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Distribution, diversity, and habitat partitioning of Scolecitrichidae species (Copepoda: Calanoida) down to 1,200 m in the Southwestern Atlantic Ocean

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Abstract: In this study, we analyzed the main distributional features of Scolecitrichidae species in the Southwestern Atlantic Ocean (northern region of Rio de Janeiro State) and determined and described their habitat partitioning, based on a night series of stratified samplings down to a depth of 1,200 m. A total of 18 species from seven genera were identified and grouped according to their depth distribution. Distinct vertical patterns of total density, richness, diversity, and evenness were observed, with a decrease in density and an increase in diversity and richness with increasing depth. The total scolecitrichid abundance was dominated by a few epipelagic migrant species (Scolecithrix danae, Scolecithricella minor, Amallothrix tenuiserrata, and Lophothrix frontalis). The nondominant species were distributed in different habitats in the mesopelagic layer (upper-mesopelagic, mesopelagic, and lower-mesopelagic species) according to their vertical patterns of abundance and occurrence in the two sampling periods (rainy and dry season). The total density of scolecitrichid copepods was positively related to temperature and nitrate, and negatively related to silicate at 1 m depth. The abundance of scolecitrichids copepods in the upper layer with warm and oligotrophic waters supports the hypothesis of the influence of different water masses on the scolecitrichid assemblage. High abundance of appendicularians (Oikopleura longicauda) at 1 m depth in the region implies a high production rate of discarded “houses”, an important dietary component for Scolecitrichidae copepods. The observed patterns of seasonal cycles and vertical distribution suggest that the diverse scolecitrichid assemblage in the region may be structured mainly according to the partitioning of vertical habitats and food resources.

Key words: Copepoda, Scolecitrichid, deep waters, Southwestern Atlantic Ocean, Tropical environment.

INTRODUCTION

The Scolecitrichidae (Copepoda: Calanoida) are widely distributed throughout the world’s oceans, with peak abundance in the tropics (Gopalakrishnan and Devi 1998, El-Sherbiny and Al-Aidaroos 2013). Scolecitrichidae are one of the most species-rich families of calanoid copepods (Boxshall

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and Halsey 2004, Kuriyama and Nishida 2006), and have generally been found from pelagic to benthopelagic regions in marine waters below 200 m (Ferrari and Markhaseva 2000, Markhaseva and Dahms 2004, El-Sherbiny and Al-Aidaroos 2013).

Like several families distributed primarily in the meso-, bathy-, and benthopelagic layers, scolecitrichids are consumers of detritus particles and play important roles in the oceanic food web, contributing to the remineralization of organic particles and transferring small organic particles to higher trophic levels (Steinberg 1995, Nishida and Ohtsuka 1997). Kuriyama and Nishida (2006) have suggested that the scolecitrichids provide an excellent model group of zooplankton for understanding the structural aspects of species diversity and of niche-partitioning in the oceanic environment, in relation to their patterns of vertical distribution, feeding specialization, and taxonomic relationships.

Currently, 32 genera are included in the family Scolecitrichidae (Razouls et al. 2005-2018), 20 of which were first described in the 21st century (Ferrari and Markhaseva 2000, El-Sherbiny and Al-Aidaroos 2013), which reflects a general rise in interest in the biology of deep ocean waters in recent years (Ferrari and Markhaseva 2000). The vertical distribution of scolecitrichids has been studied in the Atlantic, Pacific, Indian, and Antarctic oceans, however these studies have dealt with calanoid copepods as a whole (Madhupratap and Haridas 1986, Yamaguchi et al. 1999, Wishner et al. 2008) and have generally analyzed only a limited number of scolecitrichid species and/or specimens (Vyshkvartzeva 2001, Ohtsuka et al. 2002, El-Sherbiny and Al-Aidaroos 2013). Even though substantial information on the taxonomy of scolecitrichid copepods is available, their vertical distribution patterns and phylogenetic taxonomic relationships (i.e., within genera) are still poorly known (Kuriyama and Nishida 2006). Moreover, there have been no comprehensive studies of scolecitrichid zoogeography in the Southwestern Atlantic Ocean.

In the Southwestern Atlantic Ocean, most studies have investigated zooplankton distribution only in the epipelagic zone in neritic and oceanic regions (Berasategui et al. 2006, Eskinazi-Sant'anna and Björnberg 2006, Lopes et al. 2006, Dias et al. 2010, 2015, 2018, Bonecker et al. 2014, 2018), and knowledge of Scolecitrichidae distribution ranges is restricted to a few epipelagic species. Thus, information on mesopelagic and bathypelagic Scolecitrichidae in the SW Atlantic Ocean is limited (Campaner 1984, Dias et al. 2010, 2018, Bonecker et al. 2014, 2018), and their vertical distribution patterns and phylogenetic relationships have not yet been thoroughly described.

The Campos Basin is located on the SW boundary of the South Atlantic Ocean, and its copepod community has previously been investigated (Campaner 1984, Dias et al. 2010, 2015, 2018, Bonecker et al. 2014, 2018), with high (ca. 20) scolecitrichid species richness reported. The aim of this study was to investigate the abundance patterns and vertical distribution of scolecitrichid copepods in the northern region of Rio de Janeiro State in order to better understand the species diversity and habitat partitioning of this family in the deep sea (down to a depth of 1,200 m). We discuss possible mechanisms for species segregation and aspects of their temporal and geographic variability. We ascertain the potential relationships between Scolecitrichidae distribution patterns and environmental variables and contribute to elucidating the vertical distribution of this family in a tropical oceanic region.

MATERIALS AND METHODS

HYDROGRAPHY OF THE STUDY AREA

The Campos Basin occupies a portion of the Brazilian continental boundary between southern Espírito Santo (Vitória High, 20.5°S) and northern

Rio de Janeiro (Cabo Frio High, 24°S), covering an area of approximately 100,000 km^2 (Viana et al. 1998). This region is characterized by its water column structure and water mass distribution over the continental shelf and slope. The different water masses in the area have distinct temperatures, salinities, and dissolved oxygen (DO) levels that provide different habitats for pelagic species down to depths of 3,000 m.

