



# Living at the top. Connectivity limitations and summit depth drive fish diversity patterns in an isolated seamount

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**ABSTRACT:** The fish assemblages of the Galicia Bank and the closest continental slope (north-west of Spain) were analysed using otter trawls to improve our understanding of how environmental drivers structure seamount fish communities in the deep sea. The effect of environmental drivers on these assemblages was studied using multivariate techniques together with the variation in  $\alpha$  and  $\beta$  diversity across assemblages. Fish fauna in the study area was distributed in 5 different assemblages generated by the action of 3 main drivers: depth, distance to the coast and presence of cold-water corals. The observed differences in species composition among assemblages were mostly explained by species turnover across a depth gradient. The seamount summit and the continental slope showed important differences despite sharing similar depths, mainly because several species requiring shallow juvenile habitats were absent from the summit. These absences were observed in both summit assemblages inside and outside the cold-water coral reef. Our results show that in isolated seamounts with relatively deep summits, the lack of connectivity with shallower areas limits the presence of certain species, probably due to the impossibility for these species to migrate directly from shallow to deeper seabed areas. These species are replaced by species with preferences for deeper habitats, providing the fish assemblages located at the top of the summit with a deeper profile than observed in fish assemblages of the continental slope.

**KEY WORDS:** Seamount · Fish distribution · Diversity · Connectivity · Coral reef fish · Galicia Bank

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## 1. INTRODUCTION

The distribution of biodiversity has always fascinated humans, with its study and description being one of the main goals of natural history. In fact, some of the mechanisms that determine biodiversity distribution were described by the pioneers of this discipline more than 200 yr ago (e.g. von Humboldt 1807, as cited by Mendoza & Araújo 2019). Our knowledge of diversity drivers has greatly increased since then, even in the most remote ecosystems on earth such as the deep sea (Jamieson et al. 2020), although it is still

incomplete (Woolley et al. 2016). Unfortunately, the remoteness and isolation of this ecosystem does not preserve it from human impacts such as climate change, deep-sea bottom trawling, oil and gas extraction or deep-sea mining (Morato et al. 2006, 2020, Montagna et al. 2013, Watson & Morato 2013, Danovaro et al. 2017, Sweetman et al. 2017, Miller et al. 2018). Therefore, it is important to continue increasing our knowledge of diversity drivers in the deep sea, not only to improve our basic knowledge on diversity distribution but also to provide useful information for deep-sea management and conserva-

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tion (Woolley et al. 2016, Serrano et al. 2017a,b, Victorero et al. 2018, Ramiro-Sánchez et al. 2019). This is especially true for seamounts that can host valuable resources, increasing their risk of being exposed to human pressures (Victorero et al. 2018).

Seamounts comprise unique-deep sea environments, usually associated with biodiversity hotspots and vulnerable fauna (Richer de Forges et al. 2000, Serrano et al. 2017b, Victorero et al. 2018, De la Torriente et al. 2019, Eerkes-Medrano et al. 2020). Around seamounts, flow complexities are generated by oceanic currents. Such complexities include enhanced tidal currents, eddy formations, local upwelling events, internal waves or Taylor columns (Lavelle & Mohn 2010, Rogers 2018). These special features provide feeding opportunities and shallower seabed areas that are used by many fish species (Morato & Clark 2007). Furthermore, this flow specificity seems to induce nutrient retention and resuspension, enhancing the presence of habitat-forming species which, if they reach a high enough density (e.g. De la Torriente et al. 2018, 2020), can increase biodiversity by providing complexity. This higher biodiversity also offers new feeding opportunities for predators, strengthening the positive effect of complexity (Reed 2002, Ross & Quattrini 2007, Linley et al. 2017, Ramiro-Sánchez et al. 2019, De la Torriente et al. 2020). According to Rogers (2018), at large geographical scales, seamount community structure is driven by a combination of physico-chemical conditions (such as temperature, oxygen and aragonite saturation), food availability and evolutionary history. At the regional to local scale, depth is usually the main driver of community structure in seamounts (e.g. Clark et al. 2010, McClain et al. 2010, García-Alegre et al. 2014, Victorero et al. 2018, Ramiro-Sánchez et al. 2019), although other factors (substrate type, slope, currents) are also important for defining diversity patterns (McClain & Lundsten 2015, Serrano et al. 2017a, De la Torriente et al. 2018, Ramiro-Sánchez et al. 2019). In fact, at both scales (small and large), some of the direct drivers defining seamount community structure are the same (e.g. temperature, food availability, currents). At a large scale, some of these drivers show geographical variations, whereas at a small scale (e.g. seamount scale) they are usually correlated with depth (Victorero et al. 2018). All of these factors interact to create distinct seamount fish assemblages, different from the fish communities found in the closest continental margins (Tracey et al. 2004, Neat & Campbell 2011, Stefanoudis et al. 2019).

