Marine Biology (2024) 171:99
https://doi.org/10.1007/s00227-024-04418-1

ORIGINAL PAPER

The zoogeographic regionalization for cephalopoda linked to the canary current upwelling system

Amanda Luna[1] · **Ana Ramos**[1] · **Francisco Rocha**[1]

Received: 28 December 2022 / Accepted: 19 February 2024 / Published online: 24 March 2024

Abstract

Quantitative data on cephalopods collected in ten multidisciplinary surveys (20–2000 m) between 2004 and 2012, together with original oceanographic and satellite data, were analyzed using multivariate techniques. Statistical analyses were based on presence–absence matrices by species and hydrological variable indices. The results show that cephalopods are distributed in two main zoogeographical groups separated by latitude: "Temperate water" and "Tropical water" clusters. They extended by temperate and tropical regions, separated by a geographical boundary, Cape Blanc, particularly strong in the case of coastal species between these groups. For the total fauna, we have identified a third particular cephalopods' cluster, the "Upwelling" cluster (22°–17°N), characterized by a higher diversity and dominance of oceanic cephalopods. This is proposed as a new zoogeographical region that would coincide with the area of greatest productivity, intensity and permanence throughout the year of the canary current upwelling, confined between the north of Cape Blanc and the south of Mauritania. The results confirm the strong relationship between the three zoogeographical regions (temperate, tropical, and upwelling) and certain water bodies that characterize the regional hydrology. This paper deepens into the zoogeography of the cephalopods from Northwest Africa (Central-Eastern Atlantic), providing a new, more detailed insight into the region and its boundaries in relation to the oceanography.

Keywords Cephalopoda · Oceanography · Zoogeographical boundaries · CCLME · Northwest Africa · Central-Eastern Atlantic

Introduction

The distribution of marine species is globally associated with regions and provinces separated by geographical barriers, linked to the geomorphology of the seabed and water masses, and in turn strongly influenced by the regional evolutionary history, patterns of dispersal and isolation (Ekman 1953; Briggs 1974, 1995; Spalding et al. 2007; Costello et al. 2017). It also involves gradual gradients, finding large areas where organisms have variable tolerances to different physical properties of water bodies. As a result, the precise biogeographic boundaries of marine species are much more difficult to define and less well known than those of terrestrial species (Cox and Moore 2000). As a consequence, several approaches to global marine biogeographic classification have been proposed (Spalding et al. 2007, 2012; Briggs and Bowen 2012; Sutton et al. 2017).

Following the pioneering works in marine zoogeography (Ekman 1953; Hedgpeth 1957; Briggs 1974), subsequent authors have identified marine biogeographic regions and their respective limits worldwide (Briggs 1995; Longhurst 1998; Spalding et al. 2007, 2012; Briggs and Bowen 2012). These were based on different criteria, such as zoogeographic characteristics, climatic zones, levels of endemism, expert knowledge, or environmental barriers. However, due to incomplete knowledge of the distributions of most marine taxa, these classifications were based exclusively on certain species groups, primarily fishes (Domanevsky 1980). Thus, biogeographical regions may vary depending on the studied zoological group and environment (Griffiths et al. 2009). As consequence, it is considered that the fauna found in coastal and shelf areas biogeographically differs from that found

---

Responsible Editor: R. Rosa.

✉ Amanda Luna
amluna@uvigo.gal

[1] Departamento de Ecología y Biología Animal, Centro de Investigación Mariña, Universidade de Vigo, 36310 Vigo, Spain

in adjacent oceanic waters and deep-sea benthic habitats (Ekman 1953; Hedgpeth 1957; Briggs 1974; Spalding et al. 2007, 2012; Watling et al. 2013). For instance, in the case of cephalopod biogeography, Nesis (1982) discussed the general principles of faunistic and zoogeographical zoning of the shelf-bottom species, although this work had a limited scope. Other more relevant articles by this Russian author were crucial to the zoogeography of the group (Nesis 1987, 2001, 2003). Furthermore, Burukovsky (1998) conducted a significant zoogeographic study of the northwest African region, analyzing the distribution of 250 shrimp species.

In recent decades, the necessity of using biogeographic regionalization for resource assessment, biodiversity management, and marine conservation planning has highlighted the absence of a suitable global classification of marine kingdoms. Consequently, several essays have integrated current global and regional knowledge, as well as new scientific findings, such as phylogeny, to modify, redefine, and describe new world biogeographic classifications. Multivariate methods using quantitative data have recently been employed for marine regionalization (Kulbicki et al. 2013; Freitas et al. 2019; Caballero-Herrera et al. 2021). However, most reviews still analyze the biogeography of pelagic, benthic, and deep-water habitats separately (Spalding et al. 2007, 2012; Watling et al. 2013). Only Costello et al. (2017) have produced the first global map of marine biogeography, including coastal, deep-sea, pelagic, and benthic environments, across all marine taxa.

Cephalopods comprise nearly 860 species (Hoving et al. 2014; Sales et al. 2019; Fernández-Álvarez et al. 2020, 2021Santos et al. 2022) and inhabit all marine environments. Among them, benthic coastal cephalopods are one of the most well-known benthic taxa due to their commercial significance (Arkhipkin and Laptikhovsky 2006; Rocha et al. 2017). Nevertheless, achieving biogeographic regionalization for this class is challenging due to the diverse habitats its species inhabit, including neritic, oceanic, pelagic and bottom-dependent, coastal shelf, and deep-sea waters (Nesis 1982, 2003). Studying their distribution is a challenge because the species in each of these marine habitats have substantially different worldwide distribution patterns, and the ecology and biology of the species remain unknown.

The northwest coast of Africa is part of the Canary Current Large Marine Ecosystem (CCLME), which is one of the four main Eastern Boundary Upwelling ecosystems. The CCLME hosts high productivity and important fishery resources (Valdés and Déniz-González 2015). Large Marine Ecosystems usually consists of more than one biogeographic province, representing transitional zones where species from different affinities converge. The study area of our research is the CCLME, which extends from the Strait of Gibraltar to Sierra Leone border (36°–8° N), and includes the exclusive economic zones (EEZ) of seven countries (Valdés and Déniz-González 2015).

The CCLME covers both warm-temperate and tropical zones, and is an area where temperate and tropical species meet. It has been classified into different realms, provinces and ecoregions according to current worldwide classifications (Ekman 1953; Briggs 1974, 1995; Longhurst 1998; Spalding et al. 2007, 2012; Briggs and Bowen 2012). CCLME marine fauna has been included in the Lusitanian Province (Mediterranean–Atlantic Region) by Briggs (1974, 1995), in the Canary and Guinea Currents Coastal Provinces by Longhurst (1998), or in the Lusitanian and Tropical Eastern Atlantic Provinces by Briggs and Bowen (2012).

The CCLME region has been positioned in different biogeographical demarcations, but is considered one unique pelagic unit—the Canary Current Province, included in the Atlantic Warm Water Realm—by Spalding et al. (2012). However, based on the classification of the coastal and shelf areas by Spalding et al. (2007), the benthic and neritic fauna of northwest Africa could be separated by a strong geographically frontier located in Cape Blanc (approx. 21°N). This latitude would constitute the boundary between the Temperate Northern Atlantic Realm (TNAR) and the Tropical Atlantic Realm (TAR), including their respective provinces and ecoregions—Lusitanian and West African Transition provinces, and Saharan and Sahelian Upwelling ecoregions.

Although Costello et al. (2017) analyzed the distribution of 65,000 marine pelagic and benthic species in all oceans available in the ocean biogeographic information system (OBIS), the records about Canary Current cephalopods documented in this database are very few (316 records, 35 species). However, the biodiversity and distribution of cephalopod in the study area can currently be considered relatively well known, thanks to recent work (Arkhipkin and Laptikhovsky 2006; Rocha and Cheikh 2015; Rocha et al. 2017; Luna et al. 2021—Supplementary material - Table S2). Rocha and Cheikh (2015) and Rocha et al. (2017) established the bathymetric distribution, biodiversity, ecology and fisheries of cephalopods from the CCLME and Mauritanian waters, respectively. Arkhipkin and Laptikhovsky (2006) and Rocha et al. (2017) pointed out that, at the faunistic level, the CCLME region represents a transitional area where tropical, subtropical, and boreal cephalopod species mix, probably associated with bodies of water with specific characteristics, as seen in other works (Bein et al. 2023).

However, the existence of biogeographical boundaries for cephalopods in the CCLME region was still unresolved because no specific analysis focused exclusively on this class had been conducted. The only currently available information on the possible separation of the temperate and tropical cephalopod fauna in Northwest Africa is contained in the worldwide classification of Nesis (1982, 2003). This author established a unique boundary for both oceanic–pelagic and shelf-neritic species, along the Northwest African continental margin, which would also coincide with Cape Blanc. To the north and south of this latitude, the nektonic cephalopods of the shelf would be included in the Mauritanian and Guinean provinces, while the oceanic species would spread from west to east across the Atlantic, separated in the North Subtropical and Tropical zones (Nesis 2003).

This work takes advantage of the huge number of cephalopods and data collected using a consistent sampling methodology and accurate taxonomic analysis. Through multivariate analysis, it provides, the first global overview of cephalopod distribution and biogeography, with a, focus on the entire CCLME region. The study establishes the boundaries and zoogeographic patterns of cephalopods in relation to oceanographic parameters.

