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Euphausiacea diversity in a trans-oceanic transect through the South Atlantic Ocean: the first Atlantic record of *Thysanopoda astylata* Brinton, 1975

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Abstract: Information about euphausiids in central South Atlantic Ocean is scarce; hence, we investigated species composition and distribution of euphausiids along a longitudinal transect in this region, with an emphasis on *Thysanopoda*. Zooplankton samples were collected from 44 stations during the first Transatlantic Commission (Brazil–Africa). Euphausiids comprised 21,390 individuals across larval stages (nauplius, calyptopis, and furcilia) and adults. Furcilia and adults were classified to species level when possible, with a total of 19 identified species. Overall, *Euphausia* species frequency of occurrence and abundance were highest in samples collected near the African coast, while *Thysanopada* species dominated near the Brazilian coast. Of the euphausiids caught, 158 were identified as *Thysanopoda*, including 2 specimens of *T. astylata*, 6 *T. aequalis*, 3 *T. pectinata*, 2 *T. monacantha*, 2 T. *tricuspida*, and 1 *T. egregia*; 118 damaged specimens could only be identified as *Thysanopoda* spp., and 24 as *T. aequalis / T. astylata* complex because of the lack of diagnostic structures. *Thysanopada egregia* was present in samples collected down to 96 m, which increases the vertical range for this species. This report constitutes the first record of *Thysanopoda astylata* Brinton, 1975 in Atlantic waters.

Key words: euphausiids, South Atlantic, *Thysanopoda astylata*, zooplankton.

INTRODUCTION

Most of our knowledge about the biology and distribution of the 60 known species of euphausiids in the South Atlantic (Gibbons et al. 1999) is based on studies of *Euphausia superba* Dana, 1850, which were mainly conducted near Antarctica (Brinton and Antezana 1984, Montú and Oliveira 1986, Montú and Cordeiro 1986, Endo et al. 1986, Montú et al. 1994, Siegel 2015), or studies of euphausiids on the continental shelves of South America and Africa (Ramirez 1971, Montú 1977, 1982, Antezana and Brinton 1981, Lansac-Tôha 1981, Barange 1990, Curtolo et al. 1990, Barange et al. 1991, 1992, Freire 1991, Gibbons et al. 1995, Gibbons 1997, Gorri 1995, Menezes 2007, Werner 2012). There is little or no information about the biodiversity and biology of these organisms in the central regions of the Atlantic Ocean (Letessier

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et al. 2009, 2011), especially in the central South Atlantic, probably due to the scarce scientific exploration in this region compared to that in the Pacific and North Atlantic Oceans (Mauchline 1980, Gibbons et al. 1999).

Euphausia is the most-studied genus of euphausiids due to the distribution, abundance, and ecological role of its species (Brinton and Antezana 1984, Endo et al. 1986, Pillar et al. 1989, Barange and Pillar 1992, Siegel 2015, Siegel and Watkins 2016); however, even with lower abundances *Thysanopoda* can play a significant ecological role (*e.g.,* pelagic-benthic coupling, biological pump) (Schnetzer and Steinberg 2002). There are 14 known species in the genus *Thysanopoda* (Mikkelsen 1987, Baker et al. 1990, Brinton et al. 1999); nevertheless, *T. astylata* Brinton 1975, *T. minyops* Brinton 1987, and *T. spinicaudata* Brinton 1953 are still unreported in South Atlantic waters (Brinton et al. 1999), which could be associated with the scarcity of studies in this region.

This study aimed to investigate the composition and distribution of euphausiids in the upper layer (22-130 m) of the South Atlantic Ocean across a longitudinal transect profile at 30° S, with an emphasis on *Thysanopoda* species.

MATERIALS AND METHODS

The first cruise of the Transatlantic Commission (Brazil-Africa) (https://www.naval.com.br/ngb/C/C125/C125.htm) was carried out during the spring of 2009 (October-November) on board the Brazilian Navy ship Cruzeiro do Sul. A longitudinal transect was made in the central region of the South Atlantic Ocean at 30° S, beginning with station 31 over the Rio Grande Rise (RGR) off the Brazilian continental shelf (33°48'W) and ending at station 86 off the coast of South Africa (16°46' E) (Figure 1).

A total of 56 oceanographic stations were visited, and zooplankton samples were taken at 44 of them using oblique tows down to an average depth of 66 m (22-130 m) using a 60-cm diameter zooplankton net with 140-µm mesh size that filtered 295 m^3 on average per tow (see Supplementary Material - Table SI). A calibrated flowmeter (GO2030R) was attached to the mouth of the net. Temperature profiles were obtained using a CTD (Seabird - SBE 25) that was lowered down to 200 m on average (110-250 m) or ~10-20 m from the bottom on shallower casts at shelf locations. Averaged CTD data for the first 3 meters were used as surface values for each oceanographic station and plotted using ArcGIS 10.4. Zooplankton samples were most often (51.5%) collected at night (18:00-05:59 h), while 48.5% of the samples were collected during the day (06:00-17:59 h). Due to weather conditions, all activities at sampling stations 59, 64, 76, 78, 80, and 82 were aborted.

