



OPEN The effect of Mauritanian and Benguela upwelling waters on micronekton (Decapoda, Euphausiacea, and Lophogastrida) in the Southeastern Atlantic Ocean

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Eastern Boundary Upwelling Systems play a crucial role in marine productivity, supporting rich biodiversity and sustaining significant global fisheries. These dynamic regions are characterized by nutrient-rich waters that fuel complex food webs, making them vital for ecosystem functioning and fisheries management. Understanding the composition and distribution of key zooplankton groups, such as pelagic crustaceans, is essential for assessing ecosystem dynamics, particularly in the context of climate variability. In this study, we describe the community composition of pelagic crustaceans in the Mauritanian Upwelling (MU) and Benguela Upwelling System (BUS). The stations sampled in both ecosystems were grouped in relation to the water masses, with MU (10–22°N) stations associated to high temperature and salinity, and southern BUS (30–34°S) to rich oxygen waters. A total of 43 species were identified in MU and 48 in BUS, with the same number for Decapoda and Lophogastrida, but more euphausiid species in the BUS (14 and 19 species, respectively). Sergestidae was the most diverse family from Decapoda, with 13 and 14 species in MU and BUS, respectively. We found the highest abundance and biomass of pelagic crustaceans in the permanent upwelling area of the MU. Considering organisms body size, the largest individuals (surface area > 100 mm²) showed the highest frequency of occurrence in the MU. However, the smallest organisms (surface area 0–20 mm²) predominated in the BUS, probably due to a high intensity of the upwelling. Additionally, in the BUS, we identified the tropical euphausiid *Thysanopoda tricuspidata*, likely transported from the Indian Ocean by the Agulhas Current. Our results highlight the influence of large-scale oceanographic processes on pelagic crustacean distribution.

Keywords Micronekton, Biodiversity, Twilight zone, Eastern Boundary Upwelling System, Atlantic Ocean

Upwelling ecosystems are among the most productive areas of the planet. In these regions, equatorward winds driven by large-scale atmospheric pressure systems blow parallel to the coast. Thus, Ekman transport moving surface waters offshore, cause deep waters to rise and replace surface waters to conserve mass¹. There are four major eastern boundary upwelling systems: the California, Humboldt, Canary/Iberian, and Benguela. The upwelling of nutrient-rich water in these regions enhances primary production under suitable conditions², allowing these areas to yield³ 443–1157 gC·m⁻² y⁻¹. The physical processes driving upwelling formation are rather understood¹ and recent models predict upwelling intensification in future scenarios of climate change⁴. However, the long-term ecosystem impacts remain uncertain. The high productivity in upwelling systems results in dense zooplankton populations such as copepods⁵ and euphausiids^{6,7}, which serve as primary food sources for commercially important pelagic fish species⁸. Upwelling systems contribute to 22.5% of the global fish catches⁹.

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and they are characterized by short, highly efficient food chains transferring energy from lower to upper trophic levels, in contrast to oligotrophic ecosystems¹⁰.

Mid-trophic organisms play a key role in these ecosystems, linking primary producers and top predators. They are mostly organisms between 1 and 10 cm and includes macrozooplankton and jellyfish, as well as micronekton such as fish, cephalopods, large euphausiids (krill), and other shrimp-like organisms such as decapods and lophogastrids. Despite recent significant efforts to study this ecosystem, most research was focused on mesopelagic fish¹¹ limiting the comprehensive knowledge of the entire community¹². These organisms perform diel vertical migrations and feed upon small zooplankton and large phytoplankton^{13–15}, serving as prey for tunas, dolphins, and seabirds^{16–18}. Many pelagic shrimps also perform diel vertical migrations, feeding in surface layers at night and descending to deeper layers during the day. Thus, both groups transport organic carbon to deep waters^{19,20}, contributing to the so-called biological carbon pump, efficiently removing carbon from shallower layers^{21,22}.

The Canary Current, the eastern branch of the subtropical gyre in the North Atlantic Ocean, extends from the northwestern Iberian Peninsula to northwestern Africa. This wide ecosystem is divided into five subsystems²³: (1) the Galician and (2) Portuguese sub-regions, both characterized by a temperate climate, transporting North Atlantic Central Water upward, and intensifying during the spring-summer season^{24,25}. (3) The Gulf of Cádiz sub-region, highly influenced by the Mediterranean Water, showing intermittent or no upwelling because of the coastal orientation. These three sub-regions generally show lower productivity mainly due to upwelling seasonality²³. The other two sub-regions, (4) the Moroccan and (5) Mauritanian-Senegalese are characterized by wide shelves and an almost constant upwelling, displaying a much higher productivity^{23,26}. Near Cape Blanc, the Canary Current coastal upwelling converges with the Mauritanian Current forming the Cape Verde Frontal Zone²⁷. This is a highly dynamic oceanographic area frequently forming a giant filament off Cape Blanc, exporting high amounts of biogenic organic matter that originated in the coastal zone, further offshore^{28,29}.

The taxonomic studies on pelagic shrimps in the northwest African zone were conducted several decades ago. These works established the species composition³⁰, while the first detailed accounts of their vertical distribution were also provided^{31,32}. Recent studies around the Canary Islands added new species records for the area^{33,34} and also studied their vertical distribution, oceanographic conditions, and diel vertical migration^{21,35}. The southern side of the Canary Current System is even less studied. Some studies focused on the species composition of decapods in the Mauritania Upwelling (MU) using bottom trawls^{36,37}. Hoving et al.³⁸ provided interesting observations on the vertical migration of pelagic fauna using video profiles around Cape Verde archipelago. The most detailed information was provided by Díaz-Pérez et al.⁷ who described the vertical distribution of decapods, euphausiids, and lophogastrids in two oceanic stations during a latitudinal survey. These authors found low abundance and biomass values and a high diversity, typical of the subtropical ocean, and a limited influence of the oxygen minimum zones⁷.

The Benguela upwelling System (BUS) is located in southwest Africa, along the coasts of Namibia and western South Africa, from 5° to 37°S. The BUS is delimited by two fronts of warm water: (1) the Angola-Benguela front at 15°S, and (2) the Agulhas Current flowing from the Indian Ocean¹. The Angola Dome, a cyclonic feature at 10°S–10°E, drives the southward Angola Current along the continental shelf. In late summer, this warm, saline water extends into northern Namibia, while Benguela waters shift north and offshore, pushed by southeasterly winds. The convergence of these opposing currents creates an offshore flow near the frontal zone at 20°S. Seasonal southward shifts of Angolan water occur twice a year, influenced by sea level anomalies peaking in October and February^{1,39}. In the southern margin, at Cape Agulhas, cool upwelling waters meet the warm, nutrient-poor waters of the Agulhas Bank, influenced by the nearby Agulhas Current. This interaction creates a complex mix of water masses near Cape Point, where warm eddies and offshore filaments flow into the South Atlantic. The region is divided into three zones: coastal upwelling, mid-shelf stratification, and offshore oceanic influence, with seasonal variability in wind-driven upwelling and increased chlorophyll *a* during summer^{1,40}. Between 25° and 30°S is located the Lüderitz cell, with strong winds promoting a constant upwelling zone, separating this region into two subsystems: northern and southern Sections⁴¹. Both sections exhibit different periods of maximum upwelling, with autumn and spring in the northern section and spring and summer in the southern Section⁴². The latter section is strongly influenced by frequent eddies from Agulhas Current transporting species from higher latitudes⁴³.

In southern section, euphausiids were a focal point of research since the 1990s, with studies on diversity, distribution, and behaviour^{44–49}. By contrast, pelagic shrimps received much less attention. Macpherson⁵⁰ showed the distribution of decapod crustaceans in the northern subsystem and within the Lüderitz cell. In the southern subsystem, Kensley⁵¹ identified species commonly associated with coastal and oceanic waters, such as *Solenocera africana* and *Systellaspis debilis*. However, only epipelagic sampling was conducted in this study. Schukat et al.⁵² also studied the carbon flux performed by pelagic shrimps, showing the significant impact of these organisms upon the calanoid copepod population, consuming approximately 13% of the total standing stock per day in the area. Both upwelling ecosystems are influenced by similar physical processes (wind blowing parallel to the coast, Ekman transport displacing surface water offshore, and the ascent of deep water). However, local conditions within each ecosystem create different environments.

In this study, given the importance of pelagic crustaceans as a component of micronekton⁵³, we hypothesize that the contrasting environmental conditions of the Mauritanian Upwelling (MU) and the Benguela Upwelling System (BUS) drive the formation of different crustacean assemblages. To address the knowledge gap regarding decapods, lophogastrids, and euphausiids in the two regions, we analysed epi- and mesopelagic composition, spatial distribution of abundance, and biomass. The main objective of our study was to examine the spatial distribution of decapods, lophogastrids, and euphausiids abundance and biomass and identify the key factors contributing to their variability.

Material & methods

Study areas and sample collection

This study compiles data from two research cruises. The collection of samples was conducted under the required permits from Mauritania, South Africa, and Namibia. The first cruise was conducted aboard the RV Meteor (cruise M129) in August 2016 in the MU (Fig. 1A)⁵⁴, and the second set of samples were collected on the RV Sonne (cruise SO285) in the southern part of the BUS (Fig. 1B) during September 2021 (Table 1)⁵⁵. During both

