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Horizontal and vertical distribution of mesozooplankton species richness and composition down to 2,300 m in the southwest Atlantic Ocean

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ABSTRACT. We describe the species richness, distribution and composition of mesozooplankton over the continental shelf and slope, and in the water masses in the Campos Basin, southwest Atlantic Ocean. We analyzed the mesozooplankton from two oceanographic cruises (rainy and dry seasons, 2009) with samples taken in five different water masses from the surface to 2,300 m depth. In the Subsurface Water (SS), in both sampling periods, more species were recorded over the slope (rainy: 100; dry: 128) than the continental shelf (rainy: 97; dry: 104). Over the slope, species richness decreased with increasing depth: the highest values were observed in the South Atlantic Central Water (SACW), and the lowest values in the North Atlantic Deep Water (NADW), in both sampling periods. We recorded 262 species in 10 groups (Hydrozoa, Siphonophora, Ctenophora, Branchiopoda, Copepoda, Euphausiacea, Decapoda, Chaetognatha, Appendicularia e Thaliacea), with 13 new occurrences for the southwest Atlantic. Copepoda was the group with the highest species richness, containing 138 species. In both periods, the samples from SS, SACW and Antarctic Intermediate Water (AAIW)/ Upper Circumpolar Deep Water (UCDW) were clustered in different faunistic zones, based on species composition. This study confirmed that zooplankton richness in the southwest Atlantic Ocean is underestimated, and suggests that additional efforts must be directed toward a better understanding of this fairly unknown region.

KEY WORDS. Deep sea; diversity; southeastern Brazil; zooplankton.

In pelagic marine environments, biodiversity is relatively low on the continental shelf, increases in oceanic waters and, in these areas, decreases with depth (Angel 1997, Smith & Brown 2002, Lopes *et al*. 2006). The pattern of increasing diversity from coastal to oceanic waters is attributed to continental influence, causing large fluctuations in temperature/salinity gradients and productivity, which favors dominance by relatively few species. The vertical pattern reflects the decrease in food availability due to light-limited primary production in deeper waters, and the decrease in temperature from the surface to the meso- and bathypelagic layers (Rutherford *et al*. 1999). Therefore, few species are adapted to live in the pelagic realm of the deep ocean, which leads to lower species richness in these environments than in surface waters (Smith & Brown 2002).

The South Atlantic is one of the least known marine habitats, mainly with respect to some zooplankton groups (Boltovskoy *et al*. 2003). Zooplankters play a key role in the control of phytoplankton production and are a critical food source for upper trophic levels, thus structuring pelagic ecosystems (Labat *et al*. 2009).

Investigations on the epipelagic zooplankton off Brazil only began in the last century. Björnberg (1963) provided the first detailed account of epipelagic species communities, and Bassani *et al*. (1999) reviewed the state of knowledge of planktonic biota between 21°S and 23°S. Between 1998 and 2000, surveys were carried out regarding zooplankton composition and distribution down to 200 m depth, between 12°S and 22°S (Bonecker 2006, Bonecker *et al*. 2007). Epipelagic studies in neighbouring regions were carried out by Ramirez & Sabatini 2000, Eskinazi-Sant'anna & Bjönberg 2006, and Lopes *et al*. 2006. Information on the mesopelagic and bathypelagic community is nonexistent except for copepods (Dias *et al*. 2010).

The Campos Basin is located on the central Brazilian coast. This region is characterized by the presence of different water masses, whose physical and chemical properties (e.g., temperature, salinity and dissolved oxygen) provide different potential habitats for many species in the pelagic realm. Due to coastal upwelling, the southern area of the Campos Basin has been the focus of most studies, mainly on circulation, nutrients, microplankton and epipelagic mesoplankton (Valentin 1984, Valentin *et al.* 1987). In this region, as throughout the southwest Atlantic, the vertical biodiversity pattern and the composition of mesopelagic is poorly known. Knowledge of bathyplankton is very scarce everywhere in the ocean.

In order to fill the gaps in knowledge of the species richness, distribution and composition of the mesozooplankton in deep waters in the southwest Atlantic, we describe the mesozooplankton composition from the surface to 2,300 m depth in the Campos Basin. We aimed to answer three questions: 1) Is there a horizontal gradient of mesozooplankton species richness between the continental shelf and the slope? 2) Is there a vertical gradient of mesozooplankton species richness? 3) Does each water mass, which has its own environmental characteristics, have a particular mesozooplankton species composition?

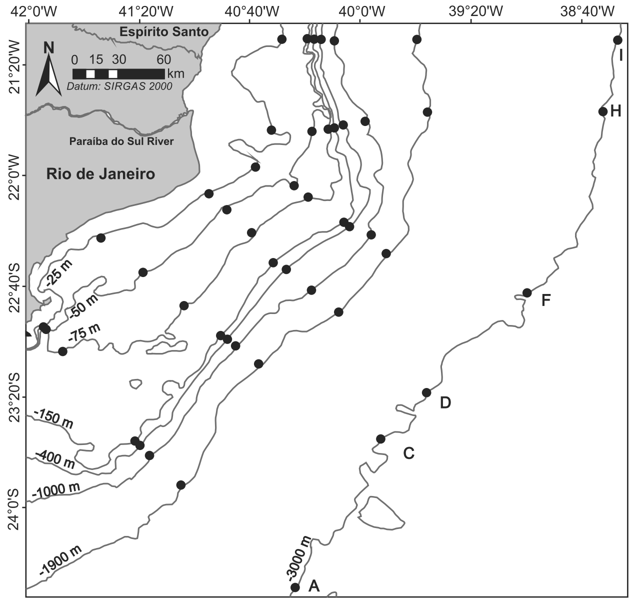

Figure 1. Sampling stations off the central Brazilian coast surveyed in this study. Lines indicate isobaths and letters indicate transects.

MATERIAL AND METHODS

The Campos Basin is located between 24°S and 20.5°S on the central Brazilian coast (Fig. 1). The climate is warm and humid, with a rainy season from November to February and a dry season from June to August (Lacerda *et al.* 2004). The continental shelf has a mean width of 100 km and the slope extends over a width of 40 km, with a 2.5° mean gradient (Viana *et al.* 1998).

The Brazilian coast is influenced by the Brazil Current, a warm and oligotrophic western boundary current. It flows from the northeast toward the southwest, as part of the South Atlantic western boundary current system (Stramma *et al.* 1990). The water-column structure and distributions of the different water masses over the continental shelf and slope of the Campos Basin are the main factors that characterize the environment, and are determined mainly by temperature and salinity (Mémery *et al.* 2000, Silveira & Schmidt 2000; Fig. 2). In the upper layers of the water column, the nutrient-poor Subsurface Water (SS) and the South Atlantic Central Water (SACW) are found. At deeper levels are the cold waters of the Antarctic Intermediate Water (AAIW), Upper Circumpolar Deep Water (UCDW), and North Atlantic Deep Water (NADW) (Mémery *et al.* 2000; Fig. 2).

Mesozooplankton (size >200 µm) samples were collected in two oceanographic cruises in 2009: February 25 to April 13 (rainy season) and August 5 to September 17 (dry season). The stations were distributed along six transects perpendicular to the coast organized in the South-North direction (A, C, D, F, H, and I). Each transect contained eight sampling stations, from the 25- to 3,000-m isobaths (25, 50, 75, 150, 400, 1,000, 1,900 and 3,000 m), four on the continental shelf and four on the slope (Fig. 1). Over the continental shelf, only Subsurface Water (SS) was collected; over the slope, samples were collected from the SS and from the other water masses, in the isobaths where they were present (Table I).

Mesozooplankton samples were collected during the night by horizontal hauls in the water-mass nuclei: Subsurface Water (SS), South Atlantic Central Water (SACW), Antarctic Intermediate Water (AAIW), and Upper Circumpolar Deep Water (UCDW; Table I). In the North Atlantic Deep Water (NADW), samples were collected by vertical hauls from the nucleus of this water mass (2,300 m) up to the limit of influence of the subjacent water mass (1,800 m), because of logisti-

Table I. Distribution of samples in water masses (continental shelf and/or slope) in the Campos Basin, central Brazilian coast, by isobaths. In parentheses, water-mass nucleus. (SS) Subsurface Water, (SACW) South Atlantic Central Water, (AAIW) Antarctic Intermediate Water, (UCDW) Upper Circumpolar Deep Water, (NADW) North Atlantic Deep Water.

