



Distribution patterns of micronektonic crustaceans (Decapoda, Euphausiacea, and Lophogastrida) in the tropical and subtropical Atlantic Ocean

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ABSTRACT

Large pelagic crustaceans are a main component of the micronekton community in the deep-sea having an important role in the food webs and the biological carbon pump. However, they are scarcely studied in comparison to other groups such as mesopelagic fish. Here, we analyse day/night and bathymetric variability in taxonomic composition, abundance, and biomass across a latitudinal transect in the Atlantic Ocean from off Brazil (15°S) to the Canary Islands (25°N). A total of 95 species were identified belonging to 9 different families, of which Euphausiidae was the most abundant family and Acanthephyridae the family contributing the most to the total biomass. We found distinct assemblages associated with Atlantic ecoregions related to the environmental variables. Diel vertical migrations were detected along the entire transect, even crossing the oxygen minimum zone, likely due to the metabolic adaptations of these organisms.

1. Introduction

The pelagic domain is the largest habitat on Earth, extending from the ocean surface to the seabed (Dawson, 2012). Since the breakthrough research of Irigoien et al. (2014) highlighting the actual global biomass of mesopelagic fish, which is significantly larger than previous estimates (Lam and Pauly, 2005), mesopelagic community is in the spotlight. It is one of the least studied ecosystems of the world's oceans, and the vast biomass that it holds attracted interest from fisheries and the marine industry (Hidalgo & Browman, 2019). The research of meso- and bathypelagic communities is still in its early stage, so it is alarming that ecosystem services that it provides can be at risk even before any of the potential consequences of fishing are fully understood (Martin et al., 2020). Most of the research efforts are nowadays directed towards studying the fish component (Proud et al., 2019), even though other micronektonic organisms of the twilight zone could also be acoustically detected using high-frequency broadband scattering systems (Peña et al., 2023). Therefore, the gap of knowledge is even more severe for other groups such as cephalopods, jellyfish, or crustaceans.

In this habitat, mesopelagic shrimps-like, among which are included euphausiids, lophogastrids, and decapods (Landeira & Fransén 2009), are considered an important trophic component, being the main prey of squids and fishes but also important consumers of plankton and tripton (Fanelli et al., 2011). However, in quantitative terms, its relevance is frequently diminished due to its effective ability to avoid sampling gears (Kaartvedt et al., 2012). Nowadays, a combination of pelagic nets and acoustics methods are used to increase precision in the estimation of their abundance and biomass (Peña et al., 2019). Decapods, euphausiids, and small pelagic fishes constitute the main part of the micronekton biomass, with 15–25 %, 35–50 %, and 20–45 % of the whole biomass, respectively (Omori, 1975). Lophogastrids are also important contributors for total abundance in many studies (Burghart et al., 2007; Miranda et al., 2020; Nishiuchi et al., 2021). The relatively high biomass of pelagic shrimps contrasts with the scarce information about spatial distribution, taxonomic composition, or abundance. Fasham and Foxton (1979) studied the faunal composition in different locations of the Atlantic Ocean between 20°N and 60°N and found higher diversity of pelagic shrimps at lower latitudes. In a region between 40°S and 40°N,

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Vereshchaka et al. (2019) reported biomass of only decapod crustaceans one order of magnitude higher than previous estimates in the Atlantic Ocean, accounting 1700 million tons. It should be noted that this estimation did not include other crustacean groups such as euphausiids or lophogastrids, which may suggest a much higher biomass of pelagic shrimps in this region.

The spatial variability of biomass and abundance of pelagic shrimps not only occurs latitudinally, but also vertically. A significant fraction of the pelagic shrimp community displays vertical migrations throughout the water column. During the day, these organisms stay at depth, where the light intensity is low, preventing the detection from visual predators. During the sunset they swim towards upper layers for foraging and return to deep waters at dawn (Lambert, 1989; Meester, 2009). This predatory and anti-predatory behaviour is an evolutionary driver for the diversification of pelagic crustaceans (Foxton, 1972a; Golightly et al., 2022). The magnitude of this migration also depends on the preference for certain oceanographic conditions, and species-specific strategies related to ontogeny and foraging behaviours (Pearre, 2003; Bollens et al., 2011). These biomass movements have a huge importance for the biogeochemical functioning of the pelagic ecosystem. On a daily basis, these micronektonic migrants ingest organic carbon in the productive shallower layers and move to deeper layers of the ocean where they respire, excrete, defecate, or they could be eaten by other deepwater predators. Therefore, this active transport of organic carbon is a key component of the so-called biological carbon pump (BCP) in the ocean. Active carbon flux mediated by micronekton can constitute a significant fraction of the total carbon transported into the mesopelagic zone such as 63–92 % in the Pacific (Pakhomov et al., 2019) and 5–35 % in the Atlantic Ocean (Hernández-León et al., 2019a). Regarding the spatial variability of this flux, Hernández-León et al. (2019a) showed that in areas of high productivity of the tropical and subtropical Atlantic Ocean, most of the vertical carbon flux was driven by the migrant zooplankton and micronekton. However, the contribution of pelagic shrimps to the total carbon transport should need more accurate biomass estimations.

The objectives of this study were (1) to describe the latitudinal changes in the abundance, biomass, and diversity of pelagic micronektonic shrimps (and shrimp-like organisms) along the Central Atlantic Ocean; (2) to quantify the vertical distribution of abundance and biomass of these assemblages, and (3) to determine distinctive vertical migration patterns throughout water column.

2. Material and methods

2.1. Study area

Sampling covered the central area of the Atlantic Ocean from 15°S to 25°N (Fig. 1). This cruise was carried out in April 2015 on board the R.V. “Hespérides” from 400 Km off the coast of Brazil to the Canary Islands in the framework of the research project “Migrants and Active Flux In the Atlantic Ocean” (MAFIA). The sampling area occupied different mesopelagic ecoregions characterized by Sutton et al. (2017): the Tropical and West Equatorial Atlantic (TWEA), Mauritania/Cape Verde (MCV), and the Central North Atlantic (CNA).

At each station, vertical profiles of temperature, conductivity, pressure, dissolved oxygen, and fluorescence were recorded using a Seabird 911Plus CTD profiler equipped with SBE dissolved oxygen and Seapoint chlorophyll fluorometer sensors. Fluorescence data from the first 200 m were converted to chlorophyll *a* (Chl-*a*) using samples collected with Niskin bottles at discrete depths for calibration (see Hernández-León et al., 2019a). Vertical sections of environmental variables were plotted using Ocean Data View software using the DIVA gridding procedure (Schlitzer, 2022).

2.2. Micronekton sampling

Micronekton samples were collected using a Mesopelagos trawl

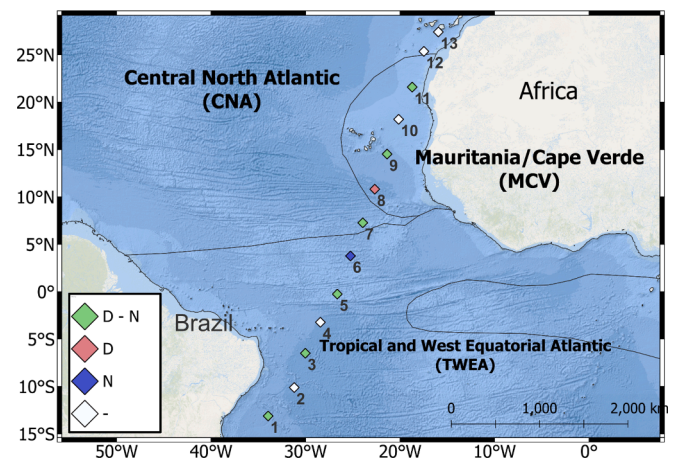


Fig. 1. Location of the sampling stations. Solid black lines delimit ecoregions established by Sutton et al. (2017). Green symbols are stations where day- and nighttime samples were collected. Red symbols stand for stations sampled only during daytime samples. Blue symbols indicate stations where only nighttime samples were obtained. White symbols define stations where only CTD casts were performed. The daylight sampling was carried out around 12:00 and the nightly at 00:00.

(Meillat, 2012) which works with a single traction cable and it has a mouth opening of 5 x 7 m and a total length of 58 m. The mesh size opening changes from 30 mm at the mouth to 4 mm near the cod-end where the multi-sampler VERDA (Castellón and Olivar, 2023) was installed. Multi-sampler VERDA is equipped with a depth sensor to monitor the net position in the water column and allowed the collection of samples in five different layers (Supl. 3): 0–100, 100–200, 200–400, 400–700, and 700–800 m. Hauls were made at 2–3 knots during day and night at every station. In those stations where the multi-sampler failed at certain depth strata, the catch was integrated from the maximum depth to the surface. The total volume of water filtered was estimated using the average mouth area of 35 m², the vessel speed, and duration of each haul. On board, organisms were sorted and fixed in 4 % buffered formalin.