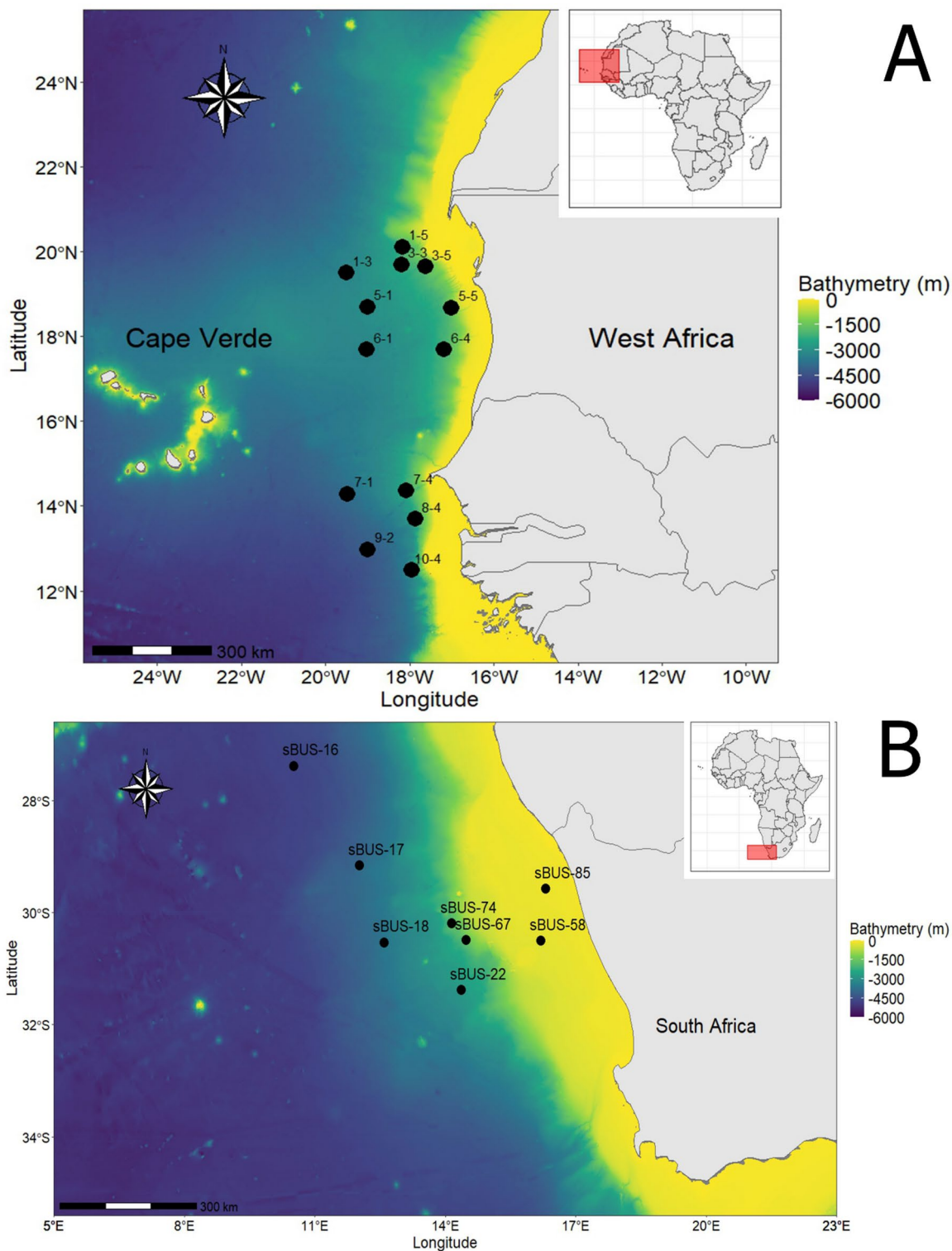


Fig. 1. Map of the sampling stations in (A) the Mauritanian Upwelling (MU) and (B) the Benguela Upwelling System (BUS). Samples obtained using the RMT8 net are represented as black dots.

Zone	St	Filtered volume (m ³)	Latitude (°N)	Longitude (°W)	Date	Layer sampled (m)	Bathymetry (m)	Light
North MU	1–3	30,878	19.49	19.51	04/08/2016	0–566	3203	D
	1–5	43,748	20.11	18.17	05/08/2016	0–566	2233	D
	3–3	38,053	19.69	18.19	08/08/2016	0–566	2270	D
	3–5	38,292	19.64	17.62	08/08/2016	0–453	1854	D
	5–1	41,246	18.70	19.00	22/08/2016	0–566	3035	D
	5–5	38,185	18.67	17.00	12/08/2016	0–566	1920	D
	6–4	32,488	17.69	17.17	14/08/2016	0–566	1990	D
	6–1	28,440	17.69	19.01	15/08/2016	0–566	3189	D
South MU	7–1	43,199	14.28	19.47	16/08/2016	0–566	3825	D
	7–4	41,090	14.36	18.07	17/08/2016	0–566	2240	D
	8–4	33,796	13.69	17.87	19/08/2016	0–566	2470	D
	9–2	38,753	12.97	18.99	20/08/2016	0–566	4229	D
	10–4	34,799	12.49	17.95	22/08/2016	0–566	2632	D
BUS	sBUS-16	86,967	– 27.38	10.51	13/09/2021	0–502	4182	N
	sBUS-17	29,619	– 29.16	12.02	13/09/2021	0–500	3869	N
	sBUS-18	93,834	– 30.53	12.59	14/09/2021	0–750	3377	D
	sBUS-22	26,848	– 31.38	14.36	18/09/2021	0–505	2771	N
	sBUS-58	19,667	– 30.50	16.19	22/09/2021	0–190	227	N
	sBUS-67	60,080	– 30.49	14.47	24/09/2021	0–505	1956	N
	sBUS-74	36,093	– 30.19	14.14	25/09/2021	0–501	1730	N
	sBUS-85	7261	– 29.57	16.30	27/09/2021	0–137	173	N

Table 1. Position, filtered volume, date, and layer sampled at the Mauritanian and Benguela upwelling systems.

cruises, salinity, temperature, dissolved oxygen, and chlorophyll-a (Chl-a) were measured using a CTD (Sea Bird Plus SBE 9) at each sampling station down to 1000–1500 m depth (0.5 m·s^{−1} descent and 1 m·s^{−1} ascent) to characterize the oceanographic conditions of each region. Monthly mean Chl-a for each cruise was obtained from satellite data provided by Copernicus Marine Services⁵⁶ with a spatial resolution of 0.25°. All data were visualized using Ocean Data View⁵⁷ and R⁵⁸, utilizing the ggplot2 package⁵⁹. Biological samples were collected using an integrated vertical approach with a RMT 8 net (mouth opening of 8 m², mesh size of 4.5 mm, and a net bucket cod-end with 1 mm mesh size) towed at 2.5–3 knots⁶⁰. In the MU, the stations were divided into two groups, Northern MU (8 stations) and Southern MU (5 stations) (Fig. 1A). In the BUS, we selected 8 stations, all located in the southern part of the upwelling system (Fig. 1B). The layer sampled (see Table 1) was determined by the bathymetry at each station.

In the MU, the filtered volume (FV) was estimated following Duncan et al.⁶¹, based on the maximum sampled depth (z), net mouth area (A), and the distance travelled by the vessel (x, in km). It was assumed that during the descent and ascent, the net followed the hypotenuse of two identical right triangles, with catheti given by half the horizontal distance covered (x/2) and the maximum sampling depth (z):

$$2 \sqrt{z^2 + \left(\frac{x}{2}\right)^2}$$

Multiplying by the net mouth area (A) and converting the distance travelled to meters gives the total filtered volume (FV):

$$FV = 2 * A \sqrt{z^2 + \left(1000 * \frac{x}{2}\right)^2}$$

In the BUS, since the depth sensor attached to the RMT malfunctioned, the filtered volume was instead estimated based on (1) the distance travelled (determined subtracting the final latitude and longitude to the initial coordinates), (2) the net's mouth opening area, and (3) the haul duration. This alternative approach followed the method described by Duncan et al.⁶² for the analysis of the mesopelagic fish catch in these samples.

Species identification and micronekton assemblages

In both cruises, samples were preserved in 4% phosphate buffered formalin. In the laboratory, the organisms were identified to the lowest possible taxonomic level using reference works^{30,63–68}. Species names were then updated according to the World Register of Marine Species⁶⁹. All the organisms of the same species in each sample were counted and divided into the filtered volume and the maximum depth sampled in each station (Table 1) to obtain abundance, as individuals per square meter (ind·m^{−2}). In the same way, these organisms were pooled and weighed together to obtain wet weight, that we divided into the filtered volume (Table 1) to obtain

biomass as grams of wet weight per square meter ($\text{gWW}\cdot\text{m}^{-2}$). All the organisms were photographed with a scale and using the software ImageJ⁷⁰, where we measured the surface area of each specimen (mm^2). The area of the organisms ranged between 0.5 and 1900 mm^2 , from small euphausiids to big penaeids.

All figures generated from abundance and biomass data, data processing, and statistical analysis were developed using R language⁵⁸ and the PRIMER-7 package⁷¹. To explore patterns in the environmental data, we conducted a Principal Component Analysis (PCA), with k-means clustering using the packages Factoextra V1.0.7⁷² and Vegan, V2.4-6⁷³, and we determined three different oceanographic groups. The environmental variables used were temperature, salinity, and oxygen averaged within the layer sampled (Table 1), chlorophyll-a, and bathymetry, standardized for this analysis.

Differences in crustacean's abundance, biomass, and size classes were assessed using a consistent statistical workflow. Prior to hypothesis testing, we used Levene's test to check for equality of variances and the Shapiro-Wilk test to assess normality. Since all tests indicated homoscedasticity but non-normal distributions, we applied the non-parametric Kruskal-Wallis test. For multivariate community analysis, abundance data were transformed with $\log(x+1)$ to calculate the resemblance matrix (Bray Curtis similarity) for cluster analysis, using group average linkage. This transformation was selected to reduce the influence of highly abundant taxa and to stabilize variance among samples, which is particularly useful when working with skewed ecological data. The $\log(x+1)$ transformation remains a widely accepted alternative in multivariate community analyses, especially when all data are expressed in consistent units. This approach follows established practices described by Legendre and Legendre⁷⁴ and Clarke et al.⁷⁵. As the cluster analysis yielded the same three groups as the PCA, differences between these oceanographic groups were tested using PERMANOVA with associated pairwise tests. A SIMPER analysis identified the contribution of key species to group similarity. Regarding organism size, spatial differences in surface body area across the PCA groups were also tested using PERMANOVA and pairwise tests, while differences in the median of the area of each species across the sampling zones were assessed with the Kruskal-Wallis test.

Finally, we tested the relationship between the environmental factors and the total abundance of the micronektonic crustaceans with Spearman correlation. The variables with the highest correlation were selected for the Redundancy Analysis (RDA). To ensure the robustness of the model and avoid multicollinearity, a stepwise selection was performed based on the Variance Inflation Factor (VIF), retaining only variables with $\text{VIF} < 10$ (specifically, temperature 0–100 m and oxygen 100–200 m). These statistical multivariate analyses were performed using the Vegan package in R⁷³.

Results

Oceanographic conditions

We found different water masses in the MU. In the northern area (Northern MU) (Fig. 2A) the subsurface layers revealed the presence of North Atlantic Central Water (NACW) with temperature oscillating between 11 and 18 °C and a salinity of 35.5–36.5. Beneath the NACW, we identified the South Atlantic Central water (SACW) characterized by a temperature ranging between 9.5 and 15 °C and a salinity of 35–35.5^{27,76}. Around 800–1200 m depth, we observed the Antarctic Intermediate Water (AAIW) with a temperature below 8 °C. The deepest water mass detected in this region was the North Atlantic Deep Water (NADW) below 1200 m depth and 4 °C⁷⁷. In contrast, sampling in the southernmost stations (Southern MU) were shallower than the northern stations, and the NADW was not detectable in the TS profiles (Fig. 2B).

In the BUS region, Ocean Surface Water (OSW) was observed from the surface to depths of 200–300 m, with salinities values ranging from 35 to 35.5, and temperature between 13 °C and 15 °C. The Modified Upwelled Water was also detected within the same depth range but exhibiting different characteristics, with temperature of 10–15 °C and salinities of 34.7–35.2. The South Atlantic Central Water (SACW) was present below 200 m depth, characterized by a salinity of 35 and a temperature of 10 °C. The Eastern South Atlantic Central Water (ESACW) was identified at approximately 600 m depth, with temperature ranging from 4 to 7 °C and salinities of 34.3–34.5. The Antarctic Intermediate Water (AAIW) was present around 1000 m depth, with a salinity of 34.4–34.5 and a temperature of 4 °C. The deepest water mass observed was the North Atlantic Deep Water (NADW), located below 1200 m depth, with temperature of 2–3 °C and a salinity of 34.7⁴².