The Brazil Current (BC) is a warm, oligotrophic western boundary current that flows southwest, as part of the South Atlantic western boundary current system (Stramma et al. 1990). The upper reaches of the water column include the nutrient-poor Tropical Water [TW; temperature (T) > 20°C; salinity (S) > 36.20] and the relatively cold, nutrient-rich South Atlantic Central Water (SACW, 142–567 m depth; 8.72°C < T < 20°C and 34.66 < S < 36.20) that flows along the continental slope at the bottom layer of the BC (Bonecker et al. 2014, Dias et al. 2015). Water masses at greater depths include the cold Antarctic Intermediate Water (AAIW, 567–1,060 m; 3.46°C < T < 8.72°C and 34.42 < S < 34.66), which flows north, has high values of phosphate, is rich in oxygen, and is less saline (Viana et al. 1998, Pedrosa et al. 2006), and the Upper Circumpolar Water (UCDW, 1,060–1,300 m; 3.31°C < T < 3.46°C and 34.42 < S < 34.66) that can be identified only by chemical analysis due to its lower levels of oxygen and higher concentration of nutrients, mainly silicates (Pedrosa et al. 2006). Finally, the North Atlantic Deep Water (NADW; 2.04°C < T < 3.31°C and 34.59 < S < 34.87) is found below the UCDW, influencing the lower continental slope below a depth of 1,300 m (Mémery et al. 2000, Silveira et al. 2000; Figure 1). This southward-flowing water mass is highly saline, oxygen-rich, and nutrient-poor compared with the Circumpolar Water (upper and lower) (Viana et al. 1998, Pedrosa et al. 2006).

SAMPLES COLLECTION AND ANALYSES

Mesozooplankton (> 200 µm) samples were collected during oceanographic cruises from February 25 to April 13, 2009 (rainy season, RS) and from August 5 to September 17, 2009 (dry season, DS). The sampling stations were distributed along six transects perpendicular to the coast (A, C, D, F, H, and I) in a north–south direction. Each transect contained eight sampling stations (four on the continental shelf and four on the slope) between the 25-m and 3,000-m isobaths (25, 50, 75, 150, 400, 1,000, 1,900, and 3,000 m; Figure 2). Zooplankton samples were not collected in transects B, E, and G. All samples were collected between 6:18 PM and 5:08 AM during the RS and between 5:57 PM and 5:46 AM during the DS (local time).

Environmental data recorded included the following: (a) water temperature and salinity at all sampling depths, namely, 1 m, 250 m, 800 m, and 1,200 m, by using a CTD sonde; (b) inorganic nutrients (nitrate, silicate, and orthophosphate), determined by standard oceanographic methods (Grasshoff et al. 1999); (c) DO, measured continuously in the water column using a sensor coupled to the CTD; and (d) suspended particulate matter (SPM), obtained from 4-L water subsamples filtered through a Whatman GF/F filter pre-combusted at 510°C for 4 h, and weighed to an accuracy of 0.0001 g. Detailed methodology and discussion of the hydrochemistry of the study area are presented elsewhere (Bonecker et al. 2014, Rodrigues et al. 2014, Dias et al. 2015, Suzuki et al. 2015).

Mesozooplankton samples were collected by horizontal hauls at the same stations and depths (1 m, 250 m, 800 m, and 1,200 m) at which the environmental parameters were recorded. Sampling depths represent the nucleus of each water mass. In the DS, no samples were collected on the 3,000-m isobaths of transects H and I, due to logistical problems. A total of 193 samples (102 in the RS and 91 in the DS) were collected using a Hydro-

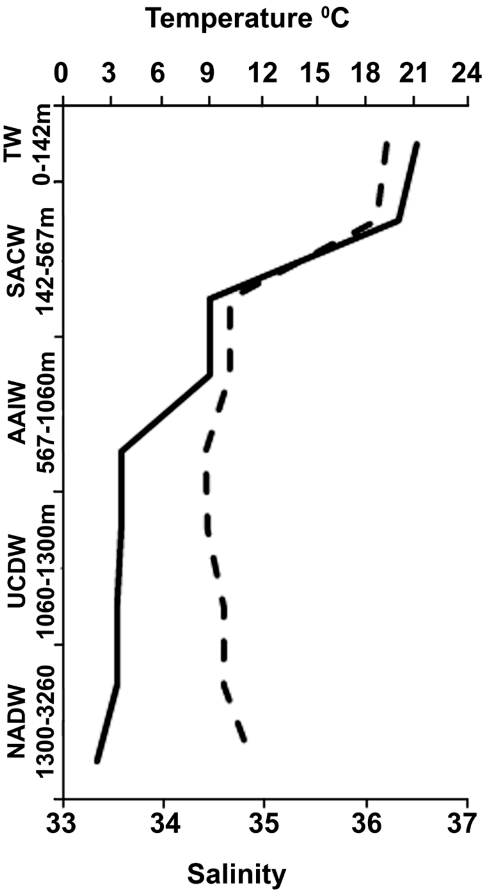

Figure 1 - Salinity and temperature of the five water masses (0-3,260 m) in the Campos Basin, central Brazilian coast, modified from Bonecker et al. (2014). Solid line, temperature; dashed line, salinity; TW, Tropical Water; SACW, South Atlantic Central Water; AAIW, Antarctic Intermediate Water; UCDW, Upper Circumpolar Deep Water; NADW, North Atlantic Deep Water.

Bios MultiNet® type midi with a 50 × 50 cm frame opening (aperture of 0.25 m^2) and dimensions of 80 cm × 90 cm × 95 cm. The MultiNet was equipped with a set of nets (mesh apertures of 200 µm) and a different net was used to sample each water mass to prevent contamination. At each predetermined depth, hauls were performed at a speed of 2 knots using an opening–closing mechanism operated by electronically transmitted commands. The depth of the haul was controlled during the entire procedure to ensure that the net was towed horizontally. At 1 m depth, 5-minute hauls were performed, whereas at 250 m, 800 m, and 1,200 m depths, the net was towed for 10 minutes because of the lower density of organisms in deeper waters. To determine the collecting depth, the MultiNet was equipped with a depth sensor. A depressor was used to maintain net stability. Water volume and haul depth data were transmitted in real-time to a shipboard computer. Filtration efficiency and water volume were determined using two flow meters: one was mounted in front of the mouth of the net and the other fixed to the outer part of the net. Filtered water volume in each sampling depth ranged from 60 to 280 m^3 (1 m), from 57 to 195 m^3 (250 m), from 83 to 269 m^3 (800 m), and from 92 to 264 m^3 (1,200 m).

Samples were immediately fixed and preserved in 4% buffered formalin. In the laboratory, the preserved samples were divided into between 1 and 10 fractions using a Folsom Plankton Splitter (Hydro-Bios, Am Jägersberg, Altenholz, Germany) (McEwen et al. 1957) and the resultant subsamples were analyzed. The degree of subsampling was adjusted to the density of the organisms so that at least 100 individuals were sorted in each sample. All the copepods were sorted, identified (adults and copepodites), and counted under a stereoscopic microscope, and the scolecitrichid copepods were identified according to the methods of Bradford-Grieve et al. (1999) and Dias and Araujo (2006). Taxon abundance per cubic meter and scolecitrichid species composition were determined for all samples. All collected specimens were deposited in the copepod collection of the Integrated Zooplankton and Ichthyoplankton Laboratory of the Universidade Federal do Rio de Janeiro.