Samples were immediately preserved in 1-L jars with 100 mL of 40% formaldehyde neutralized with borax for fixation at 4% strength when full (Steedman 1976). In the laboratory, all euphausiids were manually picked from the samples, counted, and staged. Undamaged adults and furcilia were identified to the lowest possible taxonomic level based on Brinton (1962, 1975), Mauchline and Fisher (1969), Mauchline (1971, 1980, 1984), Antezana and Brinton (1981), Baker et al. (1990), Brinton et al. (1999, 2013), Gibbons et al. (1999), and Martin and Davis (2001). No attempt was made to identify nauplius and calyptopis stages to species.

Euphausiacea compositions (taxa with at least two observations) were ordered using Non-Metric Multidimensional Scaling (MDS) and a Bray-Curtis similarity matrix after double standardization (function *dcontand* of R software vegan package) of the environmental variables. PERMANOVA analyses tested the statistical differences between groups of sampling stations and between day and night samples. Redundancy analysis (RDA) (*adespatial* package of R software) was used to extract and summarize the variations

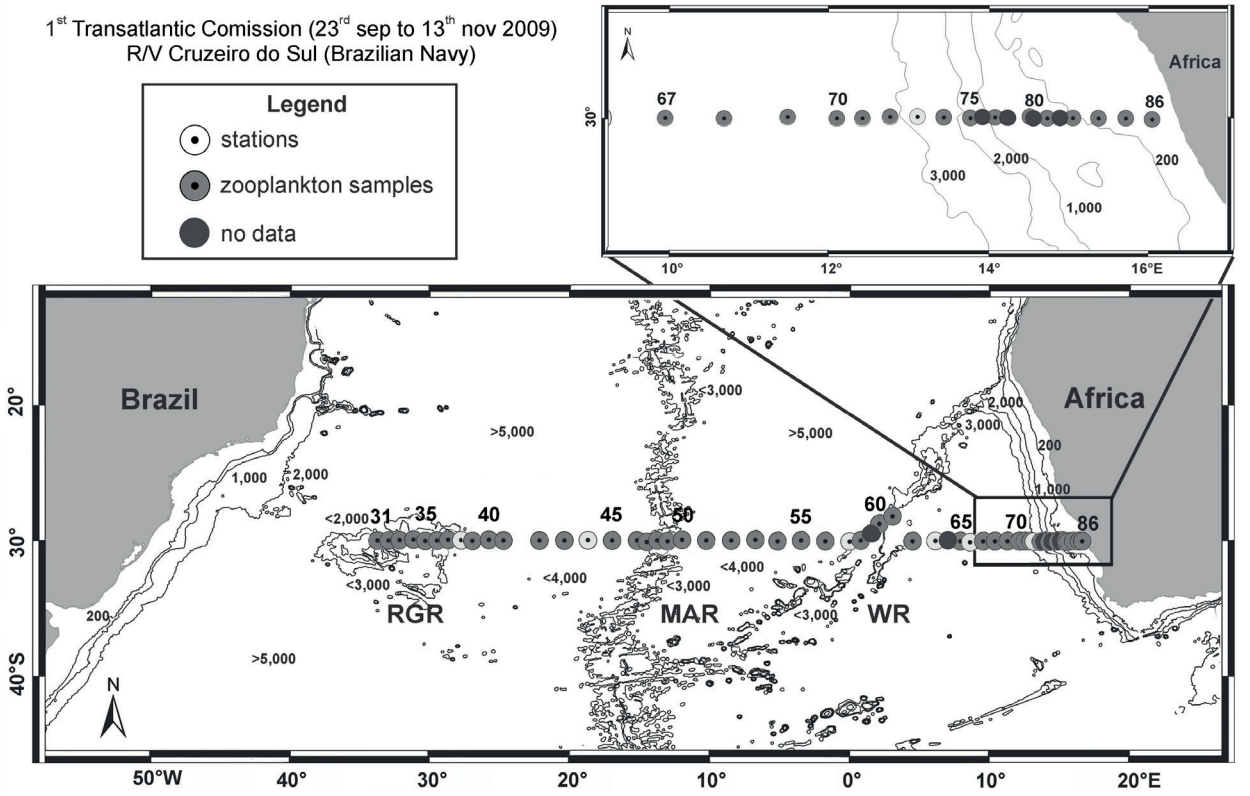

Figure 1 - Study transect through the South Atlantic Ocean at 30 °S with the 56 oceanographic stations. Bathymetry and oceanic rises are also indicated. Where: Rio Grande Rise (RGR), Mid-Atlantic Ridge (MAR), and Walvis Ridge (WR).

in the Euphausiacea composition with changes in different environmental variables (chlorophyll-*a*, temperature, salinity, and sampling depth) and euphausiid ordination was performed to observe any patterns in the composition and/or distribution of each euphausiid taxa as well as groups of taxa. The Similarity Percentage test (SIMPER) was employed to estimate the contribution (CI) of each taxon to the differences observed.