Surface Chl-a concentrations were higher along the coast of the MU exhibiting a decreasing gradient from 5 $\text{mg}\cdot\text{m}^{-3}$ in the northern region to $>1 \text{ mg}\cdot\text{m}^{-3}$ in the oceanic waters and the southern area (Fig. 3A). In the BUS, coastal waters between 17°S to 30°S exhibited elevated Chl-a concentrations, ranging from 3 to 5 $\text{mg}\cdot\text{m}^{-3}$ (Fig. 3B). The oxygen profile in the MU (Fig. 3C) showed a high variability at the surface and a minimum at 400 m depth, increasing with depth as also observed in the BUS (Fig. 3D).

A Principal Component Analysis (PCA) separated the stations into three groups, based on the sampling area (Fig. 4). MU stations were primarily associated with temperature and salinity, while BUS stations were more closely linked to oxygen concentration. A third different group was formed by stations sBUS–85, sBUS–58, both on the shelf zone of the BUS and St. 3–5 in the MU which were all characterized by high Chl-a values.

Abundance and biomass distribution

We found higher values of abundance and biomass in the northern area of the MU stations, centred around Sts. 1–5 and 5–5. These stations showed abundance values of 19.51 $\text{ind}\cdot\text{m}^{-2}$ and 10.23 $\text{ind}\cdot\text{m}^{-2}$, and biomass of 2.08 $\text{gWW}\cdot\text{m}^{-2}$ and 0.85 $\text{gWW}\cdot\text{m}^{-2}$, respectively (Fig. 5A, B). In the southernmost area of the MU, maximum values were recorded at St. 10–4, with an abundance of 3.79 $\text{ind}\cdot\text{m}^{-2}$ and biomass of 1.18 $\text{gWW}\cdot\text{m}^{-2}$. For the BUS stations, the highest abundance was recorded at St. sBUS-85 with 4.23 $\text{ind}\cdot\text{m}^{-2}$, while the maximum biomass was recorded at St. sBUS-74, with 0.44 $\text{gWW}\cdot\text{m}^{-2}$ (Fig. 5C, D). Despite variations in abundance and biomass across each sampling area (MU and BUS), these differences were not significant within each zone (MU: $p > 0.01$, $\chi^2 = 0.83$ for abundance, $p > 0.01$, $\chi^2 = 18.55$ for biomass; BUS: $p > 0.01$, $\chi^2 = 17.36$ for abundance;

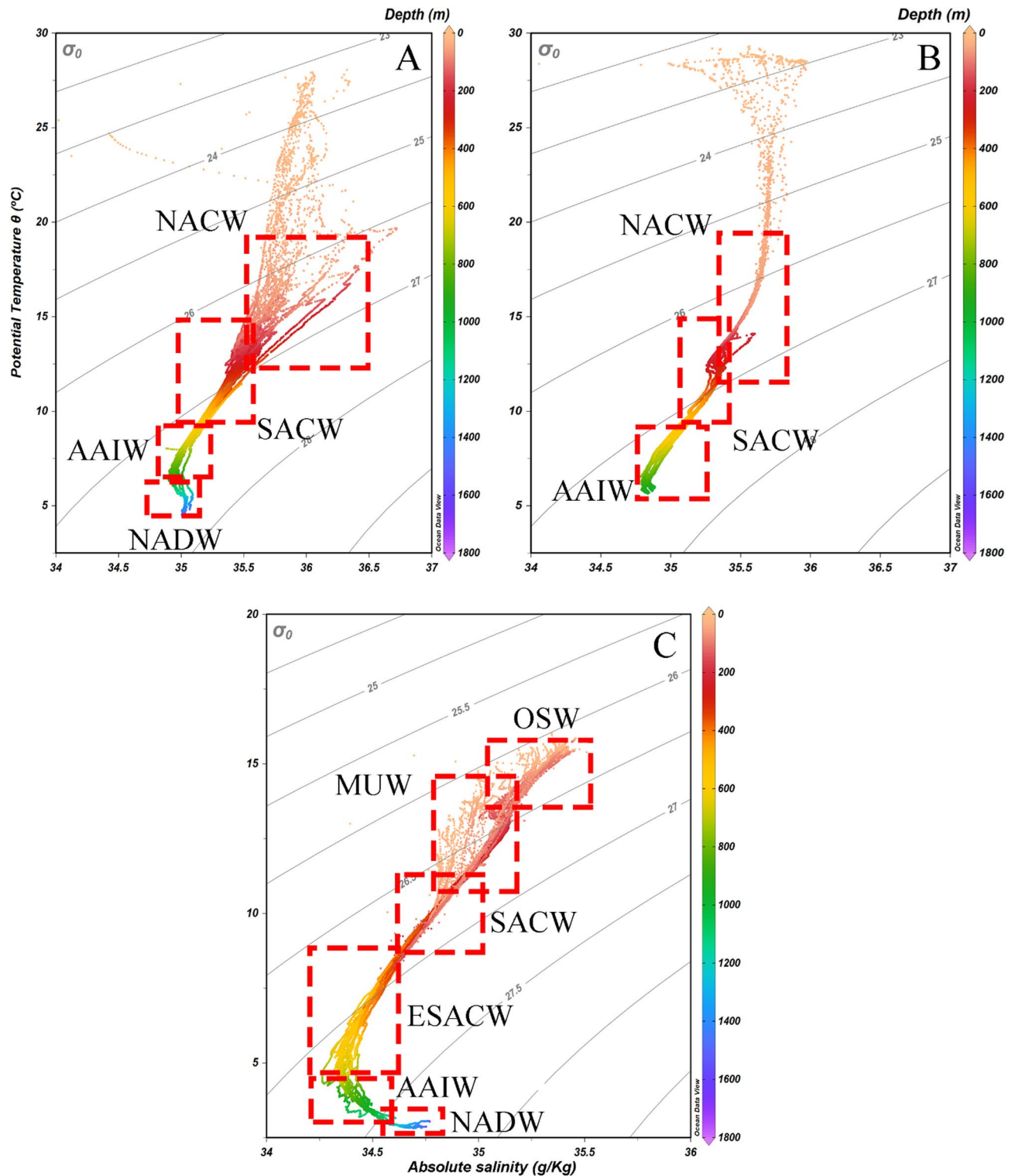


Fig. 2. Potential temperature and absolute salinity (g/kg) (TS) diagram in the Mauritanian Upwelling in (A) northern and (B) southern areas. (C) TS diagram in the Benguela Upwelling System. Density was represented in the background. Depth is represented by the colour scale. The water masses detected are represented in each figure.

$p > 0.01$, $\chi^2 = 17.58$ for biomass). However, the differences were significant for biomass and abundance ($p < 0.01$, $\chi^2: 61.397$; $p < 0.01$, $\chi^2: 43.43$) across all the stations (from MU and BUS combined).

In the MU stations, we identified 43 species belonging to 8 different families (Table 2), with Euphausiidae being the most abundant family (Fig. 6). This dominance shifted to Sergestidae southward, reaching a maximum at the

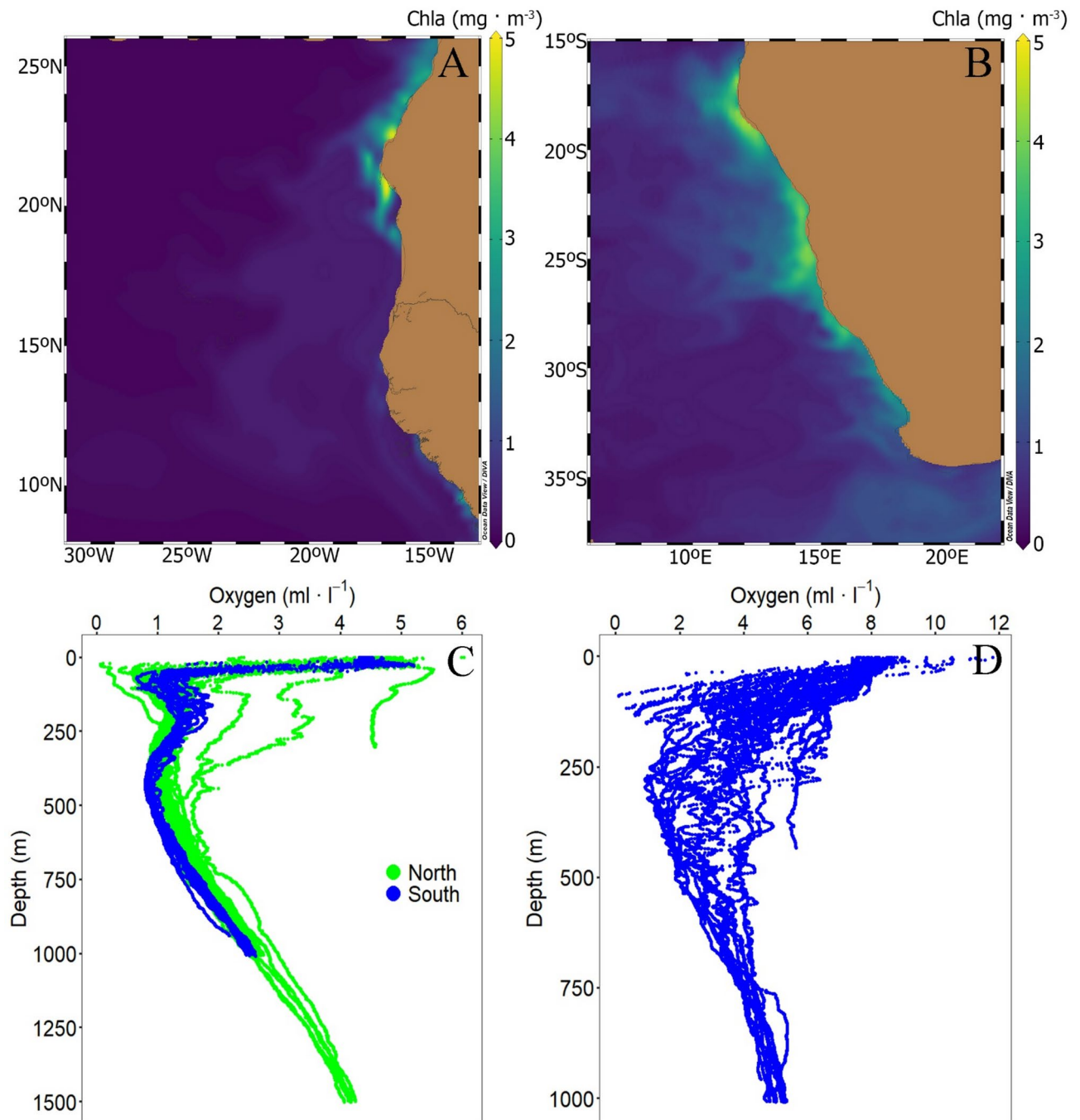


Fig. 3. Satellite data of the surface Chl-a in the Mauritanian Upwelling (MU, **A**) and the Benguela Upwelling System (BUS, **B**). Dissolved oxygen profiles (ml · l⁻¹) in the MU (**C**) and the BUS (**D**). The blue colour represents the stations from the southern area and green from the northern zone of the BUS. Chl-a data was obtained from Copernicus Marine Service (<http://marine.copernicus.eu/>).