2.3. Distribution patterns of pelagic shrimps

In the laboratory, organisms were identified to the lowest possible taxon using key bibliography (Brinton et al., 2000; Casanova, 1997; Crosnier & Forest, 1973; Perez Farfante & Kensley, 1997; San Vicente, 2016; Vereshchaka, 2000, 2009). Species names were corrected according to WoRMS (WoRMS Editorial Board, 2023). Individuals were weighted to obtain the wet weight (Ww) and converting to dry weight (Dw) using the Dw/Ww ratio of 0.179 proposed by Pakhomov et al. (2019). Then, Dw was converted into carbon units assuming that 40 % of Dw is carbon (Hernández-León et al., 2019a; Olivar et al., 2017). Finally, we standardized the abundance and biomass data using the volume of water filtered by the Mesopelagos trawl.

Abundance and biomass data were represented with R (v. 4.2.3, Posit team, 2022) and Primer-7 packages (Clarke & Gorley, 2015). Shannon diversity index (H') was calculated as $H' = -\sum P_i \ln P_i$; where P_i is the relative abundance of “*i*” species. We calculated the Weighted Mean Depth (WMD) for each taxon during the day and during the night as: $\sum_{i=1}^n P_i Z_i$, where P_i is the proportion of the taxon in the *i*th stratum, and Z_i is the mid-depth of the of the *i*th stratum. In order to compare day- and nighttime samples and different depth layers, the normality and homoscedasticity were calculated with Shapiro-Wilk normality Test and Levene’s Test, respectively (Fox & Weisberg, 2019). When the data were homoscedastic ($p < 0.05$) and no-normal ($p < 0.05$), non-parametric Kruskal-Wallis test was performed, on the other hand, ANOVA test was used for normal data. Principal Component Analysis

(PCA) was performed using temperature, salinity, oxygen, and chlorophyll *a*. For statistical analysis, we used the ecoregions defined above establishing a factor called “Province” with 3 levels. For multivariate statistical analysis, abundance data matrix was transformed using $\log(x + 1)$ to reduce the weighting of dominant species. Hierarchical cluster analysis and non-metric multidimensional scaling (nMDS) analysis were performed based on the Bray–Curtis similarities matrix. In order to classify the stations according to species abundance, a similarity profile routine (SIMPROF; $p < 0.01$; 999 permutations) was performed. Then, similarity percentage analysis (SIMPER) was used to estimate the similarity among groups and to determine which species were contributing most to characterize each group. Canonical Correspondence Analysis (CCA) was performed (“vegan” R package, v. 2.6–4, Oksanen et al., 2022) with the species’ biomass and environmental variables for each station and depth level sampled, in order to detect the environmental drivers of the biomass patterns.

3. Results

3.1. Environmental conditions

Temperature (Fig. 2A) showed a marked latitudinal gradient in the epipelagic zone, with maximum values at stations around the equator (30 °C at 5°S; St. 1–4) and lower values at higher latitudes (18 °C at 22°N; St. 12–13). A pronounced stratification was observed between 10°S and 10°N, with maximum values of 30 °C at the surface decreasing to 5 °C at 750 m depth. Further north, from 10°N northward, the stratification was less intense, and the 7.5 °C isotherm became deeper reaching 1000 m at station 13. This stratification was also observed in the mixed layer depth (Fig. 2D) following the pattern described in the temperature profile. Vertical salinity profiles allowed the detection of different water masses along the cruise (Fig. 2B). In the first 500 m and around the equator (10°S–10°N), the Eastern South Atlantic Central Water (ESACW) and the Western South Atlantic Central Water (WSACW) were detected, with an average salinity of 37 and 35.5 respectively. We found the Antarctic Intermediate Water (AAIW) with a salinity between 34 and 35 was observed below 500 m depth. The vertical oxygen gradient was pronounced between 10°S and 20°N (Fig. 2C) showing an oxygen minimum zone (OMZ) between 5°N and 20°N, extending from 200 m to 750 m depth (values lower than 50 $\mu\text{mol}\cdot\text{kg}^{-1}$). Another low oxygen region was recorded at 5°S at 500 m depth but with higher values (75 $\mu\text{mol}\cdot\text{kg}^{-1}$). Chl-*a* concentration was measured in the first 200 m of the water column (Fig. 2D). The highest values were recorded around 20°N in the oceanic upwelling off NW Africa (St. 11) with values of 6 $\text{mg}\cdot\text{m}^{-3}$. By opposite, lower values were recorded at the deep chlorophyll maximum (DCM) with values of 1–2 $\text{mg}\cdot\text{m}^{-3}$ around 50 m depth between the equator and 10°N. The DCM became deeper southward showing values of 0.5–1.5 $\text{mg}\cdot\text{m}^{-3}$. The PCA analysis (Fig. 3, Supl. 4) showed that St.1 was associated with higher temperature in the epipelagic zone and high oxygen concentration in the epi- and mesopelagic layers. Stations 3 and 5 depicted a similar pattern but also were placed in the opposite direction of salinity and temperature in the mesopelagic zone. Stations 6, 7, and 8 were closely related, and associated with less salty waters in the epipelagic zone. Stations 9 and 11 showed a high correlation with Chl-*a* associated with the upwelling zone, and also were positively related to salinity and temperature in the mesopelagic zone.

3.2. Taxonomic composition and horizontal distribution

A total of 95 species belonging to 9 families of three orders were identified, and a total abundance of 362.9 $\text{ind}\cdot 10^{-3}\text{ m}^{-3}$ and a total biomass of 4.3 $\text{mg C}\cdot\text{m}^{-3}$ (Table 2). The most abundant family was Euphausiidae which ranged between 79.4 and 229.1 $\text{ind}\cdot 10^{-3}\text{ m}^{-3}$ (Table 1) of the total abundance during day- and nighttime, respectively (Table 1). Euphausiids dominated in all stations in terms of abundance

except for St. 9 during day and night and St. 11 during the day, where we observed a mixture of all the identified families (Fig. 4). Specifically, three species of euphausiids (*Nematobrachion seppinosum*, *Euphausia hanseni*, and *Thysanopoda tricuspidata*) were the taxa most contributing to the total abundance. Thus, *T. tricuspidata* total abundance accounted 61.47 $\text{ind}\cdot 10^{-3}\text{ m}^{-3}$ during daytime, while *N. seppinosum* and *E. hanseni* were 119.89 and 92.46 $\text{ind}\cdot 10^{-3}\text{ m}^{-3}$, respectively at night. None of the other species exceeded 10 $\text{ind}\cdot 10^{-3}\text{ m}^{-3}$ of the total abundance at any time. On the other hand, Acantheephyridae, which included large specimens, was the family most contributing to the total biomass (1.8 $\text{mg C}\cdot\text{m}^{-3}$ during daytime and 0.7 $\text{mg C}\cdot\text{m}^{-3}$ at night) (Table 1) in all the stations, except for St.1 and 7 during the day and St.11 during the night where euphausiids were the most contributor to the total biomass (Fig. 4). Specifically, *Acantheephyra kingsleyi* (0.6 $\text{mg C}\cdot\text{m}^{-3}$ during the day and 0.3 $\text{mg C}\cdot\text{m}^{-3}$ during the night) and *A. purpurea* (0.4 $\text{mg C}\cdot\text{m}^{-3}$ during the day and < 0.1 $\text{mg C}\cdot\text{m}^{-3}$ during the night) were the species mostly contributing to the total biomass. The other families and species contributed less than 0.5 $\text{mg C}\cdot\text{m}^{-3}$ to the total abundance and biomass except for euphausiids (0.5 $\text{mg C}\cdot\text{m}^{-3}$ during daylight and 0.6 $\text{mg C}\cdot\text{m}^{-3}$ at night).

Latitudinal variations in terms of abundance were evident along the transect (Fig. 5A) with a gradual increase towards 20°N during the night. However, during the daytime the pattern was weaker, showing an abundance increase from St.1 to St.7 (13°S to 7°N) and a decrease until St.11 (21°N). Biomass distribution exhibited the opposite pattern (Fig. 5B). Thus, biomass increased from 13°S to 20°N during the day, whereas at nighttime the biomass increased from 13°S to 7°N, and then decreased in the northern stations. The lowest values of abundance were observed in the tropical North Atlantic around 5°N (St. 6), with abundances of 0.5 $\text{ind}\cdot\text{m}^{-2}$ and a biomass of 20 $\text{mg C}\cdot\text{m}^{-2}$. On the contrary, the highest abundance values were found at nighttime in the northernmost station exceeding 10 $\text{ind}\cdot\text{m}^{-2}$, an order of magnitude higher than equivalent daytime record (1.4 $\text{ind}\cdot\text{m}^{-2}$, St. 11, Fig. 5A), but a corresponding biomass of 30 and 10 $\text{mg C}\cdot\text{m}^{-2}$ respectively.

