

RESEARCH ARTICLE

An analytically derived delineation of the West African Coastal Province based on bivalves

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Abstract

Aim: To assess the pattern of biotic regions (BR) and their boundaries, to detect chorotypes and to relate these patterns to key environmental factors.

Location: Eastern Atlantic Ocean.

Time period: Recent.

Taxon studied: Bivalvia.

Methods: Distributions were scored for 595 species. Operational geographical units are classified hierarchically using Baroni-Urbani & Buser similarity index, clusters were assessed for statistical significance with the 'RMacoqui 1.0' software using G tests of independence, and chorotypes were inferred likewise from similarity between species distributions.

Results: Three strong biotic boundaries delimit four BR: (1) European Atlantic and Mediterranean; (2) West African, from western Sahara to southern Angola; (3) Baía dos Tigres/Namibia; and (4) Saint Helena/Ascension. The West African BR is subdivided by two weak boundaries into three subordinate BR: the tropical region proper, the north-western African transition zone and the cluster (southern Angola/São Tomé/Cape Verde Islands). Of the 429 species present in West Africa, 261 (60.7%) are endemic, and 19 genera (7.2%) are endemic. Sixteen chorotypes were identified; the European BR is correlated with chorotypes C5 (149 species mostly European and Mediterranean) and C3 (38 species mostly in northern Europe), whereas the West African BR is mainly characterized by chorotype C6 (221 species). Some discontinuous distribution patterns of tropical West African species were identified as chorotypes, but subordinate to chorotype C6. The West African BR is mainly characterized by sea surface temperature and chlorophyll; characterization without the islands also involved the extensive sandy coast. The north-western African transition region is characterized by an arid climate and few rivers and influenced by seasonal upwelling. The cluster of southern Angola, São Tomé and Cape Verdes contrasts with the remainder of West Africa in having a predominantly rocky shore.

Main conclusions: The present analyses provide an objective regionalization based on species occurrences, which supports the traditional recognition of West Africa as a major biotic region with a high level of endemism. Attention is called on that the

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unique endemic component is insufficiently represented in current marine protected areas.

KEYWORDS

biogeographic regions, bivalves, chorotypes, Lusitanian, marine biogeography, marine regionalization, marine regions, Mauritanian, Mediterranean., West Africa

1 | INTRODUCTION

The existence of differentiated biogeographical regions in the sea has been long recognized since the pioneer works of Forbes (1856) and McAndrew (1857). However, the placement of boundaries has been persistently based on authoritative decisions or on an empirical knowledge (Briggs, 1974; Ekman, 1935, 1953; Schilder, 1956), and rarely based on a formal analysis of the occurrence data of taxa (e.g. the pioneer work of Valentine, 1966, 1973). With a wealth of occurrence data being increasingly available, it becomes feasible and necessary to address those empirical units from the very basic data, namely the occurrence patterns of individual species (e.g. Belanger et al., 2012; Costello et al., 2017; Kulbicki et al., 2013). Tropical West African is unanimously recognized as one of the four major provinces for tropical coastal and shelf marine biota, together with the Caribbean, Panamanian and Indo-West Pacific (Briggs, 1974; Briggs & Bowen, 2012; Ekman, 1953; Kulbicki et al., 2013). Yet, the exact location of the boundary is unclear and the within-province biogeography is much less known than in the other tropical provinces.

A sound classification of biogeographical areas is an essential tool for analysing basic questions in historical and ecological biogeography, evolutionary biology and systematics underlying global biodiversity patterns (Lomolino et al., 2006; Valentine, 1973; Witman & Roy, 2009), and for assessing priorities for conservation planning (Spalding et al., 2007; Whittaker et al., 2005). The assessment of representativeness for the conservation evaluation also requires a previous biotic regionalization to define biogeographical contexts (Austin & Margules, 1986).

Another perspective of biogeography is to analyse species distributions by looking for shared overall distribution patterns (chorotypes; see Fattorini, 2015 for a detailed discussion of that term). Both biotic regions and chorotypes reflect species distribution, which in turn respond to environmental and historical attractors (Kreft & Jetz, 2010; Real et al., 2008). The species composition of a biotic region can be viewed as the regional superposition of several chorotypes, considered as biogeographic features with properties beyond the simple sum of their parts (Olivero et al., 2013).

Molluscs are one of the major phyla in the marine benthos, accounting for as much as one-quarter of all species (Appeltans et al., 2012) and occupying a large variety of habitats. Among these, the class Bivalvia is not only the second largest with ca. 8500 living species (Huber, 2015) but also that one with the most economically and ecologically important species, commonly outnumbering gastropods in number of individuals, if not of species. Therefore, bivalves have

attracted the attention of biogeographers as an appropriate group for large-scale analysis, for example Krug et al. (2009), Belanger et al. (2012), Jablonski et al. (2013).

The Bivalvia of tropical West Africa have been treated in a comprehensive identification guide (Cosel & Gofas, 2019). The wealth of original distribution data examined for this publication is such that it could provide a new, independent insight on the regional biogeography. Here, we aim to analyse the occurrence data therein in order to (1) test the placement of a major boundary between the Lusitanian or west European province and the West African one, (2) characterize the tropical West African biotic region and its subdivisions in terms of correlated chorotypes, species richness and levels of endemism, (3) attempt to relate the faunal break between Europe and West Africa, and the subordinate faunal breaks within the West African Province, to key environmental factors, and (4) to draw conclusions from this study regarding conservation priorities.

2 | METHODS

2.1 | Distribution data

Occurrence data for West African bivalves are based on the original material used for the elaboration of the distribution maps in Cosel & Gofas (2019). Of the 462 species treated therein, we excluded the species normally occurring on the continental slope below 200 m, the species living only in nearly fresh water, and the family Teredinidae living in driftwood. Subspecies were not distinguished. This leaves a total species pool of 429 species occurring in West Africa.

The sampling effort is unequal (see Cosel & Gofas, 2019: figure. 1.6 for details), being most thorough in Mauritania, Senegal, Cape Verde Islands, Guinea and Guinea Bissau, Côte d'Ivoire, Gabon, Congo and Angola. Mauritania and Guinea were covered by a comprehensive sampling using grabs, aimed at a sedimentological characterization of the entire continental shelf; other countries such as Côte d'Ivoire, Gabon and Angola were sampled repeatedly in particular places and not at all in others. For the remainder of West Africa, the data rely on sampling efforts that spanned the whole coast, or large parts of it, among which the most noteworthy are the mostly shore-based Mission Gruvel 1909–1910 (Dautzenberg, 1910, 1912), the expedition of R/V Atlantide in 1949 (Nicklès, 1955), the expeditions of R/V *Calypso* to the Cape Verde Islands in 1956 and Gulf of Guinea in 1959, and the Guinean Trawling Survey in 1964.

Altogether, the sampling considered in this work is representative of the second half of the 20th century as a baseline. The material figured in Cosel & Gofas (2019) is detailed in the book's supplementary material, but the distributions scored here take into account all the examined material, including the unfigured lots.

Data for distributions outside tropical West Africa were taken from the official Spanish list of marine organisms (Gofas et al., 2017) in which five areas are considered separately; from Pasteur-Humbert (1962) and Salas (1996) for Morocco; from Fauna d'Italia (Schiaparelli, 2008) in which nine regions are scored; from the list of Roscoff area (Cornet & Marche-Marchad, 1951, with online updates at <http://www.sb-roscoff.fr/fr/observation/biodiversite/especes/inventaires/inventaires-de-la-faune-et-de-la-flore-marines>) and Seaward (1990) provided the basis for distributions in Great Britain and North Sea. Portugal lacks a reliable, comprehensive checklist for the mainland coast and was therefore not included. Occurrence in the European Neogene fossil record of species currently living in West Africa (or of their close relatives) are those mentioned in Cosel & Gofas (2019).