Isobaths	Continental shelf (m)				Slope (m)			
	25	50	75	150	400	1,000	1,900	3,000
SS (1 m)	x	x	x	x	x	x	x	x
SACW (250 m)					x	x	x	x
AAIW (800 m)						x	x	x
UCDW (1,200 m)							x	x
NADW (2,300 m)								x

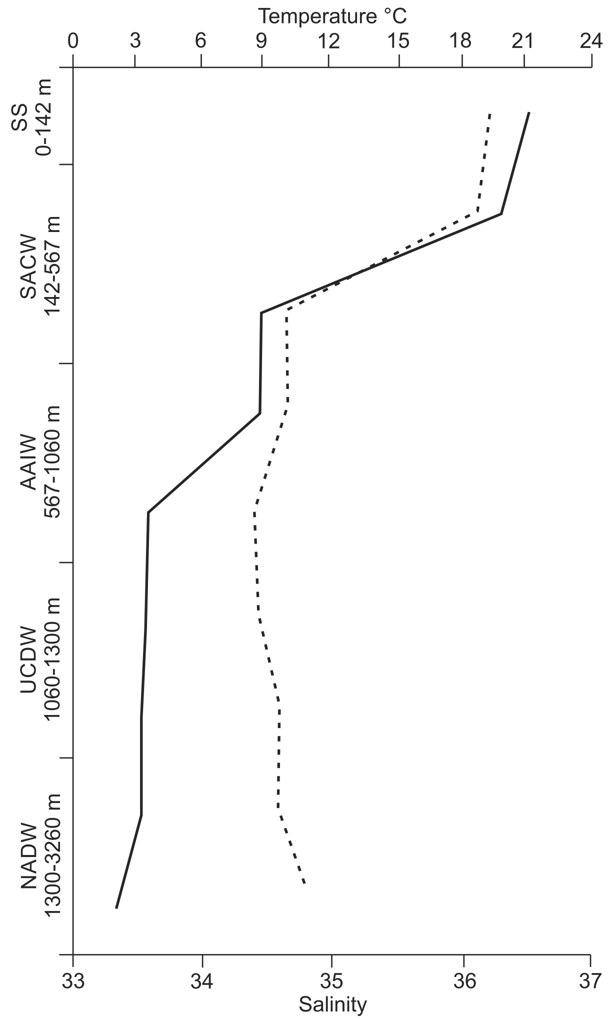

Figure 2. Salinity and temperature of the five water masses (0-3260 m) in the Campos Basin, central Brazilian coast, according to data from Mémery *et al.* (2000) and Silveira *et al.* (2000). Solid line = temperature, dashed line = salinity. SS – Subsurface Water, SACW – South Atlantic Central Water, AAIW – Antarctic Intermediate Water, UCDW – Upper Circumpolar Deep Water, NADW – North Atlantic Deep Water.

cal problems associated with the speed of water currents (Table I). Hauls were made using a *MultiNet*® type midi (Hydro-Bios, 200 µm white mesh, 50 x 50 opening of frame), with digital flow meters attached to the inner net mouth and also an external meter to assess the filtration efficiency. Different set of nets were used at each depth, to prevent sample contamination. To determine the collecting depth, the MultiNet contained a depth sensor. Both the depth and water volume were transmitted to a computer simultaneously with the hauls. The horizontal hauls were made at a speed of 2 knots, during 10 minutes or until the filtered water volume reached 50 m^3. Immediately after sampling, organisms were preserved in 4% buffered formalin. The mesozooplankton samples were obtained as part of the Habitats Project – Campos Basin Environmental Heterogeneity by CENPES/PETROBRAS.

In the laboratory, samples were divided into fractions using a Folsom Plankton Splitter (Hydro-Bios; McEwen *et al.* 1957) and at least 100 individuals per taxonomic group were sorted (Frontier 1981). The mesozooplankton taxonomic groups in this subsample were identified to species under a stereoscopic microscope and optical microscope.

All the specimens collected were deposited in the collection of the Integrated Zooplankton and Ichthyoplankton Laboratory of the Federal University of Rio de Janeiro (DZUFRJ 2007-2277, DZUFRJ 3075-4178, DZUFRJ 6726-8487, DZUFRJ 12622-16893).

We tested whether the mesozooplankton species richness varied depending on the region (continental shelf and slope) in the rainy and dry seasons, using non-parametric Mann-Whitney U test. To test differences in mesozooplankton species richness among water masses present over the slope, in both sampling periods, we used the non-parametric Kruskal-Wallis test.

We used hierarchical agglomerative cluster analyses (Q-mode) based on species composition to partition the samples into discrete groups in the rainy (69 species x 105 sampling stations) and dry seasons (69 species x 94 sampling stations). For this analysis, we used the Sørensen-Dice coefficient with average linkage method. The species composition was defined as the presence or absence of each species in each sample, and only species showing occurrence frequencies above 15% in each study period (rainy and dry seasons) were used in the analysis.

To identify the species that contributed most to the similarities and dissimilarities of the sample groups previously identified in the cluster analysis, we used the SIMPER (similarity of percentages) test. The analyses were performed using the statistical package Primer 6 (Primer-E Ltd., Luton, United Kingdom).

RESULTS

In the SS, we found more species over the slope (rainy season: 100 species, dry season: 128 species) than over the continental shelf (rainy season: 97 species, dry season: 104 species; Fig. 3) in the dry season ($p < 0.05$). On the slope, the species richness decreased with increasing depth. During the two sampling periods, we observed the highest values of species richness in the SACW (rainy season: 154 species, dry season: 141 species), and the lowest values in the NADW (rainy season: 39 species, dry season: 72 species; Fig. 3). In the rainy season, the mesozooplankton species richness showed significant differences in the NADW in relation to the other water masses, with the exception of IAW. In the dry season, the SS was significantly different from the other water masses ($p < 0.05$).

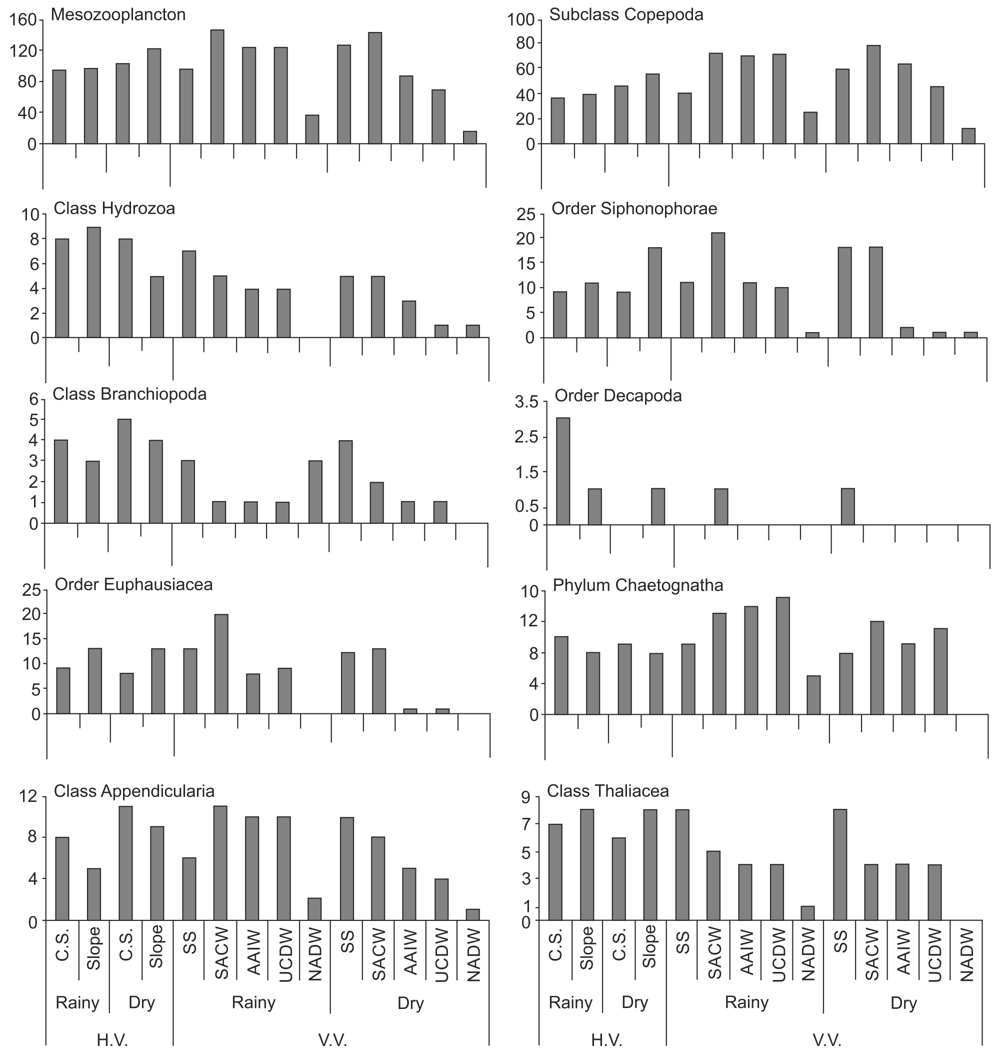

Figure 3. Horizontal distribution in the Subsurface Water, over the continental shelf and slope, and vertical distribution over the slope of species richness of each mesozooplankton group in the Campos Basin, central Brazilian coast, during the rainy and dry seasons. C.S. – Continental shelf, SS – Subsurface Water, SACW – South Atlantic Central Water, AAIW – Antarctic Intermediate Water, UCDW – Upper Circumpolar Deep Water, NADW – North Atlantic Deep Water, H.V. – Horizontal variation, V.V. – Vertical variation.

We recorded 262 species belonging to 10 zooplankton groups from 0-2,300 m depths (Table II). Copepoda was the group with the highest richness (138 species), followed by Siphonophorae (34), Euphausiacea (22), Hydrozoa (18), Chaetognatha (16), Appendicularia (14), Thaliacea (10), Decapoda (4), Branchiopoda (5) and Ctenophora (1). We found 13 new records for the southwest Atlantic Ocean: 10 Copepoda species, 1 Hydrozoa species and 2 Siphonophorae species. Among the new records, except for *Lychnagalma utricularia* (Siphonophorae) and *Laodicea indica* (Hydrozoa), which occurred in the SS, all of the other species were observed in the SACW, AAIW and/or the UCDW (Table II).

Hydrozoa. *Aglaura hemistoma* was the most frequent hydrozoan species (>70% in both sampling periods), followed by *Liriope tetraphylla* (>50% in both periods). The highest frequency of these species was recorded on the slope in the dry season and on the continental shelf in the rainy season, respectively. The SS (5 species) showed the highest number of species with exclusive occurrence in one water mass (Table II).