DATA ANALYSIS

The scolecitrichids were classified according to their vertical distribution in the studied area based on criteria developed by Kuriyama and Nishida (2006), which classified the scolecitrichid species into six groups (epipelagic migrants, interzonal

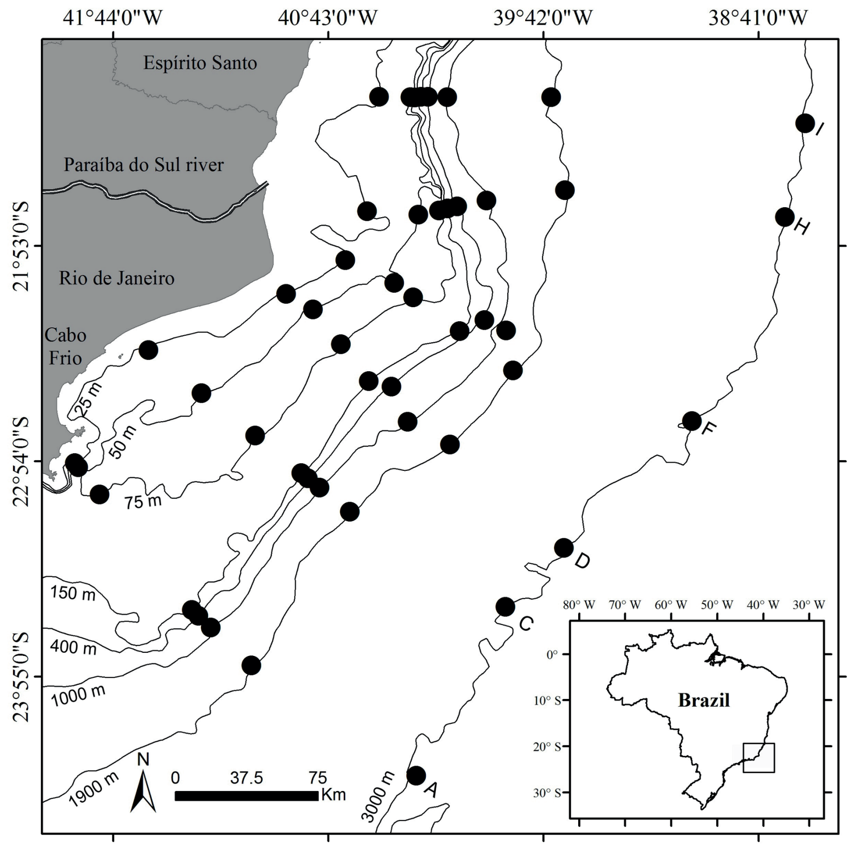

Figure 2 - Study area showing the sampling stations and collection sites (black solid circles) for specimens of scolecitrichids used in this study.

migrants, upper-mesopelagic migrants, upper-mesopelagic non-migrants, lower-mesopelagic species, and mesopelagic species) according to their distributional depths and day–night differences. These criteria were modified for adaptation to local conditions.

For comparisons of diversity between the sampling periods and depths, the Shannon–Wiener index (H′) was calculated for each station as follows:

$$H' = -\sum pi * \ln (pi),$$

where pi is the fraction of species i in the total sample. We also calculated Pielou's index of evenness. These analyses were run using the PRIMER 6.0 package (Clarke and Gorley 2006). The vertical (depth) and temporal (RS and DS) differences in density, richness, diversity, and evenness of scolecitrichids, and their interactions were analyzed using generalized linear models (GLMs) with gamma family (dispersion = 1). A low additive constant (1) was applied to the density data from each sampling station data to eliminate zero values in the matrix because the gamma family does not allow for zeros. The results were considered significant at a significance level < 0.05. The analyses were performed using R 3.1.3 (R Core Team 2015; www.r-project.org).

The influence of environmental parameters on Scolecitrichidae family distribution was analyzed using GLMs with gamma family. The descriptor was the total scolecitrichid density, whereas the environmental parameters were used as predictor variables to describe the total scolecitrichid density. Initially, a full model was designed using all the variables, and then biologically logical models were constructed containing fewer variables. To minimize collinearity effects on the results, highly correlated variables (salinity and orthophosphate) were excluded from the analysis. The environmental parameters used were temperature, SPM, dissolved oxygen (DO), nitrate (NO_3), and silicate. From the results of this full model, biologically important models were designed containing fewer predictor variables. The Akaike information criterion for small samples (AICc) was used to select the best model among those constructed. The model with the lowest AICc was considered the most plausible for describing the data, and the importance of alternative models was estimated from the difference between AIC values (ΔAICc). Models with ΔAICc ≤ 2 were also considered plausible (Burnham and Anderson 2002). The analyses were performed using R 3.1.3 (R Core Team 2015; www.r-project.org) and the MuMIn package.

RESULTS

HYDROGRAPHY

Environmental conditions during the study period have been described in detail by Bonecker et al. (2014), Rodrigues et al. (2014), Dias et al. (2015), and Suzuki et al. (2015), and are therefore only briefly summarized here and in Table I.

At 1 m depth, the lowest values of temperature and salinity were recorded during the DS, mainly at stations located in the southern part of the study area, over the continental shelf near Cabo Frio, and in the northern part, under the continental influence of the Paraíba do Sul River. During the RS, the lowest values were only recorded near Cabo Frio. At 250 m, the highest temperature values were measured under the continental influence of the Paraíba do Sul River (RS) and over the continental shelf near Cabo Frio (DS). At 800 m and 1,200 m, both temperature and salinity were relatively uniform. During the two sampling periods, the values of SPM declined above the slope compared with the continental shelf, and along the water column with increasing depth. The

TABLE I

Minimum and maximum values registered for the parameters temperature (°C), salinity, suspended particulate matter (SPM, mg L^{-1}), dissolved oxygen (DO), nitrate (µmol L^{-1}), silicate (µmol L^{-1}), and orthophosphate (µmol L^{-1}) for samples collected in the water column of the Campos Basin during the rainy (RS) and dry (DS) seasons of 2009.