The difference in taxonomic diversity was significant through the transect (Kruskall-Wallis test, $\chi^2(7) = 26.42$, $p < 0.05$) with Shannon Index values ranging from 1.6 to 2.3 (Sts 3–11, Fig. 5C). Daytime diversity increased northward reaching a maximum value of 2.5 in station 11, whereas nighttime diversity depicted a significant increase in station 3 remaining relatively constant northward, with values around 2. However, there were no differences in diversity between day and nighttime (Kruskall-Wallis test, $\chi^2(1) = 0.76$, $p > 0.05$) and depth layers (Kruskall-Wallis test, $\chi^2(3) = 0.24$, $p > 0.05$).

3.3. Vertical distribution

During the day, the highest values of abundance and biomass (Fig. 6A, C) occurred in the deeper layers of the water column (750 m), while at night they were observed in shallower layers (0–150 m). During the daytime, the maximum value of abundance (69.7 $\text{ind}\cdot 10^{-3}\text{ m}^{-3}$ Fig. 6B) and biomass (0.8 $\text{mg C}\cdot\text{m}^{-3}$; Fig. 6D) were recorded at 750 m depth (St. 7). At night, the highest values occurred in the 0–150 m depth layer with 91.8 $\text{ind}\cdot 10^{-3}\text{ m}^{-3}$ (St.11) in abundance and a biomass of 0.2 $\text{mg C}\cdot\text{m}^{-3}$ (St. 7). This higher abundance was driven by the high numbers of euphausiids which depicted diel vertical migrations throughout the transect (Fig. 7 A,B). The family Acantheephyridae showed a homogeneous distribution independently of light except in St. 9 (Fig. 7 C,D). Families Opolophoridae (Supl. 1 A,B), Pandalidae (Supl. 1C,D), Benthescymidae (Supl. 1E,F), and Sergestidae (Supl. 1G,H) were present in almost all the stations and followed the same spatial distribution pattern as the euphausiids. Distribution of Pasiphaeidae (Supl. 2A,B) and Gnathopausiidae (Supl. 1E,F) did not show any pattern, whereas Eucopiidae (Supl. 1C,D) was recorded mostly during daytime. Comparison tests of the WMD during the day and night (Kruskal-Wallis and ANOVA test) showed that most of the families displayed significant patterns of diel vertical migration, but with different range of migration

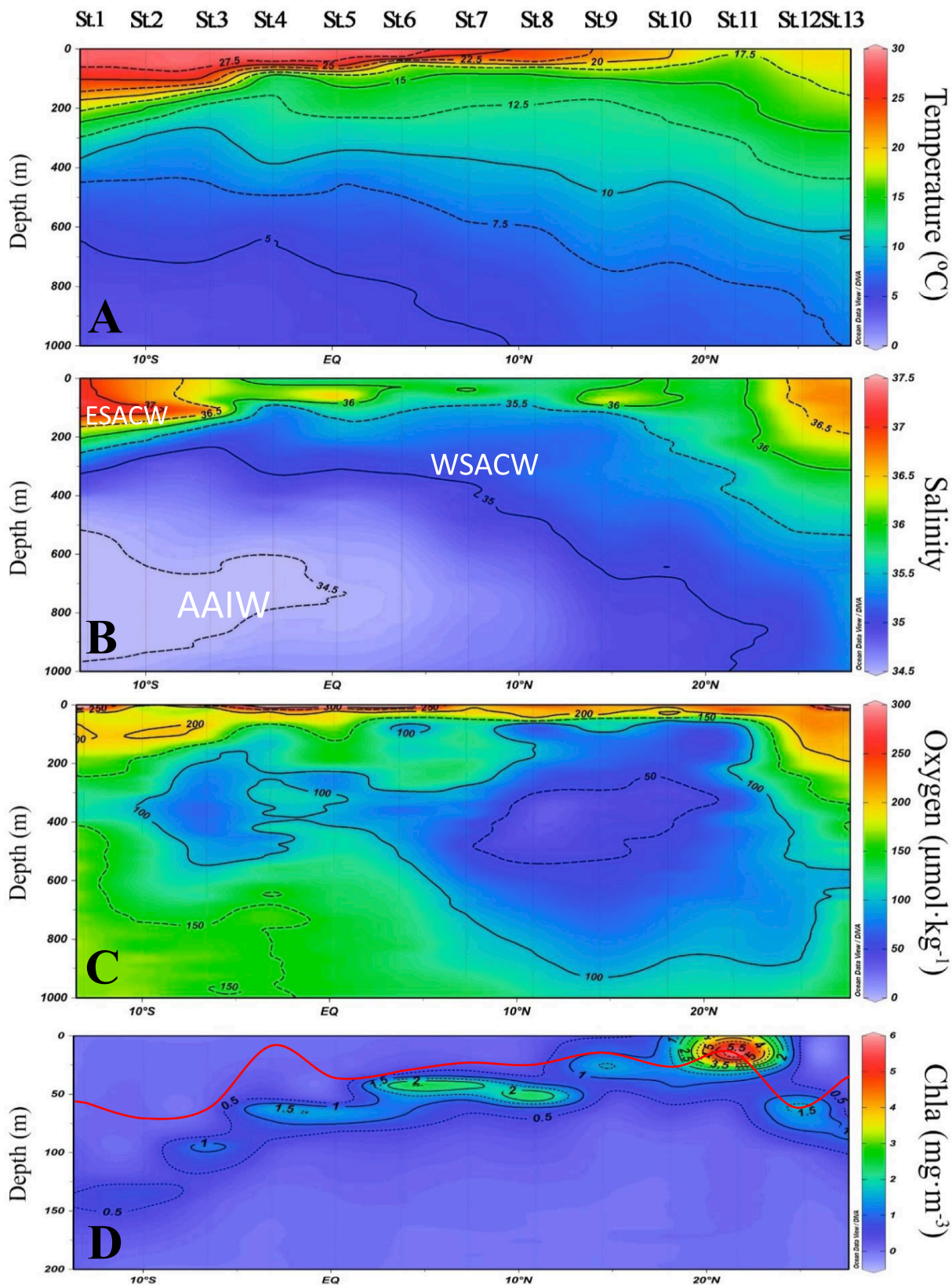


Fig. 2. Vertical distribution along the latitudinal transect of (A) temperature ($^{\circ}\text{C}$), (B) salinity, (C) dissolved oxygen ($\mu\text{mol} \cdot \text{kg}^{-1}$), and (D) chlorophyll *a* (Chla, $\text{mg} \cdot \text{m}^{-3}$), with the mixed layer depth in red. Water masses: Eastern South Atlantic Water (ESACW), Western South Atlantic Central Water (WSACW), Antarctic Intermediate Water (AAIW).

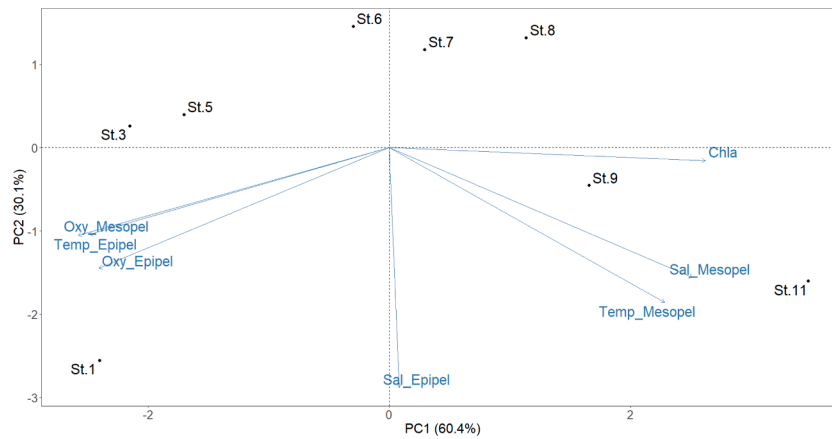


Fig. 3. Principal Component Analysis (PCA) ordination diagram of stations where the net was deployed on first and second PCA axis. The vectors corresponded to the normalized temperature, salinity, oxygen and Chla in the epipelagic (0 – 200) and mesopelagic (200 – 1000) zone. Note chla was only measured in the epipelagic zone.

(Table 1, WMD). Thus, the test showed significant differences in Ophiuridae (WMD: 616 – 197 m during the day and night, respectively, Kruskal-Wallis test, $\chi^2(1) = 6$, $p < 0.05$), Benthescymidae (454 – 199 m, ANOVA test, $F(1,9) = 8.45$, $p < 0.05$), Pandalidae (575 – 94 m, Kruskal-Wallis test, $\chi^2(1) = 3.86$, $p < 0.05$), Sergestidae (578 – 125 m, ANOVA test, $F(1,8) = 75.53$, $p < 0.05$), Pasiphaeidae (550 – 153 m, ANOVA test, $F(1,4) = 32.95$, $p < 0.05$), and Euphausiidae (424 – 145 m, ANOVA test, $F(1,10) = 13.49$, $p < 0.05$) WMD during the day and nighttime. Acanthephyridae (413 – 295 m, Kruskal-Wallis test, $\chi^2(1) = 3.33$, $p > 0.05$) and Eucopiidae (321 – 659 m, ANOVA test, $F(1,7) = 1.21$, $p > 0.05$) did not show differences in both phases and Gnathophausiidae (623 m) only showed values during night.