southernmost station (St. 10–4). The higher biomass was found for the families Sergestidae and Oplophoridae, except at St. 1–5 and 5–5, where euphausiids dominated (See Supl. 2–5). Overall, euphausiids were the largest contributors to total abundance (38.29 ind. · m⁻²) and biomass (3.22 gWW · m⁻²), followed by sergestids (6.78 ind. · m⁻² and 2.26 gWW · m⁻², respectively) (Table 2). The most abundant species and the largest contributor to the total biomass was *Euphausia hanseni* (29.99 ind. · m⁻² and 2.73 gWW · m⁻²). Other species contributed less than 5% to the total abundance, except for *E. gibboides* (2.73 ind. · m⁻²) and *Robustosergia robusta* (2.68 ind. · m⁻²). In terms of biomass, *Systellaspis debilis*, *R. robusta*, and *Deosergestes pediformis* contributed over 10% each (1.79 gWW · m⁻², 0.93 gWW · m⁻², and 0.87 gWW · m⁻²).

In the BUS stations, Euphausiidae was also the dominant family in terms of abundance (11.75 ind. · m⁻²), with a high concentration of juvenile stages at Sts. sBUS-67 and sBUS-74 (Fig. 6). An exception occurred at St. sBUS-

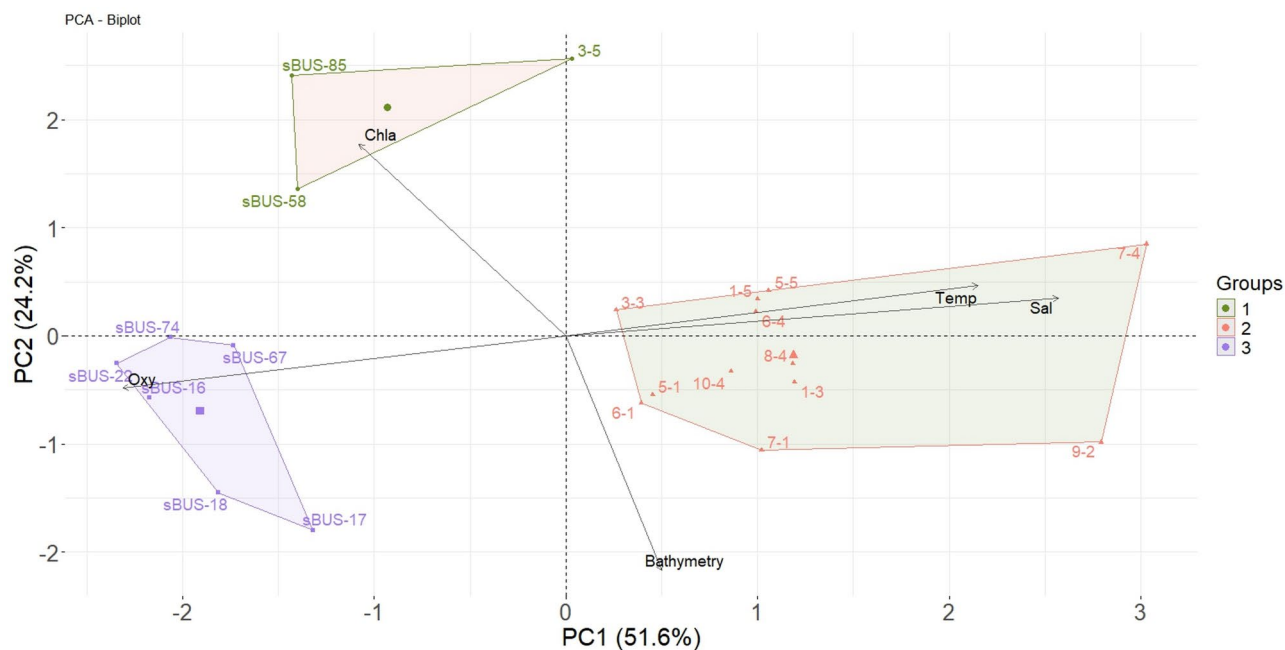


Fig. 4. Principal Component Analysis (PCA) of stations with k-means clustering forming three groups based on environmental data. Vectors corresponded to each standardized variable: temperature, salinity, oxygen, chlorophyll-a (Chla), and bathymetry. Temperature, salinity, and oxygen were averaged within the layer sampled.

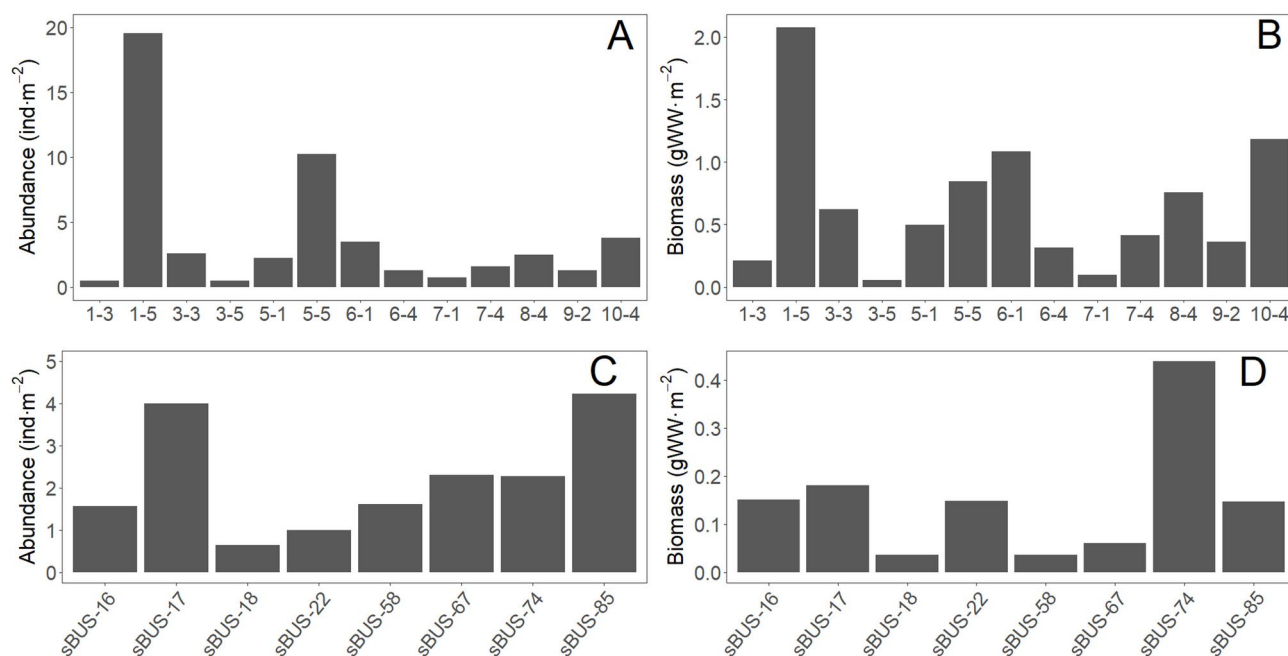


Fig. 5. Distribution of the total abundance (**A, C**) and biomass (**B, D**) of crustaceans across the Mauritanian Upwelling (top) and Benguela Upwelling System (bottom) stations. Stations are arranged from north (left) to south (right).

58 on the shelf, where Mysidae was prevalent. A total of 48 species from 9 families were identified in this region (Table 3). *Euphausia lucens* was the most abundant species (4.24 ind. $\cdot$ m⁻²), followed by juvenile stages and *Thysanoessa gregaria* (2.81 ind. $\cdot$ m⁻² and 2.62 ind. $\cdot$ m⁻², respectively). While *E. lucens* was the largest contributor to abundance at all stations, *Funchalia danae* was the primary contributor to the total biomass (0.36 gWW $\cdot$ m⁻²), only captured at St. sBUS-74.