Siphonophorae. The most frequent siphonophore species was *Diphyes bojani* (>50% in both sampling periods). *Abylopsis eschscholtzi* was the second most frequent species (>79% in the rainy season and 81% on the slope during the dry season). *Muggiaea kochi* was the most frequent species (100%

Table II. Frequency (%) of mesozooplankton species over the continental shelf (C.S.) and slope and vertical distribution in the Campos Basin, central Brazilian coast, during the rainy and dry seasons. SS – Subsurface Water, SACW – South Atlantic Central Water, AAIW – Antarctic Intermediate Water, UCDW – Upper Circumpolar Deep Water, NADW – North Atlantic Deep Water.

Taxon	Horizontal Distribution				Vertical Distribution	
	Rainy		Dry		Rainy	Dry
	C.S. (n = 24)	Slope (n = 24)	C.S. (n = 24)	Slope (n = 22)		
Class Hydrozoa						
Aglaura hemistoma Péron & Lesueur, 1810	79.2	87.5	87.5	90.9	SS/SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Amphogona apicata Kramp, 1957	–	–	–	–	SACW/AAIW/UCDW	SACW/AAIW
Bougainvillia niobe Mayer, 1894	–	–	4.3	–	–	–
Corymorpha gracilis (Brooks, 1882)	37.5	12.5	17.4	9.1	–	SS
Cunina frugifera Kramp, 1948	–	4.2	–	–	–	–
Eucheilota duodecimalis A. Agassiz, 1862	4.2	–	–	–	–	–
Eucheilota paradoxica Mayer, 1900	12.5	–	4.3	–	SACW	–
Eucheilota ventricularis McCrady, 1859	4.2	–	4.5		–	–
Laodicea indica Browne, 1905*	16.7	4.2	8.7	–	–	–
Merga violacea (Agassiz & Mayer, 1899)	–	–	–	–	SS	–
Proboscidactyla ornata (McCrady, 1857)	4.2	4.2	–	–	SS	–
Rhopalonema velatum Gegenbaur, 1856	–	4.2	–	13.6	SS	SS
Sminthea eurygaster Gegenbaur, 1857	–	16.7	–	–	SS/SACW/AAIW/UCDW	SACW/AAIW/NADW
Solmundella bitentaculata (Quoy & Gaimard, 1833)	8.3	25.0	13.0	–	SS/UCDW	–
Tetraplatia volitans (Busch, 1851)	–	–	–	9.1	–	SS/SACW
Turritopsis nutricula (McCrady, 1857)	–	–	13.0	40.9	–	SS/SACW
Zanclea medusopolypata Boero, Bouillon & Gravili, 2000	–	4.2	–	–	SS/SACW/AAIW	–
Order Siphonophorae						
Abylopsis eschscholtzi (Huxley, 1859)	79.2	87.5	21.7	81.8	SS/SACW/AAIW/UCDW	SS/SACW/UCDW
Abylopsis tetragona (Otto, 1823)	33.3	54.2	8.7	68.2	SS/SACW/AAIW/UCDW	SS/SACW
Bassia bassensis (Quoy & Gaimard, 1833)	58.3	58.3	13.0	63.6	SS/SACW/AAIW/UCDW	SS/SACW
Ceratocymba sagittata (Quoy & Gaimard, 1827)	–	–	–	4.5	–	SS
Chelophyes appendiculata (Eschscholtz, 1829)	16.7	54.2	30.4	45.4	SS/SACW/AAIW/UCDW	SS/SACW
Chuniphyes multidentata Lens & van Riemsdijk, 1908	–	–	–	–	SACW/AAIW	AAIW
Dimophyes arctica (Chun, 1897)	–	–	–	4.5	SACW	SS/SACW
Diphyes bojani (Eschscholtz, 1829)	87.5	100.0	47.9	95.4	SS/SACW/AAIW/UCDW/NADW	SS/SACW/NADW
Diphyes dispar Chamisso & Eysenhardt, 1821	–	25.0	–	–	SS/AAIW	–
Enneagonum hyalinum Quoy & Gaimard, 1827	–	–	–	–	SACW	SACW
Eudoxoides mitra (Huxley, 1859)	–	–	13.0	40.9	SACW	SS/SACW
Halistemma rubrum (Vogt, 1852)	–	–	–	–	–	SACW
Hippopodius hippopus (Forskål, 1776)	–	–	–	4.5	–	SS
Lensia achilles Totton, 1941	–	–	–	–	SACW	–
Lensia campanella (Moser, 1925)	12.5	8.3	–	9.1	SS/SACW/AAIW	SS/SACW
Lensia challengeri Totton, 1954	–	–	–	–	SACW	–
Lensia conoidea (Keferstein & Ehlers, 1860)	–	4.2	–	4.2	SS/SACW	SACW
Lensia cossack Totton, 1941	8.3	4.2	–	13.6	SS/AAIW/UCDW	SS
Lensia fowleri (H. B. Bigelow, 1911)	–	–	–	–	SACW	–
Lensia grimaldi (Leloup, 1933)	–	–	–	–	–	SACW

Continues

Table II. Continued.

Taxon	Horizontal Distribution				Vertical Distribution	
	Rainy		Dry		Rainy	Dry
	C.S. (n = 24)	Slope (n = 24)	C.S. (n = 24)	Slope (n = 22)		
Lensia havock Totton, 1941	–	–	–	–	UCDW	AAIW
Lensia hotspur Totton, 1941	–	–	–	4.5	SACW	SS
Lensia hunter Totton, 1941	–	–	–	–	AAIW	–
Lensia meteori (Leloup, 1934)	–	–	–	–	SACW/UCDW	SACW
Lensia multicristata (Moser, 1925)	–	–	–	–	SACW	SACW
Lensia subtilis (Chun, 1886)	–	–	4.3	31.8	SACW/AAIW	SS/SACW
Lensia subtiloides (Lens & van Riemsdijk, 1908)*	–	–	–	–	SACW	SS/SACW
Lychnagalma utricularia (Claus, 1879)*	8.3	–	–	–	–	–
Muggiaea kochi (Will, 1844)	50.0	16.7	100.0	77.2	SS/SACW/AAIW/UCDW	SS/SACW
Nanomia bijuga (delle Chiaje, 1841)	–	–	4.3	4.5	–	SS
Sulculeolaria chuni (Lens & van Riemsdijk, 1908)	–	12.5	–	4.5	SS/SACW/UCDW	SS
Sulculeolaria turgida (Gegenbaur, 1853)	–	–	–	4.5	–	SS
Vogtia glabra H.B. Bigelow, 1918	–	–	–	–	AAIW	–
Vogtia serrata (Moser, 1925)	–	–	–	–	–	SACW
Phylum Ctenophora					–	SS/SACW
Hormiphora plumosa L. Agassiz, 1860	–	–	–	–	SACW	–
Class Branchiopoda						
Evadne spinifera P.E. Müller, 1867	20.8	8.3	4.3	22.7	SS/NADW	SS/UCDW
Penilia avirostris Dana, 1849	37.5	4.2	91.3	63.6	SS/NADW	SS/SACW/AAIW
Pleopis polyphemoides (Leuckart, 1859)	4.2	–	21. 7	–	–	–
Pleopis schmackeri (Poppe, 1889)	–	–	8. 7	4.5	–	SS
Pseudevadne tergestina (Claus, 1877)	50.0	54.2	78. 3	72.7	SS/SACW/AAIW/UCDW/NADW	SS/SACW
Subclass Copepoda						
Acartia danae Giesbrecht, 1889	4.2	4.2	–	–	SS/SACW/AAIW/UCDW	–
Acartia lilljeborgi Giesbrecht, 1889	–	–	8.7	4.5	AAIW	SS
Acartia longiremis (Lilljeborg, 1853)	–	–	–	4.5	–	SS
Acrocalanus gracilis Giesbrecht, 1888	–	–	4.3	–	UCDW	SS
Acrocalanus longicornis Giesbrecht, 1888	79.2	95.8	39.1	59.1	SS/SACW/AAIW	SS/AAIW
Aegisthus mucronatus Giesbrecht, 1891	–	–	–	–	SACW/AAIW/UCDW	SACW/AAIW/UCDW
Aetideus giesbrechti Cleve, 1904	–	–	–	–	SACW/AAIW/UCDW/NADW	SACW/AAIW
Amallothrix dentipes (Vervoort, 1951)*	–	–	–	–	UCDW	AAIW/UCDW
Arietellus plumifer G.O. Sars, 1905*	–	–	–	–	–	SACW/AAIW
Calanoides carinatus (Krøyer, 1849)	8.3	4.2	69.6	27.3	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Calanopia americana F. Dahl, 1894	12.5	–	30.4	27.3	–	SS
Calocalanus contractus Farran, 1926	–	–	13.0	27.3	SACW/UCDW	SS/SACW/AAIW/UCDW/NADW
Calocalanus pavo (Dana, 1852)	20.8	29.2	–	9.1	SS/AAIW/UCDW	SS/AAIW
Calocalanus pavoninus Farran, 1936	45.8	58.3	30.4	45.4	SS/SACW/AAIW/UCDW	SS/SACW/AAIW
Candacia bipinnata (Giesbrecht, 1889)	4.2	–	8.7	–	SACW/AAIW/UCDW	SACW/AAIW
Candacia bispinosa (Claus, 1863)	–	–	–	–	AAIW/UCDW	–
Candacia ethiopica (Dana, 1849)	–	–	–	4.5	–	SS
Candacia longimana (Claus, 1863)	–	–	–	–	AAIW/UCDW	–
Candacia pachydactyla (Dana, 1849)	8.3	33.3	13.0	18.2	SS/SACW/AAIW/UCDW	SS/AAIW

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Table II. Continued.