The combined data matrix (West African and European coasts) summarizes occurrence data for 595 species (Appendix S1), among which 65 were marked as data-deficient and so some analyses were repeated without including them, as a test for the robustness of the results. These species were treated as data-deficient because of either taxonomic difficulty (more than one-third are Galeommatoidea, which for the same reason were excluded by Jablonski et al., 2013) or rarity/difficulty to collect (e.g. species known only or mostly from their type specimens), which make records less predictable.

Operational geographical units (OGUs) used for the classification analysis are essentially countries' EEZ (as represented in www.marineregions.org), with some exceptions. Large and/or biogeographically diverse countries (Spain, Morocco, Senegal, Angola) have been split, whereas small countries with scanty data (Benin, Ghana, Togo) have been pooled. We had several reasons for using countries rather than a grid as basic OGUs. Firstly, using a grid would have increased the bias in sampling between areas. Only two countries (Mauritania with the cruises of R/V 'Ndiago' and Guinea with the 'Sedigui' surveys) have a sampling of grabs along an evenly distributed mesh covering the entire continental shelf. For other of the more intensely sampled countries (e.g. Senegal, Côte d'Ivoire), the same sites were repeatedly sampled over decades and large areas are uncovered. Also, especially in older collections, the country is reliably documented but there are no coordinates, and those specimens could not be taken into account in a georeferenced system. A further reason is that cells are not coincident with country borders, whereas many end-users working on conservation and management issues look forward to country lists, easily deducible from our table.

Our country-based matrix comprises in total 38 OGUs spanning from the British Isles to Namibia, a large part of the western Mediterranean and the archipelagos off West Africa. The choice of a 5° grid would have involved a similar number (ca. 40, see Costello et al., 2017, Figure 3) of OGUs, with the drawbacks above mentioned. A 1° grid was not feasible taking into account the disparity in sample

density and precision of labelling. The MEOW Ecoregions, conversely, would have provided only 20 OGUs within the same scope, with some of them spanning several countries, and we rejected them as too coarse. We have considered, following Phipps (1975), that the size of the OGUs must seek the best trade-off between too many units with poor data for most of them, and too coarse units with a poor resolution.

2.2 | Classifications analysis

2.2.1 | Regionalization

The method used to objectively identify biogeographic regions (BR) and boundaries was based on Olivero et al. (2013). OGUs were classified hierarchically according to the presence/absence of bivalve species, using the Baroni-Urbani & Buser (1976) similarity index and the unweighted pair group method with arithmetic mean agglomerative algorithm (Sneath & Sokal, 1973). All clusters in the resulting classification dendrogram were assessed for statistical significance using G tests of independence (Sokal & Rohlf, 1981) and the 'RMacquie 1.0' software (<http://rmacqui.r-forge.r-project.org/>) (see more details in Olivero et al., 2013). Two types of biotic boundaries are shown in the resulting classification tree: 'weak boundaries' defined by significant similarities within the bounded region, and 'strong boundaries' defined by significant between-region dissimilarities. Thus, a coastline section that was bounded by strong borders was considered to be a 'strong BR', within which other biotic units bounded by weak borders, called 'weak BR', could nest. Consistent weak BR were characterized by a significant value of internal homogeneity (Olivero et al., 2013). Conversely, a set of clustered OGUs delimited by a significant boundary could be identified as a fuzzy biotic region if its value of internal homogeneity was not significant, thus denoting the presence of a biogeographic transition zone.

There is no consensus regarding which method is best for delimiting biogeographic regions. Quantitative techniques based on cluster analysis and similarity indices have been recently used for marine regionalization (Costello et al., 2017; Freitas et al., 2019; Kulbicki et al., 2013). Our preference went to taking into account that some biogeographic boundaries can be gradient zones or transition zones (Jacquez et al., 2000; Leung, 1987), that is that some of the areas may belong to a certain degree to more than one biogeographical region.

2.2.2 | Characterization of the biogeographical patterns with respect to spatial/environmental factors

We characterized the biogeographical patterns according to 17 variables related to spatial trends and to geophysical and hydrological factors (Table 1).

Forward-backward stepwise logistic regression analyses were used to environmentally characterize the biotic regions, using

Factor	Code	Variable	Data source
Spatial	Lat	Latitude	
	Long	Longitude	
Geophysical	Plat	Platform area (km ²)	Natural Earth
	Tid-rang	Annual mean tidal range (cm)	SND (Obst, 2017)
	Hrd	Hard substrate percentage	
Hydrological	SST-m	Mean sea surface temperature (°C)	Bio-Oracle
	SST-r	Range sea surface temperature (°C)	Bio-Oracle
	Sal-m	Mean salinity (PSS)	Bio-Oracle
	Sal-r	Range salinity (PSS)	Bio-Oracle
	Chl-m	Mean chlorophyll-a concentration (mg m ⁻³)	Bio-Oracle
	Chl-r	Range chlorophyll-a concentration (mg m ⁻³)	Bio-Oracle
	Turb	Turbidity (m ⁻¹)	Giovanni
	Upw-p	Presence of permanent upwellings	Le Lœuff & Cosel (1998)
	Upw-s	Presence of seasonal upwellings	Le Lœuff & Cosel (1998)
	Riv-larg	Distance to large rivers (km)	
	Riv-sml	Distance to small rivers (km)	
	Riv	Distance to rivers (km)	

TABLE 1 Variables used in the analysis for the spatial/environmental characterization of biogeographic regions

IBM SPSS v. 24. The analyses were performed on each BR, using the binary membership/non-membership of the OGUs in the BR (possible values: 1 or 0) as dependent variables, and the set of spatial/environmental descriptors in Table 1 as independent variables. Variable selection and parameterization along the stepwise procedure were based on score-test significance and iterative log-likelihood maximization, respectively; the goodness-of-fit regression was assessed using a chi-squared test; and the significance of variables in the regression was tested using Wald's tests (Hosmer & Lemeshow, 2000).

Spatial factors (latitude and longitude) were used, because they could point to historical reasons behind the biogeographic pattern (Legendre, 1993). The extent of the continental shelf was calculated from the surface area between the baseline (Flanders Marine Institute, 2019) and the 200-m depth (NaturalEarthdata.com), using ArcGIS 10.3 raster calculator. For quantification of the proportion of rocky shore, the coastline from each OGU was viewed in Google Earth at an altitude of ca. 2000 m. Rocky and sandy shores were scored as alternative attributes along the coastline; isolated bedrock outcrops within prevalently sandy shores, and artificial hard substrates were not taken into account. Length of coastline was determined using the ArcGIS 10.3 raster calculator.

Hydrological variables related to temperature, salinity and chlorophyll concentration were downloaded from Bio-Oracle v2.0 dataset (Assis et al., 2018; Tyberghein et al., 2012), which include conditions between 2000 and 2014. Turbidity was obtained from the 2018 annual average as for monthly data of the diffuse attenuation coefficient (KD 490 nm) (spatial resolution: 4km), which was

downloaded from Giovanni dataset (NASA Goddard Space Flight Center, 2018).

Distance to river mouths was considered, in order to take into account the influence of river run-off in the sea (Mann & Lazier, 1991). A classification was made according to each river flow in two categories: mighty rivers ($Q \geq 100 \text{ km}^3/\text{year}$) and low-flow rivers ($Q < 100 \text{ km}^3/\text{year}$). River flow data were obtained from Milliman and Farnsworth (2011). The distance to river mouths was calculated by Zonal Statistics ArcGIS 10.3.

The presence of permanent or seasonal upwellings was considered as a variable: Alboran Sea upwellings and the patterns of upwellings described by Le Lœuff & Cosel (1998).