Order/Family	Species	Abundance (ind·m ⁻²)	Rel. Abundance (%)	Biomass (gWW·m ⁻²)	Rel. Biomass (%)	Occurrence (%)
Decapoda		11.88	23.66	5.30	62.18	100
	<i>Decapod juvenile</i>	0.02	0.03	<0.01	0.04	30.8
AcanthePHYRIDAE Spence Bate, 1888		0.60	1.2	0.62	7.23	76.9
	<i>AcanthePHYRA kingsleyi</i> Spence Bate, 1888	0.34	0.67	0.34	3.65	76.9
	<i>AcanthePHYRA pelagica</i> , Risso, 1816	0.21	0.43	0.25	2.99	46.2
	<i>AcanthePHYRA purpurea</i> A. Milne-Edwards, 1881	0.03	0.06	0.01	0.17	30.8
	<i>Meningodora vesca</i> Smith, 1886	<0.01	0.01	<0.01	<0.01	7.7
	<i>Notostomus auriculatus</i> Barnard, 1950	0.01	0.02	0.01	0.07	23.1
Benthescymidae Wood-Mason & Alcock, 1891		1.97	3.93	0.49	5.71	92.3
	<i>Gennadas brevirostris</i> Bouvier, 1905	0.58	1.16	0.16	1.91	69.2
	<i>Gennadas scutatus</i> Bouvier, 1906	0.08	0.17	0.01	0.17	46.6
	<i>Gennadas sp.</i>	1.01	2.01	0.24	2.85	69.2
	<i>Gennadas talismani</i> Bouvier, 1906	0.29	0.57	0.06	0.71	46.2
	<i>Gennadas valens</i> Smith, 1884	0.01	0.02	0.01	0.08	7.7
Oplophoridae Dana, 1852		2.04	4.07	1.80	21.13	100
	<i>Oplophorus spinosus</i> Brullé, 1839	0.01	0.02	0.01	0.08	15.4
	<i>Systellaspis debilis</i> A. Milne-Edwards, 1881	2.03	4.04	1.79	21.06	100
Pandalidae Haworth, 1825		0.17	0.33	0.08	0.91	76.9
	<i>Plesionika richardi</i> Coutière, 1905	0.11	0.21	0.03	0.38	69.2
	<i>Plesionika rossignoli</i> Crosnier & Forest, 1968	0.06	0.12	0.05	0.53	38.5
Pasiphaeidae Dana, 1852		0.31	0.62	0.06	0.7	30.8
	<i>Pasiphaea semispinosa</i> Holthuis, 1951	0.31	0.62	0.06	0.7	30.8
Sergestidae Dana, 1852		6.78	13.51	2.26	26.5	100
	<i>Alloseggestes pectinatus</i> Sund, 1920	0.06	0.12	0.01	0.1	7.7
	<i>Alloseggestes sargassi</i> Ortmann, 1893	0.08	0.17	0.01	0.15	38.5
	<i>Deoseggestes corniculum</i> Krøyer, 1855	0.03	0.06	0.01	0.13	7.7
	<i>Deoseggestes henseni</i> Ortmann, 1893	0.11	0.21	0.02	0.27	46.2
	<i>Deoseggestes pediformis</i> Crosnier & Forest, 1973	2.50	4.98	0.87	10.18	84.6
	<i>Euseggestes arcticus</i> Krøyer, 1855	0.06	0.12	0.01	0.09	7.7
	<i>Gardinerosegia sp.</i>	<0.01	0.01	<0.01	0.02	7.7
	<i>Gardinerosegia splendens</i> Sund, 1920	0.10	0.2	0.03	0.33	15.4
	<i>Neoseggestes edwardsii</i> Krøyer, 1855	0.03	0.06	<0.01	0.02	15.4
	<i>Paraseggestes cylindricus</i> Vereshchaka, 2009	1.01	2.01	0.28	3.32	100
	<i>Phorcosergia grandis</i> Sund, 1920	0.01	0.01	0.01	0.12	7.7
	<i>Robustosergia extenuata</i> Burkenroad, 1940	0.04	0.08	0.06	0.76	46.2
	<i>Robustosergia robusta</i> Smith, 1882	2.68	5.34	0.93	10.88	76.9
	<i>Sergestes sp.</i>	0.01	0.01	<0.01	0.02	7.7
	<i>Sergia laminata</i> Burkenroad, 1940	0.04	0.07	0.01	0.07	15.4
	<i>Sergia sp.</i>	0.02	0.05	<0.01	0.04	15.4
Lophogastrida		0.01	0.02	<0.01	0.02	23.1
Eucopiidae G.O. Sars, 1885		0.01	0.02	<0.01	0.02	23.1
	<i>Eucopia unguiculata</i> Willemoes-Suhm, 1875	0.01	0.02	<0.01	0.02	23.1
Euphausiacea		38.29	76.3	3.22	37.77	100
Euphausiidae Dana, 1850		38.29	76.3	3.22	37.77	100
	<i>Euphausia gibboides</i> Ortmann, 1893	2.73	5.44	0.21	2.49	92.3
	<i>Euphausia henseni</i> Zimmer, 1915	29.99	59.76	2.73	32	76.9
	<i>Euphausia krohnii</i> Brandt, 1851	2.23	4.44	0.04	0.42	92.3
	<i>Nematobrachion boopis</i> Calman, 1893	0.07	0.15	0.01	0.07	15.4
	<i>Nematobrachion flexipes</i> Ortmann, 1893	0.02	0.03	<0.01	0.01	15.4
	<i>Hansarsia megalops</i> G.O. Sars, 1883	2.07	4.12	0.08	0.91	92.3
	<i>Hansarsia microps</i> G.O. Sars, 1883	0.22	0.44	0.01	0.16	53.9
	<i>Hansarsia sp.</i>	0.01	0.03	<0.01	<0.01	7.7
	<i>Stylocheiron abbreviatum</i> G.O. Sars, 1883	0.01	0.02	<0.01	<0.01	7.7
	<i>Stylocheiron elongatum</i> G.O. Sars, 1883	<0.01	0.01	<0.01	<0.01	7.7
Continued						

Order/Family	Species	Abundance (ind·m ⁻²)	Rel. Abundance (%)	Biomass (gWW·m ⁻²)	Rel. Biomass (%)	Occurrence (%)
	<i>Stylocheiron longicorne</i> G.O. Sars, 1883	0.02	0.04	< 0.01	< 0.01	30.8
	<i>Thysanopoda monacantha</i> Ortmann, 1893	0.15	0.3	0.03	0.35	84.6
	<i>Thysanopoda obtusifrons</i> G.O. Sars, 1883	0.02	0.04	< 0.01	0.03	23.1
	<i>Thysanopoda orientalis</i> Hansen, 1910	0.32	0.64	0.04	0.49	69.2
	<i>Thysanopoda tricuspidata</i> H. Milne Edwards, 1837	0.42	0.85	0.07	0.83	61.5

Table 2. Total abundance (individuals per m⁻²), relative abundance (%), total biomass (grams of wet weight per m⁻²), relative biomass (%), and occurrence (%) for each taxon in the Mauritanian Upwelling (MU).

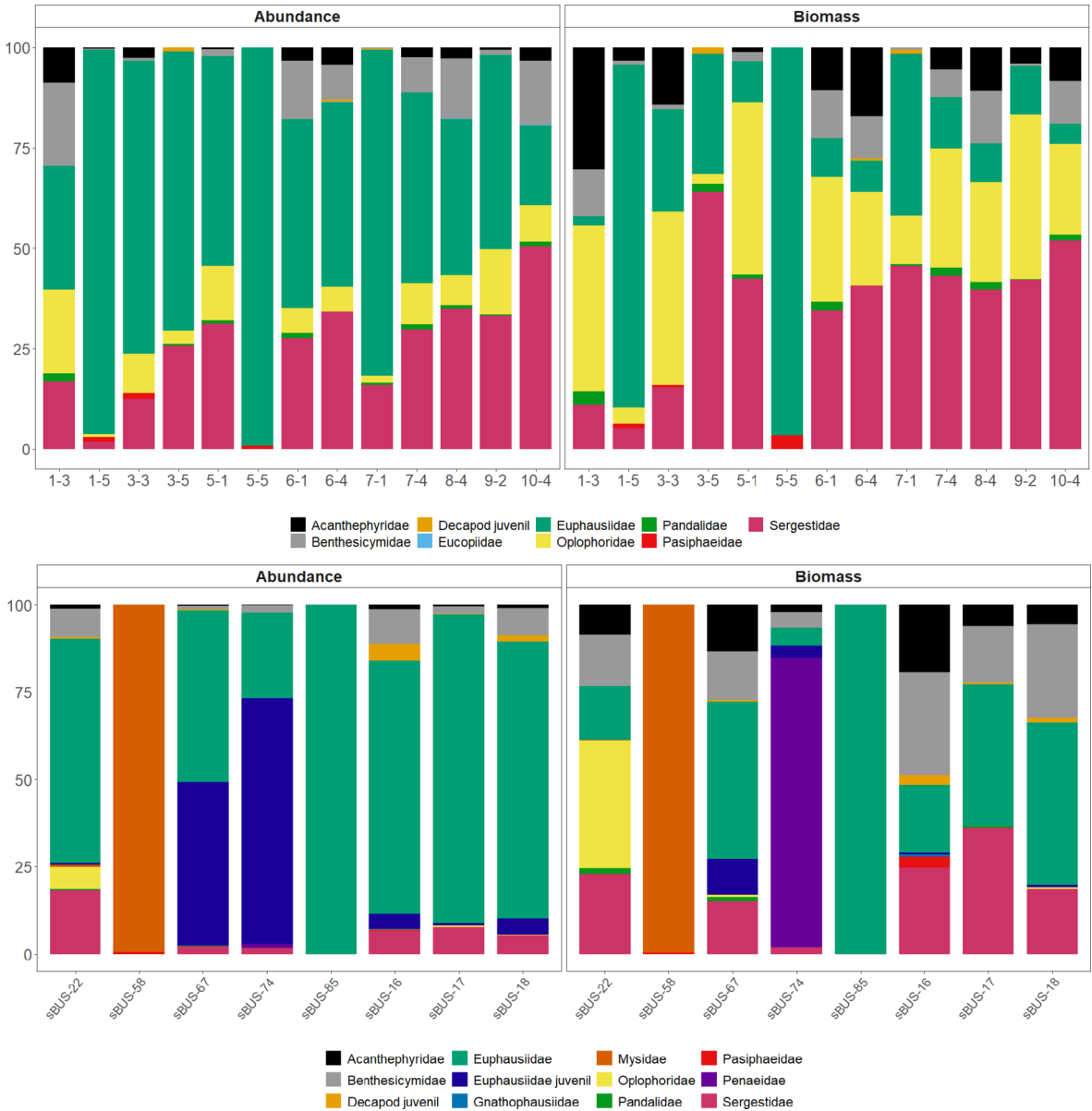


Fig. 6. Relative abundance (left) and biomass (right) of crustaceans for the different families identified in Mauritanian Upwelling (A) and Benguela Upwelling System (B). Stations are arranged from north (left) to south (right).