RESULTS

Surface temperature data showed higher temperatures westward from Walvis Ridge (near Brazil) with a decrease towards the eastern part of the transect (near Africa) where the shallower depths were recorded (see Figure S1). The highest temperature was observed in the central Atlantic (20.8 °C at station 51), while the lowest temperature was over the African shelf (16.6 °C at station 86).

Of the 21,390 euphausiids found in the samples, 711 specimens were classified as nauplius, 3,937 as calyptopis, 13,586 as furcilia, and 3,156 as adults. The stage contribution analysis for each station showed that furcilia was the most abundant stage (64%) followed by calyptopis (17%), adults (15%), and nauplius (4%) (Figure 2a). Among the 30 euphausiid taxa found, 19 species belonging to six genera were identified (Figure 2b, Table I).

Overall, euphausiid abundance averaged 264.2 organisms 100 m^{-3} and was highest near Africa, especially over the African shelf (stations 81 to 86), where the average was 1,056.0 organisms 100 m^{-3} with a maximum of 1,368.3 organisms 100 m^{-3} (Figure 2c). Significant differences in species composition were also seen between

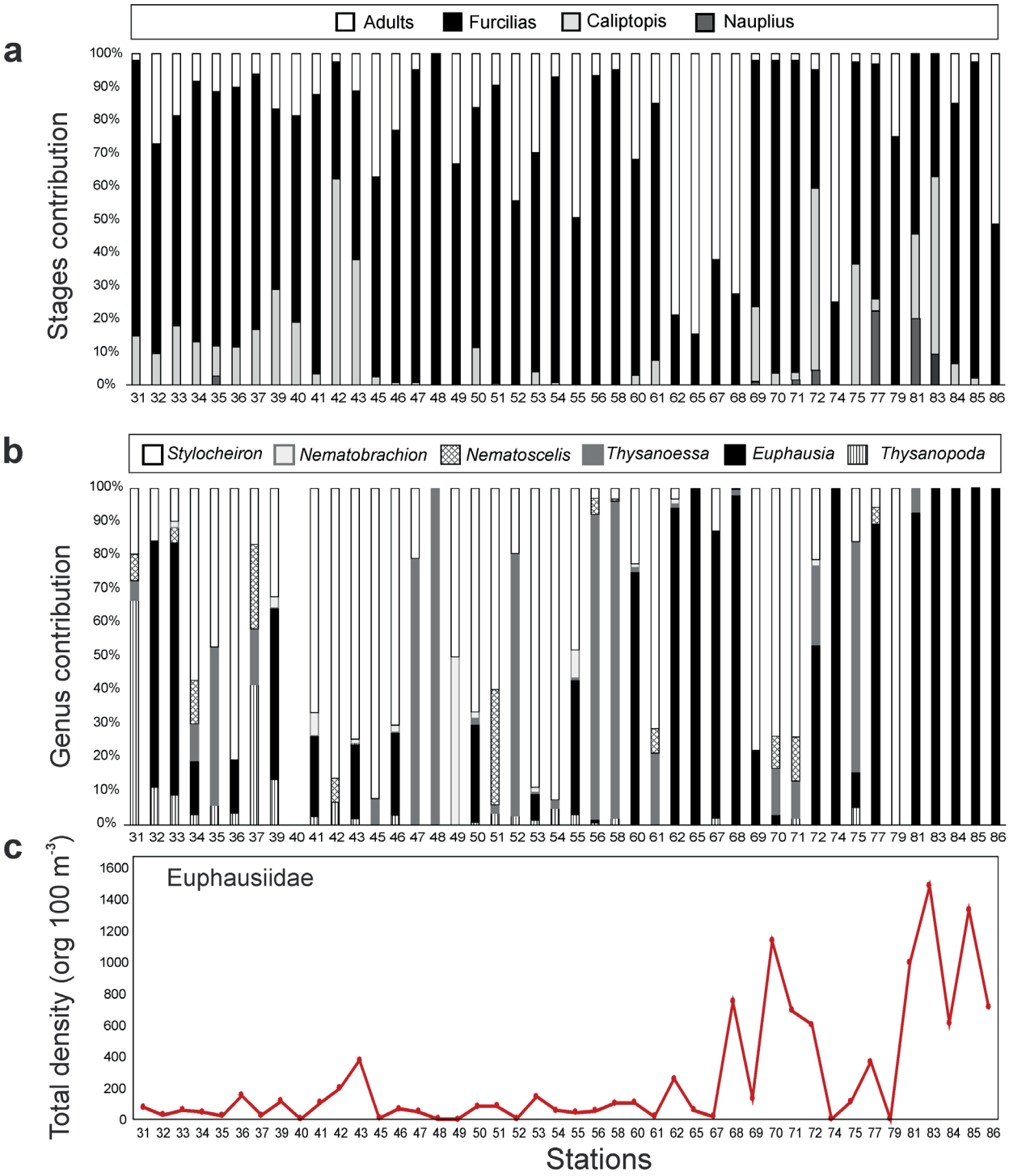

Figure 2 - (**a**) Percentage contribution of each euphausiid stage; (**b**) percentage contribution of each euphausiid genus and; (**c**) euphausiid total density (organisms 100 m^{-3}) at each station along the 30° S transect through the South Atlantic Ocean.

TABLE I

List of euphausiid taxa recorded along the 30° S transect through the South Atlantic Ocean during the First Transatlantic Commission (Brazil/Africa) in 2009 with the mean abundance (organisms 100 m^{-3}), relative abundance (RA) and frequency of occurrence (FO).

	Mean abundance	RA (%)	FO (%)
Subphylum Crustacea			
Class Malacostraca			
Superorder Eucarida			
Nauplii not id	10.643	4.029	15.91
Calyptopis not id	45.771	17.324	72.73
Furcilia not id	113.744	43.052	90.91
Adults not id	0.456	0.173	31.82
Family Euphausiidae Holt and Tattersall, 1905			
Thysanopoda monacantha Ortmann, 1893	0.011	0.004	4.55
Thysanopoda tricuspida H. Milne Edwards, 1837	0.009	0.003	2.27