Materials and methods

Our faunistic and oceanographic data were collected during ten bottom-trawling surveys between 2004 and 2012, comprising 1298 trawl stations. We have updated this data with the latest available bibliography information (Rocha and Cheikh 2015; Rocha et al. 2017; Luna et al. 2021—Supplementary material - Table S2) and satellite data. During surveys along the northwest African coast, cephalopod specimens and data were collected on board Spanish and Norwegian research vessels (*Vizconde de Eza* and *Dr Fridtjof Nansen*). The sampling covered the shelf and continental slope (from 20 to 2000 m in depth) in the region spreading between the Strait of Gibraltar and the northern border of Sierra Leone (36°–8°N) (see Fig. 1). To simplify the statistical analysis, we grouped the species into two categories based on the specifics of the studied material: coastal and slope (Arkhipkin and Laptikhovsky 2006; Ibáñez et al. 2009). Coastal species are those that mainly live near the

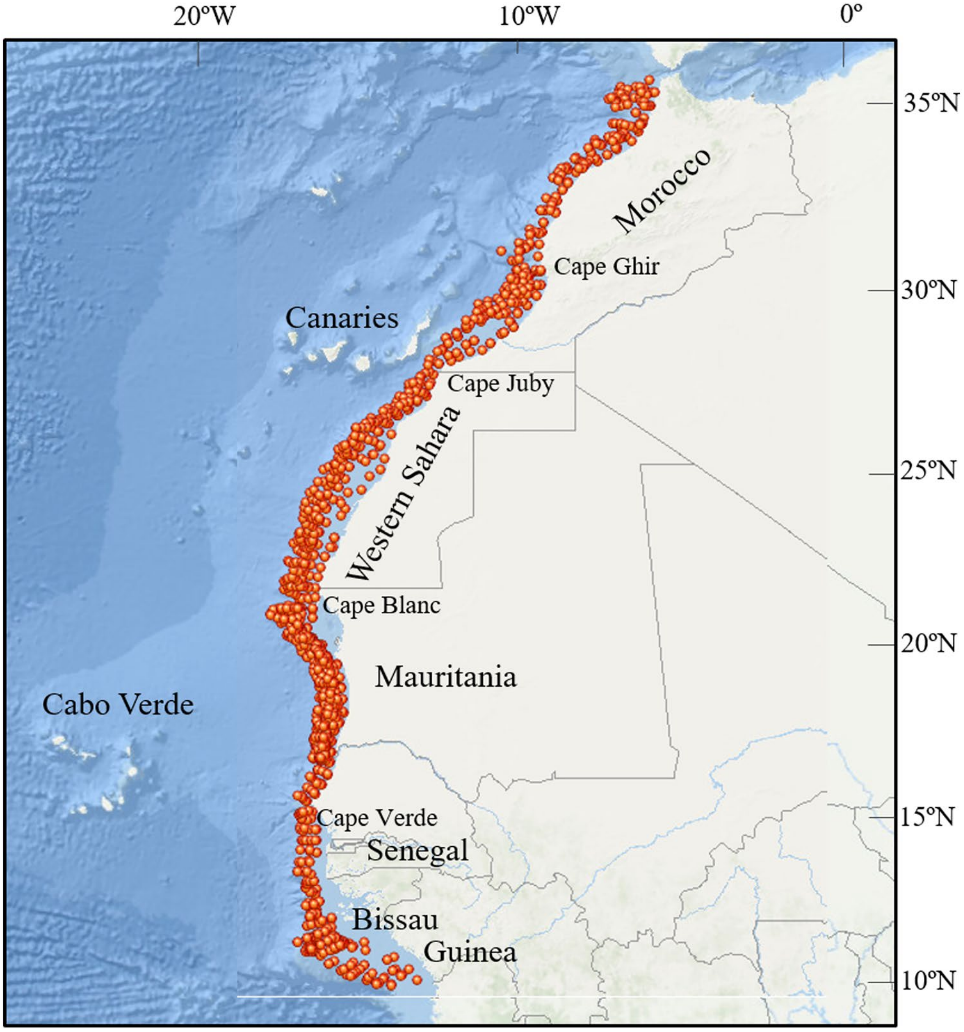


Fig. 1 Location of the stations from which the cephalopods were collected during the ten surveys conducted along the shelf and continental slope of Northwest Africa

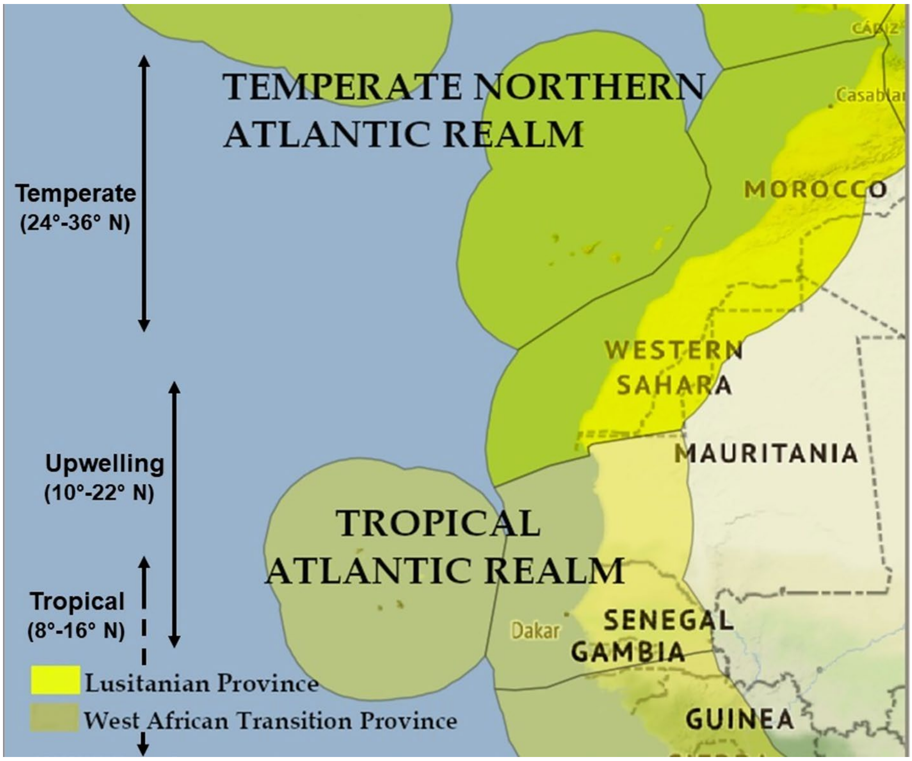
coast, on the shelf and upper slope. This category includes benthic, slope-shelf, and neritic–pelagic cephalopods associated with bottom or shelf waters. Slope species include those associated with the slope, such as deep-sea and nerito-oceanic species, and pelagic–oceanic species. It is the case of a typical representative of the nerito-oceanic eco-group *Todarodes sagittatus* (Lamarck, 1798), whose population living off the coast of Northwest Africa may occasionally stay close to the coast (Nigmatullin et al. 2002). Pelagic–oceanic species are attached to the slope category because they are collected by bottom-trawling gears. It is known as, during trawl operations, oceanic cephalopod specimens come across accidentally and, mainly, when lifting the trawl, as it climbs openly, not adequately sampling these species.

For this study, we used only the identified cephalopod species. We eliminated any for which there was doubt about correct taxonomic classification, rare species, and taxa not identified to species level. Our basis was the matrix of occurrence of 82 original species (33 coastal and 49 from the slope) taken during ten surveys.

To investigate the potential existence of biogeographic regions and boundaries in the distribution of cephalopods along the CCLME (Fig. 2), we utilized various multivariate techniques. Initially, we constructed similarity matrices by applying the Sørensen-Dice index to the presence–absence data for each species within two latitudinal degrees (between 36° and 8° N). Hierarchical agglomerative clustering and non-metric multi-dimensional scaling (nMDS) methods were used to analyze the similarity matrices. First, the analysis was performance on the total dataset, followed by the coastal species subset. The agglomerative clustering analysis employed various algorithms, with the group average (unweighted pair group method with arithmetic mean UPGMA; Clarke and Gorley 2015) being chosen due its higher cophenetic correlation.

In order to verify the possible link of the identified biogeographical communities with specific water masses that could be determining factors in the location of the faunal breaks and the corresponding biogeographical boundaries, we created a matrix of main variables characterizing the regional hydrology within one latitudinal degree. We then applied principal component analysis (PCA). During the surveys, measurements of temperature (°C), salinity (psu), and oxygen (ml L^{-1}) in the sea bottom were obtained using CDT and net-sensors. Besides, we assessed various physical and biological indexes based on latitude, including sea-surface temperature, chlorophyll a concentration (mg m^{-3}), primary production (organic carbon for all types of phytoplankton, mol m^{-2} s^{-1}), and wind stress (N m^{-2}). These assessments were made using integrated satellite data series maps available on the NOAA Climate Change Web Portal (https://psl.noaa.gov/ipcc/ocn/ccwp.html) for the entire year. Oxygen indexes (O) were estimated from a vertical Sect. (0–800 m depth) of a north–south profile taken along the northwest African coast from 34°N to 10°N (Pelegrí and Peña-Izquierdo

Fig. 2 Delimitation of the zoo-biogeographical zones found in our work for the cephalopods of the CCLME



2015). Latitude was included as one variable. To account for the different units of the variables, we used the correlation method for our PCA instead of the covariance method.