Order/Family	Species	Abundance (ind·m ⁻²)	Rel. Abundance (%)	Biomass (gWW·m ⁻²)	Rel. Biomass (%)	Occurrence (%)
Decapoda		1.47	8.31	0.80	66.74	87.5
	<i>Decapod juvenile</i>	0.11	0.62	0.01	0.48	62.5
Acanthephyridae Spence Bate, 1888		0.07	0.38	0.07	6.05	75
	<i>Acanthephyra purpurea</i> A. Milne-Edwards, 1881	0.07	0.38	0.07	6.05	75
Benthescymidae Wood-Mason & Alcock, 1891		0.44	2.48	0.13	11.12	75
	<i>Gennadas bouvieri</i> Kemp, 1909	< 0.01	0.01	< 0.01	0.06	50
	<i>Gennadas brevirostris</i> Bouvier, 1905	0.02	0.12	0.02	1.5	25
	<i>Gennadas gilchristi</i> Calman, 1925	0.13	0.74	0.04	3.19	62.5
	<i>Gennadas incertus</i> Balss, 1927	< 0.01	0.01	< 0.01	0.02	37.5
	<i>Gennadas parvus</i> Spence Bate, 1881	< 0.01	0.02	< 0.01	0.06	12.5
	<i>Gennadas scutatus</i> Bouvier, 1906	0.01	0.04	< 0.01	0.09	12.5
	<i>Gennadas sp.</i>	0.24	1.39	0.06	5.38	75
	<i>Gennadas tinayrei</i> Bouvier, 1906	0.01	0.07	< 0.01	0.19	25
	<i>Gennadas valens</i> Smith, 1884	0.01	0.07	0.01	0.55	50
Oplophoridae Dana, 1852		0.08	0.47	0.06	4.61	50
	<i>Systellaspis debilis</i> A. Milne-Edwards, 1881	0.08	0.47	0.06	4.61	50
Pandalidae Haworth, 1825		0.01	0.06	< 0.01	0.32	37.5
	<i>Plesionika richardi</i> Coutière, 1905	0.01	0.06	< 0.01	0.01	37.5
Pasiphaeidae Dana, 1852		0.01	0.07	0.01	0.42	25
	<i>Pasiphaea ecarina</i> Crosnier, 1969	< 0.01	0.06	< 0.01	0.32	12.5
	<i>Pasiphaea semispinosa</i> Holthuis, 1951	0.01	0.06	< 0.01	0.01	12.5
Penaeidae Rafinesque, 1815		0.03	0.16	0.36	30.37	12.5
	<i>Funchalia danae</i> Burkenroad, 1940	0.03	0.16	0.36	30.34	12.5
Sergestidae Dana, 1852		0.72	4.08	0.16	13.36	75
	<i>Allosergestes sargassi</i> Ortmann, 1893	0.04	0.22	0.01	0.55	50
	<i>Allosergestes sp.</i>	0.02	0.12	< 0.01	0.17	25
	<i>Deosergestes henseni</i> Ortmann, 1893	0.01	0.05	< 0.01	0.31	37.5
	<i>Deosergestes sp.</i>	0.04	0.23	0.01	0.74	62.5
	<i>Eusergestes antarcticus</i> Vereshchaka, 2009	0.01	0.04	< 0.01	0.13	50
	<i>Gardinerosergia kensleyi</i> Vereshchaka, 2000	0.02	0.1	0.01	0.56	12.5
	<i>Gardinerosergia splendens</i> Sund, 1920	0.10	0.55	0.03	2.44	12.5
	<i>Neosergestes sp.</i>	< 0.01	0.01	< 0.01	0.04	12.5
	<i>Parasergestes cylindricus</i> Vereshchaka, 2009	0.10	0.58	0.03	2.1	75
	<i>Parasergestes diapontius</i> Spence Bate, 1881	< 0.01	0.01	< 0.01	0.01	12.5
	<i>Phorcosergia burukovskii</i> Vereshchaka, 2000	0.01	0.08	0.02	1.29	12.5
	<i>Phorcosergia máxima</i> Burkenroad, 1940	< 0.01	0.02	< 0.01	0.35	12.5
	<i>Prehensilosergia prehensilis</i> Spence Bate, 1881	0.04	0.23	0.01	0.7	50
	<i>Robustosergia extenuata</i> Burkenroad, 1940	< 0.01	0.02	0.01	0.57	12.5
	<i>Robustosergia regalis</i> Gordon, 1939	< 0.01	0.01	0.00	0.03	12.5
	<i>Sergestes atlanticus</i> H. Milne Edwards, 1830	0.28	1.58	0.03	2.59	75
	<i>Sergestes sp.</i>	0.01	0.05	< 0.01	0.15	25
	<i>Sergia laminata</i> Burkenroad, 1940	0.03	0.14	0.01	0.46	37.5
	<i>Sergia sp.</i>	0.01	0.07	< 0.01	0.19	25
Lophogastrida		< 0.01	0.01	< 0.01	0.07	12.5
Gnathophausiidae		< 0.01	0.01	< 0.01	0.07	12.5
	<i>Neognathophausia gigas</i> Willemoes-Suhm, 1873	< 0.01	0.01	< 0.01	0.07	12.5
Mysida		1.62	9.19	0.04	3.04	12.5
Euphausiacea		11.75	66.6	0.34	28.33	87.5
Euphausiidae Dana, 1850		11.75	66.6	0.34	28.33	87.5
	<i>Euphausiidae juvenile</i>	2.81	15.9	0.02	1.89	75
	<i>Euphausia lucens</i> Hansen, 1905	4.24	24.03	0.15	12.33	25
	<i>Euphausia recurva</i> Hansen, 1905	1.71	9.71	0.03	2.81	75
	<i>Euphausia similis</i> G.O. Sars, 1883	0.94	5.33	0.04	3.25	75
	<i>Euphausia spinifera</i> G.O. Sars, 1883	0.04	0.22	< 0.01	0.16	50
Continued						

Order/Family	Species	Abundance (ind·m ⁻²)	Rel. Abundance (%)	Biomass (gWW·m ⁻²)	Rel. Biomass (%)	Occurrence (%)
	<i>Nematobrachion boopis</i> Calman, 1893	0.04	0.22	<0.01	0.25	37.5
	<i>Nematobrachion flexipes</i> Ortmann, 1893	0.45	2.56	0.02	1.26	62.5
	<i>Hansarsia gracilis</i> Hansen, 1910	<0.01	0.02	<0.01	0.01	12.5
	<i>Hansarsia megalops</i> G.O. Sars, 1883	0.22	1.27	0.01	0.52	75
	<i>Hansarsia microps</i> G.O. Sars, 1883	0.12	0.69	<0.01	0.28	50
	<i>Hansarsia tenella</i> G.O. Sars, 1883	0.01	0.04	<0.01	0.02	25
	<i>Stylocheiron abbreviatum</i> G.O. Sars, 1883	1.03	5.85	0.03	2.44	75
	<i>Stylocheiron longicorne</i> G.O. Sars, 1883	0.09	0.51	<0.01	0.12	75
	<i>Stylocheiron maximum</i> Hansen, 1908	0.07	0.38	0.01	0.51	37.5
	<i>Thysanoessa gregaria</i> G.O. Sars, 1883	2.62	14.86	0.03	2.58	25
	<i>Thysanopoda monacantha</i> Ortmann, 1893	0.01	0.06	<0.01	0.22	25
	<i>Thysanopoda obtusifrons</i> G.O. Sars, 1883	0.13	0.72	0.02	1.32	62.5
	<i>Thysanopoda orientalis</i> Hansen, 1910	0.01	0.08	<0.01	0.12	12.5
	<i>Thysanopoda tricuspidata</i> H. Milne Edwards, 1837	0.01	0.04	<0.01	0.11	25

Table 3. Total abundance (individuals per m⁻², relative abundance (%), total biomass (grams of wet weight per m⁻², relative biomass (%), and occurrence (%) for each taxon in the in southern Benguela Upwelling System (BUS).

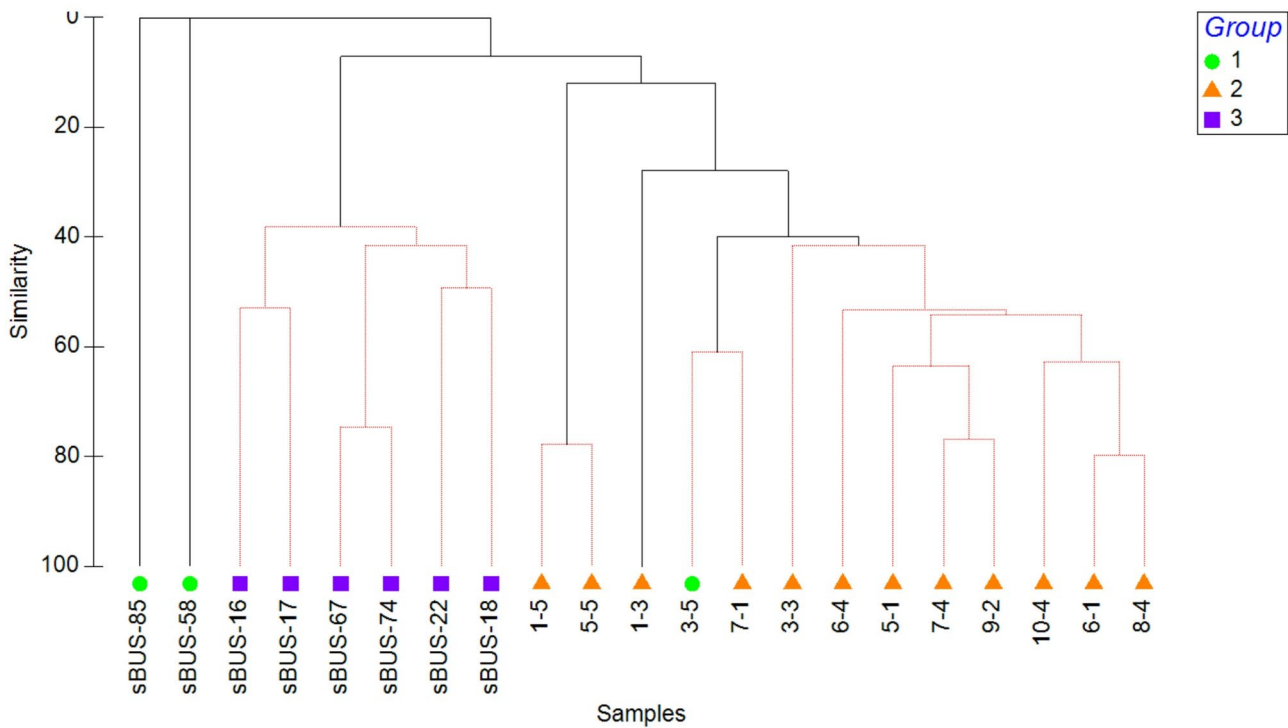


Fig. 7. Dendrogram for hierarchical clustering of station similarities (Bray Curtis) based on the abundance matrix (log(x+1) transformed). SIMPROF test showed non-significant combinations (in red), and the groups from PCA analysis are added as symbols and colours, as legend shows.

Community structure

Cluster analysis based on abundance data with log (x + 1) transformation divided the stations into two groups (Fig. 7). The PCA analysis based on environmental conditions showed two groups which were consistent with the two regions studied (MU and BUS). However, Group 1 was further split into two subgroups (sBUS-85, sBUS-58), and one station (St. 3–5) was integrated into the MU group. A PERMANOVA test revealed significant differences between these groups ($F_{(3,20)} = 5.67, p < 0.01$), though pairwise comparison showed no significant differences for Group 1 vs. Group 2 ($F_{(2,15)} = 2.61, p > 0.05$). Differences were significant for Group 2 vs. Group 3 ($F_{(2,17)} = 10.23, p < 0.05$) and Group 1 vs. Group 3 ($F_{(2,9)} = 3.60, p < 0.05$). SIMPER analysis showed the group-

Group 2 (CVFZ)				
Average similarity: 36.97				
Species	Av.Abund	Av.Sim	Contrib.%	Cum.%
<i>Hansarsia megalops</i>	0.15	5.39	14.57	14.57
<i>Euphausia krohnii</i>	0.16	5.23	14.15	28.72
<i>Euphausia gibboides</i>	0.19	5.12	13.83	42.56
<i>Systellaspis debilis</i>	0.15	5.03	13.60	56.15
<i>Deosergestes pediformis</i>	0.17	4.44	12.01	68.16
<i>Euphausia hanseni</i>	0.52	2.31	6.24	74.40
<i>Robustosergia robusta</i>	0.17	2.25	6.08	80.48
Group 3 (BCS)				
Average similarity: 43.23				
Species	Av.Abund	Av.Sim	Contrib.%	Cum.%
<i>Euphausia recurva</i>	0.24	11.16	25.82	25.76
<i>Euphausia similis</i>	0.14	8.39	19.40	45.12
<i>Stylocheiron abbreviatum</i>	0.16	7.32	16.93	62.01
<i>Euphausiidae juvenil</i>	0.30	4.34	10.05	72.03
<i>Gennadas sp.</i>	0.04	1.98	4.57	76.60

Table 4. Results of SIMPER analysis for abundance data, showing the average similarity of each group and the contribution of each species. Group 1 had zero similarities.