Differences in the WMD between day and night was tested in the most contributing species. In Acanthephyridae, the vertical distribution of *A. purpurea* (566 – 167 m, during day and night, respectively, Kruskal-Wallis test, $\chi^2(1) = 5.06$, $p < 0.05$), and *A. kingsleyi* (399 – 200 m, Kruskal-Wallis test, $\chi^2(1) = 6$, $p < 0.05$) showed differences, whereas *A. acanthitelsonis* (335 – 613 m, ANOVA test, $F(1,8) = 2.20$, $p > 0.05$), and *A. pelagica* (636 – 332 m, ANOVA test, $F(1,6) = 5.58$, $p > 0.05$) did not show any difference. In Ophiuridae, the distribution of *Systellaspis debilis* (545 – 75 m, ANOVA test, $F(1,5) = 34.8$, $p < 0.05$) showed significant differences, that was also observed in the pandalid shrimp *Plesionika richardi* (575 – 128 m, ANOVA test, $F(1,3) = 13.74$, $p < 0.05$). Moreover, the distribution of *Gennadas talismani* (651 – 199 m, ANOVA test, $F(1,7) = 26.64$, $p < 0.05$) and *Neosergestes edwardsi*, (509 – 50 m, Kruskal-Wallis test, $\chi^2(1) = 4.94$, $p < 0.05$) belonging to Benthescymidae and Sergestidae respectively, showed differences between day and night. In Eucopiidae, *Eucopia unguiculata* (389 – 642 m, Kruskal-Wallis test, $\chi^2(1) = 0.95$, $p > 0.05$) did not show significant differences in both phases of the day. In Euphausiidae, the species *Euphausia gibboides* (327 – 88 m, $F(1,6) = 6.75$, $p < 0.05$), *Nematobranchion sexspinosum* (472 – 164 m, Kruskal-Wallis test, $\chi^2(1) = 6.86$, $p < 0.05$), *Thysanopoda monacantha* (528 – 160 m, ANOVA test, $F(1,8) = 24.48$, $p < 0.05$), and *Thysanopoda tricuspudata* (576 – 73 m, ANOVA test, $F(1,4) = 40.12$, $p < 0.05$) showed significant differences.

3.4. Community structure and assemblages

Through a hierarchical cluster analysis of stations (SIMPROF test) based on the abundance and taxonomic composition, three groups were clearly identified. (Fig. 8, Fig. 9.). SIMPER analysis determined the percentage of similarity for each group and the species characterizing each group (Table 3). Group A (average similarity of 42.3 %) was formed by stations 5D, 6 N, 3D and 3 N from the TWEA ecoregion. *Thysanopoda orientalis*, *Acanthephyra kingsleyi*, and *Notostomus gibbosus* were the

species most contributing to group A, although there was a high presence of the family Euphausiidae in the total contribution. Group B was made up by stations 8D, 9D, 9 N, 7D and 7 N, showing an average similarity of 51.6 %, and constituting a transition from TWEA to MCV ecoregions. This group matched the OMZ and was characterized by high diversity, with *Euphausia gibboides*, *Acanthephyra kingsleyi*, and *Acanthephyra acanthitelsonis* as the three major contributors to the total similarity. Group C was only formed by stations 11D and 11 N from the MCV ecoregion, and with an average similarity of 44.5 %. This upwelling influenced area was dominated by families Sergestidae and Euphausiidae, and *Sergestes atlanticus*, *Acanthephyra pelagica*, and *Euphausia krohni* were the species mostly contributing to the total similarity.

The multivariate Canonical Correspondence Analysis (CCA, Fig. 10) was performed using those species that most contributed to forming the groups (see Table 3) and showed a high correlation in the first two axis (see table in Fig. 10). The first axis was negatively correlated with temperature and salinity (−0.77 and −0.96, respectively), and the second with the oxygen and Chl-a (−0.72 and −0.60, respectively). The groups of samples detected previously in the cluster analysis were also observed in the CCA. However, they showed a mixture of depth levels from stations belonging to other groups. Group A and B were both observed mainly in the positive region of the axis, but stations from group A were grouped in the positive axis of the CCA1 and group B stations in the positive part of the CCA2 axis. Group C was arranged in the negative part of both axes. Chl-a and oxygen highly influenced the biomass of group C species, while species from group A and B were in the opposite side to vectors of environmental variables.

4. Discussion

4.1. Horizontal distribution

The latitudinal patterns observed in this study regarding pelagic shrimps are consistent with the previously defined pelagic ecoregions of the central Atlantic Ocean by Sutton et al. (2017). There is scarce information about latitudinal distribution of the decapod pelagic community, and we only found comparable results from Vereshchaka et al. (2019) (Table 2). Total biomass results were slightly different and the total abundance in our study was much higher because we included the high abundant order Euphausiacea (Fig. 7 A, B). In any case, our biomass estimates were derived from individuals preserved in formalin (4 %) resulting in an underestimation of the actual carbon biomass due to the water loss caused by the formalin fixation (Howmiller, 1972).

This study found three different spatial assemblages (Group A – C,

Table 1

Total values of abundance (ind. · 10⁻³ m⁻³), biomass (g WW · 10⁻³ m⁻³), occurrence (%) and weighted mean depth (WMD), and standard deviation (SD) during the day and the night for each specie identified along the survey.