Differences in fauna species composition between seamounts and adjacent continental slopes have pre-

viously been observed in fish assemblages (Tracey et al. 2004, Neat & Campbell 2011, Stefanoudis et al. 2019), ophiuroid assemblages (O'Hara et al. 2008) and megabenthic assemblages (McClain et al. 2009). Tracey et al. (2004) suggested that some of the fish species that clearly preferred the continental slope had a preference for soft bottoms, whereas McClain, (2007) indicated that these differences can be linked to distance to the closest suitable habitat. In a similar way, Neat & Campbell (2011) explained that these differences resulted from the absence of several species with life-history stages associated with inshore habitats. These authors suggested that the isolation of the Rockall Plateau together with its relatively small area was a key constraint on fish diversity. In this sense, Porteiro et al. (2013) observed a higher richness of fish species in the Condor seamount than in other seamounts of the Azores region, attributing these differences to the shortest distance of the Condor seamount to the coast. Despite these works and potential explanations, the mechanisms behind these differences and the relative importance of each factor remain unclear.

The Galicia Bank (GB) is a seamount located 120 nautical miles from the Iberian coast. This distance to the main Spanish fishing harbours, together with the low abundance of high-value commercial species, has historically limited fisheries interests in the seamount (Bañon et al. 2016). Furthermore, the prohibition since 2002 (for Spanish vessels) of fishing on weekends and the 2010 zero catch regulation for deep-water sharks set by the European Union has greatly reduced fishing activities, which never reach high levels at the seamount (Bañon et al. 2016). The GB and the closer continental slope are mainly affected by 3 water masses that define the environmental conditions at the studied depths (Iorga & Lozier 1999, Cartes et al. 2014). From shallowest to deepest, these water masses are (1) the Eastern North Atlantic Central Water, which occupies the shallowest area of this study; (2) the Mediterranean Outflow Water, which is characterized by its higher salinity and a maximum core (with higher salinity and low oxygen concentration) at depths between 800 and 1200 m; and (3) the Labrador Sea Water, which has a core at 1800 m. The fauna that inhabits the seamount has been studied in the past (Duineveld et al. 2004, Somoza et al. 2014) and especially in recent years, with several studies (Cartes et al. 2014, 2021, Preciado et al. 2017, Serrano et al. 2017a,b) improving our understanding of the faunal communities of the GB, allowing its inclusion in the

Natura 2000 network as a site of community importance. As part of this effort, the fish fauna that inhabits this seamount has been described in detail (Bañón 2016, Bañón et al. 2016). However, how these fish communities are organized and how environmental drivers (e.g. depth, sediment characteristics, slope, temperature) affect the structure of these communities have not yet been studied.

The GB is located close to the Iberian coast, but separated by the Galicia interior basin, and is host to a cold-water reef formed by *Desmophyllum pertusum* and *Madrepora oculata* (Serrano et al. 2017a,b). These 2 features, i.e. proximity to the coast and presence of the reef, offer optimal conditions to study meso- (connectivity limitations) and micro- (coral reef presence) scale drivers of seamount fish communities. In this work, we identified the demersal fish assemblages of the GB and analysed the effect of local drivers on the distribution of these assemblages across the seamount. Furthermore, to increase our understanding of how connectivity processes can affect fish distribution in isolated seamounts, we compared the GB assemblages with the demersal assemblages of the closest upper slope, with the final aim of describing the drivers of fish diversity at local and regional scales.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study area is located off the northwest coast of Spain, on the summit of the GB and the adjacent continental slope (Fig. 1). The GB is an isolated seamount located 220 km west of the northwest Spanish shoreline and approximately 170 km from the Spanish continental shelf. It is separated from the Iberian coast by the Galicia Interior Basin, which reaches depths of 3000 m. The summit of the seamount is 75 km long (NNE–SSW direction) and 58 km wide (WNW–ESE direction), with a total surface area of 1844 km<sup>2</sup> (Serrano et al. 2017a). The shallowest part of the seamount reaches depths close to 600 m, although most of the seamount has depths ranging from 700 to 1500 m.