Depht	Sampling Periods	Temperature (°C)		Salinity		SPM (mg L^{-1})		DO (mg L^{-1})		Nitrate (µmol L^{-1})		Silicate (µmol L^{-1})		Orthophosfate (µmol L^{-1})	
		Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
1 m	Rainy Season	24.82	28.50	35.44	37.28	0.29	3.99	5.78	6.53	0.56	3.09	0.41	9.06	0.01	0.14
	Dry Season	19.64	24.89	35.71	37.12	0.15	6.50	4.36	7.75	0.37	4.85	0.31	7.89	0.02	0.44
250 m	Rainy Season	13.64	25.65	35.28	35.99	0.04	1.93	6.17	6.68	0.58	7.67	0.58	3.53	0.02	0.71
	Dry Season	12.09	16.75	35.12	35.79	0.17	0.87	6.22	6.77	1.48	11.41	1.35	7.15	0.26	0.81
800 m	Rainy Season	4.64	5.61	34.33	34.40	0.01	1.02	6.03	6.84	5.29	32.37	5.33	30.15	0.72	2.00
	Dry Season	4.39	5.33	34.34	34.46	0.22	0.67	6.08	6.67	18.18	34.72	19.85	31.31	1.69	1.95
1,200 m	Rainy Season	3.20	3.53	34.45	34.57	0.33	1.11	5.90	6.06	17.58	31.76	20.93	51.11	1.71	2.08
	Dry Season	3.19	3.45	34.54	34.67	0.13	1.05	5.76	5.89	25.42	35.33	37.54	49.88	1.79	2.07

highest values of SPM were recorded in the southern part of the study area (Cabo Frio region) during the DS. Dissolved Oxygen values were relatively homogeneous in both sampling seasons, except for those at 1 m depth, where both low and high values were obtained during the DS over the continental shelf of the northern part of the study area (under the continental influence of the Paraíba do Sul River). In both sampling periods, a nutrient pattern typical of that in oceans was observed, characterized by low values at the surface and increasing with depth. At 1 m depth, the highest values were observed over the continental shelf during the DS, particularly in the Cabo Frio region.

ABUNDANCE, OCCURRENCE, AND VERTICAL DISTRIBUTION OF SCOLECITRICHID COPEPODS

Scolecitrichidae species comprised ca. 1% of total copepod abundance, although this family was the most species-rich in the study area (13% of total copepod taxa; Bonecker et al. 2015). Although the total scolecitrichid abundance did not vary between the sampling periods, it did show variation among sample depths ($p < 0.05$). The abundance of scolecitrichids showed a distinct pattern, with the major population occurring at 1 m (mean values—RS: 6.94 ± 16.76 ind.m^{-3}; DS: 28.07 ± 88.00 ind.m^{-3}) and at 250 m (mean values—RS: 2.45 ± 2.99 ind.m^{-3}; DS: 4.85 ± 14.24 ind.m^{-3}), decreasing with depth in the two sampling periods (Figure 3a). The highest scolecitrichid abundances were recorded over the continental shelf (mean values—RS: 7.50 ± 17.48 ind.m^{-3}; DS: 32.93 ± 115.08 ind.m^{-3}) in comparison with the slope (mean values—RS: 2.82 ± 9.45 ind.m^{-3}; DS: 9.28 ± 28.40 ind.m^{-3}). The highest densities found above the continental shelf were recorded near Cabo Frio and under the influence of the Paraíba do Sul River during the DS.

Twenty-four copepod taxa were identified, including 18 species of Scolecitrichidae belonging to eight genera. *Scolecithrix danae*, *Scolecithricella minor*, *Amallothrix tenuiserrata*, and *Lophothrix frontalis* were the most frequent (≥ 5% of the total stations) and abundant (97% of the total Scolecitrichidae collected; Table II). The remaining 14 species were less abundant and frequent (Table II). During the sampling period, some species showed seasonal changes: *Scaphocalanus brevicornis*, *Scaphocalanus magnus*, and *Scolecithrix bradyi* occurred only during the RS, whereas *Scaphocalanus elongatus*, *Lophothrix latipes*, *Racovitzanus levis*, *Scaphocalanus subbrevicornis*, *Pseudoamallothrix ovata*, *Pseudoamallothrix profunda*, and *A. tenuiserrata* occurred only during the DS (Table II).

As for the total scolecitrichid density, the species richness did not vary between the sampling periods, although it did vary among the sample depths ($p < 0.05$). There were interactions between the effects of the sampling periods and depths on the diversity and evenness of scolecitrichids ($p < 0.05$). During the RS, the species richness ranged from 1 to 3, with the diversity (H′) varying from 0.00 to 1.58, whereas during the DS, the number of species varied from 1 to 4 species, and the diversity ranged from 0.00 to 2.00. In both sampling periods, the evenness ranged from 0.00 to 1.00. The number, diversity, and evenness of species showed gradual increases with depth, with an increasing trend during the DS at 800 and 1,200 m (Figure 3b). In terms of species numbers, *Scaphocalanus* was the most species-rich genus (five species observed during the sampling periods), followed by *Lophothrix* (three species). *Scaphocalanus* was represented by three species in each sampling period, whereas the species richness of *Lophothrix* increased during the DS (RS: two species, DS: three species; Table II).

In the RS, the single species that occurred at 1 m depth, above both the continental shelf and slope, was *S. danae* (continental shelf: 4.56 ± 11.98 ind.m^{-3}; slope: 4.54 ± 15.52 ind.m^{-3}). In waters above the continental shelf, this species was found at stations located in the southern (in the 150-m

TABLE II
Mean, standard deviation (ind.·m^{-3}), and occurrence frequency (%) of scolecitrichid species at different depths in Campos Basin during the two sampling periods.

Species/Stations	**Rainy season**			
	1 m	**250 m**	**800 m**	**1,200 m**
Amallothrix dentipes	-	-	-	0.01±0.04/8.33
Amallothrix tenuiserrata	-	-	-	-
Lophothrix frontalis	-	0.03±0.10/8.33	0.01±0.02/11.11	0.01±0.02/16.67
Lophothrix latipes	-	-	-	-
Lophothrix quadrispinosa	-	0.01±0.04/4.17	-	-
Pseudoamallothrix ovata	-	-	-	-
Pseudoamallothrix profunda	-	-	-	-
Racovitzanus levis	-	-	-	-
Scaphocalanus brevicornis	-	-	0.002±0.01/5.56	-
Scaphocalanus echinatus	-	0.25±1.25/4.17	0.004±0.01/11.11	-
Scaphocalanus elongatus	-	-	-	
Scaphocalanus magnus	-	-	0.004±0.02/5.56	0.01±0.03/16.67
Scaphocalanus subbrevicornis	-	-	-	
Scolecithrix danae	4.55±13.71/ 16.67	0.31±1.37/12.50	0.08±0.31/16.67	0.05±0.10/41.67
Scolecithrix bradyi	-	0.01±0.03/4.17	-	0.001±0.002/8.33
Scolecithricella dentata	-	0.20±0.81/12.50	0.01±0.02/5.56	-
Scolecithricella minor	-	1.27±2.71/29.17	0.04±0.13/16.67	-
Scottocalanus securifrons	-	0.03±0.09/12.50	-	-