Thysanopoda astylata Brinton, 1975	0.013	0.005	4.55
Thysanopoda aequalis Hansen, 1905	0.034	0.012	9.09
Thysanopoda aequalis/astylata complex	0.127	0.048	13.64
Thysanopoda pectinata Ortmann, 1893	0.060	0.023	6.82
Thysanopoda egregia Hansen, 1905	0.011	0.004	2.27
Thysanopoda spp.	0.796	0.301	36.36
Euphausia mutica Hansen, 1905	0.114	0.043	11.36
Euphausia diomedeae Ortmann, 1894	0.909	0.344	15.91
Euphausia recurva Hansen, 1905	20.995	7.947	43.18
Euphausia lucens Hansen, 1905	49.515	18.741	25.00
Euphausia similis G.O. Sars, 1883	0.398	0.150	6.82
Euphausia longirostris Hansen, 1908	0.404	0.153	13.64
Euphausia spp. (gibba group)	0.755	0.286	25.00
Euphausia spp.	4.513	1.708	34.09
Thysanoessa gregaria G.O. Sars, 1883	1.609	0.609	36.36
Thysanoessa spp.	3.400	1.287	36.36
Nematoscelis spp.	0.677	0.256	29.55
Nematobrachion flexipes (Ortmann, 1893)	0.332	0.126	29.55
Stylocheiron carinatum G.O. Sars, 1883	1.398	0.529	61.36
Stylocheiron affine Hansen, 1910	0.026	0.010	2.27
Stylocheiron suhmii G.O. Sars, 1883	2.726	1.032	47.73
Stylocheiron microphthalma Hansen, 1910	0.268	0.101	13.64
Stylocheiron abbreviatum G.O. Sars, 1883	1.379	0.521	34.09
Stylocheiron spp.	3.107	1.176	52.27

groups of sampling stations (F = 1.623; $p = 0.001$). *Euphausia lucens* (76%), *Stylocheiron carinatum* (14%), and *Thysanopoda* spp. (6%) were the species responsible for the differences observed between the west and east sections of the transect (see Table SII). Overall abundance and frequency of occurrence of *Euphausia* species were highest at stations near Africa, while those of *Thysanopoda* species were highest at those near Brazil (Figure 3).

RDA analysis showed that the factor that most influenced euphausiid species distribution was sampling depth ($r^2 = 0.118$; F = 1.626; $p = 0.037$), followed by salinity ($r^2 = 0.087$; F = 2.585; $p = 0.017$), temperature ($r^2 = 0.105$; F = 1.794; $p = 0.016$), and chlorophyll-*a* ($r^2 = 0.059$; F = 3.399; $p = 0.002$) (Figure 3). The sampling period was correlated with significant differences in species composition (F = 2.695; $p = 0.001$); *Euphausia recurva* (CI = 18%) had higher abundances in nighttime samples (Figure 3).