### 2.2. Biological samples

The fish abundance information was obtained from 2 different data sources. Data from the GB were obtained during 3 surveys carried out in July 2009, August 2010 and August 2011 (Ecomarg0709, Ban-

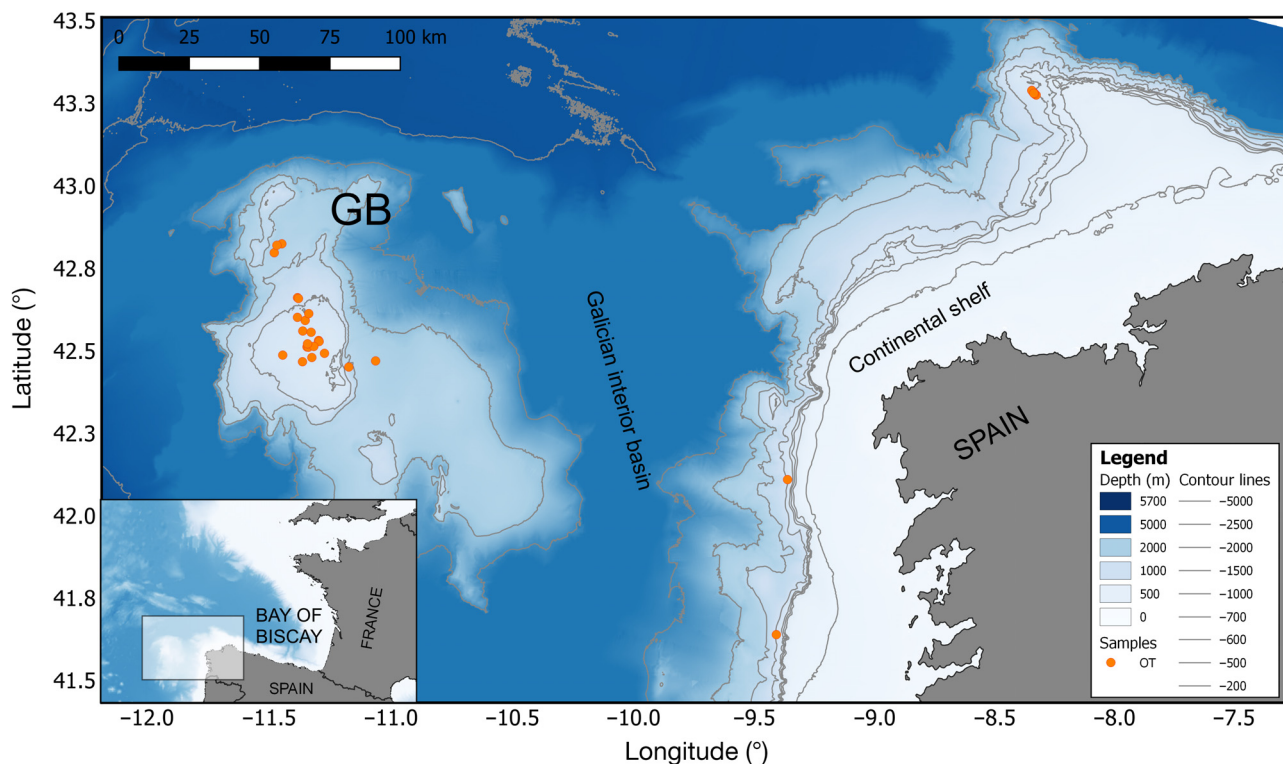


Fig. 1. Study area, showing the otter trawl (OT) sampling locations on the Galicia Bank (GB) and the adjacent continental slope

Gal0810, BanGal0811) as part of the INDEMARES project (<https://www.indemares.es/>). In total, 22 otter trawl hauls towed for 45 min at a speed of 2.8–2.9 knots were carried out across the GB at depths ranging from 650 to 1800 m (Fig. 1). Data from the continental slope were obtained during the bottom trawling Demersales survey, carried out by the Spanish Institute of Oceanography every autumn (September–October) since 1983 on the northern Spanish coast. This survey was designed according to the sampling specifications of the International Bottom Trawling Surveys working group (WGIBTS) of ICES and consists of 30 min otter trawl hauls towed at a speed of 3.0 knots, covering a wide range of depths from 50 to 900 m (ICES 2017). To obtain data from hauls that are comparable to the samples obtained in the GB, the data on the continental slope were restricted in time and space. We selected only hauls carried out on the Galician coast and deeper than 650 m to assure comparable environmental conditions with the GB, and we selected only hauls for the 2006–2015 period to assure a short time window between the different samples. Ultimately, 11 different hauls from 3 different areas were included in the analysis (Fig. 1).