Species/Stations	**Dry season**			
	1 m	250 m	800 m	1,200 m
Amallothrix dentipes	-	-	0.002±0.01/6.67	0.005±0.01/12.50
Amallothrix tenuiserrata	0.85±2.99/13.04	1.35±5.71/27.27	-	0.01±0.04/12.50
Lophothrix frontalis	0.13±0.87/2.17	0.01±0.06/4.55	-	0.002±0.004/25.00
Lophothrix latipes	-	-	0.10±0.38/6.67	-
Lophothrix quadrispinosa	-	-	-	0.004±0.01/12.50
Pseudoamallothrix ovata	-	0.03±0.12/9.09	-	-
Pseudoamallothrix profunda	-	0.001±0.01/4.55	-	-
Racovitzanus levis	-	0.01±0.05/4.55	-	-
Scaphocalanus brevicornis	-	-	-	-
Scaphocalanus echinatus	-	0.04±0.09/18.18	-	-
Scaphocalanus elongatus	-	-	-	0.001±0.02/12.50
Scaphocalanus magnus	-	-	-	-
Scaphocalanus subbrevicornis	-	-	-	0.001±0.002/12.50
Scolecithrix danae	0.33±1.19/8.70	0.02±0.07/9.09	-	-
Scolecithrix bradyi	-	-	-	-
Scolecithricella dentata	-	0.05±0.13/13.64	-	0.003±0.01/25.00
Scolecithricella minor	2.73±12.59/6.52	2.67±8.65/36.36	0.12±0.42/13.33	0.01±0.04/25.00
Scottocalanus securifrons	-	0.001±0.01/4.55	0.10±0.38/6.67	-

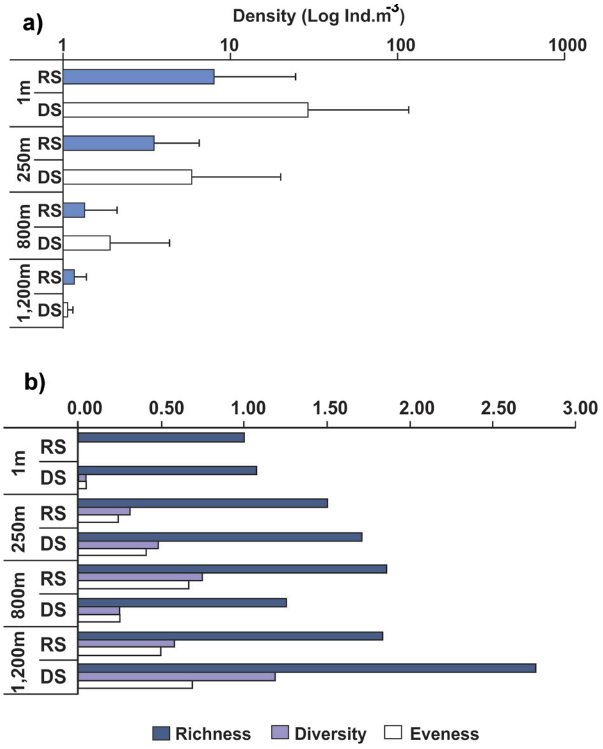

Figure 3 - Vertical distribution in the water column of the Campos Basin of the mean values: (**a**) total density and standard deviation of scolecitrichids (log ind.m^{-3}). Blue bars, rainy season (RS); open bars, dry season (DS), (**b**) scolecitrichid species richness, diversity, and evenness. Dark blue bars, richness; Navy blue bar, diversity; open bars, evenness. Rainy season (RS) and dry season (DS).

isobath) and northern (in the 50-m and 75-m isobaths) parts of the study area (Figure 4a). During the DS, *L. frontalis* (0.24 ± 1.20 ind.m^{-3})*, S. minor* (0.73 ± 3.56 ind.m^{-3}), and *A. tenuiserrata* (0.80 ± 3.63 ind.m^{-3}) were found above the continental shelf, whereas *S. danae* (0.70 ± 1.67 ind.m^{-3}), *S. minor* (4.92 ± 17.79 ind.m^{-3}), and *A. tenuiserrata* (0.90 ± 2.17 ind.m^{-3}) were found above the slope at 1 m depth (Figures 4b, 5a, b, and c). The other species occurred only in deep waters.

Scolecithricella and *Scolecithrix* were the two most abundant genera and their patterns of vertical distribution reflect the patterns of the Scolecitrichidae family as a whole (Table II). *Scolecithricella* abundance was highest at 1 and 250 m during the DS, whereas the highest density of *Scolecithrix* was mainly in the 1m layer during the RS. *Scolecithricella* showed an increase in abundance from the surface downward and peaked at 250 m (Table II).

Based on the groups proposed by Kuriyama and Nishida (2006), we classified the scolecitrichid copepods into the following four groups according to the vertical patterns of abundance observed in our study (the seasonal abundance peaks are indicated in parentheses).

Group A—Epipelagic species (with major abundance in the upper 250 m): *Scolecithrix danae* (RS), *Scolecithricella minor*, *Amallothrix tenuiserrata*, and *Lophothrix frontalis* (DS).

Group B—Upper-mesopelagic species (with major abundance in the upper mesopelagic zone, upper 800 m): *Lophothrix quadrispinosa*, *Scaphocalanus echinatus*, *Scolecithrix bradyi*, *Scolecithricella dentata* (RS), *Racovitzanus levis, Pseudoamallothrix ovata*, and *Pseudoamallothrix profunda* (DS).

Group C—Mesopelagic species (species with a broad range in the 800-m layer): *Scaphocalanus brevicornis* (RS), *Lophothrix latipes*, and *Scottocalanus securifrons* (DS).

Group D—Lower-mesopelagic species (species with a major population below 800 m): *Amallothrix dentipes*, *Scaphocalanus magnus* (RS), *Scaphocalanus elongatus*, and *Scaphocalanus subbrevicornis* (DS).

The results of the GLMs showed that the total scolecitrichid density was related to different environmental parameters. Among the competing models of the GLMs, the most plausible model indicated that total scolecitrichid density was positively related to temperature and nitrate, and negatively related to silicate (Table III).