An analysis of similarity test (unordered ANOSIM) was used using a one-way layout and 999 permutations. The test was applied to the occurrence resemblance matrix and normalized hydrological factors to determine the statistical significance of the cephalopod groupings' separation, the strength of biogeographical boundaries, and its possible relation with the water masses occurring along northwest Africa. The analyses were performed using the PRIMER v7 (Clarke and Gorley 2015) and XLSTAT (Addinsoft 2022) software.

Results

Globally, the cephalopods fauna from Northwest Africa is composed by 100 oceanic (75.2%) and 33 coastal species (24.8%). The majority of the oceanic species have Atlantic (48.1%), cosmopolitan (21.8%), amphiatlantic (11.3%), or circumglobal affinities. In contrast, the coastal species are almost exclusively of Atlantic affinity (88.0%), with a minor component of amphiatlantic species (12.0%) (Table S1).

The multivariate analysis results show a separation in three clearly differentiated groups at almost the 60% of similarity level (red lines in the dendrogram in Fig. 3a). The cophenetic correlation coefficient is high ($\rho = 0.93044$) and statistically significant ($p < 0.001$). The first cluster comprises the northernmost latitude in the temperate region, which extends from the Gibraltar Strait to the north

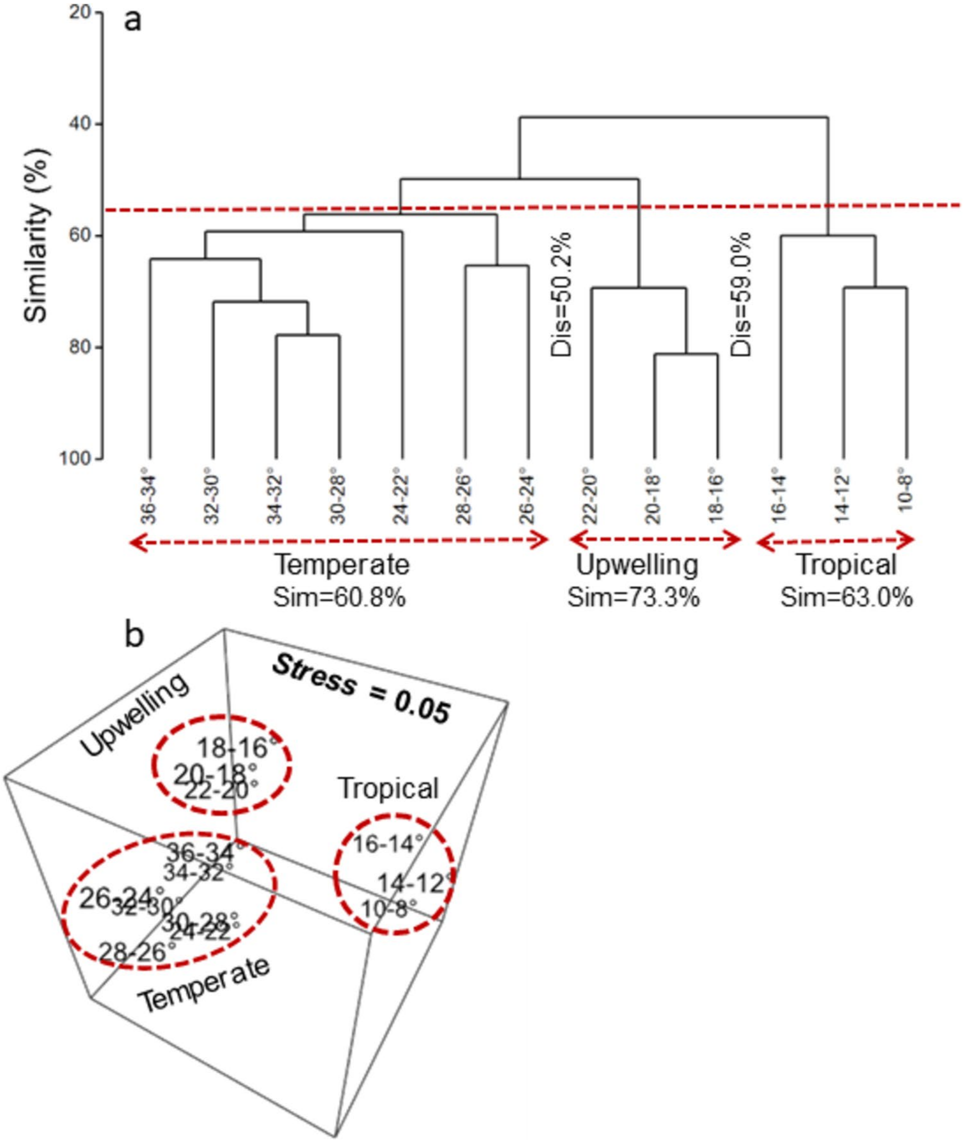


Fig. 3 Dendrogram (**a**) and three-dimensional nMDS (**b**) resulting of the multivariate analysis based on the presence–absence data by cephalopod species and two latitude-degrees (Sørensen-Dice similarity index, group average algorithm, cophenetic correlation = 0.93044)

of Western Sahara (35°–22°N, Temperate water cluster, Fig. 3a). The second group includes the latitudes of the southernmost region in the tropical area, ranging from south of Mauritania to Guinea (16°–8°N, Tropical water cluster). A third cluster groups the southern part of Western Sahara, Cape Blanc area, and almost the entire Mauritanian coast (22°–17°N). This cluster shows a stronger similarity in its faunistic composition (73.3%) compared to the temperate and tropical water clusters, which only reached 60.8% and 63.0% similarity, respectively.

The three-dimensional nMDS (Fig. 3b) confirms the latitudinal segregation in three faunistic regions, highlighting the existence of two zoogeographical boundaries in the distribution of cephalopods along the northwest African coast. In this three-dimensional representation, temperate, upwelling, and tropical units are clearly separated. The two identified boundaries were in Saharan waters (23°–21°N) and in the south of Mauritania (17°–16°N). The low stress value in the three-dimensional representation (stress = 0.05) in Fig. 3b demonstrates a better fit than the bi-dimensional representation (stress = 0.07), indicating the robustness of the similarity within the three groups and their faunal segregation.

Tables 1 (a summary of the total number and percentage of coastal and oceanic cephalopods) and 2 (a comprehensive species list in the three zoogeographical assemblages) demonstrate clear differences in the specific richness and composition of the three cephalopods clusters. The tables highlight the highest diversity and the importance of oceanic cephalopods in the upwelling zone, where these species represent almost 60% of the total. On the contrary, in temperate and, mainly, in tropical communities, diversity is lower and the fauna is dominated by coastal species (59.4% and 61.5%, respectively). It is important to note that the ‘tropical water’ cluster includes both species that are classically defined as tropical and some that are temperate-tropical, such as *Illex coindetii* (Vérany, 1839), which have been detected in the tropical realm through our analyses. On the other hand, *T. sagittatus* and *Todaropsis eblanae* (Ball, 1841) are typically temperate species that have also been found in this cluster.

To analyze the similarity and possible grouping of species, we used a second multivariate approach on the same presence–absence matrix. The resulting dendrogram in Fig. 4 shows a distinct cluster, indicating a strong association among coastal cephalopods (short species names in Supplementary material - Annex 1). The high similarity (78.8%) within this community demonstrates that it is a characteristic and robust faunistic group. The coastal cluster is separated from the oceanic cephalopods, which are divided into three groups with a low similarity level (20.0%). However, when considering the oceanic species as a whole, they exhibit a high similarity (70.5%).

Table 1 Summary of total number and percentage of coastal and oceanic cephalopods in the three biogeographical communities identified along Northwest Africa (only data from surveys)

	Temperate	Upwelling	Tropical
Total	32	35	13
Coastal	59.4	42.9	61.5
Oceanic	40.6	57.1	38.5

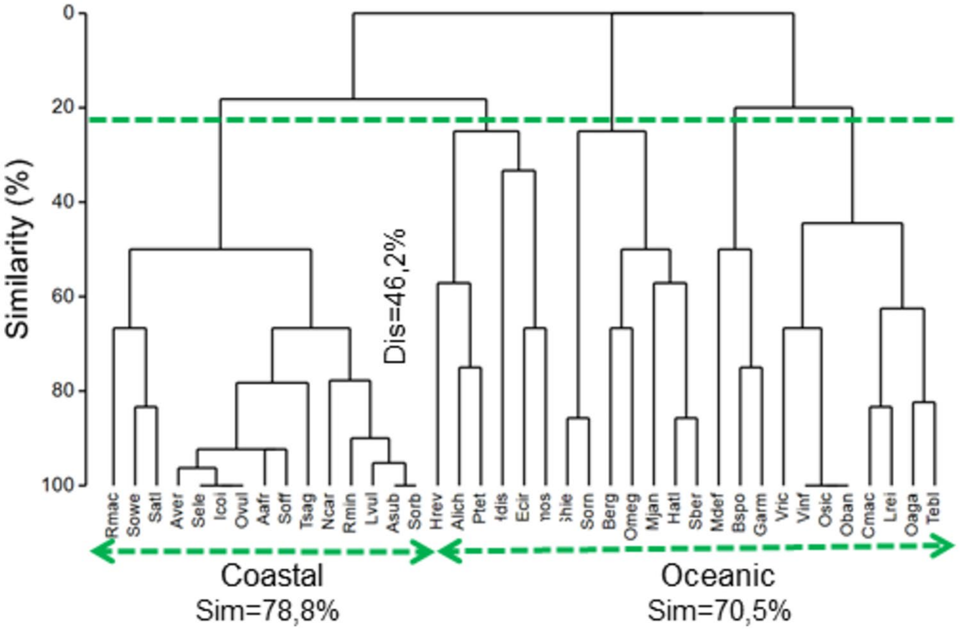


Fig. 4 Dendrogram resulting of the multivariate analysis showing the similarity among the cephalopod species based on the presence–absence data by species and two latitude-degrees (Sørensen-Dice similarity index, group average algorithm, cophenetic correlation = 0.77496). For species abbreviation see Supplementary material - Annex 1

