern Atlantic (TSA).

Shi et al., 2015). The presence of trade winds, absence of upwelling, consistent high temperatures, narrow continental shelf (< 50 km), and low inflow from estuaries (Mazzocchi and d'Alcalà, 1995) make this area important for filling gaps in scientific knowledge about functional diversity and the use of copepods as ecological indicators.

Considering the existing scientific knowledge (Cornils et al., 2010; Miyashita et al., 2009; Neumann-Leitão et al., 2008), it can be hypothesized that the variations in copepod assemblages are related to ecosystem functions. Therefore, the objective of this study was to reduce this gap by improving the understanding of pelagic ecology of the marine environment, via analysis of the assemblage of copepods based on functional trait diversity and ecological indicators.

2. Materials and methods

2.1. Study area

Our study area is located in the TSA (Fig. 1), under the influence of the Northern Brazil Current, and it is considered oligotrophic. It is located on a coastline 1038 km long with a continental shelf width of 35–90 km. This zone is immersed in the continuous subequatorial atmospheric circulation of the trade winds, which are persistent and intense throughout the year (Ferreira and Mello, 2005). The climate is dry (semiarid), and the estuaries are shallow, with low river flow (Schettini et al., 2017). Estuaries influencing this area include the Timonha and Ubatuba Rivers; the Parnaíba River Delta, an Environmental Protection Area (de Paula Filho et al., 2015); the Jaguaribe River estuary, which has the largest hydrographic basin in the semiarid coast of Brazil (Dias et al., 2016); and the Coreaú River, located in the northwestern portion of Ceará state (Miola et al., 2016). Historical flow data show a reduction in riverine contributions to the marine waters of the tropical continental shelf because of construction of dams along the hydrographic basin (Dias et al., 2013). This semiarid coast shelters tropical reefs (Soares et al., 2016) and mangrove forests (Ferreira and Lacerda, 2016).

2.2. Methodology and zooplankton sampling

Sampling was carried out on two occasions (July and October) during the dry season in 2010. Three profiles (inner, middle, and outer) were established along the continental shelf, each with 18 stations, parallel to the coast (Fig. 1).

Zooplankton samples were collected via 5-min superficial horizontal hauls using a cylindrical-conical net (mouth opening: 50 cm, mesh size: 300 μm) equipped with a General Oceanics flowmeter (General Oceanics, Miami, FL, USA). After collection, the samples were immediately fixed with 4% formaldehyde buffered with 4 g/L sodium tetraborate. Water environmental variables—salinity, dissolved oxygen (mg/L), temperature (°C), conductivity, pH, and turbidity—were measured with multiparameter probe YSI 6660.

In the laboratory, each sample was fractionated with a Motoda-type subsampler. Once the samples were split into suitable fractions, varying from 1/2 to 1/512, all copepods present in the subsamples were counted under a stereoscopic microscope (Omori and Ikeda, 1984). The species were identified based on the main literature (Björnberg, 1981; Bradford-Grieve et al., 1999; Tregouboff and Rose, 1957).

2.3. Data analysis

The density (ind.$\cdot$m^{-3}) was calculated for all species of copepods. The frequency of occurrence of each species was also calculated, with values being classified as very frequent (> 70%), frequent (70–30%), infrequent (30–10%), and sporadic (≤10%).

The assemblage of copepods was analysed using community descriptors and ecological indicator value. To describe the structure of copepod assemblages, Margalef's richness index (d), Pielou's evenness index (J′), Simpson's dominance index (λ), and the Shannon-Weaver diversity index (H′) were used. All the indexes were log (x + 1) transformed. The indicator value (IndVal) of a species was used to express species importance as ecological indicators in community classifications. An IndVal analysis calculates a single value for each species based on the fidelity and specificity of the species in relation to groups of sites, and tests for statistical significance of the associations by permutation. The IndVal of species *i* for class *j* is obtained using the equation $IndVal_{ij} = A_{ij} \times B_{ij} \times 100$, where A_{ij} is specificity, i.e., the proportion of the individuals of species *i* that are in class *j*; and B_{ij} is fidelity, i.e., the proportion of sites in class *j* that contain species *i* (Chew et al., 2015). IndVal was calculated using PC−ORD Version 6.08 (MJM software).

An extensive review of the literature on the functional traits of marine copepods was carried out. The functional traits were compiled into a matrix that included feeding type (active ambush feeding, passive ambush feeding, filter feeding, cruise feeding, or mixed feeding), trophic group (herbivore, carnivore, omnivore, detritivore, herbivore-omnivore, omnivore-carnivore, or detritivore-carnivore), and reproduction (broadcast spawner or sac spawner). The groups formed on the basis of Euclidean distance were assessed by the SIMPROF test at 5% significance.

Analysis of similarity of the oceanographic stations was conducted by a method of grouping the stations into clusters. For this purpose, we used a Bray-Curtis similarity matrix, where the raw data for species density was log-transformed. Based on this index, a cluster analysis was carried out using the unweighted pair group method with arithmetic mean (UPGMA). This multivariate analysis was used to evaluate possible patterns in the structure of the community in each part of the continental shelf (inner, middle, and outer).

The groups formed were evaluated by the SIMPROF test at the 5% significance level. A nonparametric analysis (one-way Kruskal-Wallis; KW) was performed to test significance of differences in environmental variables and community descriptors (H′, J′, λ, and d) between different profiles.

3. Results

3.1. Hydrographic conditions

There were no statistically significant differences in salinity, dissolved oxygen (mg/L), temperature (°C), conductivity, or pH among the profiles on the continental shelf. Only turbidity showed significant variation, mainly along the inner shelf (Table 1).

3.2. Copepod diversity

Overall, 38 species of copepods were identified: 20 Calanoida, 14 Cyclopoida, and 4 Harpacticoida (Table 2). Most (33) of these species are cosmopolitan, with seawide distribution. We found three species endemic to the Atlantic Ocean (*Calanopia americana*, *Labidocera nerii*, and *Farranula gracilis*) and two endemic to Brazil [*Acartia (Odontacartia) lilljeborgi* and *Pseudodiaptomus acutus*].

Calanoida was the most abundant taxon (13 families), followed by Cyclopoida (4 families) and Harpacticoida (2 families; Table 2). On the inner shelf, Temoridae (49.3% of all individuals; two species) was the most abundant family; on the middle shelf, it was Paracalanidae (43.9%, three species); and on the outer shelf, Clausocalanidae (28.7%, one species). Calanidae and Corycaeidae families were also common (Fig. 2).

Table 1
Environmental variables and values (mean and standard deviation) on the continental shelf of the semiarid coast (Tropical Southwestern Atlantic). Salinity (KW, P = 0.40), oxygen (KW, P = 0.80), temperature (KW, P = 0.82), conductivity (KW, P = 0.88), pH (KW, P = 0.96), and turbidity (KW, P = 0.0013). Different letters indicate a statistically significant difference between profiles in the environmental variable considered.

Environmental Variable	Inner shelf	Middle shelf	Outer shelf
Salinity	33.67 ± 1.41[a]	33.33 ± 1.36[a]	33.00 ± 1.32[a]
O_2 (mg/L)	4.74 ± 0.95[a]	4.84 ± 0.75[a]	5.09 ± 0.84[a]
Temperature (°C)	27.86 ± 0.41[a]	27.71 ± 0.37[a]	27.8 ± 0.26[a]
Conductivity	51.09 ± 1.94 [a]	50.67 ± 1.86[a]	50.26 ± 1.82[a]
pH	8.17 ± 0.03[a]	8.17 ± 0.04[a]	8.19 ± 0.45[a]
Turbidity	**9.28 ± 6.64[a]**	**3.5 ± 4.45[b]**	**3.22 ± 4.34[b]**

Bold value indicate the environmental variable with significant variation.

3.3. Spatial distribution and structure of the copepod assemblages

The near-shore profile (the inner shelf) had the highest density of copepods, followed by the outer and middle shelves. The highest values of richness (d) and diversity (H′) were observed on the outer and middle shelves, with the inner shelf having statistically significantly lower values for both measures. Pielou's evenness index (J′) remained constant across shelves (KW, P = 0.1296). Mean density did not show great variation between the middle and outer shelves, and the inner shelf had the highest value (Table 3).

Species that were common or exclusive to each profile are shown in Table 4. Among the organisms considered very frequent were *Paracalanus aculeatus* (adult and juvenile copepodite) and *Onychocorycaeus giesbrechti*, the latter being present in 100% of the samples analyzed. Some species were very frequent or frequent only on the middle shelf, including *A. lilljeborgi* and *Euterpina acutifrons*, while others were frequent only on the outer and inner shelf, including *Acrocalanus* cf. *longicornis*, *Temora stylifera*, *Oithona plumifera*, *Oncaea media*, *Corycaeus (Corycaeus) speciosus*, and *Undinula vulgaris* (Table 5). Along the TSA, the frequency of *T. turbinata* occurrence was higher on the inner and middle shelves, while that of congeneric native species *T. stylifera* was higher on the middle and outer shelves.