Taxa	Day					Night				
	Abundance	Biomass	Occ.	WMD (m)		Abundance	Biomass	Occ.	WMD (m)	
	(Ind. · 10 ⁻³ m ⁻³)	(mg C · m ⁻³)		Mean	SD	(Ind. · 10 ⁻³ m ⁻³)	(mg C · m ⁻³)		Mean	SD
Order Decapoda	31.6	2.2	85.7	456	218	19.9	1.1	100	212	96
Fam. Acantheephyridae	10.7	1.8	85.7	413	246	5.1	0.7	100	295	126
<i>Acanthephyra Acanthitelsonis</i>	0.9	0.3	85.7	335	234	0.8	0.3	80	613	65
<i>Acanthephyra curtirostris</i>	<0.1	<0.1	14.3	50	–	0.1	<0.1	40	509	56
<i>Acanthephyra kingsleyi</i>	2.9	0.6	85.7	399	242	2.3	0.3	80	200	68
<i>Acanthephyra pelagica</i>	4.9	0.1	57.1	636	91	1.2	0.1	80	332	200
<i>Acanthephyra purpurea</i>	0.9	0.4	71.4	566	103	0.5	<0.1	60	167	23
<i>Acanthephyra</i> sp.	<0.1	<0.1	28.6	287	283	–	–	–	–	–
<i>Ephyrina ombango</i>	0.2	<0.1	57.1	683	95	–	–	–	–	–
<i>Meningodora marptocheles</i>	0.1	<0.1	14.3	750	–	–	–	–	–	–
<i>Meningodora mollis</i>	<0.1	<0.1	14.3	550	–	<0.1	<0.1	20	550	–
<i>Meningodora vesca</i>	<0.1	<0.1	28.6	550	–	<0.1	<0.1	20	850	–
<i>Notostomus auriculatus</i>	<0.1	<0.1	14.3	550	–	–	–	–	–	–
<i>Notostomus elegans</i>	0.2	<0.1	42.9	294	384	<0.1	<0.1	20	550	–
<i>Notostomus gibbosus</i>	0.2	0.2	28.6	194	495	0.1	<0.1	60	451	219
<i>Notostomus robustus</i>	0.1	0.1	14.3	750	–	–	–	–	–	–
Fam. Oplophoridae	1.6	0.1	71.4	616	176	3.0	0.2	80	197	139
<i>Oplophorus spinosus</i>	<0.1	<0.1	28.6	206	566	0.1	<0.1	60	116	140
<i>Systellaspis cristata</i>	0.1	<0.1	42.9	610	115	0.1	<0.1	60	283	274
<i>Systellaspis debilis</i>	1.1	0.1	57.1	545	134	1.6	0.2	60	75	31
<i>Systellaspis pellucida</i>	0.2	<0.1	28.6	548	154	1.2	<0.1	60	296	268
Fam. Pandalidae	0.4	<0.1	42.9	575	166	0.2	<0.1	60	94	50
<i>Heterocarpus ensifer</i>	–	–	–	–	–	<0.1	–	20	50	–
<i>Plesionika richardi</i>	0.4	<0.1	42.9	575	166	0.2	<0.1	40	128	29
Fam. Pasiphaeidae	<0.1	<0.1	28.6	550	–	1.9	<0.1	80	153	88
<i>Parapasiphae sulcatifrons</i>	<0.1	<0.1	28.6	550	–	–	–	–	–	–
<i>Pasiphae</i> sp.	<0.1	<0.1	14.3	550	–	1.9	<0.1	80	153	88
Fam. Benthescymidae	7.2	0.1	85.7	454	210	3.9	0.1	100	199	102
<i>Benthegennema intermedia</i>	0.1	<0.1	28.6	122	177	0.1	<0.1	20	657	–
<i>Gennadas bouvieri</i>	0.3	<0.1	42.9	247	289	0.4	<0.1	60	319	36
<i>Gennadas brevirostris</i>	0.4	<0.1	57.1	409	152	0.5	<0.1	40	58	12
<i>Gennadas burkenroadi</i>	0.6	<0.1	14.3	750	–	–	–	–	–	–
<i>Gennadas kempfi</i>	0.1	<0.1	14.3	750	–	–	–	–	–	–
<i>Gennadas scutatus</i>	0.3	<0.1	28.3	642	141	0.3	<0.1	20	150	–
<i>Gennadas talismani</i>	4.5	<0.1	71.4	651	92	2.5	<0.1	80	199	72
<i>Gennadas tinayrei</i>	<0.1	<0.1	14.3	150	–	–	–	–	–	–
<i>Gennadas valens</i>	0.2	<0.1	14.3	150	–	–	–	–	–	–
<i>Gennadas</i> sp.	0.6	<0.1	42.9	449	148	0.1	<0.1	40	80	54
<i>Pelagopenaeus balboae</i>	0.1	<0.1	14.3	750	–	–	–	–	–	–
Fam. Sergestidae	11.9	0.1	71.4	578	94	5.8	0.1	100	125	65
<i>Allosergestes nudus</i>	0.1	<0.1	14.3	550	–	<0.1	<0.1	20	150	–
<i>Allosergestes pectinatus</i>	0.3	<0.1	14.3	750	–	0.3	<0.1	40	162	18
<i>Allosergestes sargassi</i>	<0.1	<0.1	14.3	50	–	–	–	–	–	–
<i>Allosergestes</i> sp.	0.1	<0.1	57.1	204	144	<0.1	<0.1	40	122	177
<i>Cornutosergestes cornutus</i>	<0.1	–	14.3	550	–	0.2	<0.1	40	50	–
<i>Deosergestes corniculum</i>	<0.1	–	28.6	166	354	0.2	<0.1	40	128	28
<i>Deosergestes henseni</i>	0.8	<0.1	57.1	642	115	0.1	<0.1	20	50	–
<i>Deosergestes pediformis</i>	<0.1	<0.1	28.6	406	177	<0.1	<0.1	20	300	–
<i>Deosergestes</i> sp.	<0.1	–	14.3	300	–	0.1	<0.1	40	150	–
<i>Eusergestes similis</i>	0.9	<0.1	14.3	212	–	0.1	<0.1	20	75	–
<i>Gardinerosergia gardineri</i>	–	–	–	–	–	<0.1	–	20	50	–
<i>Gardinerosergia splendens</i>	<0.1	<0.1	14.3	750	–	0.1	<0.1	40	77	49
<i>Neosergestes edwardsi</i>	4.8	<0.1	57.1	509	181	0.7	<0.1	60	50	–
<i>Neosergestes</i> sp.	0.1	<0.1	14.3	472	–	–	–	–	–	–
<i>Parasergestes armatus</i>	0.1	<0.1	57.1	503	192	0.2	<0.1	60	109	135
<i>Parasergestes cylindricus</i>	0.7	<0.1	57.1	527	167	0.5	<0.1	80	84	29
<i>Parasergestes</i> sp.	<0.1	–	14.3	50	–	–	–	–	–	–
<i>Phorcosergia burikovskii</i>	0.1	<0.1	14.3	550	–	<0.1	<0.1	20	50	–
<i>Phorcosergia filicla</i>	0.1	<0.1	28.6	406	177	0.1	<0.1	40	162	18
<i>Phorcosergia grandis</i>	0.2	<0.1	14.3	750	–	<0.1	<0.1	20	50	–
<i>Phorcosergia</i> sp.	<0.1	–	14.3	550	–	–	–	–	–	–
<i>Robustosergia extenuata</i>	0.1	<0.1	14.3	480	–	0.1	<0.1	40	212	106
<i>Robustosergia regalis</i>	0.1	<0.1	14.3	750	–	–	–	–	–	–
<i>Robustosergia robusta</i>	0.2	<0.1	42.9	541	16	0.7	<0.1	40	125	6
<i>Scintillosergia scintillans</i>	–	–	–	–	–	<0.1	<0.1	20	50	–
<i>Sergestes atlanticus</i>	1.0	<0.1	14.3	530	–	1.9	<0.1	20	105	–
<i>Sergestes</i> sp.	–	–	–	–	–	<0.1	<0.1	20	150	–
<i>Sergia japonica</i>	1.9	<0.1	42.9	652	95	<0.1	<0.1	40	642	141
<i>Sergia laminata</i>	0.1	<0.1	14.3	449	–	<0.1	<0.1	20	550	–
<i>Sergia tenuiremis</i>	0.2	<0.1	28.6	533	24	0.2	<0.1	20	550	–

(continued on next page)

Table 1 (continued)

Taxa	Day					Night				
	Abundance	Biomass	Occ.	WMD (m)		Abundance	Biomass	Occ.	WMD (m)	
	(Ind. · 10 ⁻³ m ⁻³)	(mg C · m ⁻³)		Mean	SD	(Ind. · 10 ⁻³ m ⁻³)	(mg C · m ⁻³)		Mean	SD
<i>Sergia</i> sp.	0.1	<0.1	14.3	750	–	0.1	<0.1	40	75	–
Order Lophogastrida	2.4	<0.1	85.7	319	297	0.5	<0.1	60	659	158
Fam. Eucopiidae	2.2	<0.1	85.7	321	302	0.4	<0.1	60	659	158
<i>Eucopia grimaldii</i>	<0.1	<0.1	14.3	550	–	–	–	–	–	–
<i>Eucopia sculpticauda</i>	0.1	<0.1	42.9	202	250	0.2	<0.1	40	642	141
<i>Eucopia unguiculata</i>	1.5	<0.1	71.4	389	284	0.2	<0.1	20	642	141
<i>Eucopia</i> sp.	0.6	<0.1	14.3	540	–	0.1	<0.1	40	850	–
Fam. Gnathophausiidae	0.2	<0.1	14.3	623	–	0.1	<0.1	40	100	–
<i>Fagegnathophausia gracilis</i>	–	–	–	–	–	<0.1	<0.1	20	50	–
<i>Gnathophausia bergstadi</i>	<0.1	<0.1	14.3	50	–	–	–	–	–	–
<i>Gnathophausia zoea</i>	0.2	<0.1	14.3	676	–	–	–	–	–	–
<i>Neognathophausia ingens</i>	–	–	–	–	–	<0.1	<0.1	40	150	–
Order Euphausiacea	79.4	0.5	100	424	160	229.1	0.6	100	145	78
Fam. Euphausiidae	79.4	0.5	100	424	160	229.1	0.6	100	145	78
<i>Euphausia gibboides</i>	3.3	<0.1	57.1	327	177	2.7	<0.1	80	88	63
<i>Euphausia hansenii</i>	0.1	<0.1	14.3	150	–	92.5	0.1	40	62	88
<i>Euphausia krohni</i>	0.9	<0.1	14.3	150	–	0.7	<0.1	20	75	–
<i>Euphausia</i> sp.	0.2	<0.1	42.9	218	324	0.1	<0.1	40	150	159
<i>Nematobrachion boopis</i>	0.7	<0.1	57.1	291	257	0.6	<0.1	100	219	122
<i>Nematobrachion flexipes</i>	–	–	–	–	–	0.1	<0.1	60	189	87
<i>Nematobrachion sexspinosum</i>	1.4	<0.1	71.4	472	105	119.9	0.3	100	164	57
<i>Nematobrachion</i> sp.	0.1	<0.1	28.6	531	26	–	–	–	–	–
<i>Nematoscelis megalops</i>	–	–	–	–	–	0.1	<0.1	20	300	–
<i>Stylocheiron armatus</i>	0.3	<0.1	14.3	50	–	–	–	–	–	–
<i>Stylocheiron carinatum</i>	<0.1	<0.1	14.3	150	–	–	–	–	–	–
<i>Stylocheiron elongatum</i>	–	–	–	–	–	0.3	<0.1	60	238	87
<i>Stylocheiron maximum</i>	–	–	–	–	–	0.1	<0.1	20	300	–
<i>Stylocheiron</i> sp.	0.4	<0.1	42.9	184	255	0.7	<0.1	60	268	57
<i>Thysanopoda cristata</i>	<0.1	<0.1	14.3	300	–	0.4	<0.1	60	263	34
<i>Thysanopoda microphthalma</i>	–	–	–	–	–	0.1	<0.1	20	150	–
<i>Thysanopoda monacantha</i>	9.3	0.1	71.4	528	142	1.4	<0.1	100	160	86
<i>Thysanopoda obtusifrons</i>	<0.1	<0.1	14.3	750	–	<0.1	<0.1	40	150	–
<i>Thysanopoda orientalis</i>	0.7	<0.1	85.7	456	168	0.8	<0.1	100	202	61
<i>Thysanopoda pectinata</i>	–	–	–	–	–	<0.1	<0.1	40	212	106
<i>Thysanopoda tricuspidata</i>	61.5	0.4	42.9	576	133	8.6	0.1	60	73	40
<i>Thysanopoda</i> sp.	0.3	<0.1	57.1	326	299	<0.1	<0.1	20	496	–

Table 2

Abundance and biomass data reported in the study area Vereshchaka et al. (2019). The biomass was converted from g WW · 10⁻³ m⁻³ to g C · 10⁻³ m⁻³ (See material and methods for more details).