We analyzed the presence–absence dataset of exclusively coastal species separately, considering the stronger cohesion of coastal cephalopods compared to oceanic species. The resulting graphics from both hierarchical clustering and nMDS (Fig. 5a, b) show identical and very marked latitudinal separation of almost 70% (in the dendrogram) with an excellent fit goodness in the three-dimensional nMDS (stress = 0.001). The northern temperate is divided into two geographical sub-regions, extending from the Strait of Gibraltar (approx. 36° N) to southern Mauritania. The tropical sub-region occupies the Senegalese, Bissauan, and Guinean shelves. A faunistic frontier located in the southern zone off Mauritania (16°–17°N), appears to divide both zoogeographic regions. Table 2 displays the main species found in the temperate and tropical components of the coastal cephalopod community identified in Northwest Africa, highlighting the exclusive species in each cluster.

The correlation circle graphics resulting from the principal components analysis display the correlations between the main oceanographic variables (red vectors) in a two-dimensional space (Fig. 5a, b). The two principal components (F1 and F2), represented on the horizontal and vertical axis, explain a high percentage of the variability (88.44%) (Fig. 5a). Although this value may be considered reliable, we have also checked the contribution of the third dimension (F3) to the total amount of information (Fig. 5b) and found it to be almost insignificant (4.64%). Latitude and certain hydrological factors directly associated to it, mainly oxygen content and salinity, are positively correlated ($\rho = 0.786$ and 0.792, respectively) (Table 3). As a result, their vectors appear grouped together and pointing to the right in the same direction (Fig. 5a). Conversely, surface temperature, which is negatively and strongly correlated with the latitude ($\rho = -0.963$) and with the oxygen content ($\rho = -0.944$), is displayed to the left in the opposite direction (Table 3). The main principal component (F1) represented in the horizontal axis was strongly influenced by these variables. The oceanographic variables related to the upwelling phenomena, mainly wind stress, and to a lesser extent chlorophyll *a* content, do not correlate with the mentioned

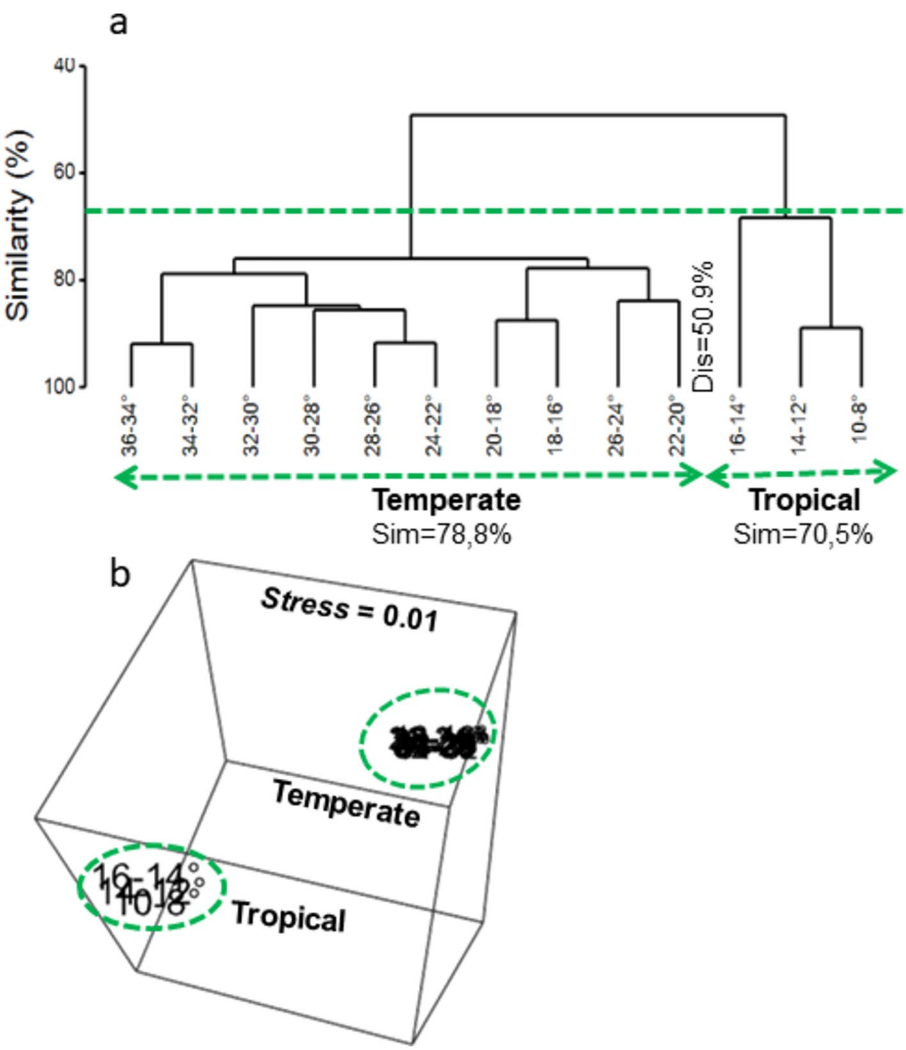


Fig. 5 Dendrogram (**a**) and three-dimensional nMDS (**b**) resulting of the multivariate analysis based on the presence–absence data by species and two latitude-degrees of coastal cephalopods (Sørensen-Dice similarity index, group average algorithm, cophenetic correlation = 0.95926)

Table 2 Main species of cephalopods in the three biogeographical zones identified along Northwest Africa in our study (in gray, the oceanic cephalopods)

Temperate	**Upwelling**	**Tropical**
Abralia (A.) *veranyi*	*Abralia* (A.) *veranyi*	*Abralia* (A.) *veranyi*
Alloteuthis africana	*Alloteuthis africana*	*Alloteuthis africana*
Alloteuthis subulata	*Alloteuthis subulata*	*Illex coindetii*
Ancistroteuthis lichtensteinii	*Bathypolypus ergasticus*	*Octopoteuthis megaptera*
Bathypolypus ergasticus	*Bathypolypus sponsalis*	*Octopus vulgaris*
Callistoctopus macropus	*Bathypolypus valdiviae*	*Opisthoteuthis agassizii*
Chiroteuthis veranii	*Brachioteuthis riisei*	*Sepia elegans*
Chtenopteryx sicula	*Callistoctopus macropus*	*Sepia hierredda*
Eledone cirrhosa	*Galiteuthis armata*	*Sepia officinalis*
Eledone moschata	*Grimalditeuthis bonplandi*	*Sepiella ornata*
Galiteuthis armata	*Haliphron atlanticus*	*Taonius pavo*
Heteroteuthis dispar	*Histioteuthis reversa*	*Todarodes sagittatus*
Illex coindetii	*Illex coindetii*	*Todaropsis eblanae*
Japetella diaphana	*Leachia atlantica*	
Liocranchia reinhardti	*Liocranchia reinhardti*	
Loligo vulgaris	*Loligo vulgaris*	
Macrotritopus defilippi	*Muusoctopus januarii*	
Magnoteuthis magna	*Neorossia caroli*	
Neorossia caroli	*Octopoteuthis megaptera*	
Octopoteuthis megaptera	*Octopoteuthis rugosa*	
Octopus vulgaris	*Octopoteuthis sicula*	
Pteroctopus tetracirrhus	*Octopus vulgaris*	
Rondeletiola minor	*Onychoteuthis banksii*	
Rossia macrosoma	*Opisthoteuthis agassizii*	
Sepia elegans	*Pteroctopus tetracirrhus*	
Sepia officinalis	*Rondeletiola minor*	
Sepia orbignyana	*Rossia macrosoma*	
Sepietta oweniana	*Sepia bertheloti*	
Sepiola atlantica	*Sepia elegans*	
Spirula spirula	*Sepia officinalis*	
Todarodes sagittatus	*Sepia orbignyana*	
Todaropsis eblanae	*Todarodes sagittatus*	
	Todaropsis eblanae	
	Vampyroteuthis infernalis	
	Vitreledonella richardi	

variables (Table 3). They pointed out in an orthogonal direction, significantly contributing to the second component (F2) (Fig. 5a). However, the third upwelling-related factor (the primary production) shows a stronger relationship with the

Table 3 Main species of the temperate and tropical components in the community of coastal cephalopods identified in Northwest Africa (in gray, species exclusive to the respective group)