The cluster analysis of the stations showed a tendency to form three groups (Fig. 3) largely corresponding to physical location. Group I included nearly all the inner-shelf stations, and groups M and O included mostly the stations on the middle and outer shelves.

3.4. IndVal analysis

Temora turbinata (IndVal = 98.9, P = 0.0002), *Clausocalanus furcatus* (IndVal = 96.1, P = 0.0002), and *Ditrichocorycaeus amazonicus* (IndVal = 95.4, P = 0.0002) were indicator species (Table 6).

3.5. Functional groups

Two major functional groups were identified, sorted by spawning strategy (Fig. 4). These were subdivided according to the trophic regime and feeding strategy, and we defined seven subgroups (Table 7).

Groups 1, 2, and 3 are sac-spawners, and groups 4, 5, 6, and 7 are broadcasters. Group 1 is species that cruise feed. The trophic regime of this group was mainly omnivore-detritivore, with the exception of the species *C. furcatus* (omnivore-herbivore) and *Sapphirina nigromaculata* (carnivore). Group 2 is mostly Cyclopoida carnivores that feed via active ambush. *O. plumifera* was the only species in this group classified as an omnivore. Group 3 consists of three species of Harpacticoida. *E. acutifrons* and *Macrosetella gracilis* did not show a defined feeding strategy and are omnivore-herbivores. *Miracia efferata* is herbivorous and a cruise feeder.

Group 4 species are active ambush carnivores, except for *Centropages velificatus*, which has a mixed feeding strategy and is an omnivore-carnivore. Group 5 was composed of the smallest number of species, with only *C. americana* and *Scolecithrix danae*; both have no defined feeding strategy and are omnivorous and omnivore-herbivore, respectively. Group 6 consists of three Calanoida omnivores, and Group 7 is composed of herbivores and omnivore-herbivores. These last two groups together include all filter feeders.

4. Discussion

4.1. Hydrographic conditions

Along the continental shelf of the TSA, turbidity was the only

Table 2
A list of the copepod species on the continental shelf (Tropical Southwestern Atlantic).

Order	Family	Species
Calanoida	Calanidae (Dana, 1849)	*Undinula vulgaris* (Dana, 1849)
		Undinula vulgaris (juvenile copepodite)
	Paracalanidae (Giesbrecht, 1893)	*Acrocalanus cf. longicornis* Giesbrecht, 1888
		Calocalanus pavo (Dana, 1852)
		Paracalanus aculeatus Giesbrecht, 1888
		Paracalanus aculeatus (juvenile copepodite)
	Eucalanidae Giesbrecht, 1893	*Subeucalanus pileatus* (Giesbrecht, 1888)
		Subeucalanus pileatus (juvenile copepodite)
	Clausocalanidae Giesbrecht, 1893	*Clausocalanus furcatus* (Brady, 1883)
	Scolecitrichidae (Giesbrecht, 1893)	*Scolecithrix danae* (Lubbock, 1856)
		Scolecithrix danae (juvenile copepodite)
	Lucicutiidae (Sars, 1902)	*Lucicutia gaussae* Grice, 1963
		Lucicutia gaussae (juvenile copepodite)
	Centropagidae (Giesbrecht, 1893)	*Centropages velificatus* (Oliveira, 1947)
		Centropages velificatus (juvenile copepodite)
	Pseudodiaptomidae (Sars, 1902)	*Pseudodiaptomus acutus* (Dahl F., 1894)
		Pseudodiaptomus acutus (juvenile copepodite)
	Temoridae (Giesbrecht, 1893)	*Temora stylifera* (Dana, 1849)
		Temora stylifera (juvenile copepodite)
		Temora turbinata (Dana, 1849)
		Temora turbinata (juvenile copepodite)
	Candaciidae (Giesbrecht, 1893)	*Candacia pachydactyla* (Dana, 1849)
		Candacia pachydactyla (juvenile copepodite)
	Pontellidae (Dana, 1853)	*Calanopia americana* Dahl F., 1894
		Calanopia americana (juvenile copepodite)
		Labidocera acutifrons (Dana, 1849)
		Labidocera nerii (Krøyer, 1849)
		Labidocera nerii (juvenile copepodite)
		Labidocera spp. (juvenile copepodite)
		Pontellopsis brevis (Giesbrecht, 1889)
		Pontellopsis perspicax (Dana, 1849)
	Acartidae (Sars, 1900)	*Acartia (Odontacartia) lilljeborgi* Giesbrecht, 1889
Cyclopoida	Oithonidae (Dana, 1853)	*Oithona plumifera* Baird, 1843
		Oithona spp.
		Oithona spp. (juvenile copepodite)
	Oncaeidae (Giesbrecht, 1893)	*Oncaea media* Giesbrecht, 1891
		Oncaea mediterranea (Claus, 1863)
		Oncaea spp. (juvenile copepodite)
		Oncaea venusta Philippi, 1843
	Sapphirinidae (Thorell, 1859)	*Sapphirina nigromaculata* Claus, 1863
		Copilia mirabilis Dana, 1852
	Corycaeidae Dana, 1852	*Corycaeus (Corycaeus) speciosus* Dana, 1849
		Ditrichocorycaeus amazonicus (Dahl F., 1894)
		Onychocorycaeus giesbrechti (Dahl F., 1894)
		Onychocorycaeus latus (Dana, 1849)
		Farranula gracilis (Dana, 1849)
		Farranula spp.
Harpacticoida	Ectinosomatidae (Sars, 1903)	*Macrosetella gracilis* (Dana, 1847)
		Microsetella rosea (Dana, 1847)
	Miraciidae (Dana, 1846)	*Miracia efferata* Dana, 1849
	Euterpinidae (Brian, 1921)	*Euterpina acutifrons* (Dana, 1847)

environmental variable with significant differences among profiles (inner, middle, and outer shelf). It showed high values on the inner shelf owing to resuspension of bottom material caused by the interaction between wave dynamics and the shallow coastal waters (Medeiros et al., 2007). In general, coastal regions are more productive than oceanic zones mainly because of the supply of nutrients and organic matter from the continent (Sigman and Hain, 2012). Drainage of estuaries and superficial flow from the continent may modify environmental characteristics of the continental shelf (e.g., the circulation and concentration of nutrients), thereby influencing the composition and distribution of the plankton community (Albaina and Irigoien, 2004; Morgan et al., 2005; Mota et al., 2017). Nonetheless, samples were collected during the dry season, when there is practically no outwelling in most estuaries along the tropical semiarid coast (Dias et al., 2013). In turbid coastal waters found on the inner shelf, the alien *T. turbinata* dominates and can be considered an ecological indicator.

4.2. Composition and characteristics of Copepoda

Calanoida is a highly important contributor to the density and biomass of marine plankton (Melo Júnior et al., 2016). Juvenile calanoids (copepodites; see Table 4) are an important member of the copepod assemblage (Favareto et al., 2009; Webber and Roff, 1995) and of the secondary production (Miyashita et al., 2009) along the tropical coast.

The calanoid copepods (family Paracalanidae) are environmentally tolerant species with a broad geographical distribution (Cornils and Blanco-Bercial, 2013), frequently found in tropical and subtropical regions (Bowman, 1971). *Paracalanus* is one of the most important genera in this family in the Brazilian neritic zone (Lopes et al., 1999), and *P. aculeatus* is the most common species, thought to belong to coastal and continental shelf regions (Bowman, 1971). *Acrocalanus longicornis* and *Calocalanus pavo* can be found in tropical regions (Björnberg, 1981; Bradford-Grieve et al., 1999).

T. turbinata (Temoridae) has consistently been found in various

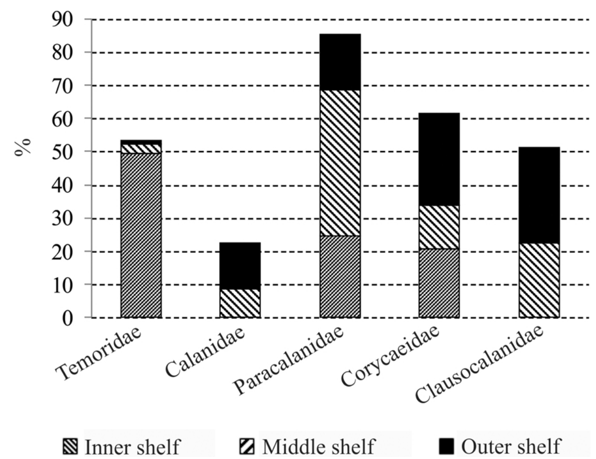


Fig. 2. Relative abundance levels of the main families of Copepoda on the continental shelf (Tropical Southwestern Atlantic).