DISCUSSION

HYDROGRAPHICAL INFLUENCES ON SCOLECITRICHID ABUNDANCE

Evaluation of factors controlling the distribution of zooplankton species is central to determining

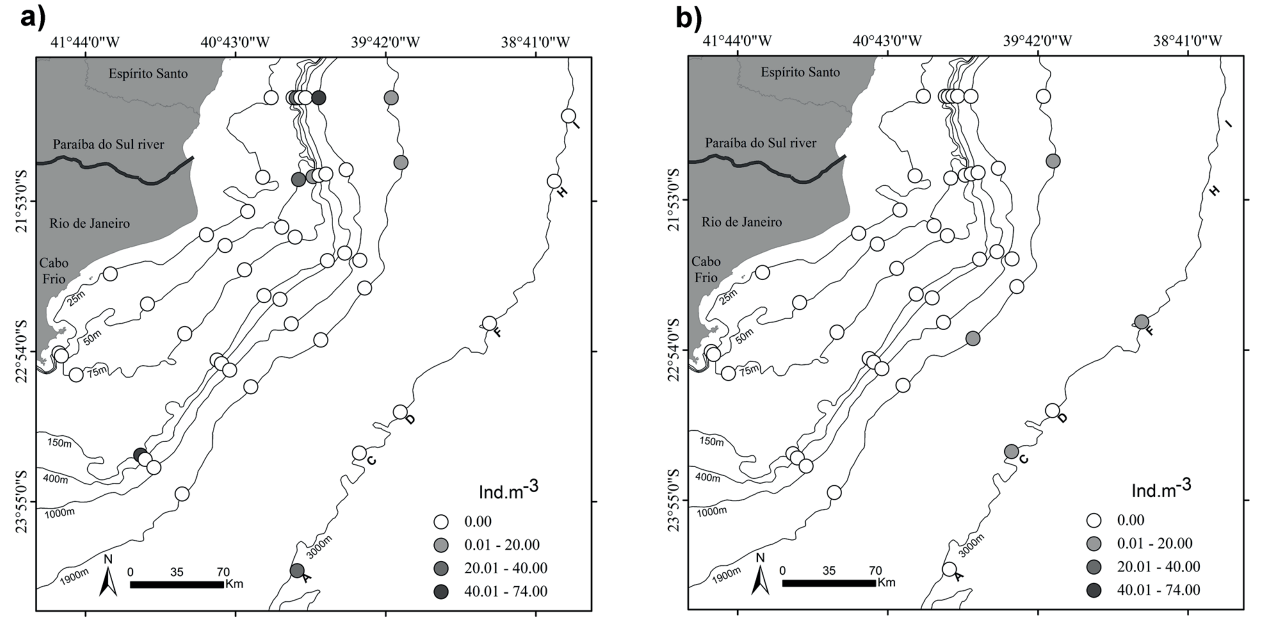

Figure 4 - Study area, showing the seasonal variation of *Scolecithrix danae* (ind.m-3) at 1 m depth, during the rainy season (**a**) and dry season (**b**).

TABLE III
Multiple regression models of environmental parameters and the total scolecitrichid density. Tem, temperature; Nit, nitrate; Sil, silicate; AICc, Akaike information criterion; w_i, weight.

	Model	AIC_c	ΔAIC_c	w_i
I	(+)Tem/(+)Nit/(-)Sil	38.95	0.00	0.12
II	(+)Tem/(-)Sil	39.88	0.92	0.07

the biological and ecological functioning of aquatic ecosystems. Although it is generally difficult to identify the main factors that explain variation in zooplankton abundance (Pinel-Alloul 1995), abiotic factors such as salinity, temperature, nutrients, DO, and pH have been identified as critical in the development of zooplankton (Quetin et al. 1996). In the present study, the distribution and abundance of scolecitrichids were related to the different oceanographic conditions that occur in the studied area. The abundance of scolecitrichids observed at a depth of 1 m over the continental shelf was positively related to changes in temperature and nitrate, and negatively influenced by the nutrient silicate. Within our study region, the upper water mass (TW) has the highest temperatures and the lowest nutrient values (Zalmon et al. 2015, Suzuki et al. 2015), which supports the hypothesis of the influence of different water masses on this copepod assemblage. The low supply of available nutrients is very transitory and small portions are derived from the decomposition of organic matter in the photic zone (Metzler et al. 1997).

The spatial distribution of oceanic organisms is determined by the interactions between organism behavior and physical oceanographic structure and processes (McManus and Woodson 2012). According to Siokou-Frangou et al. (1997), temperature fluctuations regulate the life history of all copepod species. Temperature modifies the reproductive capabilities of crustaceans in many ways (Smyly 1974). Within a suitable range, increases in temperature will increase egg production and growth rate, and shorten reproductive cycle and hatching time. However, different species living in different geographical regions may have specific temperature requirements (Li et al. 2009). According to Halsband-Lenk et

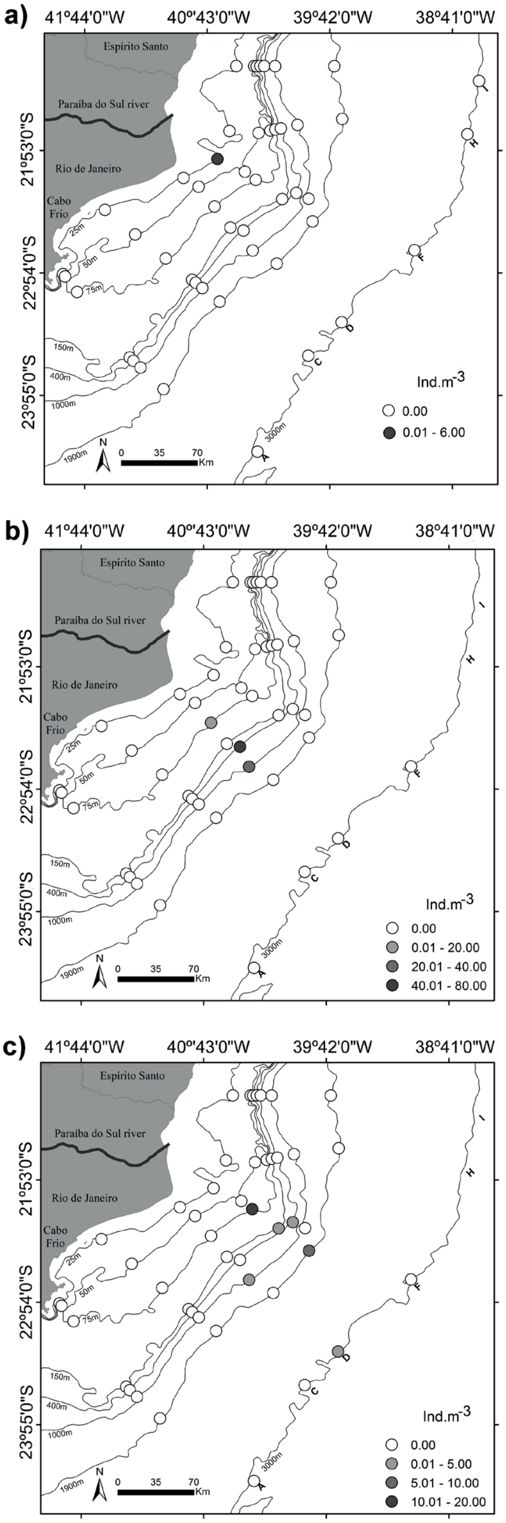

Figure 5 - Study area, showing the seasonal variation of scolecitrichid species (ind.m^{-3}) at 1 m depth, during the dry season. *Lophothrix* frontalis (**a**), *Scolecithricella minor* (**b**), and *Amallothrix tenuiserrata* (**c**).

al. (2002), the thermal tolerances of survival, reproduction and development may at least partly determine horizontal and seasonal distribution patterns of different species. Consistent with our findings for scolecitrichids in the northern region of Rio de Janeiro, the population size of several other copepods, e.g., *Oithona*, *Paracalanus*, and *Acartia* in Japan, and *Labidocera* in China, has been reported to increase with increasing temperature (Chang and Fang 2004). According to these authors, environmental factors are known to affect the distribution, species composition, and abundance of copepods.