Taxon	Horizontal Distribution				Vertical Distribution	
	Rainy		Dry		Rainy	Dry
	C.S. (n = 24)	Slope (n = 24)	C.S. (n = 24)	Slope (n = 22)		
Candacia simplex (Giesbrecht, 1889)	–	4.2	–	–	SS/UCDW	–
Candacia tenuimana (Giesbrecht, 1889)	–	–	–	–	–	SACW
Centropages furcatus (Dana, 1852)	16.7	8.3	69.6	31.8	SS	SS/SACW/AAIW/UCDW
Centropages violaceus (Claus, 1863)	–	8.3	–	4.5	SS	SS
Chiridiella atlantica Wolfenden, 1911*	–	–	–	–	–	AAIW
Chiridius gracilis Farran, 1908	–	–	–	–	UCDW	–
Chirundina streetsii Giesbrecht, 1895	–	–	–	–	SACW/AAIW	SACW/AAIW
Clausocalanus arcuicornis (Dana, 1849)	–	–	–	13.6	AAIW	SS/SACW/AAIW
Clausocalanus brevipes Frost & Fleminger, 1968	–	–	–	4.5	SACW/UCDW	SS/SACW
Clausocalanus furcatus (Brady, 1883)	100.0	95.8	95.6	100.0	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW/NADW
Clausocalanus mastigophorus (Claus, 1863)	–	–	–	–	–	SACW
Clytemnestra scutellata Dana, 1849	4.2	4.2	17.4	–	SS/SACW/AAIW	SACW
Conaea rapax (Giesbrecht, 1891)	–	–	–	–	SACW/AAIW/UCDW/NADW	SACW/AAIW/UCDW
Copilia mirabilis Dana, 1849	4.2	8.3	4.3	4.5	SS/AAIW/UCDW	SS
Corycaeus flaccus Giesbrecht, 1891	–	–	–/13.6	–	SACW	SS/SACW
Corycaeus giesbrechti F. Dahl, 1894	75.0	66.7	60.9	63.6	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW
Corycaeus latus Dana, 1849	–	–	–	–	–	SACW
Corycaeus lautus Dana, 1849	8.3	20.8	13.0	–	SS/SACW/UCDW/NADW	SACW
Corycaeus limbatus Brady, 1883	–	12.5	17.4	31.8	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW/NADW
Corycaeus speciosus Dana, 1849	37.5	45.8	13.0	31.8	SS/SACW/AAIW/UCDW/NADW	SS/AAIW/UCDW
Corycaeus typicus (Krøyer, 1849)	–	–	4.3	4.5	–	SS
Ctenocalanus citer Heron & Bowman, 1971	–	–	39.1	9.1	SACW/AAIW	SS/SACW/AAIW
Ctenocalanus vanus Giesbrecht, 1888	–	–	4.3	9.1	SACW/AAIW/UCDW	SS/AAIW
Euaugaptilus facilis (Farran, 1908)*	–	–	–	–	UCDW	AAIW
Euaugaptilus hecticus (Giesbrecht, 1892)	–	–	–	–	SACW	–
Eucalanus hyalinus (Claus, 1866)	–	–	–	–	AAIW	SACW
Euchaeta marina (Prestandrea, 1833)	–	8.3	4.3	4.5	SS/UCDW	SS/SACW/UCDW
Euchaeta media Giesbrecht, 1888	–	–	–	–	SS/SACW/UCDW	SACW
Euchirella curticauda Giesbrecht, 1888	–	–	–	–	UCDW	SACW
Euchirella messinensis messinensis (Claus, 1863)	–	–	–	–	AAIW	–
Euchirella pulchra (Lubbock, 1856)	–	–	–	–	AAIW	AAIW/UCDW
Euterpina acutifrons (Dana, 1849)	–	–	4.3	–	UCDW	–
Farranula gracilis (Dana, 1849)	75.0	100.0	34.8	77.3	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW/NADW
Farranula rostrata (Claus, 1863)	–	–	–	–	UCDW	–
Gaetanus kruppi Giesbrecht, 1903	–	–	–	–	AAIW	–
Gaetanus miles Giesbrecht, 1888	–	–	–	–	–	SACW
Gaetanus minor Farran, 1905	–	–	–	–	SACW/UCDW/NADW	SACW/AAIW
Gaetanus pileatus Farran, 1903*	–	–	–	–	–	SACW
Gaetanus tenuispinus (G.O. Sars, 1900)	–	–	–	–	SACW/AAIW/UCDW	SACW/AAIW
Haloptilus austini Grice, 1959	–	–	–	–	SACW	–
Haloptilus longicirrus Brodsky, 1950*	–	–	–	–	–	SACW
Haloptilus longicornis (Claus, 1863)	–	–	–	4.5	SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW

Continues

Table II. Continued.

Taxon	Horizontal Distribution				Vertical Distribution	
	Rainy		Dry			
	C.S. (n = 24)	Slope (n = 24)	C.S. (n = 24)	Slope (n = 22)	Rainy	Dry
Heterorhabdus austrinus Giesbrecht, 1902	–	–	–	–	AAIW	SACW/UCDW
Heterorhabdus papilliger (Claus, 1863)	4.2	–	–	–	SACW/AAIW	SACW/AAIW/UCDW
Heterorhabdus spinifrons (Claus, 1863)	8.3	12.5	4.3	13.6	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Labidocera acutifrons (Dana, 1849)	8.3	16.7	–	–	SS/SACW	–
Lophothrix frontalis Giesbrecht, 1895	–	–	4.3	–	SACW/AAIW/UCDW	SS/SACW/UCDW
Lophothrix latipes (T. Scott, 1894)	–	–	–	–	–	AAIW/UCDW
Lophothrix quadrispinosa Wolfenden, 1911*	–	–	–	–	SACW	–
Lubbockia aculeata Giesbrecht, 1891	–	–	–	–	–	SACW
Lubbockia squillimana Claus, 1863	–	–	–	18.2	SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW/NADW
Lucicutia clausii (Giesbrecht, 1889)	–	–	–	–	SACW/UCDW	SACW/UCDW
Lucicutia flavicornis (Claus, 1863)	12.5	25.0	17.4	72.7	SS/SACW/UCDW/NADW	SS/SACW/AAIW/NADW
Lucicutia gaussae Grice, 1963	–	–	–	–	SACW/AAIW/UCDW	–
Lucicutia longicornis (Giesbrecht, 1889)	–	–	–	–	UCDW	AAIW
Lucicutia magna Wolfenden, 1903	–	–	–	–	–	UCDW
Lucicutia ovalis (Giesbrecht, 1889)	–	–	–	–	SACW/AAIW/UCDW	–
Lucicutia wolfendeni Sewell, 1932	–	–	–	–	UCDW	AAIW/UCDW
Macrosetella gracilis (Dana, 1847)	37.5	75.0	–	54.5	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW/NADW
Mecynocera clausi I.C. Thompson, 1888	–	8.3	–	31.8	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Metridia brevicauda Giesbrecht, 1889	–	–	–	–	AAIW	AAIW
Metridia princeps Giesbrecht, 1889	–	–	–	–	–	AAIW
Microsetella rosea (Dana, 1849)	–	–	4.3	–	–	SACW/AAIW/UCDW/NADW
Miracia efferata Dana, 1849	–	8.3	–	–	SS/SACW/AAIW/UCDW	–
Nannocalanus minor (Claus, 1863)	62.5	75.0	34.8	59.1	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Neocalanus gracilis (Dana, 1849)	–	–	–	9.1	SACW	SS
Neocalanus robustior (Giesbrecht, 1888)	–	–	–	9.1	–	SS
Nullosetigera helgae (Farran, 1908)	–	–	–	–	SACW	SACW
Oithona nana Giesbrecht, 1892	–	–	–	–	NADW	–
Oithona plumifera Baird, 1843	25.0	25.0	43.5	45.4	SS/SACW/UCDW	SS/SACW/AAIW/UCDW/NADW
Oithona setigera Dana, 1852	–	–	17.4	22.7	SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Oithona similis Claus, 1866	25.0	16.7	13.0	36.4	SS/SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Oithona tenuis Rosendorn, 1917	–	–	–	–	SACW	–
Oncaea atlântica Shmeleva, 1967*	–	–	–	–	–	SACW
Oncaea cf. *media* Giesbrecht, 1891	29.2	33.3	43.5	40.9	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Oncaea venusta Philippi, 1843	79.2	10.0	65.2	90.9	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW/NADW
Paracalanus aculeatus Giesbrecht, 1888	87.5	50.0	43.5	27.3	SS/SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Paracalanus nanus (G.O. Sars, 1907)	–	–	–	–	–	SACW
Paracalanus parvus (Claus, 1863)	54.2	20.8	47.8	31.8	SS/SACW/AAIW/UCDW	SS/SACW
Paracalanus quasimodo Bowman, 1971	75.0	58.3	91.3	77.3	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW
Paraeucalanus sewelli Fleminger, 1973	–	–	–	–	AAIW/UCDW	AAIW
Paraeuchaeta sarsi (Farran, 1908)	–	–	–	–	SACW/AAIW/UCDW	–
Paraheterorhabdus vipera (Giesbrecht, 1889)	–	–	–	–	–	SACW
Pleuromamma abdominalis (Lubbock, 1856)	4.2	–	–	9.1	SACW/UCDW/NADW	SS/SACW/AAIW/UCDW/NADW

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Table II. Continued.