Reference	Zone	Sampling stations	Net	Depth sampled	Total abundance	Total biomass	Taxa included
					(Ind. · 10 ⁻³ m ⁻³)	(mg C · m ⁻³)	
Our study	Equatorial Atlantic (13 °S – 21.5 °N)	7 (day), 5 (night)	Mesopelagos	Epi- and mesopelagic zone	362.9	4.3	Decapoda, Lophogastrida, Euphausiacea
Vereshchaka et al. (2019)	Equatorial Atlantic (0 °S – 22 °N)	7 (night)	Borgorov-Rass	Epi- and mesopelagic zone	20.0	4.8	Decapoda
Vereshchaka et al. (2019)	Equatorial Atlantic (0 °S – 22 °N)	7 (night)	Isaacs-Kidd midwater trawl	Epi- and mesopelagic zone	6.0	0.2	Decapoda

Fig. 8). The first assemblage (Group A) comprised samples from the Tropical and West Equatorial Atlantic area (TWEA). This region, extending from 10°S to the Equator, exhibited oligotrophic properties characterized by high sea surface temperature (30 °C) and a pronounced water column stratification. Additionally, this area exhibited lower biomass and abundance values compared to other northern areas. The species found in this ecoregion were typical of tropical and subtropical regions (Judkins, 2014; Sutton & Beckley, 2022).

Group B (Fig. 8) consisted of stations from the Mauritania/Cape Verde ecoregion (MCV) and a transition zone belonging to the Central North Atlantic (CNA). Despite the strong similarity within this group, stations 8 and 9, which were influenced by the OMCZ (Fig. 2C), displayed lower abundance and biomass values but higher diversity compared to station 7 (Fig. 5). This region also exhibited high stratification, limited nutrient input, and low Chl-a concentration resulting in higher

crustacean diversity compared to areas showing higher disturbances, often disrupting spatial organization (Margalef, 1968; Andersen et al., 1997; Woodd-Walker et al., 2002). However, in this study, we observed an increase in diversity moving northward due to the co-occurrence of tropical, subtropical, and temperate species in the stations between Cape Verde and the upwelling region off NW Africa. In agreement with previous studies (Crosnier and Forest, 1973; Valdés and Déniz-González, 2015), we observed that temperature was the main environmental variable driving the distribution of pelagic shrimps. The gradual change of communities was linked to certain temperature ranges allowing the species coexistence in transition zones as observed by Fasham and Foxton (1979) and Sutton and Beckley (2022). For example, *Acanthe-phyra pelagica* was reported as subpolar-temperate species whereas *A. purpurea* as temperate-tropical (Judkins, 2014), and both were collected in St. 11. Using the same samples of this cruise, Olivar et al.

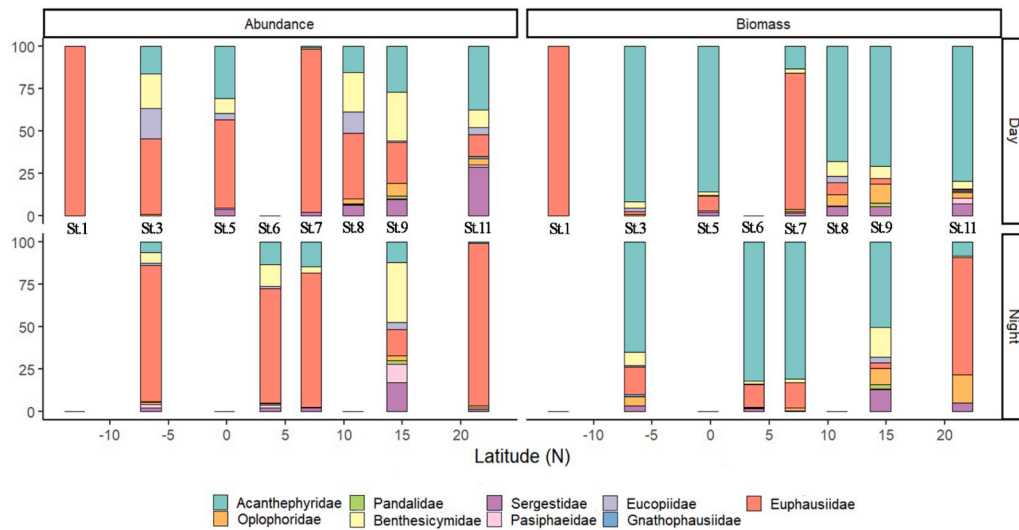


Fig. 4. Relative abundance (left) and biomass (right) (%) of each family at each latitude during day- (top) and nighttime (bottom). The net was empty in stations 1 N, 5 N, 6D and 8 N.

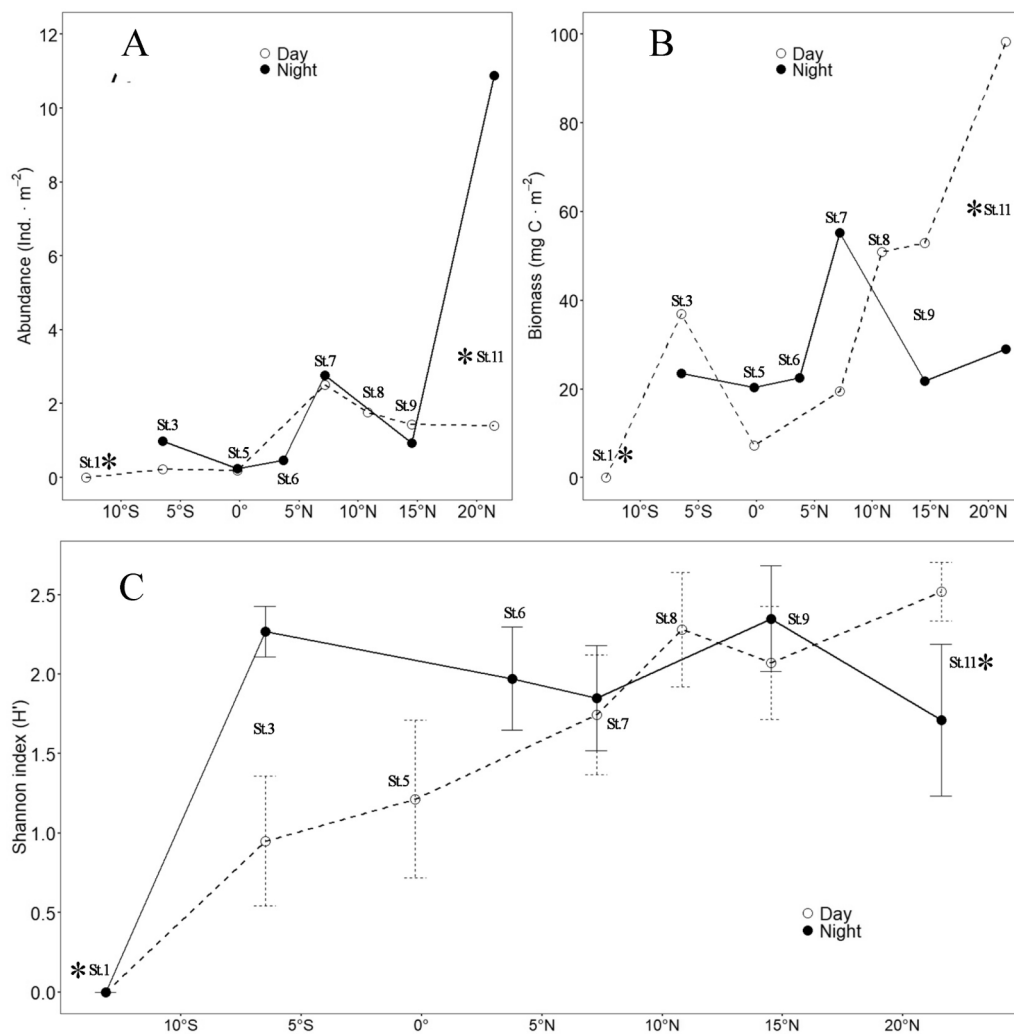


Fig. 5. Latitudinal distribution of (A) total abundance (NO · m⁻²) and (B) total biomass (g C · m⁻²). Stations 1D and 11D had different sampling range (marked as *): 0–500 and 0–200, respectively. (C) Shannon index (H') for day- (empty dots) and nighttime stations.