Table 3
The number of species (S), Margalef's richness index (d), Pielou's evenness index (J′), Shannon-Weaver diversity index (H′), and average density of the copepod community along the inner, middle, and outer shelves (Tropical Southwestern Atlantic). S (KW, $P < 0.0001$), D (KW, $P < 0.0001$), J′ (KW, $P = 0.12$), H′ (KW, $P < 0.0008$).

	Inner shelf	Middle shelf	Outer shelf
S	11.78 ± 2.49^a	16.83 ± 2.64^b	18.28 ± 3.08^b
d	4.37 ± 1.39^a	7.72 ± 2.12^b	7.18 ± 1.35^b
J′	0.84 ± 0.07^a	0.80 ± 0.06^a	0.81 ± 0.05^a
H′($\log_e$)	2.05 ± 0.20^a	2.25 ± 0.26^b	2.34 ± 0.19^b
Average density (ind/m^3)	2.49 ± 19.53	0.59 ± 3.46	0.69 ± 2.16

Different letters indicate significant differences between profiles ($P < 0{,}05$)

environments in Brazil, including coastal zones and estuaries (Ara, 2002; Silva et al., 2004; Silva et al., 2003; Sterza and Fernandes, 2006). Recognized as an exotic species on the Brazilian coast, this copepod was probably introduced through ballast water (Silva et al., 2004). *T. turbinata* is considered both coastal and oceanic (Björnberg, 1981; Bradford-Grieve et al., 1999), being extremely widespread and tolerant of a wide range of environmental conditions (Bradford, 1977). Our results indicate that this ecological indicator is more abundant on the inner shelf, which is near the estuaries and turbid coastal waters.

The species endemic to the Brazilian coast, *A. lilljeborgi* and *P. acutus*, were found only along the inner shelf adjacent to the coast. *A. lilljeborgi* is a copepod characteristic of Brazilian estuaries (Björnberg, 1981) and is considered an indicator of coastal waters (Björnberg, 1963). The copepods of the *Pseudodiaptomus* genus are the only typically estuarine ones (Björnberg, 1981; Bradford-Grieve et al., 1999) found in this study. The species *P. acutus* is very common in estuarine environments in the Tropical Atlantic (Magalhães et al., 2009; Marcolin et al., 2010; Sankarankutty et al., 1995; Silva et al., 2003).

4.3. Spatial distribution and structure of the copepod community

The results provided an insight into the distribution of copepods in three profiles parallel to the TSA (inner, middle, and outer continental shelves), giving evidence supporting the hypothesis that these profiles have different structures of copepod assemblages and mainly distinguish the inner shelf from the middle and outer shelves. The composition of the zooplankton on tropical continental shelves is characterized by a persistent gradient from the coast to the open sea (Sammarco and Crenshaw, 1984; Walter, 1989). The data presented here point to the existence of a gradient of plankton distribution even on narrow continental shelves (< 50 km). The differences between profiles are possibly due to the hydrodynamics in the region, which generates heterogeneity in the tropical water masses along this continental shelf (Dias et al., 2010).

Along the TSA continental shelf, greater diversity was observed in the outer-shelf region than in regions closer to the coast. This phenomenon probably can be explained by the fact that this is a more stable zone, richer in species, as compared to the coastal zone. This pattern is suggested by research carried out in the Gulf of Naples (Italy, west of the Mediterranean Sea) (Mazzocchi and d'Alcalà, 1995), off the northeast coast of Brazil (South Atlantic Ocean) (Cavalcanti and Larrazábal, 2004), on the northwest coast of Australia (Indian Ocean) (McKinnon et al., 2008), off Indonesia (Indian Ocean) (Cornils et al., 2010), and off east Africa (Schnack-Schiel et al., 2010). It is possible that the proximity of the middle and outer shelves to the oceanic water masses favors increased species richness as compared to the inner shelf of the coastal zone, which, according to our results, has lower copepod diversity and richness.

The density of copepods (inner shelf > middle and outer shelves) and species richness (middle and outer shelves > inner shelf) indicate the continental and oceanic influences on the zooplankton. A mixture of neritic and oceanic species was found on the middle and outer shelves; this situation made it difficult to separate these communities in a consistent way. This pattern is confirmed by the cluster analysis, which revealed lower similarity among stations in groups M and O, and greater similarity in the inner-shelf group (I). The temporal distribution of zooplankton is directly influenced by physical processes such as mixing caused by winds, tidal advection, and vortices (Fernández et al., 1993). The Macau Vortex, whose radius measures approximately 150 km (Marin, 2009), may have assisted the invasion and consequent mixing of oceanic waters with coastal waters on the continental shelf at the extreme east end of our study site.

The greater similarity between the middle and outer shelf is related to their locations, which are influenced by oceanic waters to different degrees. All the species common to both profiles (e.g., *C. pavo*, *A.* cf. *longicornis*, and *O. plumifera*) and exclusive to the outer shelf (e.g., *Candacia pachydactyla*, *Lucicutia gaussae*, and *M. efferata*) are oceanic (Bradford-Grieve et al., 1999). Because the planktonic community is

Table 4
Exclusive and common copepod species on the inner, middle, and outer shelves (Tropical Southwestern Atlantic).

	Exclusive species	Species in common
Inner shelf	*Subeucalanus pileatus* (juvenile copepodite), *Acartia* (Odontacartia) *lilljeborgi,* and *Pseudodiaptomus acutus* (adult and juvenile copepodite).	
Middle shelf	*Temora stylifera* (juvenile copepodite), *Labidocera acutifrons, Pontellopsis perspica,x* and *Pontellopsis brevis*	
Outer shelf	*Scolecithrix danae* (juvenile copepodite), *Candacia pachydactyla* (adult and juvenile copepodite), *Lucicutia gaussae,* and *Miracia efferata.*	
Inner and Middle shelf		*Labidocera nerii* (juvenile copepodite), and *Euterpina acutifrons.*
Middle and Outer shelf		*Calocalanus pavo, Acrocalanus* cf.*longicornis, Scolecithrix danae, Lucicutia gaussae* (juvenile copepodite), *Oithona plumifera, Oncaea venusta, Copilia mirabilis, Corycaeus* (Corycaeus) *speciosus,* and *Microsetella rosea.*

Table 5
Average density (Ind m^{-3}) and frequency of occurrence (%) of copepods on the inner, middle, and outer shelves (Tropical Southwestern Atlantic). Very frequent (****), frequent (***), infrequent (**), sporadic (*), and absent (−).