Taxon	Horizontal Distribution				Vertical Distribution	
	Rainy		Dry		Rainy	Dry
	C.S. (n = 24)	Slope (n = 24)	C.S. (n = 24)	Slope (n = 22)		
Pleuromamma gracilis (Claus, 1863)	–	–	17.4	31.8	SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW/NADW
Pleuromamma piseki Farran, 1929	–	12.5	–	13.6	SS/SACW/AAIW	SS/SACW/AAIW
Pleuromamma xiphias (Giesbrecht, 1889)	–	–	–	4.5	SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Pontellina plumata (Dana, 1849)	–	–	–	9.1	–	SS
Pontellopsis villosa (Brady, 1883)	–	4.2	–	–	SS	–
Racovitzanus levis Tanaka, 1961*	–	–	–	–	–	SACW
Rhincalanus nasutus Giesbrecht, 1888	–	–	–	–	SACW/AAIW	UCDW
Sapphirina nigromaculata Claus, 1863	4.2	20.8	4.3	4.5	SS/UCDW/NADW	SS/AAIW
Scaphocalanus brevicornis (G.O. Sars, 1900)	–	–	–	–	AAIW	–
Scaphocalanus curtus (Farran, 1926)	–	–	–	–	–	SACW
Scaphocalanus echinatus (Farran, 1905)	–	–	–	–	SACW/AAIW	SACW
Scaphocalanus elongatus A. Scott, 1909	–	–	–	–	–	UCDW
Scaphocalanus magnus (T. Scott, 1894)	–	–	–	–	AAIW/UCDW/NADW	–
Scaphocalanus subbrevicornis (Wolfenden, 1911)	–	–	–	–	–	UCDW
Scolecithricella dentata (Giesbrecht, 1892)	–	–	–	–	SACW/AAIW	SACW/UCDW
Scolecithricella minor (Brady, 1883)	–	–	4.3	9.1	SACW/AAIW	SS/SACW/AAIW/UCDW
Scolecithricella ovata (Farran, 1905)	–	–	–	–	–	SACW
Scolecithricella profunda (Giesbrecht, 1893)	–	–	–	–	–	SACW
Scolecithricella tenuiserrata (Giesbrecht, 1892)	–	–	8.7	18.2	–	SS/SACW/UCDW
Scolecithrix bradyi Giesbrecht, 1888	–	–	–	–	SACW/UCDW	–
Scolecithrix danae (Lubbock, 1856)	16.7	16.7	–	18.2	SS/SACW/AAIW/UCDW	SS/SACW
Scottocalanus securifrons (T. Scott, 1894)	–	–	–	–	SACW	SACW/AAIW
Subeucalanus crassus (Giesbrecht, 1888)	–	–	8.7	4.5	–	SS
Subeucalanus longiceps (Matthews, 1925)	–	–	–	–	SACW/AAIW/UCDW	–
Subeucalanus pileatus (Giesbrecht, 1888)	–	–	56.5	50.0	AAIW	SS/SACW/AAIW/UCDW
Subeucalanus subtenuis (Giesbrecht, 1888)	–	–	–	–	AAIW	SACW
Temora stylifera (Dana, 1849)	100.0	91.7	82.6	81.8	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Temora turbinata (Dana, 1849)	54.2	–	91.3	50.0	UCDW	SS/SACW/AAIW/UCDW
Temoropia mayumbaensis T. Scott, 1894	–	–	–	–	SACW/AAIW/UCDW	–
Tharybis asymmetrica Andronov, 1976*	–	–	–	–	–	AAIW
Triconia cf. *conifera* (Giesbrecht, 1891)	8.3	8.3	17.4	45.4	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Undeuchaeta major Giesbrecht, 1888	–	–	–	–	SACW/AAIW/UCDW	SACW
Undeuchaeta plumosa (Lubbock, 1856)	–	–	–	–	–	SACW/AAIW
Undinula vulgaris (Dana, 1849)	66.7	91.7	39.1	72.7	SS/SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Xanthocalanus marlyae Campaner, 1978	–	–	–	–	AAIW	–
Order Euphausiacea						
Bentheuphausia amblyops (G.O. Sars, 1883)	–	–	–	–	AAIW	–
Euphausia americana Hansen, 1911	20.8	91.7	4.3	77.3	SS/SACW/AAIW/UCDW	SS/SACW
Euphausia brevis Hansen, 1905	–	37.5	–	9.1	SS/SACW/AAIW/UCDW	SS
Euphausia pseudogibba Ortmann, 1893	–	4.2	4.3	22.7	SS/SACW/AAIW	SS/SACW
Euphausia recurva Hansen, 1905	–	16.7	–	4.5	SS/SACW	SS
Euphausia similis G.O. Sars, 1885	12.5	29.2	13.0	40.9	SS/SACW	SS/SACW

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Table II. Continued.

Taxon	Horizontal Distribution				Vertical Distribution	
	Rainy		Dry		Rainy	Dry
	C.S. (n = 24)	Slope (n = 24)	C.S. (n = 24)	Slope (n = 22)		
Euphausia tenera Hansen, 1905	8.3	29.2	–	–	SS/SACW	–
Nematobrachion flexipes (Ortmann, 1893)	–	–	–	–	SACW	–
Nematobrachion sexspinosus Hansen, 1911	–	–	–	–	SACW	SACW
Nematoscelis atlantica Hansen, 1910	33.3	37.5	13.0	59.1	SS/SACW/AAIW/UCDW	SS/SACW/UCDW
Nematoscelis microps G.O. Sars, 1883	–	4.2	–	–	SS/SACW/AAIW/UCDW	SACW
Nematoscelis tenella G.O. Sars, 1883	–	–	–	18.2	SACW/UCDW	SS/SACW
Stylocheiron abbreviatum G.O. Sars, 1883	25.0	25.0	8.7	22.7	SS/SACW	SS/SACW
Stylocheiron affine Hansen, 1910	–	4.2	–	–	SS/SACW/UCDW	–
Stylocheiron carinatum G.O. Sars, 1883	37.5	33.3	21.7	63.6	SS/SACW/UCDW	SS/SACW
Stylocheiron elongatum G.O. Sars, 1883	–	–	–	–	SACW	SACW
Stylocheiron longicorne G.O. Sars, 1883	4.2	–	–	–	SACW/UCDW	SACW
Stylocheiron suhmii G.O. Sars, 1883	–	–	–	31.8	–	SS/SACW
Thysanopoda aequalis Hansen, 1905	8.3	20.8	26.1	50.0	SS/SACW/AAIW/UCDW	SS/SACW/AAIW
Thysanopoda monacantha Ortmann, 1893	–	–	4.3	22.7	SACW	SS
Thysanopoda obtusifrons G.O. Sars, 1883	–	–	–	–	SACW/AAIW	–
Thysanopoda tricuspidata Guérin Méneville, 1837	4.2	29.2	–	9.1	SS/SACW	–
Order Decapoda						
Janicella spinicauda (A. Milne-Edwards, 1883)	–	–	–	–	SACW	–
Leander tenuicornis (Say, 1818)	4.2	–	–	–	–	–
Periclimenes longicaudatus (Stimpson, 1860)	4.2	–	–	–	–	–
Stenopus hispidus (Olivier, 1811)	4.2	8.3	–	9.1	–	SS
Phylum Chaetognatha						
Caecosagitta macrocephala (Fowler, 1904)	–	–	–	–	AAIW/UCDW	AAIW/UCDW
Decipisagitta decipiens (Fowler, 1905)	–	–	–	–	AAIW/UCDW	SACW/UCDW
Decipisagitta sibogae (Fowler, 1906)	–	–	–	13.6	SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Eukrohnia bathypelagica Alvariño, 1962	–	–	–	–	SACW/AAIW/UCDW	SACW/AAIW/UCDW
Ferosagitta hispida (Conant, 1895)	4.2	8.3	–	–	SS/SACW	AAIW
Flaccisagitta enflata (Grassi, 1881)	100.0	100.0	100.0	100.0	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Flaccisagitta hexaptera (d'Orbigny, 1836)	8.3	8.3	8.7	45.4	SS/SACW/AAIW/UCDW	SS/SACW/UCDW
Krohnitta mutabbii (Alvariño, 1969)	66.7	50.0	91.3	90.9	SS/SACW/AAIW/UCDW	SS/SACW/AAIW
Krohnitta subtilis (Grassi, 1881)	8.3	16.7	4.3	–	SS/SACW/AAIW/UCDW	SACW/UCDW
Mesosagitta minima (Grassi, 1881)	4.2	–	13.0	9.1	SS/SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Parasagitta friderici (Ritter–Záhony, 1911)	95.8	95.8	100.0	100.0	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Pseudosagitta lyra (Krohn, 1853)	–	–	13.0	–	SACW/AAIW/UCDW	SACW/AAIW/UCDW
Pterosagitta draco (Krohn, 1853)	41.7	58.3	8.7	59.1	SS/SACW/AAIW/UCDW/NADW	SS/SACW/UCDW
Sagitta bipunctata Quoy & Gaimard, 1828	4.2	–	–	–	SACW/UCDW	–
Sagitta helenae Ritter-Záhony, 1911	–	–	–	–	AAIW/UCDW	–
Serratosagitta serratodentata (Krohn, 1853)	66.7	87.5	39.1	54.5	SS/SACW/AAIW/UCDW/NADW	SS/SACW
Class Appendicularia						
Fritillaria formica Fol, 1872	37.5	20.8	21.7	45.4	SS/SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Fritillaria haplostoma Fol, 1872	4.2	–	8.7	9.1	SACW/AAIW/UCDW	SS/UCDW
Fritillaria pellucida (Busch, 1851)	12.5	–	26.1	31.8	SACW/AAIW	SS/AAIW

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Table II. Continued.