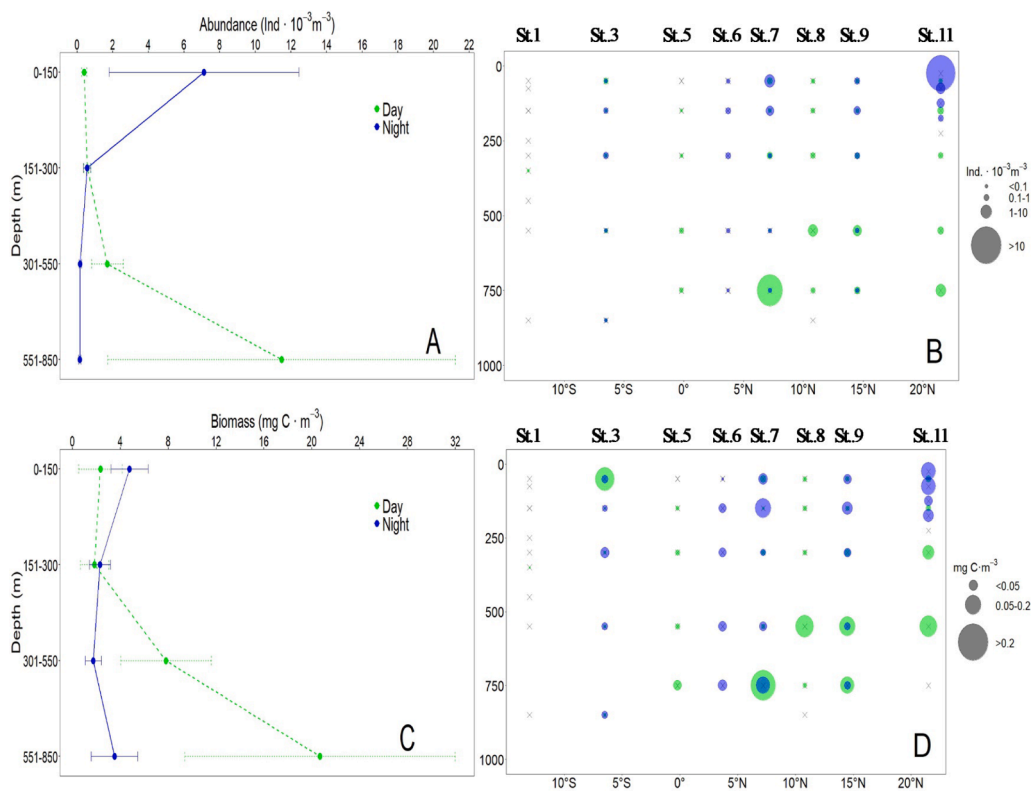


Fig. 6. Vertical distribution of abundance (top) and biomass (down) along the latitude during day- and nighttime (green and blue bubbles, respectively). Average values (\pm standard error) for all the stations at each layer are displayed in Figures A and C, and along the latitudinal transect in Figures B and D.

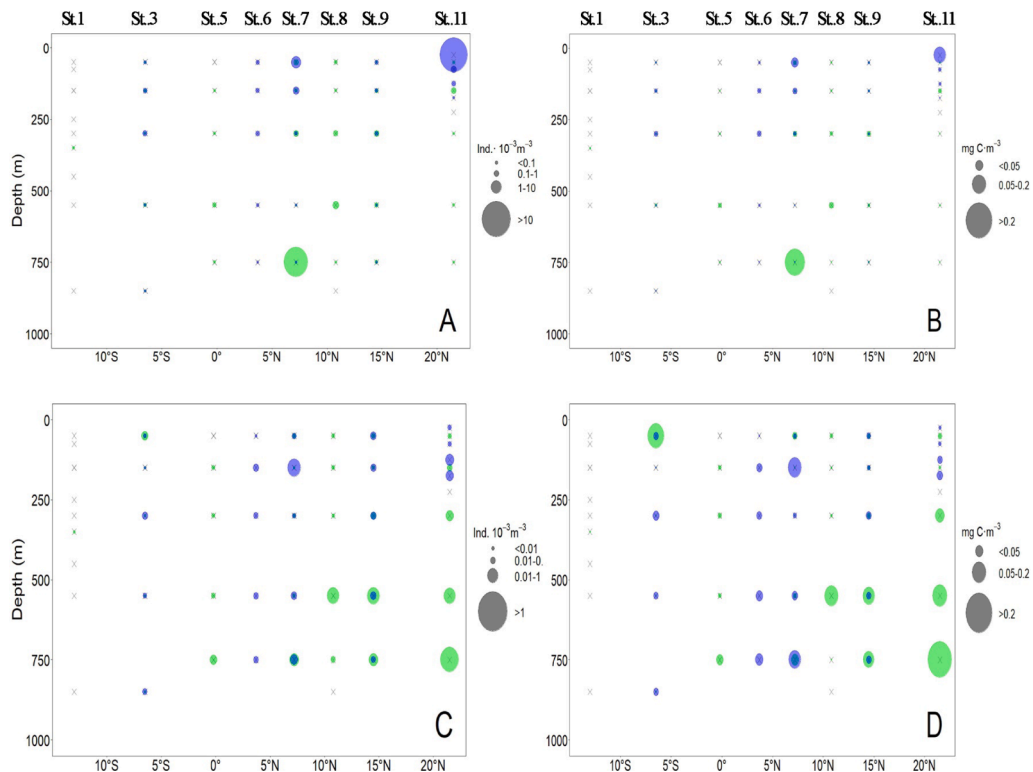


Fig. 7. Vertical and latitudinal distribution of abundance (left) and biomass (right) for families Euphausiidae (A,B) and Acanthephyridae (C,D) during day- and nighttime (green and blue bubbles, respectively).

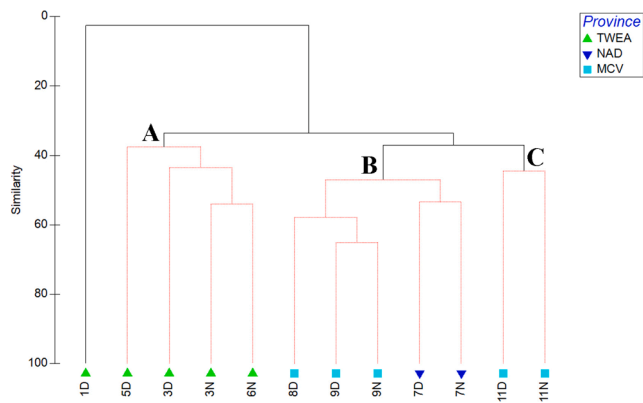


Fig. 8. Dendrogram for hierarchical clustering of station similarities (Bray Curtis) based on the abundance matrix ($\log(x + 1)$ transformed). SIMPROF test showed non-significant combinations (in red). The Province factor representing the three ecoregions sampled is also shown (Tropical and West Equatorial Atlantic, TWEA, Mauritania/Cape Verde, MCV, and Central North Atlantic, CNA).

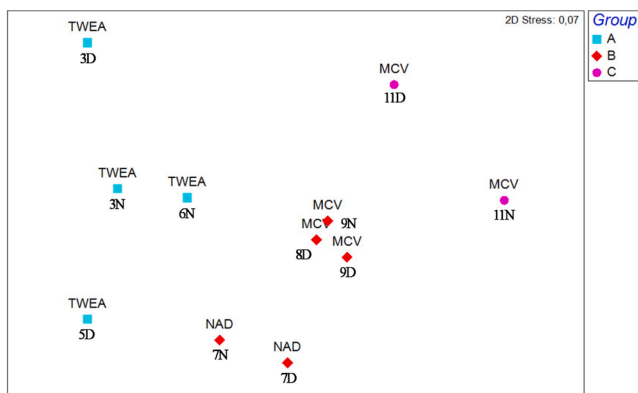


Fig. 9. Non-metric Multidimensional Scaling (nMDS) ordination of stations based on the $\log(x + 1)$ transformation abundance matrix and Bray Curtis similarities. Factor Province and groups represented in the dendrogram (Fig. 8) are also shown.

(2017) studied the mesopelagic fishes and identified a similar diversity pattern. They found that the distribution of abundance and biomass of mesopelagic fishes were influenced by the water masses, but only for those non-migrant species. They explained this pattern considering that migrant species have a wide vertical range of occurrence and were able to cross different water masses, whereas the non-migrant species were only present in deeper layers.

Group C (Fig. 8) represented day/night samples from station 11 in the MCV ecoregion. This group shared similarities with Group B but exhibited higher total (pooling together day and night samples) abundance and biomass supported by the high productivity in the oceanic upwelling region (Gabric et al., 1993). This colder and nutrient-rich water (Relvas et al., 2009; Lovecchio et al., 2018) promoted the maximum values of Chl-a along the transect. We found a positive relationship between the biomass of the species that most contributed to this group (Fig. 10) and Chl-a, which aligns with previous observations by Vereshchaka et al. (2016) in a larger area of the Atlantic Ocean.