Although all samples were collected using otter trawls, the gear was different between areas. The surveys carried out in the GB used the GOC 73 otter trawl, whereas the Demersales survey used the standardized Baca 44/60. Both gears have the same mesh size at the cod end (20 mm), a similar horizontal opening (approximately 18 m) and were trawled at very similar speeds (between 2.8 and 3 knots), with the main difference being the vertical opening (slightly higher in GOC 73 than in Baca 44/60, at 2.7 and 2 m, respectively). Ramos et al. (2002) analysed differences in catchability between both gears, concluding that both gears sample a very similar species composition with no significant differences in catchability for most of the demersal species analysed. The main differences between both gears were observed for pelagic species, which were outside the scope of this work and removed from the analysis. In both cases, net behaviour during the hauls was monitored using SCANMAR to record net geometry (net height, wingspread and spread between otter boards) as well as the actual time the net was on the bottom. This information was used to compute the swept area for each haul.

All species caught in these hauls were identified, counted and weighed to compute biomass (kg) and density (number km<sup>-2</sup>) for each species and sample (using the swept area by haul). In this work, only fish

were analysed, since previous works on GB epibenthic communities have already analysed invertebrate assemblages (Cartes et al. 2014, Serrano et al. 2017a) and their distribution (Serrano et al. 2017b).

### 2.3. Environmental data

Environmental information was obtained from a combination of georeferenced layers and *in situ* measures using the R program, version 4.02 (R Core Team 2013) for computations. Haul depth was obtained from EMODNET bathymetry ([www.emodnet-bathymetry.eu](http://www.emodnet-bathymetry.eu)) using the coordinates of the mean point of the haul and the ‘extract’ function in the ‘raster’ package (Hijmans, 2019) after resampling the original resolution (81 × 112 m) to a resolution of 1 × 1 km by applying bilinear interpolation. The slope was computed from the resampled depth layer using the function ‘terrain’ in the ‘raster’ package. Distance to coast was computed in ArcGIS using the Euclidean distance tool to generate a raster of distances. Information about sediment type (sediment size and organic matter percentages) and oceanographic variables (temperature and salinity near bottom) was collected using a USNEL box corer and a CTD Seabird SBE-911, respectively, in the same location and time where trawls were performed. Sediment was divided into 3 categories using particle size: coarse sand (>500 µm), fine sand (>62 and ≤500 µm) and mud (≤62 µm), and the composition (in percentage) of each category was computed by sample. Only 2 of these 3 variables (mud and coarse sand) were included in the analysis to avoid collinearity. Finally, total coral weight was computed for all hauls using the wet weight of coral rubble and live colonies of the 2 dominant cold-water corals present in the GB: *Desmophyllum pertusum* and *Madrepora oculata*.

### 2.4. Data analysis

To understand how fish diversity was distributed in the study area, fish communities of the GB and the adjacent continental slope were analysed using multivariate analysis. Fish density (number km<sup>-2</sup>) was used as a response variable, and was log transformed to minimize the effect of very high values. Rare species (species present in only 1 sample) were removed from the multivariate analysis (up to 39 species; see Table S1 in the supplement at [www.int-res.com/articles/suppl/m670p121\\_supp.pdf](http://www.int-res.com/articles/suppl/m670p121_supp.pdf)) to avoid high variability due to the high presence of zeros, although

they were included to compute richness and  $\alpha$  and  $\beta$  diversity. Furthermore, the analysis was focussed only on bottom-dwelling species, and mesopelagic and pelagic species were systematically removed from the data. Finally, only species classified at least to the genus level were kept in the analysis. The Bray-Curtis similarity index between samples was computed (using the function 'vegdist') to create a dendrogram applying the UPGMA algorithm with the 'hclust' function. Both functions ('vegdist' and 'hclust') are part of the 'vegan' package (Oksanen et al. 2019). The role of environmental variables as drivers of the observed fish assemblages was analysed using redundancy analysis (RDA) applying the function 'rda' in the 'vegan' package, which is based on the algorithm described by Legendre & Legendre (2012).

Species responsible for intragroup similarity (similarity percentage analysis, SIMPER) based on the groups obtained from the cluster analysis were identified using a modified version of the R code provided by Farriols et al. (2015), based on the Bray-Curtis similarity distance (Bray & Curtis 1957). Intergroup dissimilarity was determined using the function 'simper' in the 'vegan' package. Additionally, the association between a species and its more strongly associated assemblage was assessed using the indicator value (IndVal; Dufrene & Legendre 1997). Both components of IndVal were calculated (De Cáceres et al. 2012). Only species that were significantly associated with assemblages ( $p < 0.05$ ) and whose component 'A' of the IndVal (also called specificity, i.e. the probability that a sample belongs to the target assemblage) was higher than 0.5 were considered 'specific to an assemblage'. Additionally, species with  $p$ -values  $> 0.05$  but  $< 0.1$  and with an A-value of 1 (only found in 1 assemblage) are shown.