Temperate	**Tropical**
Abralia (A.) *veranyi*	*Abralia* (A.) *veranyi*
Alloteuthis africana	*Alloteuthis africana*
Alloteuthis subulata	*Eledone caparti*
Austrorossia mastigophora	*Illex coindetii*
Callistoctopus macropus	*Octopus vulgaris*
Eledone caparti	*Sepia elegans*
Eledone cirrhosa	*Sepia hierredda*
Eledone moschata	*Sepia officinalis*
Illex coindetii	*Sepiella ornata*
Loligo vulgaris	*Todaropsis eblanae*
Macrotritopus defilippi	
Neorossia caroli	
Octopus vulgaris	
Pteroctopus tetracirrhus	
Rondeletiola minor	
Rossia macrosoma	
Scaeurgus unicirrhus	
Sepia bertheloti	
Sepia elegans	
Sepia hierredda	
Sepia officinalis	
Sepia orbignyana	
Sepietta oweniana	
Sepiola atlantica	
Todaropsis eblanae	

F1 axis. The goodness of the representation of the environmental variables in the axis F1–F2 space is confirmed by the high values of the square cosines between the variable vectors and the factor axes (Table 4). Oxygen content and surface temperature (two hydrological variables whose values strongly vary along the latitudinal range), the latitude

Table 4 Spearman's rank correlation coefficients (ρ) between the main hydrological variables along northwest Africa (latitude is included)

Variables	Lat	BS	BO	ST	O	PP	Chl
BS	**0,786**						
BO	**0,792**	**0,810**					
ST	**−0,963**	**−0,802**	**−0,754**				
O	**0,889**	**0,750**	**0,755**	**−0,944**			
PP	**−0,614**	**-0,412**	**−0,705**	**0,632**	**−0,709**		
Chl	−0,180	0,082	−0,295	0,205	−0,336	**0,625**	
WS	0,079	**0,411**	−0,033	−0,085	−0,058	**0,562**	**0,730**

Lat latitude degree, *BS* bottom salinity, *BO* bottom oxygen concentration, *ST* sea-surface temperature, *O* sea-surface oxygen, *PP* primary productivity, *Chl* sea-surface chlorophyll *a*, *WS* wind stress (in bold: significant correlation)

Table 5 Squared cosines between the variable vectors and the three main factor axes

Variables/Axis	F1	F2	F3
Lat	**0.874**	0.032	0.034
BS	**0.669**	0.240	0.044
BO	**0.803**	0.001	0.163
ST	**0.895**	0.029	0.064
O	**0.899**	0.000	0.050
PP	**0.625**	0.260	0.016
Chl	0.134	**0.690**	0.000
WS	0.006	**0.916**	0.000

Lat latitude degree, *BS* bottom salinity, *BO* bottom oxygen concentration, *St* sea-surface temperature, *O* sea-surface oxygen, *PP* primary productivity, *Chl* sea-surface chlorophyll *a*, *WS* wind stress

itself (as a proxy of these variables, projected in the axis F1), and mainly wind stress (linked to axis F2) presented higher square cosines that fluctuate between 0.803 and 0.916. The square cosines of chlorophyll *a* (0.690), salinity (0.669), and primary production (0.625) are lower and present a lesser connection with the respective axes F2 and F1 (Fig. 5a). The goodness of PCA results is too confirmed by the Bartlett's sphericity test, which shows that the correlation of oceanographic variables is significant (value-*p* bilateral < 0.0001) (Table 5).

The spatial representation of the latitudinal strata, also resulting of the PCA (Fig. 6), clearly shows its strong correlation with the main physical and productive characteristics that identified the regional water masses. Temperate latitudes (23°–35°N) are in the right side of the graphic following a south–north pattern (from Western Sahara to Gibraltar Strait) which is related to the increasing in oxygen content and the decreasing in surface temperature and upwelling. On the left side of the graph are situated the lowest latitudes (16°–8°N) corresponding to tropical water masses, characterized by higher surface temperatures and low oxygen content. In the upper left part, the latitudes that would correspond to the upwelling ecoregion (22°–17°N) are sited, related to the highly productive water masses mainly linked to wind stress and chlorophyll *a*, and to a lesser extent primary production (Fig. 7).

Results of the ANOSIM test (Table 6) statistically validate the robustness of the zoogeographical cephalopods segregation, the two boundaries located between three main clusters identified through the multivariate analyses, as well as its clear relationship with the characteristics of the water masses flowing along the northwest African margin. Effectively, all-pairwise comparison, both in the case of faunistic groups and water masses, shows high values of *R* statistic and significant *p* (Table 6). ANOSIM R statistics present maximum value ($R = 1.000$) for coastal cephalopods and for the Tropical group against the Temperate and Upwelling ones. Although the differences in the cephalopod composition between the Temperate and Upwelling regions seem to be somewhat lower ($R = 0.873$), the R-value remains large, also presenting very high levels of significance ($p \leq 0.001$). This would prove the very good and clear faunistic separation, and the robustness of the zoogeographical boundaries found through our analysis, with the boundary separating the cephalopod assemblages from the Upwelling and Tropical regions being only slightly weaker ($p = 0.01$).

This faunistic separation clearly coincides with the presence of the three types of water masses, temperate, upwelling, and tropical, with different characteristics, that

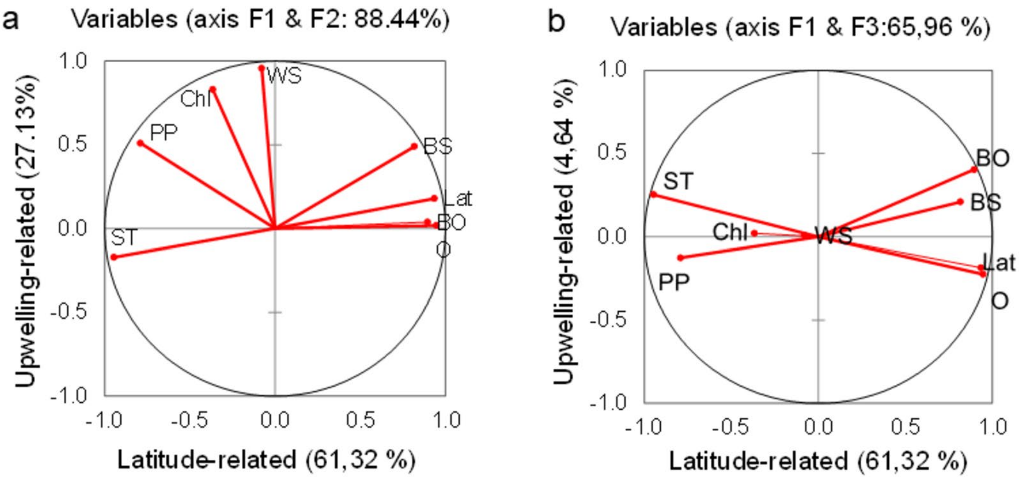


Fig. 6 Representation in the correlation circle of the hydrological variables plus the latitude (red arrows) in the two-dimensional factorial space resulting of the PCA. (*Lat* latitude degree, *BS* bottom salinity, *BO* bottom oxygen concentration, *ST* sea-surface temperature, *O* sea-surface oxygen, *PP* primary productivity, *Chl* sea-surface chlorophyll *a*, *WS* wind stress) (color figure online)

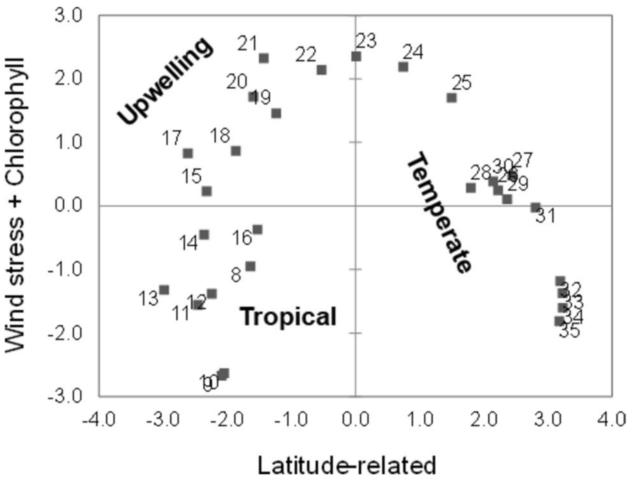


Fig. 7 Representation of the latitudinal strata in a two-dimensional space resulting of the PCA with respect to the three main axis and hydrological variables that they explain (*F1* latitude-related factors, *F2* upwelling-related)

Table 6 Results of the Bartlett's sphericity test that shows the significance of correlations among the hydrological variables

Chi-square (observed value)	272,820
Chi-square (critical value)	41,337
Degrees of freedom	28
P value (bilateral)	<0.0001
Alfa	0.05

(p value < 0.0001)

suggested the PCA, as shown by the high values of the *R* statistic, greater than 0.9 (0.919–0.947) and highly significant, in all cases.

Discussion

Biogeographic zoning and boundaries

One main subject on Northwest Africa biogeography is the location of the boundary between temperate and tropical fauna and their respective provinces, which were placed at different latitude according to diverse worldwide classifications: in Cape Verde (Senegal; Briggs 1995), at Cape Juby (northern Western Sahara; Briggs and Bowen 2012), or in Cape Blanc (northern Mauritania; Spalding et al. 2007).