A total of 158 *Thysanopoda* specimens was recorded: 2 male *T. astylata,* 6 male *T. aequalis,* 3 *T. pectinata,* 2 *T. monacantha*, 2 *T. tricuspida*, and 1 *T. egregia*. Of the remaining specimens, 118 were identified only as *Thysanopoda* spp., and 24 were grouped into a *T. aequalis / T. astylata* complex because only mature males could be differentiated based on the morphology of the third thoracic leg (see Figure S2a, b); *T. aequalis* has a long flagellum-like spinal modification (see Figure S2c) of the dactyl and propod, and *T. astylata* lacks this styliform process (see Figure S2d).

Thysanopoda averaged 1.1 organisms 100 m^{-3} (Figure 4a), with greater abundances towards the western part of the Atlantic; a density of 20.7 organisms 100 m^{-3} was recorded near the Rio Grande Rise. Individuals of the *Thysanopoda aequalis / T. astylata* complex were collected only during the night at seven stations between 033° 48.08ˈW and 003° 20.94ˈW, with densities never exceeding 3.3 organisms 100 m^{-3} (Figure 4b). *Thysanopoda astylata* males were recorded at stations 33 (032° 04.34ˈW) and 55 (003° 20.94ˈW) at depths down to 64 meters, with a maximum density of 0.3 organisms 100 m^{-3}, while *T. aequalis* males were found at four stations (stations 39, 41, 46, and 55) with a maximum density of 0.6 organisms 100 m^{-3} in samples never exceeding 80 meters in depth.

Of the remaining *Thysanopoda* species, only furcilia stages were found. *Thysanopoda pectinata* was found at three stations (stations 62, 71, and 75; Figure 4b) during day and night hours in samples from down to 92 meters, with 0.7 to 1.1 organisms 100 m^{-3}. *Thysanopoda monacantha* was also found in samples collected in both periods at stations 34 and 35 at depths down to 62 m, with densities up to 0.3 organisms 100 m^{-3}, while *T. tricuspida* was found only at station 39, during the night at depths shallower than 55 meters, at an abundance of 0.4 organisms 100 m^{-3}. Only a single furcilia *Thysanopoda egregia* was found at station 67 during daylight hours, corresponding to 0.5 organisms 100 m^{-3} (Figure 4b).

DISCUSSION

There was an obvious gradient of temperature along the studied profile, with higher temperatures towards the Brazilian coast and lower ones near the African coast. The South Atlantic is influenced by two major currents: the relatively warm and salty Brazil current to the west, and the colder and less saline Benguela current to the east. The eastern periphery of the Benguela current is characterized by an upwelling area with pronounced lower surface temperature (Shannon and Nelson 1996, Hutchings et al. 2009). The presence of cold waters over the shelf on the South African coast in this study is an indication of upwelled waters causing the surface temperature values found.

Higher euphausiid abundances were associated with the colder waters found on the eastern side of the transect. Overall species composition and abundances on the eastern side were in agreement