4.2. Vertical distribution

This study revealed diel vertical migrations (DVMs) across the transect for several families, including Opolophoridae, Pandalidae, Benthescymidae, Sergestidae, Pasiphaeidae, and Euphausiidae. However, this general pattern was not consistent for all groups. Specifically, at the

family level, Acanthephyridae did not exhibit day/night variations in WMD, primarily due to the presence of non-migrant species such as *A. acanthitelsonis*, *A. pelagica*, and those from *Notostomus*, *Meningodora*, and *Ephyrina* (Foxton, 1970; Fasham & Foxton, 1979). On the other hand, species such as *A. purpurea* and *A. kingsleyi* displayed a clear DVM behaviour as previously reported by Foxton, 1970, Foxton, 1972b). The family Eucopiidae, consisting of deep-mesopelagic and bathypelagic species (San Vicente, 2016), did not evidence DVM patterns and they were observed throughout all the water column (Suppl. 2C, D).

Euphausiidae family showed large swarming behaviour (Mauchline, 1971; Brinton et al., 2000) as an antipredator and reproductive strategy (García-Fernández et al., 2023). Euphausiids were the most abundant group, primarily due to the high population densities of *Euphausia hanseni*, *Nematobrachion sexspinosum*, and *Thysanopoda tricuspidata*. Most species within this family displayed DVM from the mesopelagic zone (400–600 m) during daytime to epipelagic waters (0–200 m) during the night (Table 1). However, the distribution pattern of *Nematobrachion boopis* and *Stylocheiron* species indicated non-vertical migration behaviours, consistent with previous reports (Kinsey & Hopkins, 1994).

All crustacean families were observed at stations 8 and 9 (Figs. 4 and 6), indicating their ability to swim in areas of low oxygen concentration (less than $50 \mu\text{mol}\cdot\text{kg}^{-1}$). Crustacean organisms are generally considered sensitive to low oxygen concentrations (Vaquer-Sunyer and Duarte, 2008) and these organisms were found at high densities within the core of OMZs (Rabalais et al., 2001; Tutas and Escribano, 2020). Physiological and anatomical adaptations enable crustaceans to effectively obtain and utilize oxygen even in low-oxygen environments. These adaptations include increased ventilation and circulatory capacity, a high gill surface area for efficient gas exchange, short distances for diffusion of oxygen between blood and water, the presence of respiratory proteins with high oxygen affinity and cooperativity (Childress & Seibel, 1998), and higher enzymatic activities (see Herrera et al., 2019, and discussion in Hernández-León et al., 2019b).

5. Conclusions

This study characterized the micronekton crustacean community consisting of shrimp-like organisms (decapods, euphausiids, and lophogastrids) in the Central Atlantic Ocean. Specifically, three distinct spatial assemblages were identified along the transect, which corresponded to previously established ecoregions (Sutton et al., 2017). These areas were primarily characterized by variations in oceanographic variables such as temperature, salinity, dissolved oxygen concentration, and chlorophyll-a levels. We observed the highest diversity in the most productive area due to the co-occurrence of tropical, subtropical, and temperate species. Diel vertical migrations were observed in several families of crustaceans, including Opolophoridae, Pandalidae, Benthescymidae, Sergestidae, Pasiphaeidae, and Euphausiidae. However, the families Acanthephyridae and Eucopiidae did not show vertical migration but had some species that showed mixed migration patterns. These vertical movements were detected all along the transect, even throughout the OMZ, due to the metabolic adaptations of these organisms as described in the literature.

CRedit authorship contribution statement

Javier Díaz-Pérez: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **José M. Landeira:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Santiago Hernández-León:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **M. José Reyes-Martínez:** Writing – review & editing, Supervision. **Juan Ignacio González-Gordillo:** Writing – review & editing, Supervision.

Table 3

Contribution of each species to the similarity in each group obtained with the SIMPER analysis. Average similarity of the group is also shown.

Group A			Group B			Group C		
Average similarity: 42.26			Average similarity: 51.63			Average similarity: 44.46		
Taxa	Contrib%	Cum.%	Taxa	Contrib%	Cum.%	Taxa	Contrib%	Cum.%
<i>Thysanopoda orientalis</i>	11.73	11.73	<i>Euphausia gibboides</i>	8.39	8.39	<i>Sergestes atlanticus</i>	10.27	10.27
<i>AcanthePHYra kingsleyi</i>	11.46	23.18	<i>AcanthePHYra kingsleyi</i>	8.08	16.47	<i>AcanthePHYra pelagica</i>	10.06	20.33
<i>Notostomus gibbosus</i>	7.99	31.17	<i>AcanthePHYra acanthitelsonis</i>	6.48	22.95	<i>Euphausia krohni</i>	9.59	29.92
<i>AcanthePHYra acanthitelsonis</i>	6.85	38.02	<i>Gennadas talismani</i>	6.43	29.38	<i>Nematobranchion sexspinosum</i>	9.45	39.37
<i>Nematobranchion sexspinosum</i>	6.85	44.87	<i>Nematobranchion sexspinosum</i>	5.94	35.32	<i>Systellaspis debilis</i>	8.66	48.03
<i>Thysanopoda monacantha</i>	6.28	51.14	<i>Thysanopoda monacantha</i>	5.51	40.83	<i>AcanthePHYra purpurea</i>	6.19	54.21
<i>Thysanopoda tricuspidata</i>	6.08	57.23	<i>Gennadas brevirostris</i>	5.42	46.25	<i>Parasergestes cylindricus</i>	5.99	60.20
<i>Gennadas bouvieri</i>	5.84	63.06	<i>Thysanopoda orientalis</i>	5.36	51.60	<i>Robustosergia robusta</i>	5.73	65.93
<i>Stylocheiron sp.</i>	5.48	68.54	<i>Neosergestes edwardsi</i>	4.75	56.35	<i>Eusergestes similis</i>	5.54	71.48
<i>Gennadas talismani</i>	4.69	73.24	<i>AcanthePHYra purpurea</i>	4.09	60.44	<i>Gennadas sp.</i>	4.79	76.26
<i>Eucopeia unguiculata</i>	4.67	77.90	<i>Systellaspis debilis</i>	3.93	64.37	<i>Sergia sp.</i>	4.77	81.03
<i>Bentheogennema intermedia</i>	3.74	81.65	<i>Thysanopoda tricuspidata</i>	3.79	68.16	<i>Euphausia hanseni</i>	4.60	85.64
<i>Thysanopoda cristata</i>	3.52	85.16	<i>Deosergestes henseni</i>	3.28	71.44	<i>Nematobranchion boopis</i>	3.26	88.90
<i>Nematobranchion boopis</i>	3.31	88.47	<i>AcanthePHYra pelagica</i>	3.25	74.70	<i>Thysanopoda orientalis</i>	3.09	91.99
<i>Euphausia gibboides</i>	1.46	89.93	<i>Plesionika richardi</i>	2.95	77.65			
<i>AcanthePHYra purpurea</i>	1.31	91.25	<i>Parasergestes cylindricus</i>	2.52	80.17			
			<i>Nematobranchion boopis</i>	2.02	82.20			
			<i>Systellaspis pellucida</i>	1.66	83.86			
			<i>Parasergestes armatus</i>	1.58	85.44			
			<i>Eucopeia unguiculata</i>	1.41	86.85			
			<i>Gennadas scutatus</i>	1.28	88.13			
			<i>Robustosergia robusta</i>	1.06	89.19			
			<i>Sergia japonica</i>	1.00	90.19			

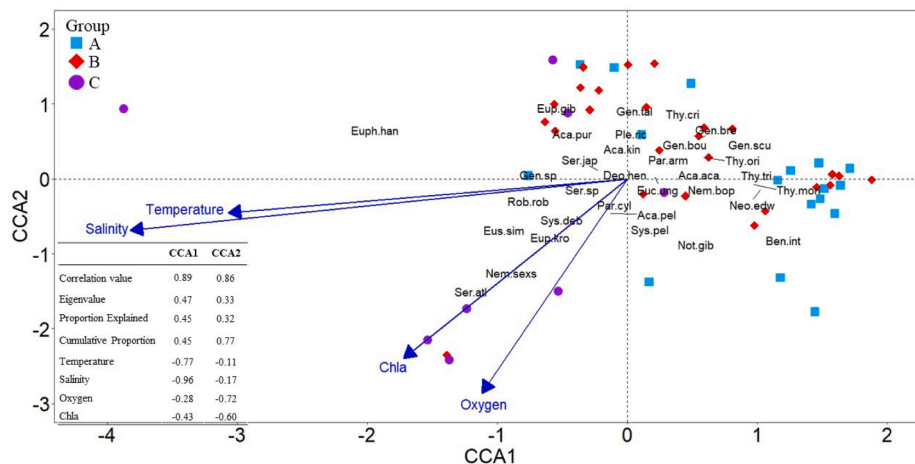


Fig. 10. Canonical Correspondence Analysis (CCA) with environmental variables (Temperature, Salinity, Oxygen, and Chla) and the species that most contributed to forming the cluster groups. Abbreviations of those species are shown, the complete name is shown in Table 3. Correlation of the first and second axis, the variance explained, and the correlation between environmental variables and each axis are shown in the table.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: [Javier Diaz-Perez reports financial support was provided by University of Las Palmas de Gran Canaria].

Data availability

I have shared the link to my dataset in the manuscript

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2024.103331>.

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