Mean density (number  $\text{km}^{-2}$ ) and biomass ( $\text{kg km}^{-2}$ ) were calculated for each fish assemblage obtained from the cluster analysis. Differences in  $\alpha$  diversity were examined by using species richness (average number of species per sample) and the Shannon-Wiener index ( $H'$ , using  $\log_2$ ; Shannon 1948) including rare species (only present in 1 sample). These analyses were performed using the 'specnumber' and 'diversity' functions in the 'vegan' package. Significant differences among fish assemblages for all metrics were examined by using the nonparametric Kruskal-Wallis test (Kruskal & Wallis 1952). As a complementary analysis,  $\beta$  diversity (Whittaker 1960) was calculated to measure variation in species composition (Anderson et al. 2011) among fish assemblages in the study area using the same data applied

to  $\alpha$  diversity analysis. To identify the processes driving differences in species composition between assemblages, we used the  $\beta$  diversity partition proposed by Baselga & Orme (2012) to distinguish between species replacement, i.e. maintaining similar levels or richness (i.e. turnover), and changes in species richness (Soininen & Hillebrand 2007, Ulrich & Almeida-Neto 2012, Legendre 2014). Therefore, total  $\beta$  diversity (Sørensen dissimilarity:  $\beta\text{SOR}$ ) was calculated using the 'betapart.core' and 'beta.multi' functions of the 'betapart' package (Baselga et al. 2012) on occurrence data (presence-absence) and subsequently deconstructed into 2 processes, the  $\beta\text{SIM}$  index (Simpson dissimilarity), which represents species turnover, and the  $\beta\text{SNE}$  index (richness difference component of Sørensen dissimilarity), which shows the loss or gain of species.

Finally, to analyse in detail the effect of depth on fish diversity distribution, 2 different analyses were performed: (1) the centre of gravity (CoG) value of each species was calculated to sort the species from shallowest to deepest affinities; and (2) the community weighted mean depth (CWMD) for each haul was computed to measure the mean depth niche of the fish catch of each haul. These values were used to compare the depth preferences of the fish assemblages of the seamount summit and the continental slope. The CoG of each species was computed using data from the Demersales historical survey (for the period 1993–2015) and data from the GB applying the following formula:

$$\text{CoG} = \frac{\sum x_i \times z_i}{\sum x_i} \quad (1)$$

where  $x_i$  is the biomass of the species in sample  $i$  and  $z_i$  is the depth in this sample.

The CWMD was computed for each haul using the same methodology as that applied by Punzón et al. (2020) for the community weighted mean temperature but using depth instead of temperature. This method allows us to assign a value of CWMD to each haul based on the preferred depth of the catch and weighted by the abundance of each species in the haul. A limitation to this approach was that the mean depth value for the species only present on the continental slope could not be properly computed using only the samples of this work because of the relatively shallow depth distribution of the Demersales survey in comparison with the samples from the GB. To overcome this limitation, we downloaded all available records in the global open-access Ocean Biodiversity Information System (OBIS, <https://obis.org/>) for species caught in our samples, and we used

these records to compute a preferred depth for each species using the mean depth value of all records (Table S2 in the Supplement). These records were filtered using the same methodology as that applied by Morato et al. (2020) to keep only data with good agreement between the associated depth at its location and the recorded depth in the OBIS database. Finally, differences between the CWMD and mean real depth by haul were calculated and used to compare the mean depth preferences of the fish communities between the summit (combined hauls from both summit assemblages) and the continental slope. All analyses and graphs were made using the R program, version 4.02 (R Core Team 2013), whereas the maps were created using QGIS, version 3.12 (QGIS Development Team 2009).

### 3. RESULTS

#### 3.1. Fish assemblages

In total, 114 different fish species sampled in 33 hauls were analysed in this work. From the initial set of species, 39 were found only once (Table S1) and were removed from the multivariate analysis, although they were included in the richness and diversity analysis. Otter trawl samples were clustered into 5 groups except for 1 haul which did not show similarity with other samples and was classified as 'unassigned' (Fig. 2a). Depth was the main driver structuring fish assemblages. The first dichotomy separated the samples from the deepest part of the GB (seamount flanks assemblage, formed by samples from 1498 to 1785 m depth, Table 1) from the rest of the samples. The second dichotomy ( $\approx 60\%$  dissimilarity) was related with distance to coast and separated the continental slope assemblage (formed by samples from the continental shelf break, with distance to coast values ranging from 30 to 70 km) from the GB samples (more than 200 km away from the coast, Table 1). The third dichotomy ( $\approx 50\%$  dissimilarity) was again depth-related and separated samples of the seamount summit from samples of the seamount break assemblage (formed by samples from 784 to 1064 m depth). Finally, a fourth dichotomy ( $\approx 35\%$  dissimilarity) separated seamount summit samples with coral (seamount summit with coral assemblage) from samples without or with very little coral (seamount summit assemblage, Table 1). The locations of these assemblages within the study area are shown in Fig. 2b.