	Inner shelf		Middle shelf		Outer shelf	
	Ind m^{-3}	F	Ind m^{-3}	f	Ind m^{-3}	F
Undinula vulgaris (Dana, 1849)	0.00	*	0.66	****	0.87	****
Undinula vulgaris (juvenile copepodite)	0.03	**	2.23	****	4.48	****
Acrocalanus cf. longicornis Giesbrecht, 1888	0.00	–	0.22	***	0.94	****
Calocalanus pavo (Dana, 1852)	0.00	–	0.01	**	0.93	****
Paracalanus aculeatus Giesbrecht, 1888	1.43	****	3.44	****	0.70	****
Paracalanus aculeatus (juvenile copepodite)	31.12	****	10.83	****	3.85	****
Subeucalanus pileatus (Giesbrecht, 1888)	0.05	**	0.05	**	0.13	***
Subeucalanus pileatus (juvenile copepodite)	0.02	*	0.00	–	0.00	–
Clausocalanus furcatus (Brady, 1883)	0.05	**	7.43	****	11.12	****
Scolecithrix danae (Lubbock, 1856)	0.00	–	0.03	**	0.01	**
Scolecithrix danae (juvenile copepodite)	0.00	–	0.00	–	0.01	*
Lucicutia gaussae Grice, 1963	0.00	–	0.00	–	0.04	*
Lucicutia gaussae (juvenile copepodite)	0.00	–	0.00	*	0.04	**
Centropages velificatus (Oliveira, 1947)	1.01	****	0.11	***	0.13	**
Centropages velificatus (juvenile copepodite)	0.56	****	0.07	**	0.01	**
Pseudodiaptomus acutus (Dahl F., 1894)	0.08	**	0.00	–	0.00	–
Pseudodiaptomus acutus (juvenile copepodite)	0.01	*	0.00	–	0.00	–
Temora stylifera (Dana, 1849)	0.01	*	0.24	****	0.24	***
Temora stylifera (juvenile copepodite)	0.00	–	0.08	**	0.00	–
Temora turbinata (Dana, 1849)	55.52	****	0.39	****	0.10	**
Temora turbinata (juvenile copepodite)	9.42	****	0.26	***	0.03	**
Candacia pachydactyla (Dana, 1849)	0.00	–	0.00	–	0.03	**
Candacia pachydactyla (juvenile copepodite)	0.00	–	0.00	–	0.00	*
Calanopia americana Dahl F., 1894	1.15	***	0.38	****	0.90	**
Calanopia americana (juvenile copepodite)	0.85	****	0.47	****	0.06	**
Labidocera acutifrons (Dana, 1849)	0.00	–	0.05	**	0.00	–
Labidocera nerii (Krøyer, 1849)	0.05	**	0.04	**	0.03	**
Labidocera nerii (juvenile copepodite)	0.02	**	0.03	**	0.00	–
Labidocera spp. (juvenile copepodite)	0.23	***	0.64	***	0.23	****
Pontellopsis brevis (Giesbrecht, 1889)	0.00	–	0.00	*	0.00	–
Pontellopsis perspicax (Dana, 1849)	0.00	–	0.00	*	0.00	–
Acartia (*Odontacartia*) *lilljeborgi* Giesbrecht, 1889	0.85	***	0.00	–	0.00	*
Oithona plumifera Baird, 1843	0.00	–	0.43	***	1.17	****
Oithona spp.	0.66	***	0.04	***	0.03	**
Oithona spp. (juvenile copepodite)	0.00	–	0.03	**	0.05	**
Oncaea media Giesbrecht, 1891	0.00	*	0.00	***	0.00	****
Oncaea mediterranea (Claus, 1863)	0.02	–	0.32	–	1.79	*
Oncaea spp. (juvenile copepodite)	0.00	–	0.00	–	0.01	*
Oncaea venusta Philippi, 1843	0.00	–	0.01	*	0.03	**
Sapphirina nigromaculata Claus, 1863	0.00	–	0.00	–	0.00	*
Copilia mirabilis Dana, 1852	0.00	–	0.04	*	0.02	**
Corycaeus (*Corycaeus*) *speciosus* Dana, 1849	0.00	–	0.15	***	0.47	****
Ditrichocorycaeus amazonicus (Dahl F., 1894)	9.03	****	0.35	****	0.11	***
Onychocorycaeus giesbrechti (Dahl F., 1894)	17.91	****	2.80	****	1.85	****
Onychocorycaeus latus (Dana, 1849)	0.00	*	0.01	**	0.16	****
Farranula gracilis (Dana, 1849)	0.01	**	0.59	***	7.40	****
Farranula spp.	0.24	***	0.42	****	0.74	****
Macrosetella gracilis (Dana, 1847)	0.13	**	0.11	**	0.09	***
Microsetella rosea (Dana, 1847)	0.00	–	0.00	*	0.00	*
Miracia efferata Dana, 1849	0.00	–	0.00	–	0.01	**
Euterpina acutifrons (Dana, 1847)	1.24	****	0.02	**	0.00	–

unevenly distributed (Berasategui et al., 2006) and is often structured in patchy assemblages, there is a close relation between this community and the characteristics of the marine environment (Nybakken and Bertness, 2004). Despite the high densities of zooplankton along the inner shelf of the semiarid coast, the oligotrophic waters of the Northern Brazil Current and the significant lack of continental water drainage result in a relatively homogeneous environment (Dias et al., 2010). The historical flow data show a reduction in the contribution of river flow into the continental shelf waters because of increases in the number of dams built along the river basins in the region (Dias et al., 2013) and the occurrence of extreme droughts in this region (Marengo et al., 2016).

4.4. Functional groups

The functional groups described for the continental shelf off the TSA coast highlight the connections of species through their ecological functions. The use of traits with functional diversity potentially enables a more mechanistic understanding of variation and regulation of zooplankton communities than is possible with taxonomic diversity alone (Pomerleau et al., 2015). Functional group characteristics that were defined here are the spawning strategy, trophic regime, and feeding strategy. The spawning strategy is regulated by the weight of a female, environmental temperature, and food (Blaxter et al., 1998; Bunker and Hirst, 2004). Broadcaster species often show development of eggs within shorter periods, when compared with sac spawners (Kiørboe and Sabatini, 1995). The trophic regime is diverse, with most being omnivorous species and the rest predominantly herbivorous, carnivorous, or

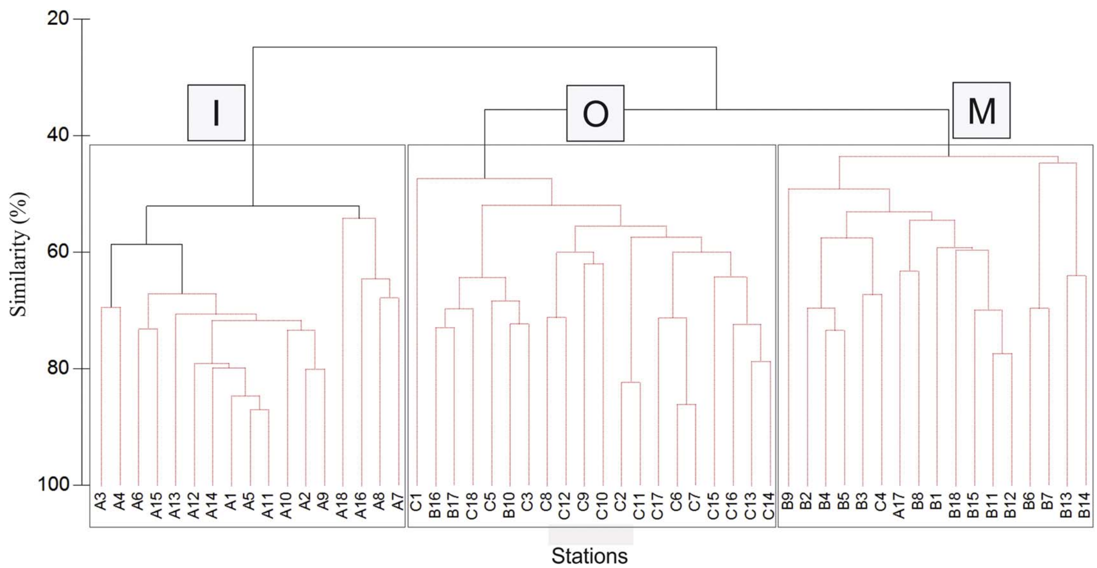


Fig. 3. Clusters of the copepod assemblages on the continental shelf (Tropical Southwestern Atlantic) showing groups I, M, and O. I: Inner Shelf, M: Middle Shelf, O: Outer Shelf. Groups are based on the SIMPROF test with a 5% significance level (gray dotted line).

Table 6
Indicator values (IndVal analysis) of the copepod assemblages on the inner, middle, and outer continental shelves (Tropical Southwestern Atlantic). S.D. = Standard Deviation. Maxgrp: Maximo Group.

Taxa	Maxgrp	Value (IV)	Mean	S.D.	p
Nauplius Copepoda	2	5.0	6.9	2.89	0.6499
Calanoida (Copepodite juvenile)	2	20.0	18.4	5.23	0.3077
Acartia (*Odontacartia*) *lilljeborgi*	1	70.4	16.7	5.86	0.0002
Acrocalanus cf. longicornis	3	71.4	27.3	5.99	0.0002
Calanopia americana	1	44.4	40.0	8.14	0.2749
Calocalanus pavo	3	52.3	20.7	5.86	0.0002
Candacia pachydactyla	3	21.1	9.5	4.51	0.0306
Centropages velificatus	1	73.4	31.8	6.75	0.0002
Clausocalanus furcatus	3	**96.1**	33.3	7.78	0.0002
Labidocera acutifrons	2	9.2	9.4	4.54	0.4017
Labidocera nerii	2	25.1	20.8	5.52	0.1910
Labidocera spp. (Copepodite juvenile)	2	36.4	30.6	6.32	0.1696
Lucicutia gaussae	3	30.0	11.0	4.61	0.0044
Paracalanus aculeatus	1	64.0	53.7	5.69	0.0384
Pontellopsis perspicax	2	11.1	5.8	3.64	0.2018
Pseudodiaptomus acutus	1	17.6	7.7	3.98	0.0244
Scolecithrix danae	3	20.1	9.6	4.75	0.0516
Subeucalanus pileatus	3	16.8	21.1	6.14	0.7329
Temora stylifera	2	38.0	25.5	6.05	0.0412
Temora turbinata	1	**98.9**	48.9	13.57	0.0002
Undinula vulgaris	3	57.5	32.5	5.22	0.0010
Copilia mirabilis	3	14.2	10.6	4.98	0.2324
Corycaeus (*Corycaeus*) *speciosus*	3	82.1	25.3	6.76	0.0002
Ditrichocorycaeus amazonicus	1	**95.4**	42.6	8.33	0.0002
Onychocorycaeus giesbrechti	1	80.5	48.2	7.83	0.0002
Onychocorycaeus latus	3	51.6	20.1	5.49	0.0002
Farranula gracilis	3	83.9	30.6	7.27	0.0002
Farranula spp.	3	56.0	38.3	5.26	0.0016
Oithona plumifera	3	91.2	28.6	6.42	0.0002
Oithona spp.	1	47.9	35.7	8.57	0.1008
Oncaea (Copepodite juvenile)	3	5.3	5.6	0.26	1.0000
Oncaea media	3	89.4	32.4	8.77	0.0002
Oncaea venusta	3	10.3	9.5	4.60	0.3691
Sapphirina nigromaculata	2	5.6	5.6	0.26	0.6461
Euterpina acutifrons	1	75.4	20.0	6.84	0.0002
Macrosetella gracilis	3	27.7	23.6	6.57	0.2268
Microsetella rosea	2	4.0	6.2	3.35	0.6571
Miracia efferata	3	10.5	5.6	3.81	0.3273

Bold value indicate the main ecological indicators.

detritivorous (Calbet, 2008; Turner, 2004). In feeding, there are three strategies developed by copepods: (1) capture the prey by straining the water (filtering), (2) wait for prey to pass by then attack it (active ambush), or (3) capture the prey that arrives to the predator via movement of water (cruise) (Kiørboe and Sabatini, 1995).