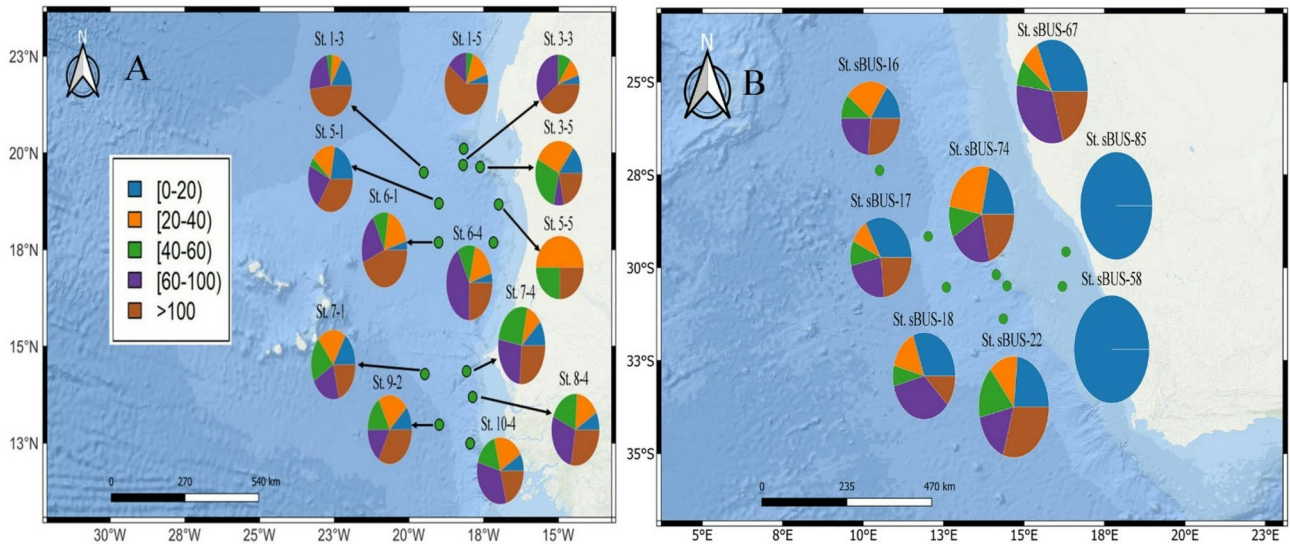


Fig. 8. Proportion of the mean area (mm²) at each station for Cape Verde Frontal Zone (A) and Benguela Upwelling System (B) sampling areas.

specific similarities and the most relevant species. Group 1 had zero within-group similarity (Table 4). Group 2 had an average similarity of 36.97%, driven primarily by *Hansarsia megalops*, *Euphausia krohnii*, *E. gibboides*, *Systellaspis debilis*, *Deosergestes pediformis*, *E. hanseni*, and *Robustosergia robusta*. Group 3 exhibited a higher similarity (43.23%), with dominant species including *E. recurva*, *E. similis*, *Stylocheiron abbreviatum*, juvenile stages of euphausiids, and *Gennadas* sp.

Size of organisms varied significantly across latitudes (χ^2 : 1743.9, p-value < 0.01), with larger individuals observed in the northern zone of the MU, diminishing in size towards the south (Fig. 8, and Supl. 1, 5, 6). PERMANOVA test confirmed significant differences in organism size between PCA-defined groups ($F_{(3,20)} = 6.75$, $p < 0.01$). All pairwise comparisons were significant (1 vs. 2: $F_{(2,15)} = 3.86$, $p < 0.05$; 2 vs. 3: $F_{(2,17)} = 12.85$, $p < 0.05$; 1 vs. 3: $F_{(2,9)} = 4.29$, $p < 0.05$). However, a Kruskal-Wallis test comparing the median of the size of each species (measured as surface body area) across stations showed no significant differences ($p > 0.05$) (see Supl. Table 1).

Influence of environmental factors on micronekton community structure

Total abundance of the micronektonic crustaceans showed a high correlation with surface temperature (0–100 m), surface and subsurface salinity (0–100, 100–200 m), and oxygen (0–100, 100–200 m) (Fig. 9). However,

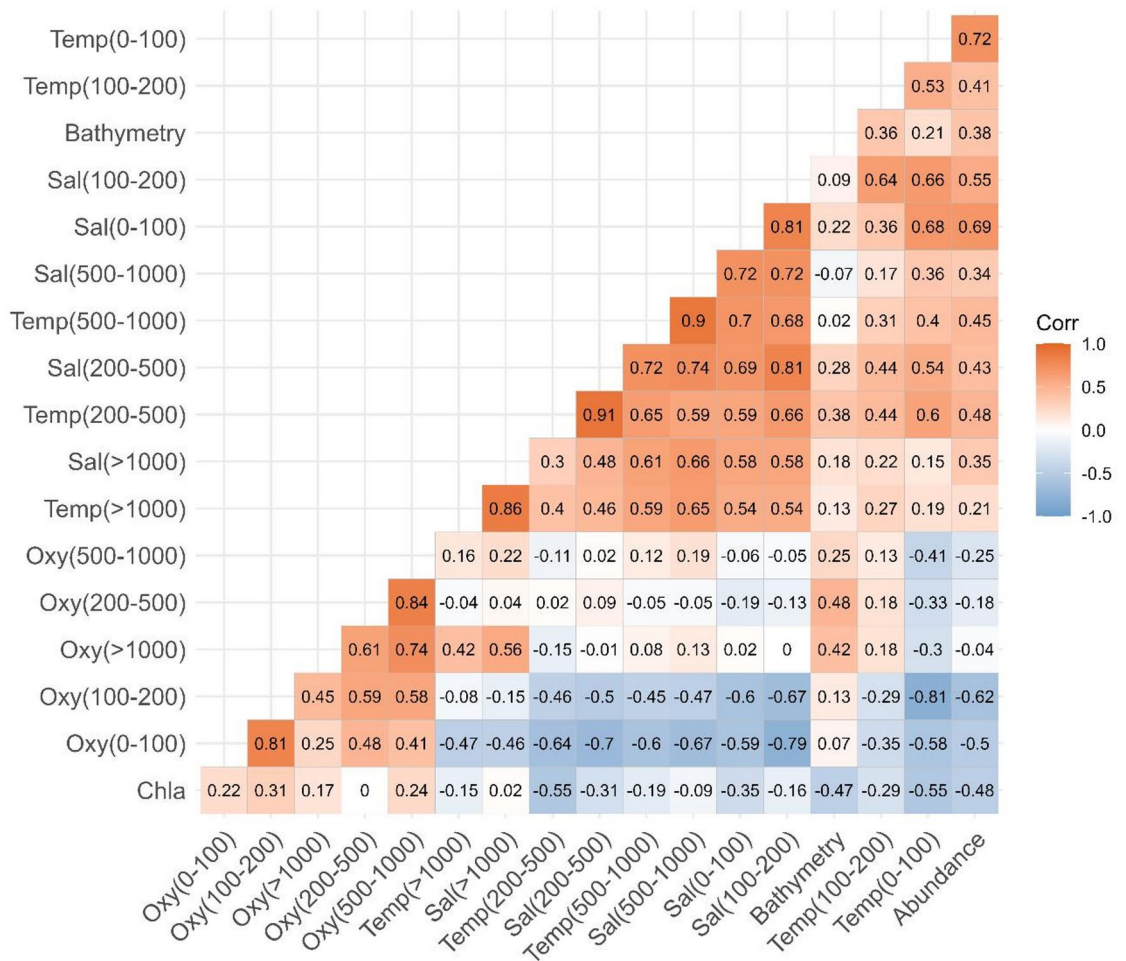


Fig. 9. Heatmap of the correlation (Spearman) between the environmental variables at different depth layer and the total abundance. Red and blue values stand for positive and negative correlation, respectively.

the Redundancy Analysis showed with VIF criteria ($VIF < 5$) that the environmental drivers explaining most of the total abundance were the temperature (0–100 m) and subsurface oxygen (100–200 m) (Fig. 10). The model explained 12.03% of the total adjusted variance, showing a marginally significant trend ($p = 0.057$). The first axis (RDA1: 60.8%) was strongly associated with the subsurface oxygen gradient, effectively separating stations from the Benguela Upwelling System (BUS) from the Mauritanian Upwelling (MU). The second axis (RDA2: 39.2%) was primarily driven by surface temperature, reflecting the thermal stratification differences between the sampled regions.

Discussion

In the present study, we described the community composition of micronektonic crustaceans in the Mauritanian Upwelling (MU) and in the southern Benguela Upwelling System (BUS), highlighting the significant influence of environmental factors in the species distribution. As expected, different water mass characteristics were observed between MU and BUS. In the MU, salinity and temperature were higher, with NACW and SACW shaping the community structure as previously observed by Tiedemann et al.⁷⁸. By contrast, the BUS was characterized by well-oxygenated waters from the Lüderitz upwelling cell⁴⁰ and a large and highly productive area with higher Chl-a levels. However, shallower stations located on the continental shelf with high Chl-a levels in both regions did not show evident environmental differences due to the strong upwelling signature.