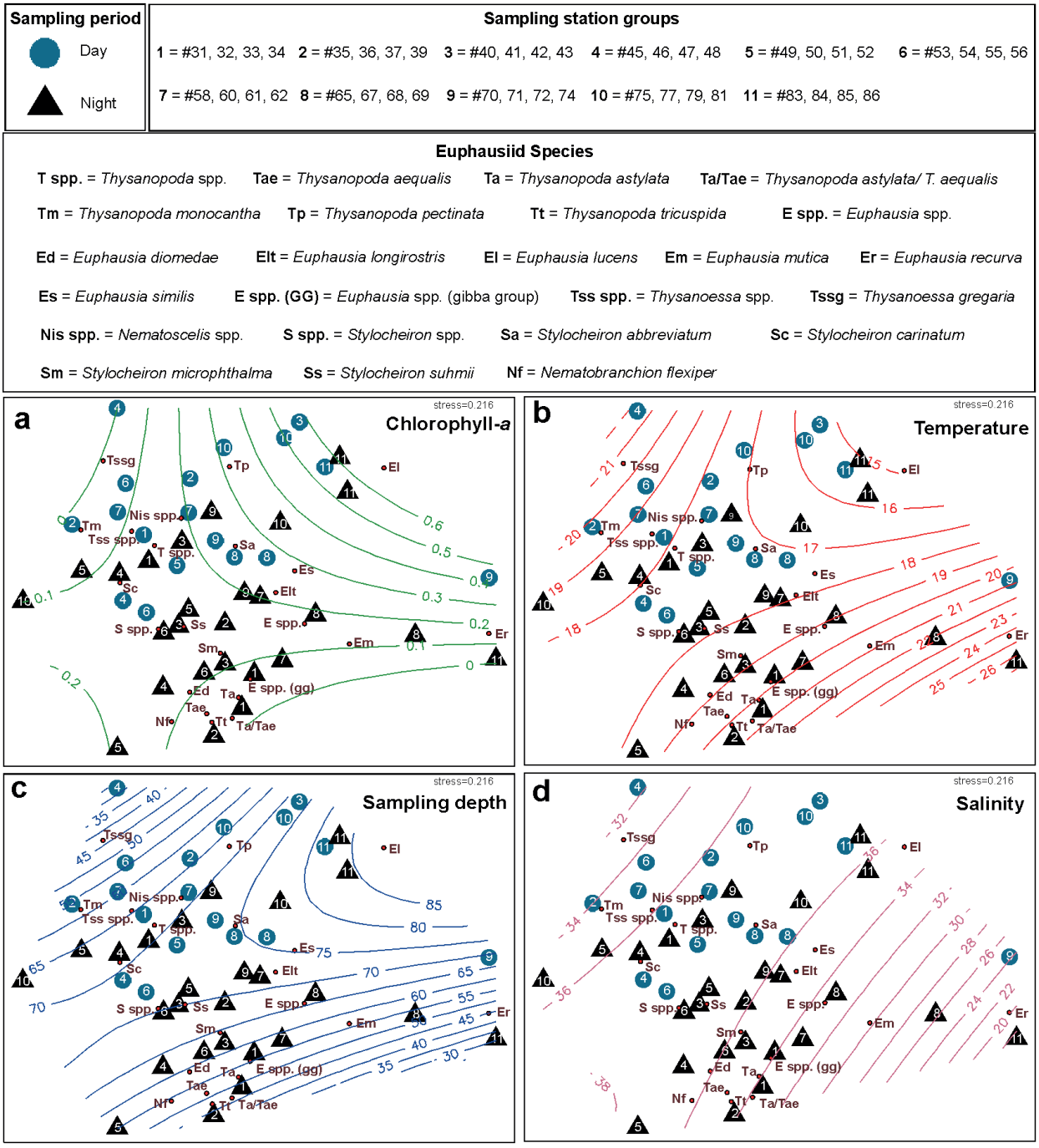

Figure 3 - MDS ordination based on Bray-Curtis similarity and euphausiid species composition (44 samples) from a Brazil-Africa cruise and different environmental variables: (**a**) chlorophyll-*a*; (**b**) temperature; (**c**) sampling depth; (**d**) salinity.