The spawning strategy subdivided the copepods of the continental shelf into sac spawners and broadcasters. Most of the Calanoida are broadcasters, while Cyclopoida and Harpacticoida are sac spawners (Blaxter et al., 1998; Melo-Júnior, 2009). Sac spawners showed cruise and active ambush feeding strategies, while the broadcasters were mostly filter feeders, a result also reported by Benedetti et al. (2016).

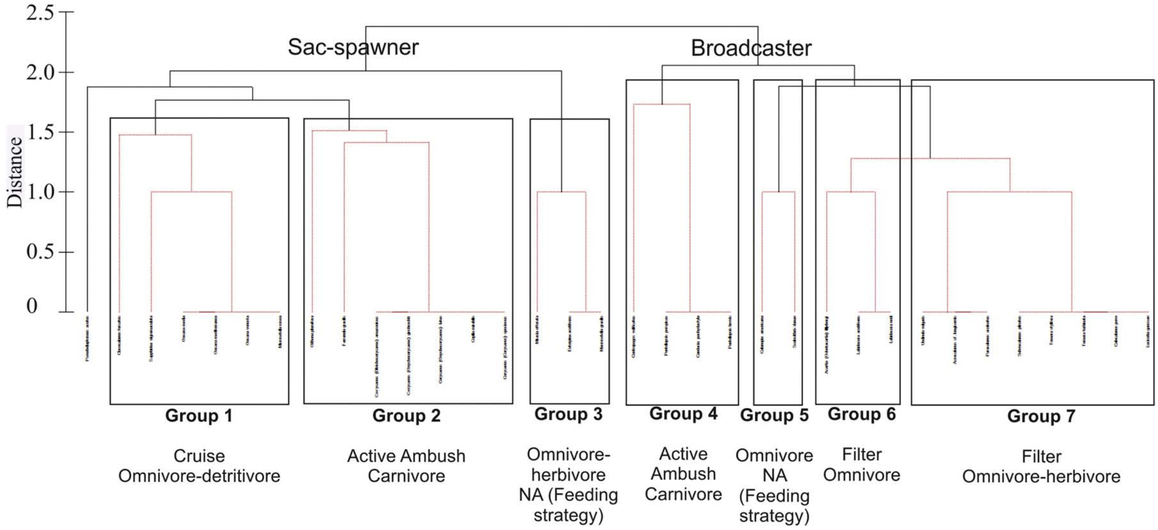
The cruise strategy, whose species were classified here as functional group 1, is not very efficient because copepods push water away when they move, allowing only a small fraction of the prey to be intercepted (Kiørboe, 2011). In this group, we find all *Oncaea* species. This genus is abundant in most oceans (Kattner et al., 2003) and feeds mainly on surface materials such as particles, bacteria, and integument or the fluid of gelatinous macrozooplankton (Go et al., 1998).

Cyclopoida, here represented by *Corycaeus* species (group 2), are mainly carnivores that feed on copepod nauplii (Turner, 1984) and capture food actively (Boltovskoy, 1999). Active ambush (groups 4 and 6) is common among smaller pelagic copepods, primarily of the genus *Oithona*, while cruise feeding dominates among the larger species. Three species of Harpacticoida were compiled into functional group 3. This order is very diverse in their diet, feeding on bacteria (Rieper, 1978), microalgae (Carman and Thistle, 1985), and metazoan tissues (Seifried and Dürbaum, 2000), and they may resort to parasitism.

C. americana and *S. danae* are the only members of group 5. *C. americana* is endemic to the Atlantic Ocean and has a strong habit of vertical migration with a night or twilight pattern (Turner et al., 1979). It is a frequent and even abundant species in continental shelf waters throughout Brazil (Boltovskoy, 1981). *S. danae* has oceanic distribution (Bradford-Grieve et al., 1999) and consistent vertical migration (Hassett and Boehlert, 1999). It is saprophagous and eats discarded Larvacea houses and copepodite carapaces (Ohtsuka et al., 1993). Filter feeders, gathered in groups 6 and 7, are all Calanoida. This order is mostly filter feeding and herbivorous or omnivorous (Kouwenberg, 1994), feeding on algae, bacteria, small animals, and debris.

4.5. IndVal analysis

Most plankton species are considered excellent bioindicators of



Functional groups	**Group 1**	*Clausocalanus furcatus, Sapphirina nigromaculata, Oncaea media, Oncaea mediterranea, Oncaea venusta,* and *Microsetella rosea*
	Group 2	*Oithona plumifera, Farranula gracilis, Ditrichocorycaeus amazonicus, Onychocorycaeus giesbrechti, Onychocorycaeus latus*, and *Copilia mirabilis*
	Group 3	*Miracia efferata, Euterpina acutifrons* and *Macrosetella gracilis*
	Group 4	*Centropages velificatus, Pontellopsis perspicax, Candacia pachydactyla,* and *Pontellopsis brevis*
	Group 5	*Calanopia americana* and *Scolecithrix danae*
	Group 6	*Acartia (Odontacartia) lilljeborgi* and *Labidocera nerii*
	Group 7	*Undinula vulgaris, Acrocalanus cf. longicorns, Paracalanus aculeatus, Subeucalanus pileatus, Temora stylifera, Temora turbinata, Calocalanus pavo*, and *Lucicutia gaussae*

Fig. 4. Identification of seven functional groups of copepods on the continental shelf (Tropical Southwestern Atlantic).

environmental influences because they have a short life cycle and respond quickly to changes in the environment (Costa et al., 2004). *T. turbinata*, *C. furcatus*, and *D. amazonicus* were found to be ecological indicators of the continental shelf by the IndVal analysis. This test identified these three species according to the fidelity and specificity in relation to groups of sites (inner, middle, and outer shelf).

In the functional group analysis, these three species (ecological indicators) have distinct functional traits. Because functional groups are a set of species with or without phylogenetic affinity, which share similar functional traits and that respond similarly to environmental conditions (Lavorel et al., 1997), we propose that there is only a small niche overlap. For example, their feeding strategies are different; therefore, there is no competition for food. Another relevant result is that these species have been reported in different areas of the continental shelf. *T. turbinata* and *D. amazonicus* show higher density in the near-shore waters, while *C. furcatus* in the outer-shelf waters close to the shelf break. Thus, these species can be considered ecological indicators of the different continental shelf waters.

T. turbinata is an especially important ecological indicator, because this species did not occur in Northeastern Brazil before 1993 (Araujo

Table 7
Trait characteristics of the seven identified functional groups of copepods on the continental shelf (Tropical Southwestern Atlantic). NA = not available.

Funcional trait	Category	Functional groups							
		Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Total number of species
Spawning strategy	Broadcaster	0	0	0	4	2	3	8	17
	Sac-spawner	6	7	3	0	0	0	0	16
Trophic group	Herbivore	0	0	1	0	0	0	3	4
	Omnivore	0	1	0	0	1	2	0	4
	Carnivore	1	6	0	3	0	0	0	10
	Omnivore-Herbivore	1	0	2	0	0	0	5	8
	Omnivore-Carnivore	0	0	0	1	0	1	0	2
	Herbivore-Detritivore	0	0	0	0	0	0	0	0
	Omnivore-Detritivore	4	0	0	0	1	0	0	5
Feeding type	Filter	0	0	0	0	0	3	8	11
	Active ambush	0	6	0	3	0	0	0	9
	Mixed	0	0	0	1	0	0	0	1
	Cruise	6	0	0	0	0	0	0	6
	NA	0	1	3	0	2	0	0	6

and Montú, 1993) and it now dominates several coastal and estuarine areas (Silva et al., 2004). This species may have been introduced in ballast water or transported by currents along the Brazilian coastline. Nevertheless, additional studies are necessary to confirm its origin. Before the identification of *T. turbinata*, the only species of this genus in Brazilian coastal waters was *T. stylifera* (Ferreira et al., 2009). In our results, the congener *T. stylifera* is now common on the middle and outer shelf. *T. turbinata* is a widespread coastal and oceanic species (Björnberg, 1981; Bradford-Grieve et al., 1999), tolerant of a wide range of conditions in its environment (Bradford, 1977). Ara (2002) suggested that the potential for genetic adaptation and effective acclimation of *T. turbinata*, along with tolerance to temperature, salinity, and pollution, favor its advance in continental waters. Our results indicate that this exotic species is abundant on the middle shelf and mainly on the inner shelf. This species has adapted to the environment near outfall outlets, which may act as a bottleneck to other zooplankton species less tolerant to pollution in coastal waters (Tseng et al., 2008). Despite the ecological and socioeconomic relevance, it is alarming how little is known about marine bioinvasions, especially those driven by small invertebrates and microscopic organisms (Marques, 2011). Among these mostly ignored organisms, zooplankton is an important albeit neglected component of biological invasions, and the potential repercussions on the trophic ecology and community equilibrium of marine systems are poorly understood.