Taxon	Horizontal Distribution				Vertical Distribution	
	Rainy		Dry		Rainy	Dry
	C.S. (n = 24)	Slope (n = 24)	C.S. (n = 24)	Slope (n = 22)		
Fritillaria sargassi Lohmann, 1896	4.2	–	–	–	AAIW	–
Fritillaria tenella Lohmann, 1896	–	–	–	–	SACW/UCDW	SACW
Oikopleura albicans (Leuckart, 1853)	–	–	13.6	–	SACW/AAIW/UCDW	SS
Oikopleura cophocerca (Gegenbaur, 1855)	–	4.2	4.3	40.9	SS/SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW/NADW
Oikopleura cornutogastra (Gegenbaur, 1855)	–	–	8.7	9.1	UCDW	SS/SACW
Oikopleura dioica Fol, 1872	–	–	13.0	–	–	–
Oikopleura fusiformis Fol, 1872	54.2	37.5	52.2	77.3	SS/SACW/AAIW/UCDW	SS/SACW
Oikopleura gracilis Lohmann, 1896	–	–	–	–	SACW	–
Oikopleura intermedia Lohmann, 1896	4.2	–	26.1	18.2	SS/SACW/AAIW/UCDW	SS/SACW/AAIW
Oikopleura longicauda (Vogt, 1854)	100.0	100.0	100.0	100.0	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Oikopleura rufescens Fol, 1872	66.7	87.5	17.4	59.1	SS/SACW/AAIW/UCDW/NADW	SS/SACW
Class Thaliacea						
Brooksia rostrata (Traustedt, 1893)	16.7	8.3	–	–	SS	–
Dolioletta gegenbauri (Uljanin, 1884)	20.8	45.8	52.2	54.5	SS/SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Doliolina mülleri (Krohn, 1852)	29.2	8.3	30.4	40.9	SS/SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Doliolum nationalis Borgert, 1893	83.3	87.5	100.0	100.0	SS/SACW/AAIW/UCDW/NADW	SS/SACW/AAIW/UCDW
Iasis zonaria (Pallas, 1774)	–	–	–	4.5	–	SS
Ritteriella retracta (Ritter, 1906)	–	4.2	–	–	SS	–
Salpa fusiformis Cuvier, 1804	8.3	16.7	26.06	54.5	SS	SS
Thalia cicar van Soest, 1973	4.2	–	–	9.1	SACW	SS
Thalia democratica (Forskal, 1775)	50.0	41.7	56.5	86.4	SS/SACW/AAIW/UCDW	SS/SACW/AAIW/UCDW
Weelia cylindrica (Cuvier, 1804)	–	4.2	4.3	22.7	SS	SS

* New occurrence for the southwest Atlantic.

frequency) on the continental shelf in the dry season. The SACW (8 species) and SS (5 species) contained the most species with exclusive occurrence in one water mass (Table II).

Ctenophora. Two ctenophore species were recorded in the study period. *Beroe* sp. occurred only in the AAIW, and *Hormiphora plumosa* in the SACW (Table II).

Branchiopoda. *Pseudevadne tergestina* was the most frequent branchiopod species, and peaked in frequency on the continental shelf during the dry season. *Penilia avirostris* was the second most frequent species and was most frequent on the continental shelf, during the dry season. Only *Pleopis schmackeri* was recorded exclusively in the SS (Table II).

Copepoda. *Clausocalanus furcatus* was the most frequent copepod species (>90%) in both sampling periods. *Temora stylifera* was the second most frequent species (>80% in both periods), with a peak frequency on the continental shelf in the rainy season. The SACW contained the most species exclusive to that water mass (19), followed by the AAIW (10 species, Table II).

Euphausiacea. *Euphausia americana* was the most frequent euphausiacean species, with a peak frequency on the slope, in both sampling periods (>70%). *Stylocheiron carinatum* was the second most frequent species (>20% in both periods), with a peak frequency in the dry season, on the slope. In the SACW, we observed the highest number of species that occurred exclusively in one water mass (3 species; Table II).

Decapoda. Decapods occurred only in the SS and SACW, mostly in the rainy season. Only *Stenopus hispidus* occurred on both the continental shelf and the slope. *Leander tenuicornis* and *Periclimenes longicaudatus* were recorded only on the continental shelf, in the rainy season (Table II).

Chaetognatha. *Flaccisagitta enflata* was the most frequent chaetognath species, and occurred at all sampling stations throughout the study period. *Parasagitta friderici* was the second most frequent species. This species was found at all stations during the dry season and at 90% of the stations during the rainy season (Table II).

Appendicularia. The most frequent appendicularian species was *Oikopleura longicauda*, which occurred at all stations throughout the study period. The second most frequent species was *Oikopleura fusiformis*, which peaked in frequency on the slope during the dry season. The SACW contained the most species that occurred in only one water mass (2 species; Table II).

Thaliacea. *Doliolum nationalis* was the most frequent thaliacean, observed at all sampling stations throughout the study period. *Thalia democratica* was the second most frequent species and showed a frequency peak on the slope in the dry season. Five species occurred exclusively in the SS (Table II).

Cluster analysis indicated the formation of groups at a 55% similarity level during the rainy season (Fig. 4) and at a 40% similarity level during the dry season (Fig. 5).

During the rainy season, the arrangement of these groups indicated three faunistic areas: A) comprising mainly the samples from the SS; B) comprising the samples from the SACW, AAIW and UCDW, mainly; and C) comprising the samples of SACW, in the south and north regions of the study area (Fig. 4). The other samples were not associated with any of the large groups (over ten samples; Fig. 4). Among the species that contributed most to the similarity within the faunistic areas in the rainy season, *Oncaea venusta* (Copepoda), *Oikopleura longicauda* (Appendicularia), *Parasagitta friderici*, *Flaccisagitta enflata* (Chaetognatha), *Doliolum nationalis* (Doliolidae) and *Diphyes bojani* (Siphonophorae) contributed to the similarity of all groups, while other species contributed to the formation of only one faunistic zone (Table III).

During the dry season, the arrangement of the groups indicated three faunistic areas: A) comprising the samples of SS; B) comprising the samples of SACW, mainly; and C) comprising the samples of AAIW and UCDW (Fig. 5). The other stations were not associated with any of the large groups (over ten samples; Fig. 5). Some species contributed to the similarity of only one faunistic area, while *Parasagitta friderici*, *F. enflata*, *O. venusta* and *O. longicauda* contributed to the similarity of all groups (Table III).

Some of the rare species (occurrence frequency below 15% in the study period) were recorded in only one faunistic zone. The SS showed 29 exclusive species, e.g., *Cunina frugifera*, *Sulculeolaria turgida*, *Hippopodius hippopus*, *Pleopis polyphemoides*, *Centropages violaceus*, *Calanopia americana* and *Pontellina plumata* (Table II). In SACW, 34 species were exclusive to this faunistic zone, e.g., *Enneagonum hyalinum*, *Lensia achilles*, *Gaetanus*

Table III. Mesozooplankton species contributing (up to a total of 50%) to the similarity of faunistic zones during the rainy and dry seasons, over the continental shelf and slope in the Campos Basin, central Brazilian coast (SIMPER). (SS) Subsurface Water, (SACW) South Atlantic Central Water, (AAIW) Antarctic Intermediate Water, (UCDW) Upper Circumpolar Deep Water.

SS Group	%	SACW/AAIW/UCDW Group	%	SACW Group	%
Rainy season					
Flaccisagitta enflata	5.40	*Oncaea venusta*	5.22	*Decipisagitta sibogae*	5.72
Oikopleura longicauda	5.40	*Oikopleura longicauda*	5.22	*Oithona similis*	5.72
Clausocalanus furcatus	5.16	*Parasagitta friderici*	4.77	*Doliolum nationalis*	5.72
Parasagitta friderici	4.99	*Clausocalanus furcatus*	4.41	*Oncaea venusta*	5.72
Temora stylifera	4.98	*Flaccisagitta enflata*	4.34	*Flaccisagitta enflata*	5.72
Diphyes bojani	4.61	*Doliolum nationalis*	4.01	*Parasagitta friderici*	5.72
Oncaea venusta	4.17	*Temora stylifera*	3.98	*Oikopleura longicauda*	4.71
Farranula gracilis	4.09	*Nannocalanus minor*	3.66	*Lubbockia squillimana*	3.97
Acrocalanus longicornis	3.92	*Pterosagitta draco*	3.63	*Nematoscelis tenella*	3.95
Doliolum nationalis	3.91	*Oikopleura fusiformis*	3.59	*Krohnitta subtilis*	3.89
Aglaura hemistoma	3.63	*Farranula gracilis*	3.28		
		Triconia cf. *conifera*	2.95		
		Diphyes bojani	2.93		
SS Group	**%**	**SACW Group**	**%**	**AAIW/UCDW Group**	**%**
Dry season					
Doliolum nationalis	5.54	*Decipisagitta sibogae*	11.15	*Caecosagitta macrocephala*	9.1
Oikopleura longicauda	5.54	*Oncaea venusta*	11.15	*Parasagitta friderici*	8.99
Parasagitta friderici	5.54	*Parasagitta friderici*	11.15	*Conaea rapax*	8.51
Clausocalanus furcatus	5.29	*Triconia cf. conifera*	8.52	*Oncaea venusta*	8.44
Flaccisagitta enflata	5.26	*Flaccisagitta enflata*	7.54	*Calanoides carinatus*	7.80
Krohnitta mutabbii	4.63	*Heterorhabdus papilliger*	5.98	*Clausocalanus furcatus*	6.73
Aglaura hemistoma	4.62			*Rhincalanus cornutus*	6.48
Muggiaea kochi	4.53				
Paracalanus quasimodo	3.84				
Penilia avirostris	3.62				
Temora stylifera	3.59				