2.2.3 | Biotic characterization of regions based on chorotypes

The chorotypes of bivalve species were analysed following the method outlined by Olivero et al. (2011). Chorotype analysis is similar to the above-described regionalization, but now, we analyse the similarity between species distributions (based on shared OGUs) instead of between OGUs (based on shared taxa). This analysis does not predefine the number of resulting chorotypes. All groups of distributions meeting the requirements for forming chorotypes to the highest level (i.e. maximizing within-group similarity) were considered chorotypes provided that they were significantly clustered. Similarity values, clustering and statistical significance based on G tests of independence were calculated using the 'RMacoqui 1.0'

software (<http://rmacoqui.r-forge.r-project.org/>) (see more methodological details in Olivero et al., 2011). When a chorotype showed disaggregated diversity cores (i.e. the chorotype species were geographically grouped in separated areas), these areas were considered 'subchorotypes' (Olivero et al., 2011) if they corresponded to different clusters of species in the hierarchical classification and these clusters were statistically significant.

The correlation between biotic regions and chorotypes was tested using Spearman's coefficient. This involves the correlation between the membership of each OGU in a region but not in the rest of the study area, on the one hand, and the number of species of a particular chorotype in those OGUs, on the other hand (see Olivero et al., 2013). The degree of membership of an OGU in a region but not in the rest of the study area was calculated using the fuzzy difference tool:

$$\mu_{BR-RSA}(OGU_i) = \min \{ \mu_{BR}(OGU_i), 1 - \mu_{RSA}(OGU_i) \}$$

where μ is 'degree of membership', BR is 'biotic region', and RSA is 'rest of the study area', being $\mu_{BR}(OGU_i)$ and $\mu_{RSA}(OGU_i)$ obtained with RMacouqi 1.0.

2.3 | Levels of endemism

The percentage of endemic species has been retained as an essential feature for the characterization of marine provinces (Briggs & Bowen, 2012). Species were scored as endemic to the West African biotic

region determined by the analysis, when they were present in one or more of the OGUs comprised therein and absent elsewhere.

3 | RESULTS

3.1 | Regionalization

Three strong biotic boundaries are identified that delimit four BR for bivalves in the eastern Atlantic and north-western Mediterranean areas (Figures 1 and 2; Table 2): (1) a European BR from Morocco and Canary Islands to all European Atlantic and Mediterranean areas included in the study; (2) a properly West African BR that is defined from the western Sahara to the south of Angola; (3) Baía dos Tigres and Namibia; and (4) Saint Helena and Ascension.

The BR are well characterized by logistic regressions (Figure 1). The equation for the European BR exclusively involves the spatial factor, with northern latitudes. The West African BR is environmentally characterized by high annual mean sea surface temperature and high range (annual variation) of chlorophyll values. The north-western Africa BR is also characterized by high range of chlorophyll and the large distance to major rivers. The western African tropical BR comprises an extensive continental shelf, with negative correlation with rocky substrate and with high annual mean sea surface temperature. Baía dos Tigres and Namibia are characterized by southern latitudes and cooler annual mean sea surface temperature. St. Helena and Ascension are positively correlated with the distance to rivers.

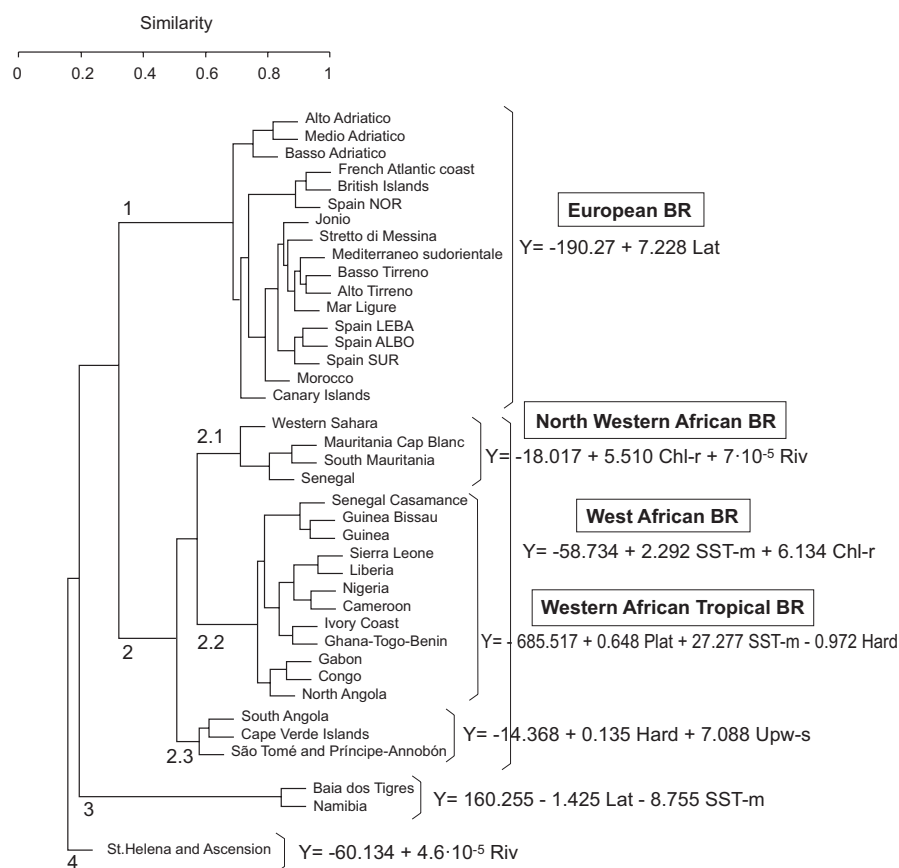


FIGURE 1 Classification of the operational biogeographic units in European and West African coastal areas, based on the similarity of their bivalve species (Baroni-Urbani & Buser's, 1976 index). Equations are the logit functions for the boundaries with significant logistic regression

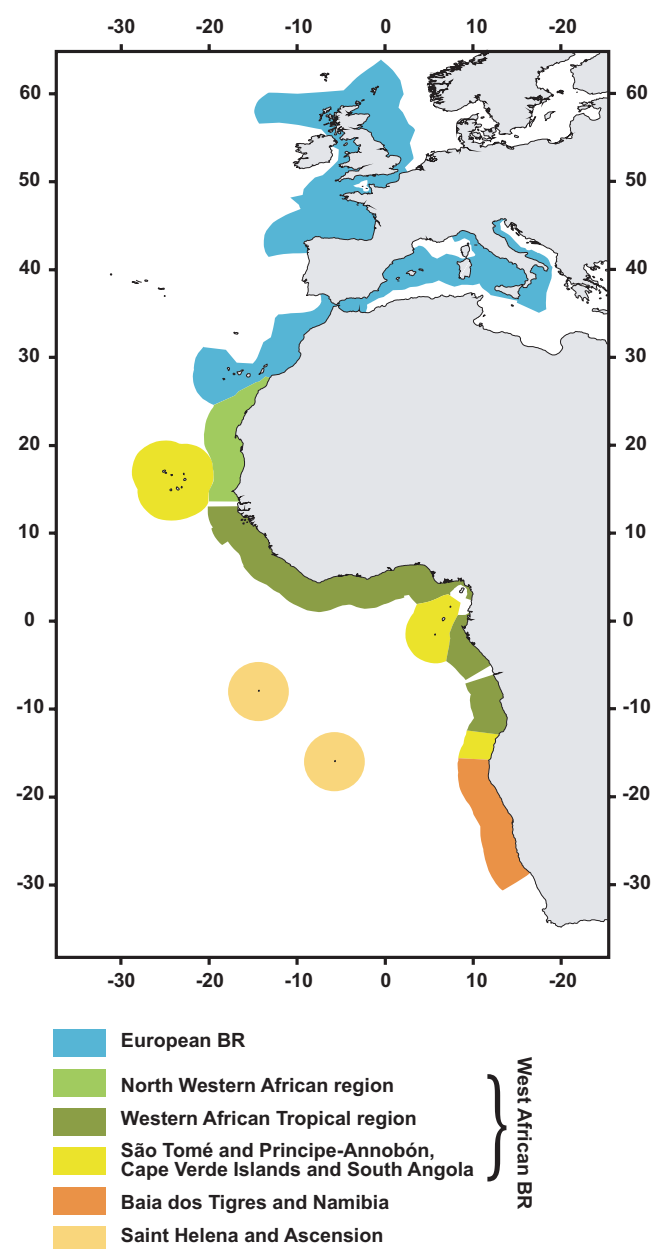


FIGURE 2 Biotic regions in European and West African coastal areas as determined in the present analysis

The West African BR is subdivided by two weak boundaries into three subordinate BR (Figures 1 and 2; Table 2): (2.1) western Sahara, Mauritania and Senegal (northern part) that are identified as a fuzzy BR or biogeographic transition zone named north-western African region, (2.2) the western African tropical region from Senegal (Casamance) to Angola (northern part), and (2.3) a third set of locations that comprises the southern part of Angola, the islands of São Tomé and Príncipe-Annobón, and the Cape Verde Islands.