A clear separation between assemblages was also observed in the RDA biplot where samples are dis-

tributed across 2 diagonal axes (Fig. 3b). The first axis (from the bottom left to the top right) separates the continental slope assemblage (red points) from the GB assemblages. The key factors segregating assemblages along the RDA1 axis were distance to coast (as a proxy for GB versus continental slope) together with correlated sediment variables (mud, organic matter and coarse sand percentages), although other factors such as coral weight and slope also had an important effect on this axis. Sediment variables showed differences between assemblages, with higher values of mud percentage and organic matter in the continental slope than in the seamount summit more characterized by sands with low values of organic matter (Table 1). Furthermore, the 2 assemblages from the seamount summit also showed important differences in coral weight by haul as well as in the frequency of coral in the hauls. The second axis (from left to right) was mainly a depth gradient from the continental slope assemblages to the seamount flanks assemblages, with the summit assemblages in a central location. In addition to depth differences, the seamount flanks also showed lower salinity and temperature values than the other assemblages. The species distribution in the RDA axis (Fig. 3a) showed good agreement with the results observed in the SIMPER analysis (Table 2). Characteristic species from seamount flanks, such as *Rouleina attrita*, *Coelorinchus labiatus*, *Coryphaenoides guentheri* or *Etmopterus princeps*, are on the bottom right side of the biplot, following the depth effect. Characteristic species from the continental slope assemblage, such as *Galeus melastomus*, *Chimaera monstrosa*, *Trachyrincus scabrus* and *Coelorinchus caelorhincus*, are in the bottom-left corner (following the 'distance to coast' axis), whereas species from the seamount summit assemblages, such as *Mora moro*, *Notacanthus bonaparte* and *Epigonus telescopus*, occupied an upper central location in the biplot. Finally, some of the most ubiquitous species, such as *Hoplostethus mediterraneus*, *Etmopterus spinax*, *Nezumia aequalis* and *Lepidion lepidion*, were in the upper left corner of the biplot, following the depth effect but ignoring the distance to coast effect since they were present in both areas (GB and continental slope)

#### 3.2. Indicator species and diversity

Fish assemblages of the continental slope and summit of the seamount showed higher values of density (number  $\text{km}^{-2}$ ), biomass ( $\text{kg km}^{-2}$ ), species richness