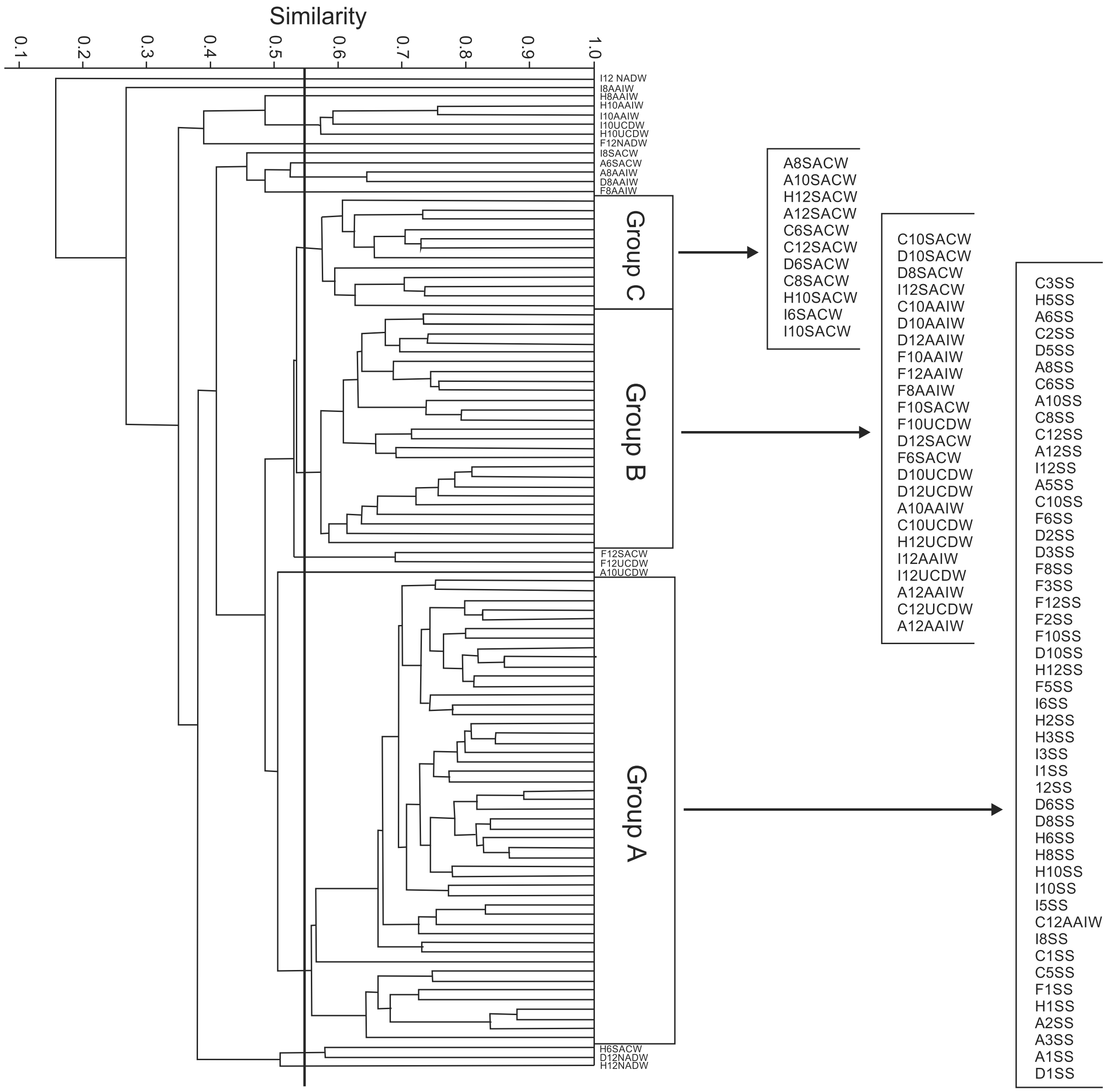

Figure 4. Cluster analysis based on species composition in samples from the water masses in the Campos Basin, central Brazilian coast, during the rainy season. For the analysis, the Sørensen-Dice coefficient with average linkage method was used. Different groups indicate faunistic zones, defined at 55% similarity. In data labels: the first letter indicates transect, number indicates station, and the letters after station number indicate water masses (SS – Subsurface Water, SACW – South Atlantic Central Water, AAIW – Antarctic Intermediate Water, UCDW – Upper Circumpolar Deep Water, NADW – North Atlantic Deep Water).

pileatus, *Candacia tenuimana*, *Lophothrix quadrispinosa*, *Nematobrachion flexipes* and *Stylocheiron elongatum* (Table II). In the AAIW/UCDW faunistic zone, 28 species showed exclusive records, e.g., *Lensia havock*, *Gaetanus kruppi*, *Euaugaptilus facilis*, *Lophothrix latipes*, *Scaphocalanus brevicornis*, *Scaphocalanus elongatus*, and *Caecosagitta macrocephala* (Table II).

DISCUSSION

The species richness and the composition of the zooplankton were primarily associated with the water masses present in the region. In the southwest Atlantic, as in most plankton studies elsewhere, the plankton fauna has mainly been sur-

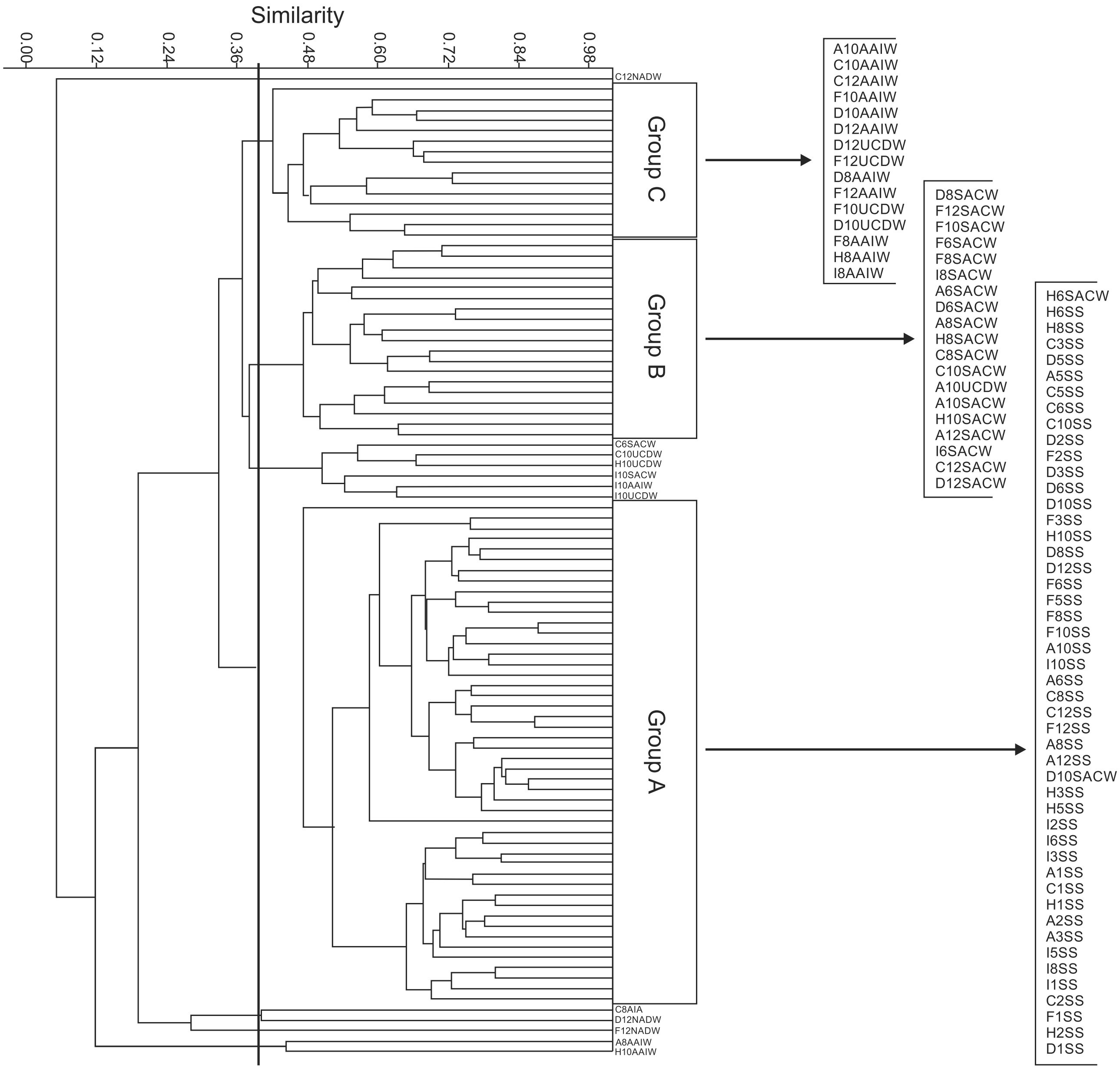

Figure 5. Cluster analysis based on species composition in samples from the water masses in the Campos Basin, central Brazilian coast, during the dry season. For the analysis, the Sørensen-Dice coefficient with average linkage method was used. Different groups indicate faunistic zones, defined at 40% similarity. In data labels: letters indicate transect, number indicate station, SS – Subsurface Water, SACW – South Atlantic Central Water, AAIW – Antarctic Intermediate Water, UCDW – Upper Circumpolar Deep Water, NADW – North Atlantic Deep Water, SS – Subsurface Water, SACW – South Atlantic Central Water, AAIW – Antarctic Intermediate Water, UCDW – Upper Circumpolar Deep Water, NADW – North Atlantic Deep Water.

veyed in the upper layers (0-200 m; Björnberg 1963, Bassani *et al.* 1999, Ramírez & Sabatini 2000, Bonecker 2006, Eskinazi-Sant'Anna & Björnberg 2006, Lopes *et al.* 2006), and the mesopelagic is better studied but about the bathypelagic we know very little (Dias *et al.* 2010). This study showed that the increase in depth is correlated with a decrease in the number of zooplankton species. In general, a decrease in diversity is expected with increasing depth (Angel 1997, Robison 2004). Dias *et al*. (2010) observed a reduction in richness from the first few meters of the water column down to 2,300 m in the vertical distribution of copepods in the Campos Basin. In the present study, the highest species richness was observed in the first 250 m in the SACW, decreasing down to 2,300 m depth in the NADW. According to SMITH & BROWN (2002), the rapid declines of temperature and productivity associated with the increasing depth are the primary causes of this pattern of diversity decrease from 200 m depth to the deep ocean.