The north-western African region, delimited by a weak biotic boundary, shows a positive but not significant internal homogeneity index, and so it is identified as a fuzzy BR or biogeographic transition zone. The same applies to Baía dos Tigres and Namíbia. Although the southern part of Angola, São Tomé and Príncipe-Annobón, and the Cape Verde Islands are geographically distant, they are recovered as a consistent BR, but with a much lower internal homogeneity index and significance. The remaining BR, delimited by strong or weak boundaries, are consistent with a high internal homogeneity value.

Within the western Africa tropical region, there is no strong signal for significant grouping subsets of OGU. However, some localities in the cluster show a greater similarity: Senegal (Casamance), Guinea Bissau and Guinea share the same node with more than 90% similarity; Sierra Leone and Liberia are more similar to Nigeria and Cameroon (90%) than to Ivory Coast and Ghana-Togo-Benin (85%), although they are not contiguous locations; and Gabon, Congo and the northern part Angola are more similar to each other (80%) than they are to the rest of the West African OGUs.

The same analysis, performed without 65 data-deficient species, yields a very similar topology. The strong biotic boundaries and the topology of the West African cluster are not altered, the only difference in the topology being that the northern and middle Adriatic OGUs cluster with the remaining Mediterranean OGUs rather than with southern Adriatic.

3.2 | Biotic characterization of regions based on chorotypes

Sixteen chorotypes and five gradual patterns were identified for bivalve species, the latter not considered significant chorotypes (Table 3). The Appendix S1 indicates for each species the pertinence

TABLE 2 Significant boundaries between location clusters of the dendrogram shown in Figure 1

Cluster A	Cluster B	DS	G(S)	DW	G(W)	IHA	G(IHA)	IHB	G(IHB)
2	1	0.742	475.946**	0.721	390.409**	0.549	193.969**	0.892	402.914**
1+2	3	0.675	87.199**	0.463	63.074**	-0.055	62.869**	0.981	2.384 ^{ns}
1+2+3	4	0.648	35.258**	0.432	31.573**	-0.136	31.573**	1	-
2.1	2.2	-0.4	14.841**	0.318	40.131**	0.318	3.268 ^{ns}	0.318	37.834**
2.1+2.2	2.3	-0.224	ns	0.557	49.226**	0.448	47.93**	0.665	4.103*

Note: DS > 0 and a significant G(S) indicate the presence of a strong biotic boundary; DW > 0 and a significant G(W) indicate a weak biotic boundary between clusters; IH is the internal homogeneity index, and IH > 0 and a significant G(IH) indicate that the cluster can be considered a consistent BR (otherwise, the cluster is a fuzzy BR or biogeographic transition zone). Statistical significance associated with the G tests (degrees of freedom = 1): ns = $p \geq .05$; * $p < .05$; ** $p < .005$; and -: not applicable because the cluster is composed by a single OGU. BR are named as in Figure 1.

TABLE 3 Chorotypes for bivalves in the eastern Atlantic

	NS	IH	G	P	West African supra-region	European supra-region	Baia dos Tigres and Namibia	St. Helena and Ascension	North Western African region	Western African Tropical region	Cape Verde Islands, S. Angola and São Tomé
Chorotypes	C1	5	0.557	15.519	0	0.377*					-
	C2	27	0.734	616.671	0	0.392*					-
	C3	44	0.485	283.978	0	-	0.860**		0.399*	-	0.381*
	C4	10	0.693	111.501	0						
	C5	154	0.614	7402.894	0	-	0.901**		0.392*	-	0.406*
	C6	221	0.54	4797.039	0	0.819**	-			0.573**	-
	C7	8	0.896	133.383	0	0.446**	-			0.328*	
	C8	13	0.892	363.1	0	-	0.574**	-	-	-	
	C9	12	0.506	38.996	0			0.493**		0.387*	
	C10	10	0.698	92.317	0			0.418**			
	C11	3	0.928	12.003	0.001						
	C12	3	0.92	11.502	0.001						
	C13	21	0.562	442.012	0	0.376*	-	0.416**			
	C14	10	0.55	37.223	0						
	C15	3	0.975	16.983	0						
	C16	3	0.797	6.389	0.011						
Subchorotypes	C6(1)	23	0.117	47.586	0						
	C6(2)	13	0.138	28.875	0						
	C6(3)	19	0.024	4.447	0.035						

Note: NS, number of species; IH, index of internal homogeneity; G, independence G tests (with p -value). The following columns represent Spearman's correlation coefficients between BR and chorotypes. Greyscale highlights increasingly positive significant correlations (* $p < .01$; ** $p < .05$), '-' denotes negative and significant correlation, and blank values denote non-significant.

to the chorotypes. The correlation of the BR with chorotypes is also represented in Table 3. The most representative chorotypes are shown in Figure 3a–f.

The European BR is highly and positively correlated with chorotypes C5 and C3. Chorotype C5 includes 149 widespread species, mostly distributed in the European Atlantic and the Mediterranean Sea and a few extending to West Africa. Chorotype C3 comprises 38 species mostly distributed in northern Europe.

The West African BR is mainly characterized by chorotype C6 with 221 species, being positively correlated with the BR as a whole, and also with the tropical subregion (Table 3). To a lesser extent, chorotype C2 is also correlated with the Africa BR, including 27 species, but all of these extend to at least part of the European OGUs. Other chorotypes (C1, C7 and C13) are less strongly correlated and/or hold few species. There is no chorotype geographically coincident with the north-western African region; chorotypes C3 and C5 are only weakly positively correlated with it and include mostly European species. The remaining chorotypes comprise few species and show a lesser correlation with the biogeographic region.

The discontinuous distribution patterns of tropical African species reported by Cosel & Gofas (2019) were significantly identified as chorotypes, but all of them subordinate to chorotype C6. Three discontinuous subchorotypes were detected (Figure 4a–c), including

species that are not present in Sierra Leone and Liberia and/or Nigeria and Cameroon.

3.3 | Species richness and endemism

Of the 429 species of our matrix (Appendix S1) present in the West African OGUs from western Sahara to S. Angola, 261 (60.8%) are endemic to the West African BR. Of the 169 non-endemic species present in West Africa, most are shared with Europe and Morocco, but a few are present in the western Atlantic or in Southern Africa.

At a lower hierarchical level, the north-western African region (western Sahara, Mauritania and Senegal) holds 294 spp., of which only 9 (3.1%) are endemic, 135 (45.9%) are part of the broader endemic species pool (261 species) of West Africa, and the remaining 150 are mostly shared with Europe and/or Morocco. The tropical region shows the highest species richness with 357 spp., of which 72 (20.1%) are endemic and 221 (61.9%) are a subset of the 261 West African endemics.