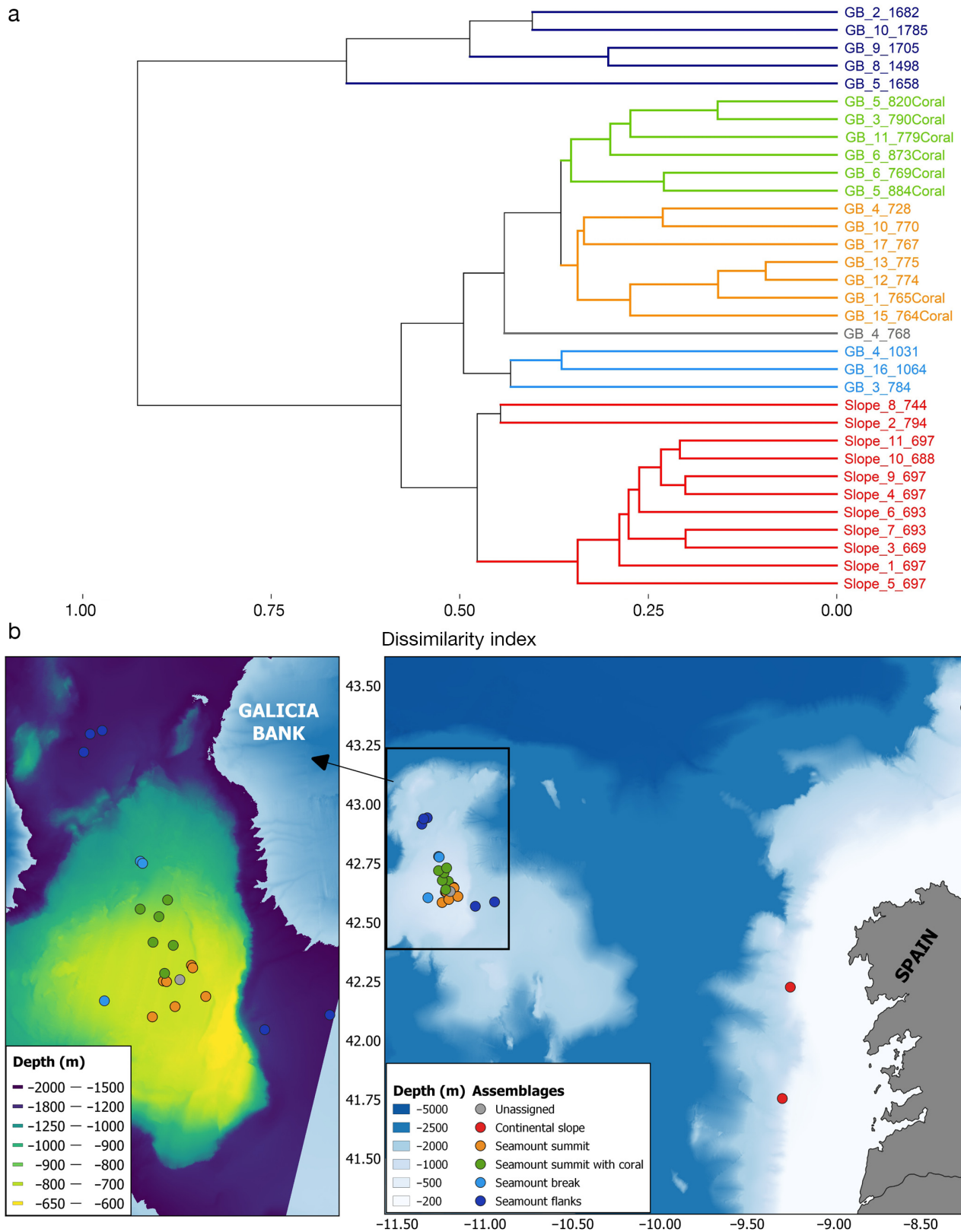


Fig. 2. (a) Bray-Curtis dissimilarity clusters of fish assemblages based on log-transformed density at sampled stations. Labels indicate location ('GB' for samples from the Galicia Bank and 'Slope' for samples from the continental slope), depth (m) and coral presence (for samples with presence of *Desmophyllum pertusum* and/or *Madrepora oculata*). Colours correspond with assemblages shown in (b). (b) Otter trawl sample locations in the study area by fish assemblage

Table 1. Mean, SD, maximum and minimum value of each environmental variable for each fish assemblage

Assemblage		Depth (m)	Distance to coast (m)	Salinity	Coarse sand (%)	Mud (%)	Organic matter (%)	Coral weight (kg km <sup>2</sup> )	Temp. (°C)	Slope
Continental slope	Mean	706	70775	35.82	1.36	21.13	3.00	0.00	11.32	3.01
	SD	34	16978	0.10	0.68	3.28	0.41	0.00	0.22	2.82
	Max	794	79158	36.00	1.99	28.21	3.26	0.00	11.60	10.00
	Min	669	30083	35.63	0.00	19.10	1.79	0.00	10.90	1.46
Seamount summit	Mean	769	198320	35.75	20.38	0.36	1.78	1.38	11.05	0.41
	SD	5	2012	0.02	5.80	0.53	0.11	2.35	0.08	0.50
	Max	775	200564	35.77	23.29	1.17	1.94	5.43	11.13	1.29
	Min	764	195635	35.74	10.05	0.00	1.70	0.00	10.99	0.11
Seamount summit with coral	Mean	802	199793	35.87	15.59	0.44	1.60	134.25	11.13	0.76
	SD	54	3854	0.10	5.17	0.68	0.18	143.43	0.14	0.55
	Max	884	205139	35.99	23.29	1.82	1.81	400.00	11.28	1.71
	Min	728	193041	35.74	10.57	0.00	1.36	0.00	10.93	0.11
Seamount break	Mean	960	206621	35.99	23.14	1.13	1.55	0.00	11.01	1.21
	SD	153	1157	0.03	3.45	0.22	0.16	0.00	0.41	0.71
	Max	1064	207762	36.03	25.13	1.38	1.74	0.00	11.48	1.64
	Min	784	205448	35.97	19.16	1.00	1.46	0.00	10.77	0.39
Seamount flanks	Mean	1665	201942	35.31	4.72	13.32	1.79	0.00	5.93	1.25
	SD	105	21070	0.06	2.35	18.89	0.97	0.00	0.39	0.63
	Max	1785	218048	35.38	6.43	46.31	3.24	0.00	6.36	2.28
	Min	1498	174797	35.27	1.90	2.72	1.12	0.00	5.65	0.76