For cephalopods, Nesis (2003) suggested that the main patterns of faunistic zonation should coincide with continental shelves and open ocean, because both realms are affected by the general scheme of oceanic circulation. Like this, the author identified for shelf, neritic, and oceanic cephalopods a unique boundary along Northwest Africa, which matches in Cape Blanc. Northern and southern of this latitude, shelf-nektonic cephalopods were associated to Mauritanian and Guinean Provinces. Oceanic species, which spread from western to eastern through the Atlantic, were separated in the North Subtropical and Tropical Zones (Nesis 2003). The boundary proposed by Nesis (2003) matches that of Spalding (2007) for the coastal shelf fauna.

Cape Blanc, effectively constitutes the area where the main regional hydrological feature in the northwest Africa margin—Cape Verde Frontal System—is located. The front which stretches from Cape Blanc to Cape Verde Islands is an oceanic frontier where water bodies of subtropical and tropical origin converge (Pastor et al. 2015; Pelegrí et al. 2017). After the first studies on marine fauna from the African Atlantic coast, Cape Blanc in Mauritania (20° 47' N) has proved to be a zoogeographical barrier where a drastic faunistic change occurred for fish and benthic fauna (Domanevsky 1980; Le Loeuff and von Cosel 1998).

Nevertheless, some researchers have suggested that the turnover between temperate and tropical northwest Africa biota must take place, at least for some particular benthic invertebrates, not at Cape Blanc, but somewhere along the Mauritanian–Senegalese margin. The coast that stretches between Cape Blanc and the south of Cape Timiris (Mauritania) to Cape Verde (Senegal) is considered a hydrological transitional zone between tropical and temperate fauna (Le Loeuff and von Cosel (1998)). Throughout this area, the marine fauna of continental shelf shallow-water reaches its southern limit and is replaced by a tropical fauna native to West Africa (van Soest 1993; Matos-Pita et al. 2017). Thus, it is known that in Mauritania, some invertebrate taxa, as sponges, echinoderms or hydrozoans, have stronger affinity with the Atlantic–Mediterranean elements than with the tropical ones (van Soest 1993; Calero et al. 2017). On the contrary, Matos-Pita et al. (2017) highlighted the predominance of tropical species (45% of the total) in the decapod

Table 7 Results of the ANOSIM test showing the *R* statistic values and the significance level (*p*) of the separation between the three biogeographical cephalopod clusters and water masses identified along north-west African coast

	Biogeographical region	Cluster		Water masses	
Total cephalopods	Global	0.954	***	0.947	***
	Temp vs Upw	0.873	***	0.919	***
	Temp vs Trop	1.000	***	0.977	***
	Upw vs Trop	1.000	**	0.921	***
Coastal	Temp vs Trop	1.000	***		

Temp temperate, *Upw* upwelling, *Trop* tropical

$^{***}p \leq 0.001$, $^{**}p = 0.01$

crustaceans (Brachyura) communities off Mauritania. In general, the proportion of species with Atlantic–Mediterranean affinities is higher in the Banc d'Arguin (northern Mauritania), while the Guinean fauna is more abundant in the southern zone. Rocha et al. (2017) argued that the abundant and diverse Mauritanian cephalopod's fauna is mainly composed of a mixture of species with tropical, temperate, and cold affinities.

In the present work, we had tried to test the possible coincidence with the worldwide biogeographic classifications previously established (Domanevsky 1980; Briggs 1995; Spalding et al. 2007; Briggs and Bowen 2012; Costello et al. 2017) and, particularly, with the studies of Nesis on the cephalopods (1982, 2003). For the whole cephalopod community, we have identified two main boundaries separating three different faunistic regions at the 60% of similarity level (Fig. 2). These limits would be located northern Cape Blanc, in south of Saharan waters (22°–21° N), and southern Mauritania (16°–17° N). Our north boundary matches with the zone where some previous works placed the main biogeographical limit for the worldwide coastal fauna (Domanevsky 1980; Spalding et al. 2007) and for coastal and oceanic cephalopods (Nesis 1982, 2003) in the CCLME region (Figs. 3–5).

Some species found in temperate and tropical clusters have quite extensive ranges, covering the Mediterranean Sea and the Eastern Atlantic from the subarctic or north part of boreal zones to the coast of Angola, Namibia, or South Africa. There are a few species that should be highlighted here (Jereb and Roper 2005, 2010; Jereb et al. 2016). It is remarkably that the temperate species *Sepia officinalis* Linnaeus, 1758, distributed from southern Norway to 20°N and very rare to 16°N, it is present in the tropical cluster (see Table 7). *Austrorossia mastigophora* (Chun, 1915) a historically tropical species, is found in the temperate cluster (see Table 2). The group of tropical species includes *Octopus vulgaris* Cuvier, 1797*, I. coindetii, T. eblanae,* and *S. elegans* Blainville, 1827, which are also widely distributed in the temperate zone, being generally located outside the studied area (see Table 2). This could be due to a change in the distributional patterns of some of these species with the recent increase in global temperatures, such it could be the same case in some other octopods (*Eledone cirrhosa* (Lamarck, 1798)*, E. moschata* (Lamarck, 1798)*, Scaeurgus unicirrhus* (Delle Chiaje [in Férussac & d'Orbigny], 1841), and *Macrotritopus defilippi* (Vérany, 1851)*;* document in preparation). Besides, it should be borne in mind that nets designed for scientific sampling have a certain selectivity and efficiency (Clarke 2003; Eleftheriou & Moore 2013). In consequence, it is necessary to complement the sampling of an area with other techniques, such as the sampling by teutophagous predators (Luna et al. 2022, 2024; Xavier et al. 2022), in order to have a more complete view of the biodiversity of the area (Clarke 2003).

Proposing a new zoogeographic ecoregion

There is a particular zoogeographical unit characterized by a higher diversity and dominance of oceanic cephalopods, located between the north-temperate and south-tropical waters of the studied area. It is associated with the upwelling, and may be defined as the "Cape Blanc upwelling" ecoregion. Spalding et al. (2007) pointed out that among the features that define an ecoregion could be upwelling phenomena, nutrient inputs, temperature regimes and currents. These authors remarked that endemism level, which seems very low for cephalopods in northwest African region, is not a determinant key in the identification of these marine units. In accordance with Spalding' definition, the Cape Blanc upwelling ecoregion, at approximately between 22° and 17°N, is adjacent to the Sahara Desert. It coincides with the most productive zone of the CCLME that spreads over the Western Saharan and Mauritanian coasts. This area experiences almost continuous upwelling throughout the year, with stronger upwelling intensity and higher quality of upwelled waters (Arístegui et al. 2009; Pelegrí and Peña-Izquierdo 2015; Pelegrí et al. 2017). In addition, this region experiences high deposition rates of Sahara Desert particles carried by the wind. This enhances productivity, maintains high biodiversity, and supports important populations of commercial species such as cephalopods (Arístegui et al. 2009; Ramos et al. 2017).

The hydrological factors that have the most influence in the area, and which vary throughout the latitudinal range, are the oxygen content and the sea surface temperature. These factors, along with wind stress, promote the productivity of the waters. The Cape Blanc upwelling ecoregion would be placed between the northern boundary where the Canary Current separates from the coast and the permanent year-round upwelling generates a giant filament that transport offshore high productivity waters (Sangrà 2015). The southern boundary would be located south of Mauritania and seems to be the main biogeographic frontier in the cephalopod's distribution along the CCLME. It separates cold temperate from tropical species and is particularly important for coastal species.

Despite their low endemicity, shelf-benthic and bottom-associated neritic species are the most common cephalopods in the CCLME region. They form a compact group with high internal similarity (78.8%), clearly separated from the oceanic ones by the multivariate analysis. This southern boundary seems to match the limit in which the favorable winds for the winter upwelling decrease and where the tropical water masses dominate for most of the year (Arístegui et al. 2009; Pelegrí et al. 2017; Moctar et al. 2020). Although many mobile tropical species can migrate to warmer higher latitudes in summer, most are restricted to the 20 °C winter limits (Briggs 1995). According to Burukovsky (1998), the permanence of cold upwelled waters the central and northern Mauritanian coastal shelf could be a northward limiting factor for the distribution of tropical species. This author, in line with our results, identified both temperate (21°N) and tropical (17°N) boundaries in the shelf of the northwest African coasts and distinguished, as a consequence of an increase in summer upwelling, the existence of anti-ecotones (zones without endemics species and with low biodiversity) located symmetrically to the equator. In addition, the resulting drop in temperature at the bottom as a consequence of this phenomena makes it possible to find species that belong to more temperate zones than expected according to the temperature observed in that period. As pointed out by Le Loeuff and von Cosel (1998), the factor that determines the degree of affinity between the tropical and temperate regions is it would not be the geographic distance but the presence of seasonal upwelling in the colder waters. In our work, tropical species are distributed south of 17°N on the coasts of Senegal and Guinea-Bissau. The presence of the mouth of the Senegal River (around 16°N), the only permanent river on the Mauritanian coast, could be one of the environmental keys to species distribution and the delimitation of biogeographical frontiers. The strong decrease in salinity during the rainy season could prevent the migration of stenohaline species, contributing to the separation of the temperate and tropical biota (Domanevsky 1980; Le Loeuff and von Cosel 1998).