The cluster that comprises South Angola, São Tomé, Príncipe and Annobón, and Cape Verde Islands totalizes 200 spp., of which only 21 are shared by all three OGUs. Each one of these three OGUs has its own endemic species: 7 in the Cape Verdes, 5 in South Angola

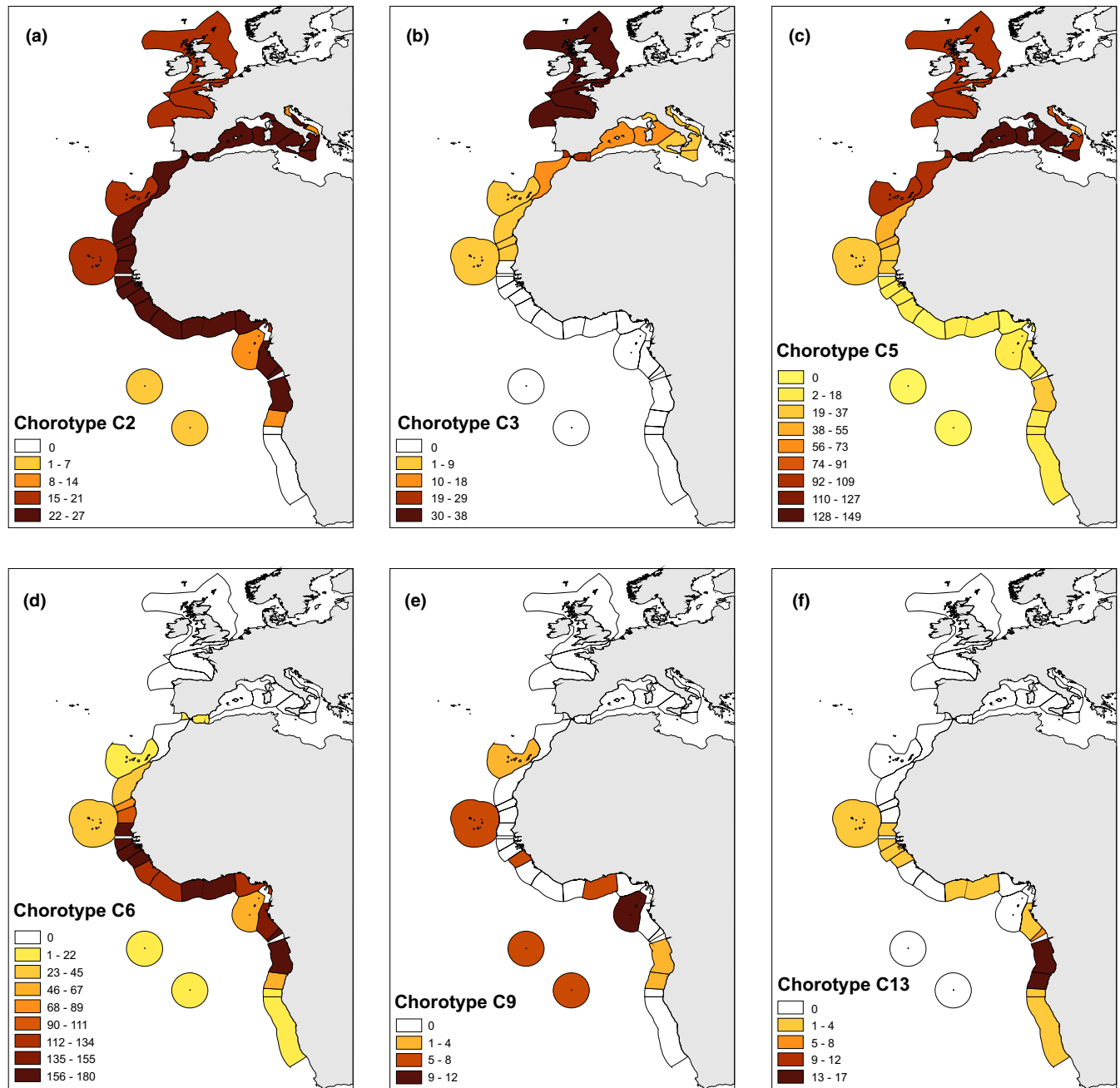


FIGURE 3 A selection of the most representative chorotypes, showing a high positive correlation with one or more biogeographic regions, and comprising a higher number of species (see Table 3 for species numbers). The colour scale and corresponding numbers represent species richness in each OGU

and 2 in the Gulf of Guinea islands (Figure 5), but there is no species endemic to the cluster and present in more than one of its component OGUs. Most of the species present there are widely distributed (including amphi-Atlantic species such as *Pinna rudis*, *Hyotissa mcgintyi* and *Papyridea soleniformis*).

In the European BR (including the Canary Islands and Morocco), our matrix includes a total of 301 species, of which 145 spp. (48.1%) are endemic and 165 spp. (54.5%) are absent in West Africa.

At the genus level, the 429 species in the matrix represent 264 genera, of which 19 (7.2%, Table 4) are endemic to the West African supraregion but only two (the Lymnecardiine genera *Acanthocardia* Gray, 1851 and *Cerastoderma* Poli, 1795) are endemic to the European supraregion. Many of these genera, nevertheless, have a fossil record in Europe, outside the current tropical West African BR; those are listed also in Table 4 with the appropriate sources.

Considering individual OGUs, species richness ranges from 78 to 258, with very few species endemic to a particular OGU (Figure 5).

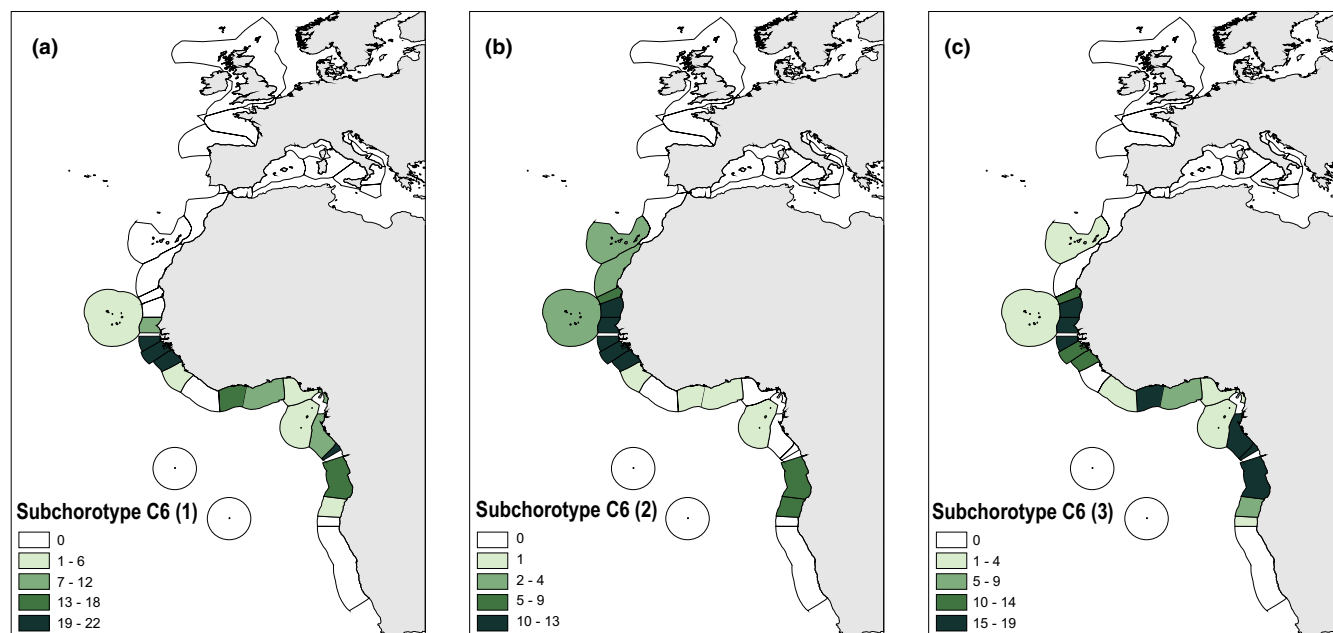


FIGURE 4 Discontinuous subchorotypes of chorotype C6

3.4 | Gaps of knowledge

Baía dos Tigres and Namibia cluster outside the West African supra-region but the occurrence data totalize only 18 species. Whereas Baía dos Tigres (sampled from shore and by dredging in August 1985 by SG) is genuinely species-poor because of the homogeneity of its sandy habitats, Namibia is one of the deepest gaps of knowledge in World faunistic records.