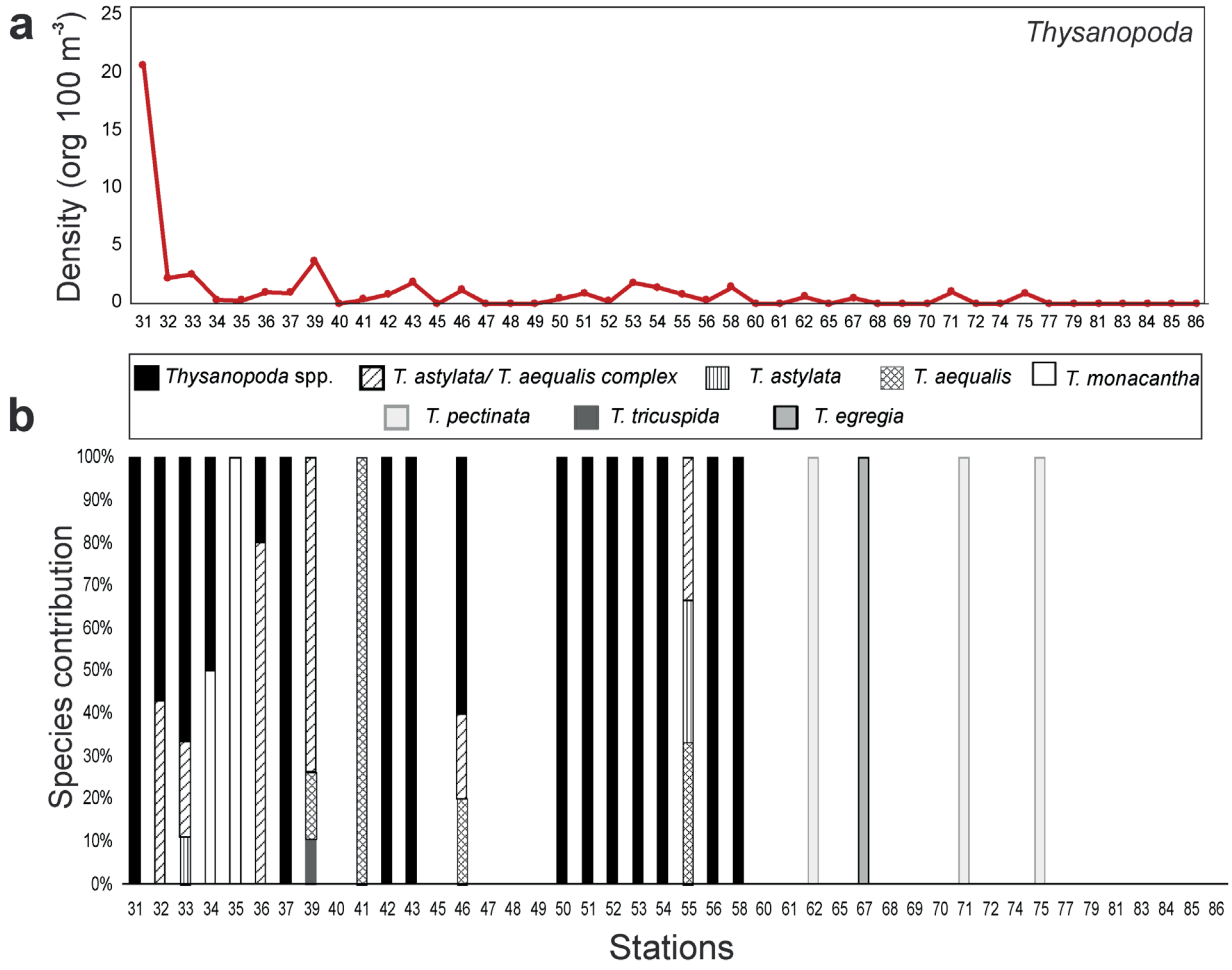

Figure 4 - (**a**) *Thysanopoda* total density (organisms 100 m^{-3}), and (**b**) percentage contribution of each *Thysanopoda* species at each station along the 30° S transect through the South Atlantic Ocean.

with what has been published previously, with *Euphausia* species being dominant in the Benguela upwelling system. This region is one of the most productive coasts of the world's oceans (Hutchings 1992), where euphausiids and copepods can dominate the mesozooplankton (Ekau et al. 2010). There were also trends in overall distribution, like an increase in the abundance of *Euphausia* species near the African continent, while *Thysanopoda* species were more abundant closer to Brazil. According to Pillar et al. (1992) and Werner and Buchholz (2013), in the coastal upwelling of Africa, *Euphausia lucens*, *E. americana*, *E. gibboides, E. hanseni, E. recurva, Nyctiphanes capensis*, and *N. megalops* have the highest biomass and abundances. However, of these only *E. lucens* and *E. recurva* were recorded in the current work.

Our data probably underestimated euphausiid abundances, as we only sampled the upper epipelagic stratum with a small ring net fitted with a fine mesh, which was most suitable for sampling smaller stages (i.e., furcilia, calyptopis, and nauplii) that cannot avoid the net. For this reason, the adult euphausiid distribution presented in this study should be interpreted with caution, as the adults are strong migrators (Barange 1990) and could avoid capture by net. Although our net was not the proper gear to fully sample this community,

the results presented here give important insight into the near-surface distribution of these animals and could corroborate some studies that indicate plankton are dispersed from the Indian Ocean to the Atlantic through transport along the African coastline rather than through the Drake passage (D'Amato et al. 2008).

According to Robledo and Mujica (1999), temperature and salinity are the main environmental variables that affect the distribution patterns (vertical and horizontal) of euphausiids, and in the current work the species found were within the known temperature and salinity values reported for them (Antezana and Brinton 1981).

Thysanopoda pectinata, T. monacantha, and *T. tricuspida* are mesopelagic species, with adults usually restricted to thermocline depths (Brinton et al. 1999). In the South Atlantic, these species occur from 0 to 35° S, with *T. pectinata* being reported at 0-30° S, *T. monacantha* at 20-35° S and *T. tricuspida* at 0-35° S (Brinton et al. 1999, Gibbons et al. 1999). In the present study, all three species were within their reported ranges, with *T. pectinata* being found only towards the eastern side of the transect, while *T. monacantha* and T. *tricuspida* were found on the western side, near Rio Grande Rise. Only a single *Thysanopoda egregia* furcilia was found bearing the characteristic ripple marks on the posterior and lateral parts of the carapace, the short sixth pleomere, and big eyes (Brinton 1962, 1975, Brinton et al. 2013). According to Gibbons et al. (1999), *T. egregia* is a bathypelagic species usually associated with seamounts (Siegel 2015). In the present study, it was collected during the day at a station close to the Walvis Ridge at a tow down to 96 m, which increases the known vertical range of this species; it was previously caught only at depths below 300 m (Brinton et al. 1999).