The study by Arkhipkin and Laptikhovsky (2006) was conducted precisely in the highly productive zone of the CCLME, which extends along the South of the Sahara and the Banc d'Arguin, and highlights the association of cephalopod species with boreal and tropical affinities with specific water masses. These authors noted that the boreal nektonic squids, such as *Loligo vulgaris* Lamarck, 1798, *T. sagittatus* or *Alloteuthis subulata* (Lamarck, 1798), are linked to the cold waters of the Sahara and Canary currents or to coastal upwelling areas, respectively. On the other hand, the widely distributed temperate–tropical cephalopods *I. coindetii* and *T. eblanae* seem to avoid the cold upwelling areas, and occupy the water masses of tropical origin. This selective preference for certain water masses leads to a clear bathymetric stratification of the cephalopods recorded, not only for this highly productive zone (Arkhipkin and Laptikhovsky 2006), but also for Mauritania and the CCLME zone in general (Rocha and Cheikh 2015; Rocha et al. 2017). Most of the cephalopods that Arkhipkin and Laptikhovsky (2006) associate with cold or tropical water masses (as *L. vulgaris* and *T. sagittatus*, or *I. coindetii* and *T. eblanae*), have a wide distribution, as evidenced by their presence in the three zoogeographical regions that we have characterized in the region. Although some cephalopod species are linked to cold or tropical water masses, what seems to characterize the Cape Blanc upwelling ecoregion at the faunistic level is its higher diversity and abundance of oceanic–pelagic cephalopods. The appearance of these "accidental" species in waters where they would not be expected, could be due to punctual incursions of foreign water masses, to particularly strong global ENSO phenomena (El Niño-Southern Oscillation, Indeje et al. 2000; Omondi and Lin 2023) or to climate change. In an area of fisheries interest such as the northwest Atlantic coast of Africa, a detailed zoogeographical classification of this group is essential, not only to expand the knowledge of basic scientific information, but also to assess the priorities for fisheries exploitation and conservation planning in a climate change scenario (Spalding et al. 2007; Whittaker et al. 2005).

Conclusions

We propose a new zoogeographical regionalization for the benthic and pelagic cephalopod fauna in the Northwest African waters. Our proposal integrates the analysis of current data and considers existing biogeographical approaches. Our approach has the novelty to merge the result of different analyses to strengthen and provide more robustness to our proposal for a new zoogeographic area linked to the complex phenomena of the upwelling for the cephalopod fauna.

For all cephalopods, we have identified two main boundaries that separates three different faunistic regions (60% similarity). These boundaries are located at the northern Cape Blanc in south of Saharan waters (22°–21°N) and southern Mauritania (16°–17°N). These boundaries match the previously known main biogeographical limit for worldwide cephalopods (Nesis 1982, 2003) and fish fauna (Domanevsky 1980) in the CCLME region. This would form a particular zoogeographical unit characterized by a higher diversity and dominance of oceanic cephalopods: The Cape Blanc Upwelling Ecoregion. This suggested new ecoregion is characterized by the permanence of a stronger and intense upwelling through all the year (Arístegui et al. 2009; Pelegrí and Peña-Izquierdo 2015; Pelegrí et al. 2017) and influenced by high deposition rates of Sahara Desert particles transported by the winds. The Cape Blanc Upwelling Ecoregion coincides with the most productive zone of the CCLME that spreads over the Western Saharan and Mauritanian coasts, maintaining a high biodiversity and important populations of commercial species as the cephalopods (Arístegui et al. 2009; Ramos et al 2017).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-024-04418-1.

Acknowledgements We would like to express our gratitude to the *EcoAfrik* team at the University of Vigo and the Spanish Institute of Oceanography for their assistance during the various cruises. Their help and support, as well as access to the valuable cephalopod collections and data, were greatly appreciated. We also extend our thanks to Chingis Nigmatullin and the anonymous reviewers for their constructive comments, which provided very valuable clarifications and recommendations to improve the original manuscript. Thanks to Alejandro Escánez for his precise and valuable contributions in enhancing the original manuscript. This publication is *EcoAfrik* number 49.

Author contributions Amanda Luna: Conceptualization, Data curation, Formal analysis, Investigation, Writing original draft, Review. Ana Ramos: Conceptualization, Resources, Formal analysis, Investigation, Writing original draft, Review, Supervision. Francisco Rocha: Conceptualization, Resources, Investigation, Writing original draft, Review, Supervision.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. Funding for open access charge: Universidade de Vigo/CISUG.

Data availability Data available on request from the authors.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval We did not require animal ethics approval for this research because we used animals sampled from licensed fishing vessels by the FAO. All applicable international, national, and/or institutional guidelines for sampling, care and experimental use of organisms for the study have been followed. This manuscript complies with the Ethical Rules applicable for this journal.

References

Addinsoft (2022) XLSTAT statistical and data analysis solution. https://www.xlstat.com.

Arístegui J, Barton ED, Álvarez-Salgado XA, Santos AMP, Figueiras FG et al (2009) Sub-regional ecosystem variability in the canary current upwelling. Prog Oceanogr 83:33–48. https://doi.org/10.1016/j.pocean.2009.07.031

Arkhipkin A, Laptikhovsky V (2006) Allopatric speciation of the teuthid fauna on the shelf and slope of Northwest Africa. Acta Univ Carol, Geol 49:15–19

Bein B, Lima FD, Lazzarotto H, Rocha LA, Leite TS, Lima SMQ, Pereira RJ (2023) Population genomics of an *Octopus* species identify oceanographic barriers and inbreeding patterns. Mar Biol 170:161. https://doi.org/10.1007/s00227-023-04307-z

Briggs JC (1974) Marine zoogeography. McGraw-Hill, New York, p 475

Briggs JC (1995) Global biogeography. In: Briggs JC (ed) Developments in Palaeontology and Stratigraphy, 14th edition. Elsevier, Amsterdam, pp 452.

Briggs JC, Bowen BW (2012) A realignment of marine biogeographic provinces with particular reference to fish distributions. J Biogeogr 39(1):2–30. https://doi.org/10.1111/j.1365-2699.2011.02613.x

Burukovsky RN (1998) On distribution of shrimps (Crustacea, Decapoda, Natantia) in West African waters. Zoologichesky Zhurnal (moscow) 77(7):778–787 ((**In Russian with English abstract**))

Caballero-Herrera JA, Olivero J, von Cosel R, Gofas S (2021) An analytically derived delineation of the West African Coastal Province based on bivalves. Divers Distrib. https://doi.org/10.1111/ddi.13454

Calero B, Ramil F, Ramos A (2017) Echinoderms of the Mauritanian Deep-Sea waters. In: Ramos A, Ramil F, Sanz JL (eds) Deep-sea ecosystems off Mauritania. Research of marine biodiversity and habitats in the Northwest African margin, Springer, Dordrecht, pp 445–480

Clarke MR (2003) Searching for deep sea squids. In: Warnke K, Keupp H, Boletzky Sv (eds). Coleoid cephalopods through time. Berliner, Paläobiologische Abhandlungen 3: 49–59.

Clarke K, Gorley R, 2015. Getting started with PRIMER v7. PRIMER-E: 20. Plymouth, Plymouth Marine Laboratory.

Costello M, Tsai P, Shan Wong P, Kwok Lun Cheung A, Basher Z, Chaudhary C (2017) Marine biogeographic realms and species endemicity. Nat Commun 8:1057. https://doi.org/10.1038/s41467-017-01121-2

Cox CB, Moore PD (2000) Biogeography, an ecological and evolutionary approach, 595, 6th edn. Blackwell Sciences, Oxford, p 428

Domanevsky LN (1980) Ichthyogeographic complexes and their structure off the Atlantic coast of Africa. Problems of marine biogeography. Abstracts of papers delivered at the All-Union Conference. Kafanov AI (Eds.). Vladivostok: 35–36 (In Russian).

Ekman S (1953) Zoogeography of the sea. Sidgwick and Jackson (eds). London. 418 pp.

Eleftheriou A, Moore DC (2013) Macrofauna techniques. In: Methods for the study of marine benthos. Wiley-Blackwell, US. 477 pp.

Fernández-Álvarez FÁ, Braid HE, Nigmatullin CM, Bolstad KS, Haimovici M, Sánchez P, Sajikumar KK, Ragesh N, Villanueva R (2020) Global biodiversity of the genus *Ommastrephes* (Ommastrephidae: Cephalopoda): an allopatric cryptic species complex. Zool J Linn Soc 190(2):460–482. https://doi.org/10.1093/zoolinnean/zlaa014

Fernández-Álvarez FÁ, Sánchez P, Villanueva R (2021) Morphological and Molecular assessments of Bobtail Squids (Cephalopoda: Sepiolidae) reveal a hidden History of Biodiversity. Front Mar Sci 7:632261. https://doi.org/10.3389/fmars.2020.632261

Freitas R, Romeiras M, Silva L, Cordeiro R, Madeira P et al (2019) Restructuring of the 'Macaronesia' biogeographic unit: a marine multi-taxon biogeographical approach. Sci Rep 9(1):1–18. https://doi.org/10.1038/s41598-019-51786-6

Griffiths H, Barnes D, Linse K (2009) Towards a generalized biogeography of the Southern Ocean benthos. J Biogeogr 36:162–177. https://doi.org/10.1111/j.1365-2699.2008.01979.x