ABUNDANCE, OCCURRENCE, AND VERTICAL DISTRIBUTION OF SCOLECITRICHIDAE COPEPODS

A vertical distribution pattern is commonly observed in oceanic mesozooplankton, characterized by an overall decline in numbers and biomass with increasing depth in the deep sea (Weikert et al. 2001, and references therein). The results obtained in the present study are consistent with the pattern reported in vertical distribution studies in oceanic areas of the Southwestern Atlantic Ocean (Dias et al. 2010, 2018, Bonecker et al. 2014, 2018), with a decrease in density and an increase in diversity and richness with depth. The same pattern was observed by Weikert et al. (2001) and Siokou-Frangou et al. (2013) for deep-sea plankton communities in the oligotrophic Levantine Sea in the Eastern Mediterranean.

Dominance is often considered indicative of successful evolution (Madhupratap and Haridas 1986, Briggs 1974). Despite their known vertical distribution pattern (Table IV), in this study the major populations of *S. danae, S. minor, A. tenuiserrata,* and *L. frontalis* were recorded in the upper 250 m, in neritic as well as oceanic waters.

Copepods consume marine snow or particles attached to it. Appendicularians are also important contributors to the vertical flux through fecal pellets and houses (Turner 2015). Scolecitrichids such as *S. minor*, one of the most frequent and abundant scolecitrichids in the region, are typically considered to be detritus feeders (Yamaguchi et al. 1999). While no quantitative data on detrital abundance in the Campos Basin are available at present, the concentration of suspended particulate matter was lower in deep water than in shallow water (Pedrosa et al. 2006). In our study region, appendicularians (mostly *Oikopleura longicauda*) are an abundant mesozooplanktonic group, with higher densities in the upper layers (Bonecker et al. 2014, 2018, Carvalho and Bonecker 2016). A high abundance of appendicularians at 1 m depth implies a high production rate of discarded "houses" (a source of detritus) that can be an important dietary component for Scolecitrichidae copepods (Ferrari and Steinberg 1993, Yamaguchi et al. 1999).

All the dominant Scolecitrichidae species showed the vertical patterns of abundance of epipelagic species and can be considered epipelagic migrants due to their distribution throughout the entire water column (1, 250, 800, and 1,200 m). The other species were considered mesopelagic zone dwellers.

Scolecithrix danae is numerically the most abundant and widespread species of Scolecitrichidae and is relatively common in the surface and subsurface layers during both the day and night (T.C. Gopalakrishna, unpublished data). In the present study, *S. danae* was found throughout the water column down to a depth of 1,200 m, with higher abundances being recorded in the 1m layer in both sampling periods. Vervoort (1965) detected *S. danae* inhabiting intermediate and subsurface layers, closer to the surface at night and in comparatively deep water during the day. This species was also recorded by Wheeler (1970) at depths between 4,100 and 2,200 m.

Scolecithricella minor is a small calanoid copepod widely distributed throughout the high latitude seas of both the northern and southern hemispheres, occurring in the epi- and mesopelagic zones (Roe 1984). However, despite the widespread distribution and potential importance of *S. minor* in the trophodynamics of pelagic systems, information on its life cycle is extremely limited (Yamaguchi et al. 1999). *Scolecithricella minor* is typically considered a detritus feeder, and in the southern Japan Sea is distributed below the thermocline in the daytime and ascends at night (Yamaguchi et al. 1999). These authors recorded the distribution of this species to depths of 700 m, with an abundance peak between 100 and 400 m. In our study, this species was found during both sampling periods, with greater abundance being recorded in the 1 m and 250 m layers, mainly during the DS.

Amallothrix tenuiserrata was recorded only during the DS. It was found in greater abundance in the 1m and 250m depth levels, with reduced densities in the 1,200m layer. In a study of zooplankton in which day–night samples were collected from the euphotic zone of the Indian Ocean, Gopalakrishnan (T.C. Gopalakrishna, unpublished data) considered this species to be a strong migrant, undertaking nocturnal migrations in neritic and oceanic waters. *Amallothrix tenuiserrata* inhabits intermediate depths up to the surface, and according to Gopalakrishnan (T.C. Gopalakrishna, unpublished data), in the Indian Ocean this species is most abundant in the highly saline upwelling waters of the Arabian Sea and warm tropical low saline surface waters of the Bay of Bengal. The occurrence of *A. tenuiserrata* only during the DS in the present study can be related to unstable conditions due to the mobility of the TW-SACW interface, an increase in which is associated with the higher temperatures of the ocean–atmosphere interface (Tsuchiya et al. 1994, Mémery et al. 2000).

Although *Lophothrix frontalis* may be classified as epipelagic–abyssopelagic, in the present study this species was found mainly in the subsurface water during the DS. Gopalakrishnan (T.C. Gopalakrishna,

TABLE IV
Scolecitrichid copepod distribution range (m) in the study area, classification according to the references (E, epipelagic; M, mesopelagic; B, bathypelagic; A, abyssopelagic), and references relating to the occurrence of scolecitrichid copepods: Southwestern Atlantic (1, Björnberg 1963; 2, Björnberg 1965; 3, Campaner 1984; 4, Campaner 1985), other localities (1, Grice and Hulsemann 1965; 2, Roe 1972; 3, Gopalakrishnan (T.C. Gopalakrishna, unpublished data); 4, Roe 1984; 5, Madhupratap and Haridas 1986; 6, Bradford-Grieve et al. 1999; 7, Yamaguchi et al. 1999; 8, Kuriyama and Nishida 2006; 9, Razouls et al. 2005-2018).