4 | DISCUSSION

4.1 | Regionalization support

There is general agreement, since Ekman's (1935, 1953) classical work, on that there are at least four tropical coastal provinces (Indo-West Pacific, Panamanian, Caribbean and West Africa) separated by either oceanic barriers or land bridges (Isthmus of Panama and Suez; see Cowman & Bellwood, 2013; Toonen et al., 2016). No such barriers are relevant for the northern and southern boundaries of the West African Province examined here, which are therefore to be delimited by environmental gradients and prone to be flanked with transition zones. There are nevertheless some discrepancies on (1) where exactly to place borders and (2) which position in the hierarchy should be given to further subdivisions.

Ekman (1953: 56) wrote 'Examination of a number of animal groups on the west coast of Africa, for instance by the expedition led by W. Michaelsen, has made it probable that the boundaries of the tropical faunal region, indefinite though they are, should be placed in the north roughly at Cape Verde (15°N.) and in the south in the southern part of Angola, roughly at Mossamedes (15°S.) or possibly a little further south, near Great Fish Bay [now Baía dos Tigres]

(16°–17°S)' but also (p. 55) regarded his 'Mauritanian' biogeographic region extending from the Strait of Gibraltar to Cap Vert (Senegal) as 'a mixed fauna forming a transition to the northern warm temperate fauna', therefore considered it together with the properly tropical West African 'Guinea' fauna. Briggs (1974) had also set the southern limit of his 'Lusitanian' (i.e. temperate European) province on the Cape Verde peninsula, but this was revised by Briggs and Bowen (2012) who wrote 'From southern Morocco, at Cap Juby (i.e. the northern limit of western Sahara), the Tropical Eastern Atlantic (TEA) Province extends south to Mossamedes, Angola'. The offshore islands of the Cape Verdes, São Tomé and Príncipe were included, and this latter view fully agrees with our results based on bivalves.

Based on occurrence data available in the Ocean Biogeographic Information System <<https://obis.org/>>, and on clustering 5° cells using Jaccard's coefficient, Costello et al. (2017) recognized 'Gulf of Guinea' as one of their 18 coastal marine realms, but depicted as extending from southern Senegal to southern Angola, without the NW African margin. For West African bivalves, we refrained from bringing in the OBIS data because of the scarcity of registered records in that part of the world ocean (e.g. *Senilia senilis*, which is one of the flagship endemics of WAF at the genus level, was represented by one point in Luanda at the time of writing). We believe that the discrepant placement of the northern boundary of the tropical West African BR in that study reflects a gap in data rather than a genuinely different conclusion.

Until recently, the Cape Verde Islands were considered to belong to a broader 'Macaronesian' Province until this was rebutted by Freitas et al. (2019). Kulbicki et al. (2013), based on reef fishes, did not assess the northern limit of their 'Eastern Atlantic Province' along the continental shelf but included therein both the Cape Verde Islands and the Canaries. However, a strong bias was introduced by the scope of their analysis, where the European Atlantic and the

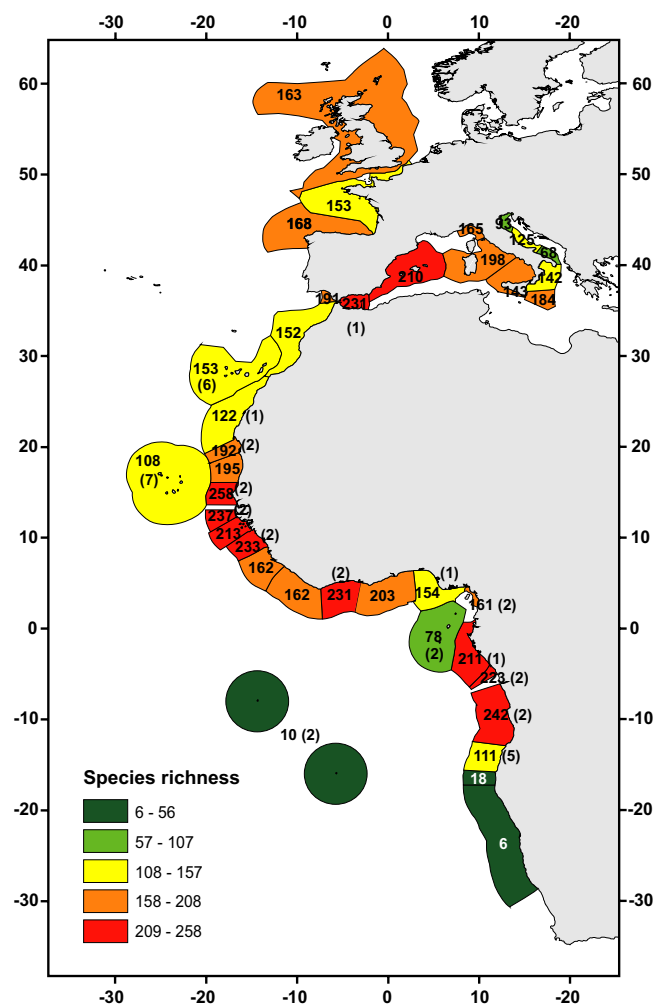


FIGURE 5 Bivalve species richness of each OGU (in brackets, number of species endemic to the OGU)

Mediterranean were not considered and therefore the Canaries and Madeira clustered with West Africa because no other eastern Atlantic biotic units were represented.

So far, fish have been the main basis for worldwide analytical assessments of marine biogeographical regions because 'Reef fishes represent one of the best candidates to conduct a quantitative assessment of biogeographical regions worldwide owing to their high diversity (with nearly 6,500 species), their well-known taxonomy, and the well-documented geographical distributions of a very large number of species' (Kulbicki et al., 2013; see also Briggs & Bowen, 2012). We consider that marine bivalves, with 8422 accepted species (WoRMS Editorial Board, 2021), fulfilled their claim to provide another large, reasonably well-known group with diverse morphology and habitat.

Our results recognize the West African tropical marine province as empirically known, but for the first time supported by analysis of individual species distributions in a major group of benthic invertebrates and given statistical support. A major boundary is found between a temperate European BR and a tropical West African BR, to be placed between Morocco and western Sahara and not around

TABLE 4 Genera endemic to the West African supraregion (from Cap Blanc to S. Angola)

Genera	No. of species	Fossil in Europe
<i>Costatoleda</i> Roth von Telegd, 1914	1	Yes (Cosel & Gofas, 2019)
<i>Senilia</i> Gray, 1842	1	Yes (Lozouet & Gourgues, 1995)
<i>Lazariella</i> Sacco, 1899	1	Yes (Sacco, 1899)
<i>Cardiocardita</i> Anton, 1838	5	Not traced
<i>Crassatina</i> Kobelt, 1881 (s. str.)	6	Yes (Essl, 2011)
<i>Lamylucina</i> Cosel, 2006	2	
<i>Pompholigina</i> Dall, 1901	1	
<i>Cardium</i> Linnaeus, 1758	2	No (Ter Poorten & La Perna, 2017)
<i>Bucardium</i> Gray, 1853	1	Yes (Ter Poorten & La Perna, 2017)
<i>Europocardium</i> Popov, 1977	4	Yes (Popov, 1977)
<i>Rostrimacoma</i> Salisbury, 1934	2	
<i>Nasopharus</i> Cosel, 1993	2	
<i>Sinupharus</i> Cosel, 1993	4	
<i>Sinucultellus</i> Cosel, 1993	1	
<i>Barymactra</i> Cossmann, 1909	1	Yes (Cossmann & Peyrot, 1909)
<i>Leptospisula</i> Dall, 1895	1	
<i>Huberimactra</i> Cosel & Gofas, 2018	2	
<i>Lamysia</i> Huber, 2015	1	
<i>Parvicirce</i> Cosel, 1995	1	Unsure (Cosel & Gofas, 2019)

Cap Vert as suggested by Ekman (1953) and more recently by Briggs (1974) and Costello et al. (2017), definitely including Mauritania and Senegal in the tropical West African BR. The area that comprises western Sahara, Mauritania and Senegal (northern part) is nevertheless in agreement with the concept of a broad transition zone as defined by Ferro & Morrone (2014): a geographical area of overlap, where physical features allow the mixture and the co-occurrence of two or more biotic components, in this case, Europe and Morocco on the one side and tropical West Africa proper on the other. The pattern of similarity of the subsets that formed the western Africa tropical region agrees with the empirical regions named by Le Lœuff & Cosel (1998) and represented in Cosel & Gofas (2019: 41). In our analysis, Saint Helena and Ascension remained outside of the West African cluster, supporting their recognition as a separate province by Briggs & Bowen (2012) and Kulbicki et al. (2013). Huber (2015) suggested that, notwithstanding strong boundaries and high levels of endemism, remote locations such as islands should be grouped with neighbouring large biotic regions when their species numbers fall below an arbitrary threshold (150 species in his treatment of marine bivalves).