Both sampling areas, MU and BUS, are highly influenced by seasonality^{27,40} and, consequently, the abundance and biomass data presented in this study is a snapshot for the respective seasons. In the MU, during the cold season (winter and spring), Trade Winds are displaced southward, enhancing productivity in this region. Conversely, during the warm season, this displacement ceases, and the highest primary production is concentrated in the permanent upwelling area^{23,27}. This pattern aligns with our findings, where the highest abundance and biomass values were observed in the northern area of the MU (Sts 1–5 and 5–5), while the southern zone exhibited the lowest values. In the BUS, the stations were located south of the Lüderitz upwelling cell, a region influenced by mesoscale oceanographic structures such as eddies from Agulhas current, and local-scale processes including strong coastal winds, Ekman transport, and the northward Benguela jet⁷⁹. It is known that during the active upwelling season (spring), although community assemblages remain stable, community

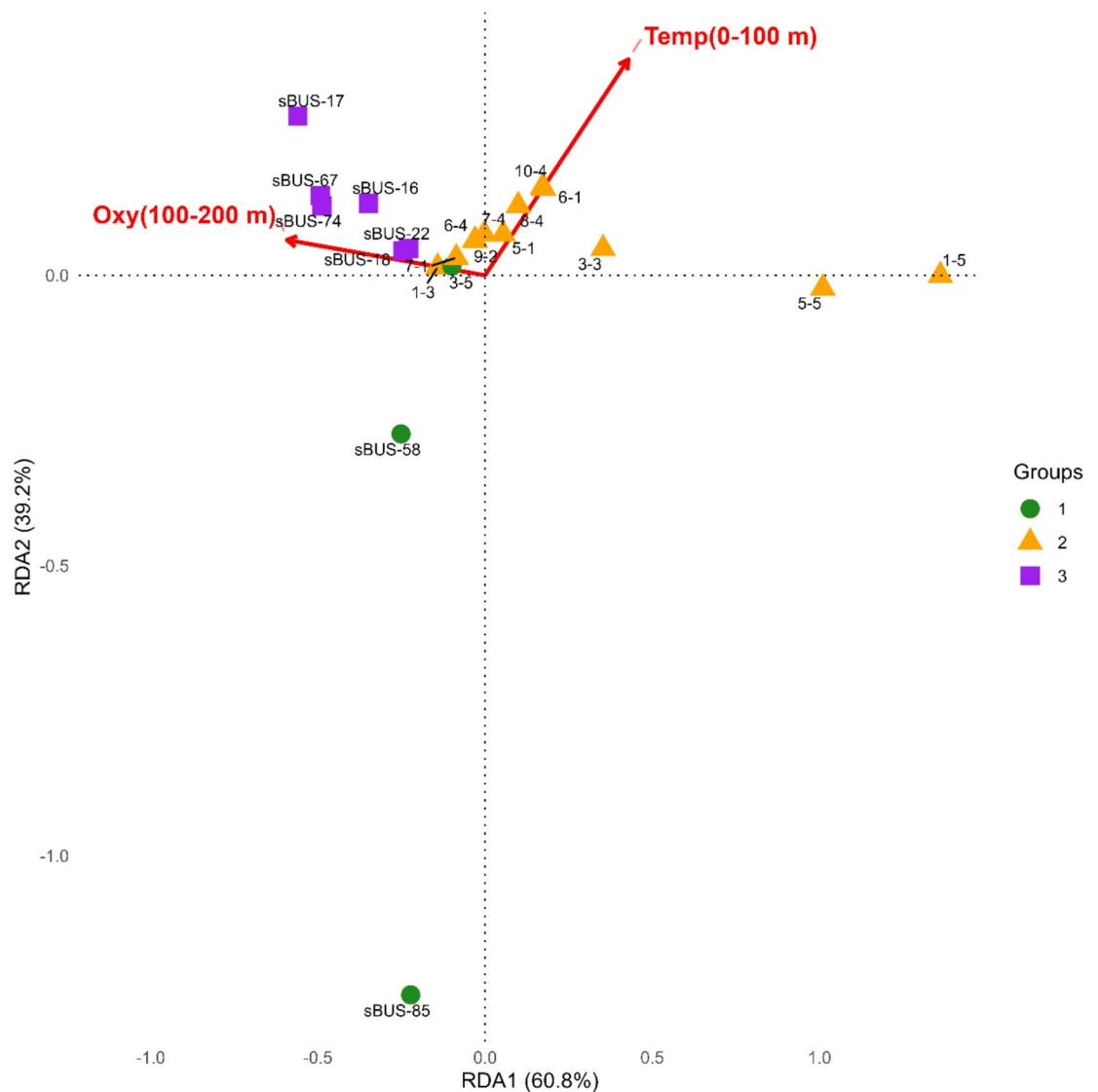


Fig. 10. Redundancy analysis (RDA) biplot showing the influence of environmental factors on the micronektonic crustaceans' abundance in the MU and BUS. Symbols represent sampling stations, color-coded and shaped according to the three main faunal clusters identified by hierarchical clustering (Group 1: green circles; Group 2: orange triangles; Group 3: purple squares). Red vectors indicate environmental drivers: surface temperature (Temp 0–100) and subsurface dissolved oxygen (Oxy 100–200). Vector length and direction reflect the strength and correlation of each variable with the ordination axes. The model was significant (ANOVA, $p = 0.057$), explaining 12.03% of the total adjusted variance.

diversity decreases⁵⁰. Our samples from this zone were collected during September, representing the community for a high-productivity scenario. Although high-nutrient areas typically favour larger phytoplankton and shorter trophic chains that efficiently transfer energy to higher levels^{80,81}, the high prevalence of small crustaceans observed in our BUS samples may reflect a transient seasonal response. Smaller components of the pelagic food web, including larvae, often have shorter generation times and could rapidly increase in abundance following algal blooms. Therefore, the disparity in size structure between the two systems likely results from the timing of our sampling, capturing a temporary pulse of smaller organisms responding to the active upwelling season in the BUS.

In the BUS, we also observed a high abundance of individuals within the 0–20 mm² body area range, while other size ranges were less abundant compared to those from MU, where the > 100 mm² range was the most abundant. Additionally, in the BUS, the smallest taxa, including juvenile and adult stages of euphausiids were found predominantly in sBUS-85, sBUS-58, sBUS-74, and sBUS-67. These stations coincided with shallower bathymetry in our sampling area. The presence of small prey organisms combined with the favourable environmental conditions near the coast, creates suitable nursery zones for commercially important fish species⁸². Notably, a study by Verheye et al.⁸³ highlighted a decline in the size of various zooplankton taxa, including euphausiids, attributed to the intensification of upwelling processes driven by global warming. In the

MU, as described in Sect. 3.2, there was a transition from euphausiids to sergestids moving from north to south. Sergestids, Benthescymidae, and caridean families identified in the MU feed on various crustacean groups, mainly copepods, ostracods, and euphausiids^{13,14,84,85}, although larger species also consume fish⁸⁶. Euphausiids are omnivorous and, in some areas, act as major zooplankton predators¹⁹. This observed succession of families likely reflects the convergence of their feeding strategies. In the northern MU, which is the most productive zone, euphausiid populations can grow rapidly, whereas in the south, larger predatory families dominate, limiting euphausiid populations through predation and competition for food. Thus, community structure in the MU appears to be influenced not only by physical processes but also by biological interactions. Similarly, Romagnan et al.⁸⁷ reported that both physical and biological drivers, including top-down control, shape zooplankton communities in the Northwestern Mediterranean Sea.

Abundance and biomass of micronektonic crustaceans were obtained using a RMT8 net in the two upwelling areas. The net was fitted with a mesh size ranging from 4.5 mm to 1 mm in the cod end, suitable for capturing epipelagic and mesopelagic species^{61,62}. However, it is important to note that all hauls in the MU and in sBUS-18 were conducted during daylight hours. Capturability of the identified taxa may be reduced due to the avoidance of organisms due to the visibility of the net⁸⁸. In addition, since most of the sampled organisms exhibit diel vertical migrations, part of this community could have been missed due to net avoidance. Furthermore, the smallest euphausiids could pass through the 4.5 mm mesh size of the net. Despite these limitations, we identified 43 different species in the MU, including 27 Decapoda, and 1 Lophogastrida. Judkins⁸⁹ reported 34 species in the MU, sampling a larger number of stations and deeper layers, which accounted for the detection of deep mesopelagic and bathypelagic species such as *Acanthephyra acanthitelsonis* and *Ephyrina ombango*⁹⁰. In the BUS, we identified the same number of species of Decapoda and Lophogastrida as in the MU but we found a higher number of species (48 species), mainly due to the presence of a higher number of euphausiid species. Acanthephyridae species were rather abundant in most samples as observed in previous studies about mesopelagic crustaceans^{7,53}. However, we found a remarkable diversity of Benthescymidae species in the BUS, with nine species of *Gennadas* identified. Kensley⁵¹ reported eight species of *Gennadas* in the same region, differing in two species, *Gennadas clavicornis* and *Gennadas brevis*, out of a total of 11 species documented in the southern African waters⁵¹. Sergestidae emerged as the most diverse family of Decapoda in both regions, with 13 and 14 species in the MU and the BUS, respectively. This high number of species could be attributed to their different adaptations to the pelagic environment, such as photophores for countershading and communication⁹¹, as well as specialized structures for predation and evasion⁹². These findings underscore the complex ecological roles and evolutionary adaptations of micronektonic crustaceans in these upwelling ecosystems⁹³.

Despite the higher number of stations sampled in the MU, the BUS exhibited higher diversity among euphausiids, with 6 genera and 19 different species, compared to 5 genera and 14 species in the MU. These results align with previous studies as Andersen et al.⁹⁴ reported the same number of euphausiid species in the MU, suggesting a correlation between lower diversity and higher productivity characteristic of the area. Conversely, in the BUS, Barange et al.⁴⁷ documented 21 species of euphausiids. This disparity in the number of species highlights how the complex interplay of physical processes in the BUS fosters environmental heterogeneity and higher diversity⁴⁸. An example of such ecological complexity is the frontal zone located at the shelf break in the southern area of the Benguela system. This front acts as a biogeographical boundary, segregating populations of *Euphausia recurva* and *E. lucens*, with the former recorded in oceanic waters and the latter closer to the coast⁹⁵. In our study, juvenile euphausiids were densely concentrated in sBUS-67 and sBUS-74, and it is plausible that these individuals belonged to *E. recurva*. The higher diversity observed may also result from species transported by the high mesoscale activity in these areas. For instance, Duncan et al.⁶² reported the incursion of mesopelagic fishes into the BUS due to seasonal jets, as previously described by Hulley and Lutjeharms⁹⁶. A similar phenomenon was observed in this study with *Thysanopoda tricuspidata*, which is a tropical euphausiid species typically found between 20°N and 20°S⁶⁵, but recorded in the BUS sampling area, likely transported by Agulhas rings (sBUS-17, sBUS-18, Supl. 2–5). Similarly, in the Gulf stream, tropical species such as *Neosergestes edwardsii* and *Gennadas scutatus* were observed moving northward into temperate and subarctic waters, while subpolar species such as *Eusergestes arcticus* migrated equatorward^{89,97}. These shifts in distribution underscores the role of ocean currents and mesoscale features in shaping community composition and increasing regional biodiversity in upwelling systems.

Conclusion

Our study highlights the strong influence of oceanographic conditions on the community structure of micronektonic crustaceans in the MU and BUS. The contrasting productivity levels and environmental heterogeneity between these systems contributed to differences in species composition, size distribution, and diversity patterns. While the MU supported larger organisms associated with lower productivity, the BUS exhibited higher euphausiid diversity, likely driven by mesoscale processes and seasonal dynamics. These findings provide valuable insights into the ecological complexity of upwelling systems and their role in structuring pelagic communities.

Data availability

Data will be available under request.

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Author contributions

JDP contributed to write the original draft, formal analysis, data curation, reviewing and editing. SHL and JML contributed to conceptualization, supervision, reviewing and editing. HF, SD, and TD contributed to reviewing and editing.

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Declarations

Conflict of interest

All co-authors declare no financial interests or personal relationships which may be considered.

Ethical approval

This study relies on the analysis of zooplankton and micronekton samples (crustaceans). No specific ethical approval or animal care protocol was required for this research in accordance with the local legislation and institutional guidelines.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-026-47770-6>.

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