Species	Distribution range	Classification	Southwestern Atlantic	Other localities
Amallothrix dentipes	800 and 1,200	M-B		4/6/9
Amallothrix tenuiserrata	1, 250 and 1,200	E	3/4	3/5/6/9
Lophothrix frontalis	1, 250, 800 and1,200	E-A	2	2/3/6/8/9
Lophothrix latipes	800	E-B	4	4/6/9
Lophothrix quadrispinosa	250, 800 and 1,200	M-B		6/9
Pseudoamallothrix ovata	250	E-M	3/4	3/4/6
Pseudoamallothrix profunda	250	M-B	3/4	2/6/8/9
Racovitzanus levis	250	M		1/2/9
Scaphocalanus brevicornis	800	E-B	2	1/2/4/6/8/9
Scaphocalanus echinatus	250 and 800	E-B	3/4	1/2/3/6/8/9
Scaphocalanus elongatus	1,200	M-A		1/2/6/8/9
Scaphocalanus magnus	800 and 1,200	E-B		1/2/4/6/8/9
Scaphocalanus subbrevicornis	1,200	M-B	2	2/6/8/9
Scolecithrix danae	1, 250, 800 and 1,200	E-M	1/2/4	1/2/3/5/6/8/9
Scolecithrix bradyi	250 and 1,200	E-M	2/4	1/2/3/5/6/8/9
Scolecithricella dentata	250, 800 and 1,200	E-M	1/2/3/4	1/2/3/4/5/6/8/9
Scolecithricella minor	1, 250, 800 and 1,200	E-B		4/6/7/9
Scottocalanus securifrons	250 and 800	E-B	4	2/3/4/5/6/8/9

unpublished data) found that, in the north Indian Ocean, *L. frontalis* inhabits high-salinity intermediate and deep waters, rising to the surface layers during the night. This author found *L. frontalis* only in night hauls, and the total absence in day hauls indicated its nocturnal occurrence in surface waters, consistent with diurnal vertical migration. In our study, all samples were collected during the night and this can explain the higher abundance of *L. frontalis* in 1-m-depth samples compared to the deeper samples. Remarkably, even some meso- and bathypelagic scolecitrichid species ascend to the surface as a part of the diurnal migration (Gopalakrishnan and Balachandran 1992, Kuriyama and Nishida 2006, and references therein).

Of the species classified as mesopelagic, *Amalothrix dentipes*, *Lophothrix quadrispinosa,* and *Racovitzanus levis* have only recently been recorded from the Southwestern Atlantic Ocean (Bonecker et al. 2014). In the present study, the upper-mesopelagic species *L. quadrispinosa* has been reported at 250 m depths over the SACW influence, during the RS, and at 1,200 m over the UCDW influence during the DS. This species has also been reported from the North Atlantic, South Pacific, and Indian oceans (Bradford-Grieve et al. 1999, Razouls et al. 2005-2018), and Owre and Foyo (1964) reported its occurrence at depths of 584 m and 1,750 m in the Florida region. *Racovitzanus levis,* which in the present study was collected at 250 m depths over the SACW influence during the

DS, has also been reported from the North Atlantic, Pacific, and Indian oceans (Harding 1974, Razouls et al. 2005-2018). Roe (1972) reported this species off the Canary Islands (North Atlantic) at depths of 450 m in diurnal hauls and 360 m in night hauls, whereas in the northeast Atlantic, Grice and Hulsemann (1965) found specimens of *R. levis* at depths of 400–1,000 m, and Deevey and Brooks (1977) recorded its presence at depths between 0 and 1000 m in the Sargasso Sea off Bermuda. Furthermore, Harding (1974) cited the occurrence of *R. levis* in a vertical tow at 3,000–4,000 m.

In our study, the lower-mesopelagic species *A. dentipes* was collected at 1,200 m, above the UCDW influence, during the RS, and at 800 and 1,200 m depths during the DS. This species has also been reported from the Central South Atlantic, South Pacific, and Indian oceans, and the Antarctic and Sub-Antarctic regions (Bradford 1973, Bradford-Grieve et al. 1999, Razouls et al. 2000). According to Bradford-Grieve et al. (1999), this species typically occurs in Antarctic waters, occasionally reaching the Convergence, and more rarely in the Southern Atlantic (36°). In the North East Atlantic, Roe (1984) reported the occurrence of *A. dentipes* at 250–600 m depths.

Divergences between the occurrences of species recorded in the present study (water masses below 250 m depth) and those reported previously could be attributed to the circulation of water masses, which may have been a potential vehicle of dispersal for these species. *Amalothrix dentipes* and *L. quadrispinosa* are classified as meso-bathypelagic, and *R. levis* as mesopelagic. As few species have restricted areas of abundance, inconsistencies in the distributions of these species indicate that the data available are still too limited to demarcate the zones of occurrence of most species, in view of the lack of studies in deep habitats in the Southwestern Atlantic Ocean.

Data on Scolecitrichidae species are limited and scattered, with only a few previous studies available for comparison with the present results on the vertical distribution of each species (Table IV). Kuriyama and Nishida (2006) studied the distribution patterns of 43 scolecitrichid species occurring in Sagami Bay from the surface down to 1,000 m depth. Although the vertical ranges of hauls were smaller, the depth distributions in Sagami Bay are similar to those observed in the present study for most of the 11 common species compared. Both Kuriyama and Nishida (2006) and the present study recorded *S. brevicornis, S. echinatus, S. danae, S. bradyi, S. dentata*, and *S. securifrons* in deeper strata. Yamaguchi et al. (1999) analyzed the vertical migration, population structure, and life cycle of *Scolecithricella minor* in Toyama Bay (southern Sea of Japan) and found a vertical distribution pattern comparable to the distribution recorded in the present study. Roe (1984) reported the vertical distribution patterns of 14 species, sampled through hauls performed at four depths (100, 250, 450, and 600 m) in the Northeast Atlantic. Seven of the species recorded in this study showed vertical distribution patterns that were narrower than those recorded in the present study. The same author (Roe 1972), has reported vertical patterns, with respect to the day–night distribution, off the Canary Islands that are comparable to the distribution patterns of 13 species recorded in the present study. *Racovitzanus levis*, *Scaphocalanus brevicornis,* and *Scaphocalanus elongatus,* which were distributed in the mesopelagic layers in the present study, have been found to occur only in much deeper layers (below 5,000 m) in the northeast Atlantic (Grice and Hulsemann 1965).

CONCLUSIONS

The aim of this paper was to review our current understanding of scolecitrichid copepod biodiversity in the northern region of Rio de Janeiro State. In the present study, we recognized the following patterns in the species diversity of scolecitrichids in relation to their depth distribution, abundance, and taxonomic groupings: (1) contrasting vertical patterns between abundance and species diversity, which is a common phenomenon in pelagic copepods in general, being repeated in all genera and in the family as a whole; and (2) a trend of vertical segregation in a small number of epipelagic migrants in contrast to a considerably larger number of meso- and bathypelagic nondominant species. These patterns suggest that the scolecitrichid assemblages in the region may be structured, and that this is mainly due to the partitioning of vertical habitats and food resources.

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AUTHOR CONTRIBUTIONS

SLCB designed the study, participated in fieldwork and revised the paper; COD and AVA analyzed the data and wrote the paper.

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