Taking into account the boundaries detected in the analysis and the levels of endemism within these boundaries, the biogeographic units resulting from the analysis should be given a rank in a hierarchical system. Level of endemism (see below) is the main basis for doing so, but Kulbicki et al. (2013) wrote that 'There is currently no universally accepted terminology for a biogeographical hierarchy'. Briggs (1974) and Briggs & Bowen (2012) ranked regions at the highest hierarchical level, and recognized provinces (mapped in Toonen et al., 2016) based on an arbitrary threshold of 10% endemic species (of fish, in their data). In their scheme, tropical West Africa belongs in the 'eastern Atlantic region', which comprises Provinces: Lusitania, Black Sea, Caspian, Aral, Tropical Eastern Atlantic, Benguela, St Helena, Ascension, Tristan-Gough, and Amsterdam-St Paul. We find the setting of a threshold for endemism quite confusing, in the absence of a theoretical background for its determination.

4.2 | Characterization of the biogeographic regions

The West African BR is mainly characterized by the mean sea surface temperature and the range of chlorophyll. Characterization of tropical West Africa without the islands also involved substrate with the negative correlation of rocky shore reflecting the extensive sandy coast (Bird & Schwarz, 1985). As a difference with the islands, the extension of the shelf also characterized the tropical West Africa proper.

The north-western African transition region from west Sahara to Senegal is characterized by an arid-desert climate, lowest rainfall and few important rivers. The hydrological conditions that are influenced by seasonal upwelling present during the Northern Hemisphere winter-spring (Pelegri & Benazzouz, 2015) are strongly influenced by important seasonal variation of chlorophylls.

The cluster that comprises Angola, Sao Tomé and Príncipe-Annobón and the Cape Verde Islands does not hold any species endemic to the cluster and present in two or in all three OGUs. These three OGUs contrast with the remainder of tropical West Africa in having a predominantly rocky shore, and this rather than a shared history likely drives the occurrence of the species.

The European BR was only characterized by the latitudinal spatial factor for its more northerly location. Baía dos Tigres and Namibia were marked by the spatial trend in the southern part and also by low sea surface temperature. Latitude is highly correlated with sea surface temperature, but also involves a historical factor. It is understood that this spatial factor with its historical component is crucial in temperate BR, where the environmentally similar areas in the opposite hemisphere may be far away and beyond the species' potential for dispersal. This is less important in the tropical BR.

In a global scale, the processes that mainly determine the distribution and availability of the primary environmental resources, and therefore the species' distribution, are latitudinal and seasonal variation (Mackey & Lindenmayer, 2001). It must be borne in mind that most of the factors that determine the habitats required by each species (e.g. substrate and sediment texture, freshwater input) are to

be determined at a very local scale and that the large OGUs as used in this study may only reflect large-scale trends.

The empirical patterns of bivalve distribution along the west Africa recognized by Cosel & Gofas (2019: 40) based on visual similarity of the distribution maps and on continuous versus discontinuous ranges were mostly supported by the analysis. Chorotype C6 with 221 included species (more than half of the species present in the area) is found as the hallmark of the tropical West African province, with a highly significant correlation of 0.819 between chorotype and BR. Cosel and Gofas (2019) also pointed out a rather high number (155 species, approximately one out of every three) showing a disjunct distribution. The latter patterns are recognized as chorotypes in the analysis, but subordinate to the broader West African chorotype C6 (see Figure 3d). Not mentioned by Cosel and Gofas (2019) are 'bridge species, whose ranges cross the tropical/extratropical boundary' as defined by Jablonski et al. (2013). Some of these either belong to the Euro-West African chorotype C2 or to the essentially European chorotype C5, or are not recognized as part of a chorotype (see Appendix S1).

Belanger et al. (2012) found that bivalve biogeographic structure can be predicted accurately by very few readily available oceanographic variables (temperature, salinity, productivity), with temperature alone predicting 53%–99% of the present-day structure along coastlines. This suggests that bivalve distributions are more likely to reflect large-scale oceanographic structure than smaller differences in local conditions. As Belanger et al. (2012) pointed out, the biogeographic units do not represent obligate associations of taxa but are composed of sets of species responding in similar ways to this limited set of environmental variables. As water masses and their boundaries are altered in response to global climate change, the biogeographic structure of benthic marine assemblages is also likely to change. The behaviour of water masses under climate change will also have important evolutionary effects in terms of creating novel combinations of selective pressures within biogeographic units, and erecting or eliminating barriers.

The delineation of biotic regions is dynamic with geological time and climatic changes (Vermeij, 2012). Monegatti & Raffi (2001: Figure 5) listed as represented in the European Neogene 22 (8.4%) of the species here found as endemic to the modern West African biotic region, and at the genus level (Table 3 herein), 8 of the 19 bivalve genera now endemic to West Africa were present in the European Neogene. The presence of the so-called 'Senegalese hosts' is also well documented in the Mediterranean as recently as isotopic stage MIS5 (ca. 130 Ky) based on gastropods (Taviani, 2015), but surprisingly, data regarding bivalves are scarce; Cuerdo (1987) reported seven tropical west African bivalves from the Pleistocene of Mallorca, of which six are today West African endemics and one (*Eastonia rugosa*) that is in progress inside the Mediterranean. This number is raised to 15 (5.7% of current West African endemic bivalves) by Bellomo (1998, unpublished doctoral thesis). Nevertheless, West Africa seems to contribute little to current faunal shifts reflecting the ongoing climate change (Vermeij, 2012). The 'Senegalese hosts' reported in the Mediterranean Pleistocene are too few to trigger

profound differences in the position of faunal boundaries, but show how fast faunal elements can disperse and occupy new areas in reaction to changing environmental conditions.

4.3 | Species richness and endemism

Of the 429 species of our matrix present in the West African OGUs from Mauritania to S. Angola, 261 (60.8%) are endemic to West Africa (including western Sahara but excluding Baía dos Tigres). Huber (2015: 32) provided an overview of bivalve species numbers and endemism based on a list of 8500 species worldwide and on their distribution in 17 'core areas' defined as holding at least 150 species, of which at least 25% are endemic to the area. The 150 species threshold was intended to exclude small, remote islands, which have a high rate of endemism but a limited area and few species, not comparable to large biogeographic regions such as tropical West Africa. He briefly discussed the arbitrary threshold of 25% of species to be endemic, considering Briggs' (1995) threshold of 10% 'too low' but pointing out that a 50% threshold would not be met by, for example, Arctic, Mediterranean, Peruvian or Argentinean area.