Despite being reported as important species in tropical pelagic webs, little information is available about the ecology of the small copepods *C. furcatus* and *D. amazonicus* (both ecological indicators according to our results). *C. furcatus* is a widespread species, with occurrence in epipelagic subtropical oceans (Frost, 1968) and oligotrophic waters (Peralba and Mazzocchi, 2004). It is very common in the North Atlantic Ocean waters (Grice and Hart, 1962) as well as the Brazilian continental shelf (Valentin and Monteiro-Ribas, 1993). *D. amazonicus* occurs in lower abundance in areas where *O. giesbrechti* (Björnberg, 1963) is overabundant. It is observed frequently in waters with salinity of 34 ppt. These two species of the genus *Corycaeus* have already invaded San Francisco Bay through ballast water and Chilean waters through ballast or other means (Hidalgo et al., 2010). This is a relevant topic for research, because in the future, other invasive species may be introduced overseas, and thus, may affect the zooplankton structure and their roles.

In conclusion, the composition and ecological indicators along the continental shelf of the TSA suggest that there are differences in the structure of the assemblages depending on the distance from the coast and functional traits. The copepod assemblage varies among the shelf profiles, from the inner to the outer shelf. *Temora turbinata* (alien species), *Clausocalanus furcatus*, and *Ditrichocorycaeus amazonicus* (native species) were found to be ecological indicators. These species have different functional traits and distinct cross-shelf distributions, where the alien species dominates the turbid coastal waters, and *C. furcatus* is an indicator of outer-shelf waters. Thus, these species can be considered ecological indicators of the different continental shelf waters. The results also underscore the need to understand functional diversity and ecological indicators (native and exotic species) in tropical marine ecosystems. To better understand this relation, it is important to conduct long-term monitoring including sampling stations in the oceanic domain and temporal series.

Conflicts of interest

None.

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References

Albaina, A., Irigoien, X., 2004. Relationships between frontal structures and zooplankton communities along a cross-shelf transect in the Bay of Biscay (1995–2003). Mar. Ecol. Prog. Ser. 284, 65–75. http://dx.doi.org/10.3354/meps284065.

Ara, K., 2002. Temporal variability and production of temora turbinata (Copepoda: calanoida) in the cananéia lagoon estuarine system, São paulo, Brazil. Sci. Mar. 66, 399–406. http://dx.doi.org/10.3989/scimar.2002.66n4399.

Araujo, H.M.P., Montú, M., 1993. Novo registro de *Temora turbinata* (Dana, 1949) (Copepoda, Crustacea) para águas atlânticas. Náuplius 1, 89–90.

Barton, A.D., Pershing, A.J., Litchman, E., Record, N.R., Edwards, K.F., Finkel, Z.V., Kiørboe, T., Ward, B.A., 2013. The biogeography of marine plankton traits. Ecol. Lett. 16, 522–534. http://dx.doi.org/10.1111/ele.12063.

Benedetti, F., Gasparini, S., Ayata, S., 2016. Identifying copepod functional groups from species functional traits. J. Plankton Res. 38, 159–166. http://dx.doi.org/10.1093/plankt/fbv096.

Berasategui, A.D., Menu Marque, S., Gómez-Erache, M., Ramírez, F.C., Mianzan, H.W., Acha, E.M., 2006. Copepod assemblages in a highly complex hydrographic region. Estuar. Coast. Mar. Sci. 66, 483–492. http://dx.doi.org/10.1016/j.ecss.2005.09.014.

Björnberg, T.K.S., 1963. On the marine free-living copepods off Brazil. Boletim do Instituto Oceanográfico 13, 03–142. http://dx.doi.org/10.1590/S0373-55241963000100001.

Björnberg, T.S.K., 1981. Copepoda Mar del Plata. In: Boltovskoy, D. (Ed.), Atlas del Zooplancton del Atlántico Sudoccidental y Metodos de Trabajo con el Zooplancton Marino. INIDEP, pp. 587–679.

Blaxter, J.H.S., Douglas, B., Tyler, P.A., Mauchline, J., 1998. The Biology of Calanoid Copepods. Academic Press.

Boltovskoy, D., 1981. Atlas del zooplancton del Atlantico Sudoocidental y métodos de com el zooplancton marino. Mar del Plata: INIDEP.

Boltovskoy, D., 1999. South Atlantic zooplankton Backhuys Publishers, Leiden.

Bowman, T.E., 1971. The distribution of calanoid copepods off the southeastern United States between cape hatteras and Southern Florida. Smithsonian Contrib. Zool. 96, 1–58.

Bradford, J.M., 1977. Distribution of the pelagic copepod temora turbinata in New Zealand coastal waters, and possible trans-tasman population continuity. New Zealand J. Mar. Freshw. Res. 11, 131–144. http://dx.doi.org/10.1080/00288330.1977.9515666.

Bradford-Grieve, J.M., Marhaseva, E.L., Rocha, C.E.F., Abiahy, B., 1999. Copepoda. In: Boltovskoy, D. (Ed.), South Atlantic Zooplankton. Backhuys Publishers, Leiden, pp. 869–1098.

Bunker, A.J., Hirst, A.G., 2004. Fecundity of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature and body weight. Mar. Ecol. Prog. Ser. 279, 161–181. http://dx.doi.org/10.3354/meps279161.

Calbet, A., 2008. The trophic roles of microzooplankton in marine systems. ICES J. Mar. Sci.: J. du Conseil. 65, 325–331. http://dx.doi.org/10.1093/icesjms/fsn013.

Carman, K.R., Thistle, D., 1985. Microbial food partitioning by three species of benthic copepods. Mar. Biol. 88, 143–148. http://dx.doi.org/10.1007/BF00397161.

Cavalcanti, E.A.H., Larrazábal, M.E.L.d., 2004. Macrozooplâncton da Zona Econômica Exclusiva do Nordeste do Brasil (segunda expedição oceanográfica − REVIZEE/NE II) com ênfase em Copepoda (Crustacea). Rev. Brasil. de Zool. 21, 467–475. http://dx.doi.org/10.1590/S0101-81752004000300008.

Chew, L., Chong, V.C., Ooi, A.L., Sasekumar, A., 2015. Vertical migration and positioning behavior of copepods in a mangrove estuary: interactions between tidal, diel light and lunar cycles. Estuar. Coast. Mar. Sci. 152, 142–152. http://dx.doi.org/10.1016/j.ecss.2014.11.011.

Cornils, A., Blanco-Bercial, L., 2013. Phylogeny of the paracalanidae giesbrecht, 1888 (Crustacea: copepoda: calanoida). Mol. Phylogenet. Evol. 69, 861–872. http://dx.doi.org/10.1016/j.ympev.2013.06.018.

Cornils, A., Schulz, J., Schmitt, P., Lanuru, M., Richter, C., Schnack-Schiel, S.B., 2010. Mesozooplankton distribution in the Spermonde Archipelago (Indonesia, Sulawesi) with special reference to the Calanoida (Copepoda). Deep Sea Res. Part II 57, 2076–2088. http://dx.doi.org/10.1016/j.dsr2.2010.09.011.

Costa, M.F., Eskinazi-Leça, E., Neumann-Leitão, S., 2004. In: Bagaço, E. (Ed.), Bioindicadores Da QualidadeAmbiental. Oceanografia: Um Cenário Tropical, Recife (p. 761).

Costa, B.N.S., Pinheiro, S.C.C., Amado, L.L., de Oliveira Lima, M., 2016a. Microzooplankton as a bioindicator of environmental degradation in the Amazon. Ecol. Indic. 61, 526–545. http://dx.doi.org/10.1016/j.ecolind.2015.10.005.