In SS, the slope showed higher species richness than the continental shelf in the dry season. This trend to increasing diversity toward the oceanic region was discussed by Lopes *et al.* (2006), and has been observed in many studies comparing neritic and oceanic areas (e.g., RAKHESH *et al.* 2006, ZHANG *et al.* 2009). The tropical oceanic regions are oligotrophic (BOLTOVSKOY 1981) and low concentrations of nutrients are associated with more stable environments (ANGEL 1993). This characteristic result higher richness in ocean regions than in neritic areas (ANGEL 1993).

The most frequent species of each mesozooplankton group found on the continental shelf and slope of the Campos Basin have been observed along the Brazilian coast (e.g., GUSMÃO *et al.* 1997, LOPES *et al.* 1999, DIAS *et al.* 2010). We found 13 new records for the southwest Atlantic Ocean; until the present study, the distribution areas of these species in the Atlantic Ocean had been recognized only from the North Atlantic, central South Atlantic and/or southeast Atlantic (BOUILLON 1999, SUÁREZ & GASCA 1989, GASCA 2002, RAZOULS *et al.* 2000, 2013; Table IV).

In both sampling periods, the samples from SS, SACW and AAIW/UCDW were clustered in different faunistic zones. The species compositions of the AAIW and UCDW were not distinct, probably due to their similar circulation patterns (REID 1989), salinity and temperature (REID 1989, MÉMERY *et al.* 2000; Fig. 2). Some rare species (occurrence frequency below 15%) showed a bathymetric distribution restricted to a single faunistic zone (SS, SACW and AAIW/UCDW). The vertical distributions previously recorded for most of these species concords with the results of this study (BRADFORD-GRIEVE *et al.* 1999, BOUILLON 1999, CASANOVA 1999, GIBBONS *et al.* 1999, PUGH 1999).

Understanding the distribution patterns of species or higher taxa is more complicated than understanding the patterns of density and biomass, since species do not react uniformly to a given environment. Water-mass characteristics and smaller-scale oceanographic features affect the habitat and bathymetric distribution of these species (FERNÁNDEZ-ÁLAMO & FÄRBER-LORDA 2006). The occurrence of epipelagic species (e.g., *Clausocalanus furcatus* and *Penilia avirostris*) in the meso-bathypelagic zones can be attributed to: 1) contamination, 2) sampling of dead individuals, or 3) increase in their depth distribution. The hypothesis of contamination is unlikely because the sampling was done with a multinet, which has a robust opening-closing mechanism and is suitable for stratified depth samples (SAMEOTO *et al.* 2000). In addition, different set nets were used at each depth. Another possibility is that specimens of epipelagic species recorded in deep water masses were dead individuals in the process of settling. This hypoth-

Table IV. New records for the southwest Atlantic of the mesozooplankton species collected in this study, with the previously known distribution.

Taxon	Previously known distribution	References
Hydrozoa		
Laodicea indica	Southeast Atlantic, Pacific and Indian	NAVAS-PEREIRA & VANNUCCI (1991), BOUILLON (1999), CAIRNS *et al.* (2009)
Siphonophorae		
Lensia subtiloides	North Atlantic and Indian	GASCA (2002), THIBAULT-BOTHA *et al.* (2004)
Lychnagalma utricularia	North Atlantic and Mediterranean	MILLS *et al.* (1996), GASCA (2002)
Copepoda		
Amalothrix dentipes	Central South Atlantic, South Pacific, Indic, Antarctic and Subantarctic regions	BRADFORD-GRIEVE *et al.* (1999), RAZOULS *et al.* (2000, 2013)
Arietellus plumifer	North Atlantic, Central South Atlantic, Southeast Atlantic, Pacific, Indian and Mediterranean	SUÁREZ & GASCA (1989), BRADFORD-GRIEVE *et al.* (1999), RAZOULS *et al.* (2000, 2013)
Chiridiella atlantica	Central South Atlantic	BRADFORD-GRIEVE *et al.* (1999), RAZOULS *et al.* (2013)
Euaugaptilus facilis	North Atlantic, Central South Atlantic, Southeast Atlantic, Pacific and Indian	BRADFORD-GRIEVE *et al.* (1999), RAZOULS *et al.* (2000, 2013)
Gaetanus pileatus	North Atlantic, Central South Atlantic, Southeast Atlantic, Pacific, Indian and Subantarctic region	THUESEN *et al.* (1998), BRADFORD-GRIEVE *et al.* (1999), RAZOULS *et al.* (2000, 2013)
Haloptilus longicirrus	North Atlantic, Central South Atlantic, Southeast Atlantic, North Pacific, Indian and Antarctic	ERRHIF *et al.* (1997), BRADFORD-GRIEVE *et al.* (1999), RAZOULS *et al.* (2000, 2013)
Lophothrix quadrispinosa	North Atlantic, South Pacific and Indian	BRADFORD-GRIEVE *et al.* (1999), RAZOULS *et al.* (2000, 2013)
Oncaea atlantica	Central South Atlantic, North Pacific, Indian, Mediterranean and Red Sea	BRADFORD-GRIEVE *et al.* (1999), NISHIBE *et al.* (2009), RAZOULS *et al.* (2000, 2013)
Racovitzanus levis	North Atlantic, Pacific and Indian	HARDING (1974), RAZOULS *et al.* (2000, 2013)
Tharybis asymmetrica	North Atlantic and Southeast Atlantic	BRADFORD-GRIEVE *et al.* (1999), RAZOULS *et al.* (2000, 2013)

esis cannot be ruled out, since we did not use any technique, such as neutral red stain for crustaceans, which could distinguish dead from living individuals (Marcus *et al.* 2004, Tang *et al.* 2006, Jessopp 2007). Otherwise, the extension of the depth distribution is possible, in view of the lack of studies in deep habitats in the southwest Atlantic Ocean.

Some species that contributed to the delimitation of all groups, occurring from the surface to the deep water masses, were previously classified as epipelagic until this study, e.g., *Parasagitta friderici* (Casanova 1999, Liang & Vega-Pérez 2001), while the other species had been recorded from the deep ocean, e.g., *Oncaea venusta*, *Flaccisagitta enflata*, and *Doliolum nationalis* (Ozawa *et al.* 2007, Weikert & Godeaux 2008, Dias *et al.* 2010). In the SS, during both study periods, *Corycaeus giesbrechti* and *Liriope tetraphylla* contributed to the delimitation of this group. These species are characteristic of the epipelagic region (Lopes *et al.* 1999, Buecher & Gibbons 2000, Benovic *et al.* 2005), although *C. giesbrechti* has been recorded in the upper 500 m of the Sargasso Sea off Bermuda (Deevey 1971), and down to 1,000 m in the Campos Basin (Dias *et al.* 2010). In the SACW, *Decipisagitta sibogae* and *Krohnitta subtilis* contributed to the delimitation of this group in the two periods. These species were classified as mesopelagic by Casanova (1999). *Decipisagitta sibogae* has been recorded between 200-600 m in the Sargasso Sea (Pierrot-Bults & Nair 2010) and *K. subtilis* has been recorded at 600-800 m in the Pacific Ocean (Ozawa *et al.* 2007, Pierrot-Bults & Nair 2010) and at 400 m off the Chilean coast (Ulloa *et al.* 2000). All species that contributed most to the similarity of the group from deep water masses in both sampling periods are classified as mesopelagic or bathypelagic, except *Dolioletta gegenbauri*, *Oikopleura fusiformis*, and *Rhincalanus cornutus*, which are classified as epipelagic. *Dolioletta gegenbauri* is a common species off the Brazilian coast in areas under the influence of coastal and tropical water (Lopes *et al.* 2006). *Oikopleura fusiformis* is found in coastal and oceanic waters and is more frequent in the latter (Bonecker & Carvalho 2006). Until this study, *O. fusiformis* had not been recorded in the mesopelagic and bathypelagic regions. Although it has been classified as epipelagic (Bradford-Grieve *et al.* 1999), *R. cornutus* was observed below 600 m off the coast of Florida, USA (Moore & O'Berry 1957), in the upper 500 m in the Sargasso Sea off Bermuda (Deevey 1971), and below 2,000 m in the Campos Basin (Dias *et al.* 2010).

The sample grid and number of zooplankton groups included in this study are more extensive than any previous study in the southwest Atlantic Ocean, and helped to fill the gap in understanding mesozooplankton vertical distribution. The results of this study extended the vertical distribution of some zooplankton species previously classified as epi-mesopelagic species. We confirmed that zooplankton richness in the southwest Atlantic Ocean is currently underestimated, and we suggest that additional efforts must be directed toward a better understanding of this fairly unknown region.

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