According to Brinton (1975) and Brinton et al. (1999), *T. aequalis* and *T. astylata* usually co-occur in parts of the Pacific and the Indian Ocean, but not in the Atlantic, where only *T. aequalis* was previously reported between 50 °N and 35 °S. Considering that, we could infer the possibility of transport of this species from the Indo-Pacific region into the Atlantic through the Agulhas Leakage (Richardson 2007). The "absence" of *Thysanopoda* in the Atlantic could be associated with the presence of environmental barriers (Barange et al. 1992) or, more likely, with poor sampling, lack of diagnostic features, or the scarcity of basin-wide studies in the Southern Atlantic, along with the difficulties in identifying these species in plankton samples. In South Atlantic waters, basin-wide studies of the distribution and abundance of euphausiids are lacking, and most current knowledge is based on presence/absence data from historical literature such as 19th century treatises and expedition reports (Gibbons et al. 1999); quantitative data are generally limited to studies conducted after the second half of the 20th century in coastal zones in the western South Atlantic and the eastern South Atlantic (see Table SIII).

According to Constanzo and Guglielmo (1976), identification of *T. astylata* in plankton samples requires the presence of mature adult males with the third leg undamaged by the sampling process. Luckily, some adult male specimens of *Thysanopoda aequalis* and *T. astylata* found during the present study were in good condition, each with at least one of their third thoracic legs intact. The two adult male specimens of *T. astylata* found in this study were collected at stations 33 (032° 04.34ˈW), near the Rio Grande Rise, and 55 (003° 20.94ˈW) (Figure 1); both showed the characteristics described by Brinton (1975), Baker et al. (1990), and Brinton et al. (1999). Samples at both of those stations were taken at night, which could justify these individuals' presence at relatively shallow depths (Table SIII); Brinton et al. (1999) reported that adults can be found at depths of 25-200 m after dusk. The current study could not verify morphological differences between Pacific/Indian Ocean and Atlantic specimens, which could

exclude the possibility of allopatric separation; confirmation will require molecular tools.

Based on our results, we believe that the absence of records of *Thysanopoda minyops* and *T. spinicaudata* in the South Atlantic is also related to the lack of samples from the deeper strata of the central area of the South Atlantic, since the first one is an abyssopelagic (4000-6000 m) species and the second is bathypelagic (1000-4000 m) and reported in other oceans (Central North Pacific and Indian) (Brinton 1987, Brinton et al. 1999, Siegel 2015).

CONCLUSIONS

i) A total of 19 euphausiid species belonging to six genera were recorded along a transect in the South Atlantic Ocean at 30° S;

ii) Overall euphausiid abundances increase towards Africa. *Euphausia* species are more common in the eastern Atlantic (Africa), while *Thysanopoda* species are more common in the western Atlantic (Brazil);

iii) *Thysanopoda* averaged 1.1 organisms 100 m^{-3}, and in the western part of the Atlantic (near Rio Grande Rise) had a density of 20.7 organisms 100 m^{-3};

iv) *Thysanopoda* egregia was caught in samples collected down to 96 m, which increases the vertical range for this species.

v) The present study is the first record of *Thysanopoda astylata* in Atlantic waters. Until this study, 60 euphausiid species were described in South Atlantic waters (Gibbons et al. 1999). Since there is no previous record of *T. astylata*, the number of described euphausiid species in the South Atlantic is now 61.

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AUTHOR CONTRIBUTIONS

Erik Muxagata contributed with sampling design, samples analyses, writing, reviewing and editing; Carla Neme Barbosa contributed with samples analyses and writing; Vanessa Ochi Agostini contributed with data analyses, writing, reviewing and editing.

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SUPPLEMENTARY MATERIAL

Table SI - Zooplankton data for the South Atlantic Ocean during the First Transatlantic Commission (Brazil-Africa) in 2009, showing the stations, sampling dates, sampling time, coordinates, local ocean depth and sampling depth.

Table SII - SIMPER test to identify the contribution index (CI) of euphausiid species between sampling stations toward the western (Brazil) and eastern (Africa) sides of the South Atlantic Ocean.

Table SIII - Main literature about euphausiid distribution in South Atlantic waters.

Figure S1 - Sea surface temperature and temperature vertical profile along the 30 °S transect through the South Atlantic Ocean.

Figure S2 - Adult males of (**a**) *Thysanopoda astylata* and (**b**) *T. aequalis*. Details show (**c**) the dactylus of the third thoracic leg of *T. astylata,* and (**d**) the long flagellum spine modification of the dactylus of the third thoracic leg of *T. aequalis*.