Costa, B.N.S., Pinheiro, S.C.C., de Oliveira Lima, M., Amado, L.L., 2016b. Microzooplankton as an indicator of environmental quality at an industrial complex in the Brazilian Amazon. Ecol. Indic. 66, 220–229. http://dx.doi.org/10.1016/j.ecolind.2016.01.033.

Díaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655. http://dx.doi.org/10.1016/S0169-5347(01)02283-2.

Dias, C.d.O., de Araujo, A.V., Paranhos, R., Bonecker, S.L.C., 2010. Vertical copepod assemblages (0–2300 m) off southern Brazil. Zool. Stud. 49, 230–242. http://zoolstud.sinica.edu.tw/Journals/49.2/230.pdf.

Dias, F.J.S., Castro, B.M., Lacerda, L.D., 2013. Continental shelf water masses off the Jaguaribe River (4S), northeastern Brazil. Cont. Shelf Res. 66, 123–135. http://dx.doi.org/10.1016/j.csr.2013.06.005.

Dias, F.J.S., Castro, B.M., Lacerda, L.D., Miranda, L.B., Marins, R.V., 2016. Physical characteristics and discharges of suspended particulate matter at the continent-ocean interface in an estuary located in a semiarid region in northeastern Brazil. Estuarine Coast. Shelf Sci. 180, 258–274. http://dx.doi.org/10.1016/j.ecss.2016.08.006.

de Paula Filho, F.J., Marins, R.V., de Lacerda, L.D., Aguiar, J.E., Peres, T.F., 2015. Background values for evaluation of heavy metal contamination in sediments in the Parnaíba River Delta estuary, NE/Brazil. Mar. Pollut. Bull. 91, 424–428. http://dx.doi.org/10.1016/j.marpolbul.2014.08.022.
Favareto, L.R., Perbiche-Neves, G., Serafim-Júnior, M., Sartori, L., 2009. Selectivity of plankton nets over planktonic Copepoda in two sub-tropical estuaries. Acta Limnol. Bras. 21, 67–77. http://www.ablimno.org.br/acta/pdf/v21n1_210104.pdf.
Fernández, E., Cabal, J., Acuña, J.L., Bode, A., Botas, A., García-Soto, C., 1993. Plankton distribution across a slope current-induced front in the southern Bay of Biscay. J. Plankton Res. 15, 619–641. http://dx.doi.org/10.1093/plankt/15.6.619.
Ferreira, A.C., Lacerda, L.D., 2016. Degradation and conservation of Brazilian mangroves, status and perspectives. Ocean Coast. Manage. 125, 38–46. http://dx.doi.org/10.1016/j.ocecoaman.2016.03.011.
Ferreira, A.G., Mello, N.G.d.S., 2005. Principais sistemas atmosféricos atuantes sobre a região nordeste do Brasil e a influência dos oceanos Pacífico e Atlânctico no clima da região. Rev. Bras. Climatol. 1. http://dx.doi.org/10.5380/abclima.v1i1.25215.
Ferreira, C.E.L., Junqueira, A., Villac, M.C., Lopes, R.M., 2009. Marine bioinvasions in the Brazilian coast: brief report on history of events, vectors, ecology, impacts and management of non-indigenous species. Biol. Invas. Mar. Ecosyst. 459–477. http://dx.doi.org/10.1007/978-3-540-79236-9_27.
Frost, B., 1968. Revision of the Genus Clausocalanus (Copepoda: Calanoida), with Remarks on Distributional Patterns in Diagnostic Characters.
Gismervik, I., 2006. Top-down impact by copepods on ciliate numbers and persistence depends on copepod and ciliate species composition. J. Plankton Res. 28, 499–507. http://dx.doi.org/10.1093/plankt/fbi135.
Go, Y., Oh, B.C., Terazaki, M., 1998. Feeding behavior of the poecilostomatoid copepods Oncaea spp. on chaetognaths. J. Mar. Syst. 15, 475–482. http://dx.doi.org/10.1016/S0924-7963(97)00038-9.
Grice, G.D., Hart, A.D., 1962. The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. Ecol. Monogr. 32, 287–309. http://dx.doi.org/10.2307/1942377.
Hassett, R.P., Boehlert, G.W., 1999. Spatial and temporal distributions of copepods to leeward and windward of Oahu, Hawaiian Archipelago. Mar. Biol. 134, 571–584. http://dx.doi.org/10.1007/s002270050572.
Hidalgo, P., Escribano, R., Vergara, O., Jorquera, E., Donoso, K., Mendoza, P., 2010. Patterns of copepod diversity in the Chilean coastal upwelling system. Deep Sea Res. Part II 57, 2089–2097. http://dx.doi.org/10.1016/j.dsr2.2010.09.012.
Kattner, G., Albers, C., Graeve, M., Schnack-Schiel, S., 2003. Fatty acid and alcohol composition of the small polar copepods, Oithona and Oncaea: indication on feeding modes. Polar Biol. 26, 666–671. http://dx.doi.org/10.1007/s00300-003-0540-x.
Kiørboe, T., Sabatini, M.E., 1995. Scaling of fecundity, growth and development in marine planktonic copepods. Mar. Ecol. Progr. Ser. 120, 285–298. http://dx.doi.org/10.3354/meps120285.
Kiørboe, T., 2008. A Mechanistic Approach to Plankton Ecology. NJ: Princeton University Press, Princeton.
Kiørboe, T., 2011. How zooplankton feed: mechanisms, traits and trade-offs. Biol. Rev. 86, 311–339. http://dx.doi.org/10.1111/j.1469-185X.2010.00148.x.
Kouwenberg, J.H.M., 1994. Copepod distribution in relation to seasonal hydrographics and spatial structure in the northwestern mediterranean (Golfe du Lion). Estuar. Coast. Mar. Sci. 38, 69–90. http://dx.doi.org/10.1006/ecss.1994.1005.
Lavorel, S., McIntyre, S., Landsberg, J., Forbes, T.D.A., 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol. Evol. 12, 474–478. http://dx.doi.org/10.1016/S0169-5347(97)01219-6.
Litchman, E., Ohman, M.D., Kiørboe, T., 2013. Trait-based approaches to zooplankton communities. J. Plankton Res. 35, 473–484. http://dx.doi.org/10.1093/plankt/fbt019.
Lopes, R.M., Brandini, F.P., Gaeta, S.A., 1999. Distribution patterns of epipelagic copepods off Rio de Janeiro (SE Brazil) in Summer 1991/19992 and winter 1992. Hydrobiologia 411, 161–174. http://dx.doi.org/10.1590/S1679-87592006000300001.
Magalhães, A., Leite, N.d.R., Silva, J.G.S., Pereira, L.C.C., Costa, R.M.d., 2009. Seasonal variation in the copepod community structure from a tropical Amazon estuary, Northern Brazil. Anais da Academia Brasileira de Ciências 81, 187–197. http://dx.doi.org/10.1590/S0001-37652009000200005.
Marcolin, C.R., Conceição, B.L., Nogueira, M.M., Mafalda-Júnior, P., Johnsson, R., 2010. Mesozooplankton and Ichthyoplankton composition in two tropical estuaries of Bahia, Brazil. Check List 6, 210–216. http://dx.doi.org/10.15560/6.2.210.
Marengo, J.A., Torres, R.R., Alves, L.M., 2016. Drought in Northeast Brazil—past, present, and future. Theor. Appl. Climatol. 1–12. http://dx.doi.org/10.1007/s00704-016-1840-8.
Marin, F.d.O., 2009. A Subcorrente Norte do Brasil ao Largo da Costa do Nordeste. Instituto Oceanográfico da Universidade de São Paulo Universidade Federal de São Paulo, São Paulo (p. 115).
Marques, A.C., 2011. Invasives: sea of data still to come. Science 19, 936. http://dx.doi.org/10.1126/science.333.6045.936-a.
Mazzocchi, M.G., d'Alcalà, M.R., 1995. Recurrent patterns in zooplankton structure and succession in a variable coastal environment. ICES J. Mar. Sci.: J. du Conseil. 52, 679–691. http://dx.doi.org/10.1016/1054-3139(95)80081-6.
McKinnon, A.D., Duggan, S., De'ath, G., 2005. Mesozooplankton dynamics in nearshore waters of the Great Barrier Reef. Estuar. Coast. Mar. Sci. 63, 497–511. http://dx.doi.org/10.1016/j.ecss.2004.12.011.
McKinnon, A.D., Duggan, S., Carleton, J.H., Böttger-Schnack, R., 2008. Summer planktonic copepod communities of Australia's North West Cape (Indian Ocean) during the 1997-99 El Niño/La Niña. J. Plankton Res. 30, 839–855. http://dx.doi.org/10.1093/plankt/fbn043.
Medeiros, P.R.P., Knoppers, B.A., dos Santos Júnior, R.C., de Souza, W.F.L., 2007. Aporte fluvial e dispersão de matéria particulada em suspensão na zona costeira do rio São Francisco (SE/AL). Geochim. Brasil. 21, 212–231. http://ppegeo.igc.usp.br/index.php/geobras/article/viewFile/10435/9860.
Melo Júnior, M., Marcolin, C.R., Miyashita, L.K., Lopes, R.M., 2016. Temporal changes in pelagic copepod assemblages off Ubatuba, Brazil. Mar. Ecol. 37, 877–890. http://dx.doi.org/10.1111/maec.12366.
Melo-Júnior, M., 2009. Produção secundária e aspectos reprodutivos de copépodes pelágicos ao largo de Ubatuba (SP, Brasil). Instituto Oceanográfico. Universidade de São Paulo, São Paulo (p. 186).
Miola, B., de Morais, J.O., de Souza Pinheiro, L., 2016. Trace metal concentrations in tropical mangrove sediments, NE Brazil. Mar. Pollut. Bull. 102, 206–209. http://dx.doi.org/10.1016/j.marpolbul.2015.11.039.
Miyashita, L.K., de Melo Júnior, M., Lopes, R.M., 2009. Estuarine and oceanic influences on copepod abundance and production of a subtropical coastal area. J. Plankton Res. 31, 815–826. http://dx.doi.org/10.1093/plankt/fbp039.
Morgan, C.A., Robertis, A., Zabel, R.W., 2005.. Columbia River plume fronts. I. Hydrography, zooplankton distribution, and community composition. Mar. Ecol. Prog. Ser. 299, 19–31. http://dx.doi.org/10.3354/meps299019.
Mota, E.M.T., Garcia, T.M., Freitas, J.E.P., Soares, M.O., 2017. Composition and cross-shelf distribution of ichthyoplankton in the Tropical Southwestern Atlantic. Region. Stud. Mar. Sci. http://dx.doi.org/10.1016/j.rsma.2017.05.001.
Neumann-Leitão, S., Sant'anna, E.M.E., Gusmão, L.M.D.O., Do Nascimento-Vieira, D.A., Paranaguá, M.N., Schwamborn, R., 2008. Diversity and distribution of the mesozooplankton in the tropical Southwestern Atlantic. J. Plankton Res. 30. http://dx.doi.org/10.1093/plankt/fbn040.
Nybakken, J., Bertness, M.D., 2004. Marine Biology: An Ecological Approach. Benjamin Cummings.
Ohtsuka, S., Kubo, N., Okada, M., Gushima, K., 1993. Attachment and feeding of pelagic copepods on larvacean houses. J. Oceanogr. 49, 115–120. http://dx.doi.org/10.1007/BF02234012.
Omori, M., Ikeda, T., 1984. Methods in Marine Zooplankton Ecology. J. Wiley & Sons, New York.
Peralba, À., Mazzocchi, M.G., 2004. Vertical and seasonal distribution of eight Clausocalanus species (Copepoda: calanoida) in oligotrophic waters. ICES J. Mar. Sci.: J. du Conseil. 61, 645–653. http://dx.doi.org/10.1016/j.icesjms.2004.03.019.
Pomerleau, C., Sastri, A.R., Beisner, B.E., 2015. Evaluation of functional trait diversity for marine zooplankton communities in the Northeast subarctic Pacific Ocean. J. Plankton Res. 37, 712–726. http://dx.doi.org/10.1093/plankt/fbv045.
Rieper, M., 1978. Bacteria as food for marine harpacticoid copepods. Mar. Biol. 45, 337–345. http://dx.doi.org/10.1007/BF00391820.
Sammarco, P.W., Crenshaw, H., 1984. Plankton community dynamics of the central Great Barrier Reef Lagoon: analysis of data from Ikeda et al. Mar. Biol. 82, 167–180. http://dx.doi.org/10.1007/bf00394100.
Sankarankutty, C., Lins Oliverira, J.E., Cunha, K.M.F., Silva, A.C.C., Barroca, E.V.G., 1995. Further observations on zooplankton of the Potengi estuary (Natal, Rio Grande do Norte, Brazil) with special reference to the larvae of Brachyura (Crustacea, Decapoda). Rev. Brasil. de Zool. 12, 273–301. http://dx.doi.org/10.1590/s0101-81751995000200007.
Schettini, C.A.F., Valle-Levinson, A., Truccolo, E.C., 2017. Circulation and transport in short, low-inflow estuaries under anthropogenic stresses. Region. Stud. Mar. Sci. http://dx.doi.org/10.1016/j.rsma.2017.01.004.
Schnack-Schiel, S.B., Mizdalski, E., Cornils, A., 2010. Copepod abundance and species composition in the Eastern subtropical/tropical Atlantic. Deep Sea Res. Part II 57, 2064–2075. http://dx.doi.org/10.1016/j.dsr2.2010.09.010.
Seifried, S., Dürbaum, J., 2000. First clear case of carnivory in marine Copepoda Harpacticoida. J. Nat. Hist. 34, 1595–1618. http://dx.doi.org/10.1080/00222930050117503.
Shi, Y.Q., Sun, S., Zhang, G.T., Wang, S.W., Li, C.L., 2015. Distribution pattern of zooplankton functional groups in the Yellow Sea in June: a possible cause for geographical separation of giant jellyfish species. Hydrobiologia 754, 43–58. http://dx.doi.org/10.1007/s10750-014-2070-7.
Sigman, D.M., Hain, M.P., 2012. The biological productivity of the ocean. Nat. Educ. Knowl. 3, 21. http://www.nature.com/scitable/knowledge/library/the-biological-productivity-of-the-ocean-70631104.
Silva, T.A., Neumann-Leitão, S., Schwamborn, R., Gusmão, L.M.O., Nascimento-Vieira, D.A., 2003. Diel and seasonal changes in the macrozooplankton community of a tropical estuary in Northeastern Brazil. Rev. Brasil. de Zool. 20, 439–446. http://dx.doi.org/10.1590/S0101-81752003000300012.
Silva, A.P., Neumann-Leitão, S., Schwamborn, R., Gusmão, L.M.O., Silva, T.A., 2004. Mesozooplankton of an impacted bay in North Eastern Brazil. Braz. Arch. Biol. Technol. 47, 485–493. http://dx.doi.org/10.1590/S1516-89132004000300020.
Soares, M.O., Rossi, S., Martins, F.A.S., Carneiro, P.B.M., 2016. The forgotten reefs: benthic assemblage coverage on a sandstone reef (Tropical South-western Atlantic). J. Mar. Biol. Assoc. United Kingdom 1–8. http://dx.doi.org/10.1017/s0025315416000965.
Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57, 573–583. http://dx.doi.org/10.1641/b570707.
Sterza, J.M., Fernandes, L.L., 2006. Zooplankton community of the Vitória Bay estuarine system (Southeastern Brazil): Characterization during a three-year study. Braz. J. Oceanogr. 54, 95–105. http://dx.doi.org/10.1590/S1679-87592006000200001.
Tregouboff, G., Rose, M., 1957. Manuel de Planctonologia Méditerraneénne. C.N.R.S., Paris.