Huber (2015) estimated 600 species, including the deep sea, in his 'core region' of West Africa, coming close to the estimate of 620 in Cosel and Gofas (2019), and 59% endemism, very close to our own estimate of 60.8% based on shelf species only. The species richness and level of endemism of tropical West African bivalves rank high among Huber's 'core areas', only surpassed in both species number and percentage of endemic species by the Indo-Pacific (3300 species, 76% endemic), the Caribbean (950 species, 68% endemic) and the Pacific Panamic (840 species, 72% endemic); Japan (1080 species, 39% endemic) and Mediterranean (650 species, 35% endemic) hold more species but lower percentages of endemics, whereas New Zealand (420 species, 80% endemic) and southern Australia (530 species, 80% endemic) surpass West Africa in percentage of endemics. All other (9) of Huber's 'core areas' rank lower. West African bivalves also rank well above the average of 42% of species unique to the realms of Costello et al. (2017) based on 65,000 species of all taxa (of which 1840 bivalves); that study found 57% endemism for their 'Gulf of Guinea' realm, also quite close to our estimate.

At a lower hierarchical level within West Africa, both species richness and levels of endemism drop. The north-western African region holds 294 spp., of which only 9 (3.1%) are endemic to that subregion. The western African tropical region shows the highest species richness with 357 spp., of which 72 (20.1%) are endemic to that subregion. At the level of any particular OGU, levels of endemism are extremely low (Figure 5).

Estimates of bivalve species richness worldwide were provided by Jablonski et al. (2013) based on 5726 Recent species (excluding the deep sea and the taxonomically uncertain Galeomatoidean families) in 1° grid cell that intersected their geographic range polygon. Their figures for Europe and West Africa are overestimated: Senegal to Ghana were represented in the range of 301–400 species, whereas our OGUs range from 154 to 258 species. The same holds

for the Mediterranean and western Europe also scored in the 301–400 interval, whereas the number of species in each of the Spanish demarcations ranges from 168 to 231 species (Gofas et al., 2017), and Fauna d'Italia totalizes 225 bivalve species (Schiaparelli, 2008). Cape Verdes, which hold 108 species in our matrix, and Canaries, which hold 153 species, were nevertheless correctly assessed.

Chaudhary et al. (2016) suggested that species richness is highest in mid-latitudes and dips near the Equator. Global bimodality is interpreted by Yasuhara et al. (2020) as a consequence of present-day temperatures in the tropics being beyond the upper thermal tolerances of some species. In West Africa, this effect might be attenuated because the intertropical sea surface temperatures are not as high as in other parts of the world (e.g. the so-called 'Coral Triangle'). At the local scale considered here, there is indeed a dip in the equatorial zone (Figure 5), which can be explained by insularity (São Tomé and Príncipe) or the presence of the Niger Delta (Nigeria). Nevertheless, the peaks are coincident with the better-explored areas (Senegal to Guinea, Côte d'Ivoire and Congo to Angola, see Cosel & Gofas, 2019, figure 1.6) therefore may be an artefact. Our data with OGUs of unequal size and with an unequal sampling effort are therefore of limited significance for the evaluation of latitudinal gradients of species richness.

4.4 | Conservation issues

Our results report that 261 species present in the West African BR (60.8%) are endemic and that 33 of those are known from only a single West African OGU (7 in the Cape Verdes, 5 in southern Angola and 2 in the Gulf of Guinea islands). At a higher taxonomic level that reflects phylogenetic uniqueness, there are 19 genera (7.2%) endemic to the tropical West African BR. This calls for an evaluation of conservation perspectives for those taxa.

Species to be considered for conservation issues, in addition to being endemic, must be suitable both for the dissemination of their values to the non-scientific public, and for the follow-up and monitoring of a marine protected area (Ducarme et al., 2012). These may be 'flagship species' that serve as symbols to stimulate conservation awareness, and 'vulnerable' species that are known to be less resistant to environmental changes than others in the community.

In the first category, we would consider the ark-shell *Senilia senilis* Linnaeus, 1758 commercially exploited for food or bait, the large cardiid *Cardium costatum* Linnaeus, 1758 and *C. maxicostatum* ter Poorten, 2007, the world's largest tellinid *Rostrimacoma cancellata* (Sowerby II, 1873) and the two local radiations of *Crassatina* spp. and *Cardiacardita* spp. represented by 9 and 5 species, respectively. In the second category, a special mention should go to the conspicuous *Hinnites corallinus* Sowerby, 1827, which lives together with the relict gastropod *Trochita* cf. *trochiformis* (Born, 1778) in shallow rocky overhangs of some inlets in southern Angola—a unique and very fragile biotope for which there should be conservation concern.

There are very, very few marine protected areas in West Africa, and all of them are rated as 'Less protected/Unknown' in the Marine Protection Atlas (Marine Protection Institute, 2021 <<https://mpati>

as.org/zones>), most noteworthy are Banc d'Arguin (a large National Park in Mauritania roughly coincident with our 'Mauritania: Cap Blanc area' OGU), then the Saloum National Park in Senegal, the Bijagos Archipelago Biosphere Reserve in Guinea Bissau and several 'Réserves Aquatiques' in Gabon. Nothing is reported from Guinea to Cameroun nor in the Cape Verde and Gulf of Guinea islands, nor in Congo and Angola despite the astounding contribution of the latter to West African marine biodiversity. The MPAs of the Saloum, Bijagos and Gabon admittedly provide a representation of all of the genus-level endemics but still, the large gap of protection from Guinea to Cameroon is unacceptable. West Africa has little tradition of shellfish exploitation and farming, but three large oyster species (*Striostrea denticulata* (Born, 1778), *Crassostrea tulipa* (Lamarck, 1819) and *Saccostrea cucullata* (Born, 1778) are worth a mention, and the latter has no West African population within a MPA. The lack of any marine protected area is particularly sensitive in those OGUs (Cape Verdes and southern Angola) that harbour local endemics, and would be even more critical if endemic gastropods (e.g. Conidae, see Peters et al. (2013), and the above-mentioned *Trochita*) were taken into account. Representativeness of MPAs can be summarized using the chorotypes; in this case, chorotype C6 (the tropical West African BR globally) is represented in existing MPAs but chorotypes C9 and C13 (the islands of Gulf of Guinea and southern Angola respectively) are not.

5 | CONCLUSIONS

This study brings overwhelming support for the recognition of a tropical West African coastal province (not including the Islands of St. Helena and Ascension), with a moderate species richness but with a proportion of endemic species ranking high among the major biotic regions of the World. This natural heritage is badly underrepresented in current conservation schemes, taking into account the scarcity of formal marine protected areas in West Africa.

The present analyses provide an objective regionalization, in which each cluster is individually assessed and could potentially be considered to represent a biogeographic unit entity (Olivero et al., 2013). In contrast to other analyses, the resulting number of biotic regions and the degree of fuzziness for partitioning do not need to be assigned *a priori* (Kreft & Jetz, 2010). This methodological approach, combining fuzzy logic and statistics, avoids arbitrary decisions in the definition of biogeographic regions. In addition, the robustness of classification has been tested in the analysis against changes in species composition (e.g. it has produced the same output when performed without 65 data-deficient species) showing a high stability.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The supplementary material containing the detailed distribution data used in this work is available from <<https://doi.org/10.5061/dryad.00000004w>>. Distribution data used in the analysis: Also available from <<https://doi.org/10.5281/zenodo.5653589>>. Sources as described in the Section 2.

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BIOSKETCH

Rudo von Cosel is a bivalve taxonomist, who collected a large part of the material examined over three decades with the support of IRD (French overseas research agency) and MNHN, Paris. RvC identified the material and used it for a comprehensive identification manual (Cosel & Gofas, 2019). **Serge Gofas**, also a molluscan taxonomist at MNHN Paris and later at the University of Málaga, Spain (UMA), helped to finalize the book and conceived this study. SG compiled the Spanish molluscan checklist (Gofas et al., 2017) and selected other sources for distributions. **Jesús Olivero** teaches zoology at UMA and contributed to develop the Macoqui method used in this study. **José Antonio Caballero-Herrera** prepares his PhD at UMA focusing on relating molluscan biogeography to environmental and biological factors. JAC processed the data, selected and acquired the sources for environmental data, and produced the illustrations. SG, JO and JAC contributed jointly to the redaction.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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