Hedgpeth J (1957) Marine biogeography. Geol Soc Am Mem 67(1):369–382

Hoving HJT, Perez JAA, Bolstad KS, Braid HE, Evans AB, Fuchs D, Xavier JCC (2014) The study of deep-sea cephalopods. Adv Mar Bio 67:235–359. https://doi.org/10.1016/B978-0-12-800287-2.00003-2

Ibáñez C, Camus P, Rocha F (2009) Diversity and distribution of cephalopod species off the coast of Chile. Mar Biol Res 5:374–384. https://doi.org/10.1080/17451000802534873

Indeje M, Semazzi FHM, Ogallo LJ (2000) ENSO signals in East African rainfall seasons. Int J Climatol 20:19–46. https://doi.org/10.1002/(SICI)1097-0088(200001)20:1%3c19::AID-JOC449%3e3.0.CO;2-0

Jereb P, Roper C (2005) Cephalopods of the world. An annotated and illustrated catalogue of species known to date, 1. Chambered nautiluses and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae). FAO Species Catalogue for Fishery Purposes 4. FAO, Rome, p 273

Jereb P, Roper C (2010) Cephalopods of the world. An annotated and illustrated catalogue of species known to date, 2. Myopsid and Oegopsid Squids. FAO Species Catalogue for Fishery Purposes 4. FAO, Rome, p 605

Jereb P, Roper C, Norman M, Finn J (2016) Cephalopods of the world. An annotated and illustrated catalogue of species known to date, 3. Octopods and Vampire Squids. FAO Species Catalogue for Fishery Purposes 4. FAO, Rome. 370 p.

Kulbicki M, Parravicini V, Bellwood DR, Arias-González E, Chabanet P et al (2013) Global biogeography of reef fishes: a hierarchical quantitative delineation of regions. PLoS ONE 8(12):e81847. https://doi.org/10.1371/journal.pone.0081847

Le Loeuff P, von Cosel R (1998) Biodiversity patterns of the marine benthic fauna on the Atlantic coast of tropical Africa in relation to hydroclimatic conditions and paleogeographic events. Acta Oecol 9(3):309–321. https://doi.org/10.1016/s1146-609x(98)80035-0

Longhurst A (1998) Ecological geography of the sea. Academic Press, San Diego, p 398

Luna A, Rocha F, Perales-Raya C (2021) A review of cephalopods (phylum: mollusca) of the canary current large marine ecosystem (central-east atlantic, african coast). J Mar Biolog Assoc 101(1):1–25. https://doi.org/10.1017/s0025315420001356

Luna A, Sánchez P, Chicote C, Gazo M (2022) Cephalopods in the diet of Risso's dolphin (*Grampus griseus*) from the Mediterranean Sea: a review. Mar Mamm Sci 38(2):725–741

Luna A, Escánez A, Marrero J, Íñiguez E, Pérez JA, Sánchez P (2024) Early prey intake of a short-finned pilot whale (*Globicephala macrorhynchus* Gray, 1846, Cetacea: Delphinidae) in the Canary Islands. Insights in the early hunting behavior of the species. Ecol Evol 14(3):11139. https://doi.org/10.1002/ece3.11139

de Matos-Pita SS, Castillo S, Ramil F (2017) Contribution to the knowledge of the deep brachyuran fauna (Crustacea: Decapoda) in waters off Mauritania (NW Africa). J Mar Biolog Assoc 97(6):1273–1305. https://doi.org/10.1017/s002531541600062x

Moctar SM, Ramos A, de Matos-Pita SS, Ramil F, Krakstad JO (2020) Seasonal variations in the diversity and structure of decapod communities in the changing hydrological scenario of the northwest African upwelling. Mar Biodivers 50(3):1–18. https://doi.org/10.1007/s12526-020-01058-8

Nesis KN (1982) Zoogeography of the World Ocean: comparison of the zonality and regional division of the shelf (according to cephalopods). Nauka Publishing House, Marine biogeography. Moscow, pp 114–134 (**In Russian**)

Nesis KN, Levitov BS, Burgess LA (1987) Cephalopods of the world: Squids, cuttlefishes, octopuses, and allies. H. Publications Inc, Ltd., for the English translation, T.F

Nesis KN (2001) West-Arctic and East-Arctic distributional ranges of cephalopods. Sarsia 86(1):1–11

Nesis KN (2003) Distribution of recent Cephalopoda and implications for Plio-Pleistocene events. In: Warnke K, Keupp H, Boletzky Sv, eds. Coleoid cephalopods through time. Berliner Paläobiol Abh 3:199–224.

Nigmatullin ChM, Laptikhovsky VV, Moustahfid H (2002) Brief review on the ecology in the North African population of arrow squid Todarodes sagittatus (Cephalopoda: Ommastrephidae). Bull Mar Sci 71(2):581–590

Omondi OA, Lin Z (2023) Trend and spatial-temporal variation of drought characteristics over equatorial East Africa during the last 120 years. Front Earth Sci 10:1064940. https://doi.org/10.3389/feart.2022.1064940

Pastor M, Vélez-Belchí P, Hernández-Guerra A (2015) Water masses in the Canary Current Large Marine Ecosystem. In: Váldes L, Déniz-González I (eds) Oceanographic and biological features in the Canary Current large marine ecosystem, IOC-UNESCO, Paris 115:73–79

Pelegrí JL, Peña-Izquierdo J (2015) Eastern boundary currents off Northwest Africa. In: Váldes L, Déniz-González I, editors. Oceanographic and biological features in the Canary Current Large Marine Ecosystem, IOC-UNESCO, Paris. 115:81–92.

Pelegrí J, Peña-Izquierdo J, Machín F, Meiners C, Presas-Navarro C (2017) Oceanography of the Cape Verde Basin and Mauritanian Slope Waters. In: Ramos A, Ramil F, Sanz J (eds) Deep-sea ecosystems off mauritania: research of marine biodiversity and habitats in the Northwest African margin. Springer, Dordrecht, pp 119–153

Ramos A, Sanz JL, Pelegrí JL, Fernández-Peralta L, Pascual P, Ramil F, Castillo S, García-Isarch E, Rocha F, Gil M, Calero B (2017) An overview on biodiversity and ecosystems off Mauritanian deep-waters. In: Ramos A, Ramil R, Sanz JL (eds) Deep-sea ecosystems off Mauritania: Research of marine biodiversity and habitats in the Northwest African margin: 615–660. Springer, Dordrecht

Rocha F, Cheikh I (2015) Cephalopods in the Canary Current Large Marine Ecosystem. In: Valdés L, Déniz-González I (eds) Oceanographic and biological features in the canary current large marine ecosystem. UNESCO, Paris, p 245

Rocha F, Fernández-Gago R, Ramil F, Ramos A (2017) Cephalopods in Mauritanian Waters. In: Ramos A, Ramil F, Sanz J (eds) Deep-sea ecosystems off Mauritania: research of marine biodiversity and habitats in the Northwest African margin. Springer, Dordrecht, pp 394–417

Sales JBL, Haimovici M, Ready JS, Souza RF, Ferreira Y et al (2019) Surveying cephalopod diversity of the Amazon reef system using samples from red snapper stomachs and description of a new genus and species of octopus. Sci Rep 5956(9):1–16. https://doi.org/10.1038/s41598-019-42464-8

Sangrà P (2015) Canary Islands eddies and coastal upwelling filaments off North-west Africa. Oceanographic and biological features in the Canary Current Large Marine Ecosystem. IOC Technical Series 115. UNESCO, Paris, p 105

Santos JM, Bolstad KS, Braid HE (2022) Two new 'bottletail squids' (Cephalopoda: Sepiadariidae: Sepioloidea) from New Zealand, with new observations on *Sepioloidea pacifica* (Kirk, 1882). Mar Biodiver 52:26. https://doi.org/10.1007/s12526-021-01247-z

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA et al (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Am Inst Biol Sci Bull 57:573–583. https://doi.org/10.1641/b570707

Spalding M, Agostini V, Grant S, Rice J (2012) Pelagic provinces of the world: a biogeographic classification of the world's surface pelagic waters. Ocean Coast Manag 90:19–30. https://doi.org/10.1016/j.ocecoaman.2011.12.016

Sutton TT, Clark MR, Dunn DC, Halpin PN, Rogers AD et al (2017) A global biogeographic classification of the mesopelagic zone. Deep Sea Res Oceanogr Res Pap 126:85–102. https://doi.org/10.1016/j.dsr.2017.05.006

Valdés L, Déniz-González I (2015) Oceanographic and biological features in the Canary Current Large Marine Ecosystem. IOC Technical Series 115. UNESCO, Paris, p 383

Van Soest R (1993) Distribution of sponges on the Mauritanian continental shelf. Hydrobiologia 258:95–106. https://doi.org/10.1007/bf00006189

Watling L, Guinotte J, Clark MR, Smith CR (2013) A proposed biogeography of the deep ocean floor. Prog Oceanogr 111:91–112. https://doi.org/10.1016/j.pocean.2012.11.003

Whittaker RJ, Araujo MB, Jepson P, Ladle RJ, Watson JE, Willis KJ (2005) Conservation biogeography: assessment and prospect. Divers Distrib 11(1):3–23. https://doi.org/10.1111/ddi.12402

Xavier JC, Golikov AV, Queirós JP, Perales-Raya C, Rosas-Luis R, Abreu J, Cherel Y (2022) The significance of cephalopod beaks as a research tool: an update. Front Physiol. https://doi.org/10.3389/fphys.2022.1038064