Tseng, L., Kumar, R., Dahms, H., Chen, Q., Hwang, J., 2008. Monsoon-Driven Succession of Copepod Assemblages in Coastal Waters of the Northeastern Taiwan Strait. Zool. Stud. 47, 46–60. http://zoolstud.sinica.edu.tw/Journals/47.1/46.pdf.
Turner, J.T., Collard, S.B., Wright, J.C., Mitchell, D.V., Steele, P., 1979. Summer distribution of pontellid copepods in the neuston of the eastern Gulf of Mexico continental shelf. Bull. Mar. Sci. 29, 287–297 (http://www.ingentaconnect.com/contentone/umrsmas/bullmar/1979/00000029/00000003/art00001).
Turner, J.T., 1984. The Feeding Ecology of Some Zooplankters That Are Important Prey Items of Larval Fish. US Department of Commerce National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
Turner, J.T., 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool. Stud. 43, 255–266. http://zoolstud.sinica.edu.tw/Journals/43.2/255.pdf.
Valentin, J.L., Monteiro-Ribas, W.M., 1993. Zooplankton community structure on the east-southeast Brazilian continental shelf (18–23 S latitude). Cont. Shelf Res. 13, 407–424. http://dx.doi.org/10.1016/0278-4343(93)90058-6.
Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional!. Oikos 116, 882–892. http://dx.doi.org/10.1111/j.2007.0030-1299.15559.x.
Walter, C.T., 1989. Review of the new world species of *Pseudodiaptomus* (Copepoda: calanoida), with a key to the species. Bull. Mar. Sci. 45, 590–628. http://www.ingentaconnect.com/contentone/umrsmas/bullmar/1989/00000045/00000003/art00005.
Webber, M.K., Roff, J.C., 1995. Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. Mar. Biol. 123, 481–495. http://dx.doi.org/10.1007/bf00349227.