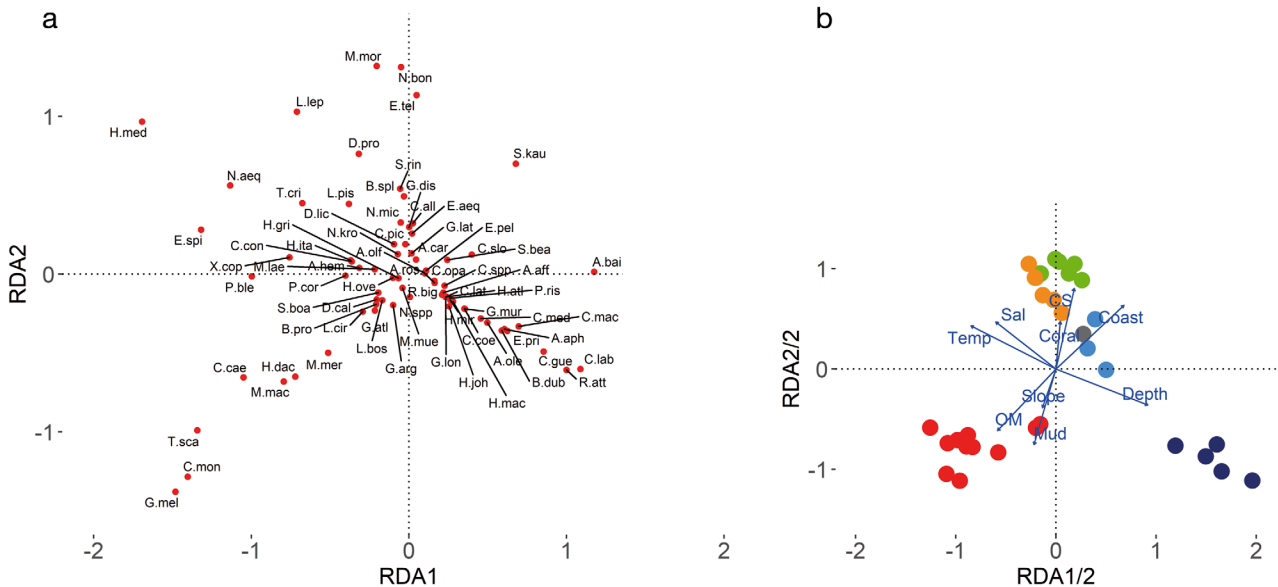


Fig. 3. (a) Species distribution across redundancy analysis (RDA) space (RDA1 explains 31% of the variance, RDA2 explains 21.2%). The species are coded with the first letter of the genus and the first 3 letters of the species name (complete names and abbreviation are shown in Table S2 in the Supplement). (b) Sample distribution across RDA space (the values were divided by 2 to facilitate comparisons with Fig. 2a). Colors representing fish assemblages are as in Fig. 2b. Arrows indicate the effect (direction) and importance (length) of each environmental variable in the RDA (Temp: temperature; Sal: salinity; Coast: distance to coast; Coral: coral weight; OM: organic matter; CS: coarse sand)

and Shannon-Wiener diversity than those assemblages from the seamount break and the seamount flanks (Fig. 4), although these differences were only statistically significant for density ( $p < 0.01$ , Kruskal-

Wallis chi-squared = 15.88,  $df = 4$ ). Total  $\beta$  diversity was high ( $\beta$ SOR = 0.77, Table 3), indicating high dissimilarity among fish assemblages. The main process governing this differentiation was species replace-



Table 2. Cumulative contributions to the similarity (Sim%) by fish assemblage

Species	Sim%
<b>Continental slope</b>	
<i>Hoplostethus mediterraneus</i>	11.5
<i>Galeus melastomus</i>	21.61
<i>Nezumia aequalis</i>	31.5
<i>Chimaera monstrosa</i>	40.66
<i>Trachyrincus scabrus</i>	48.67
<i>Phycis blennoides</i>	55.75
<i>Etmopterus spinax</i>	62.65
<i>Lepidion lepidion</i>	68.41
<i>Coelorinchus caelorhincus</i>	73.9
<i>Xenodermichthys copei</i>	78.53
<b>Seamount summit</b>	
<i>Hoplostethus mediterraneus</i>	13.82
<i>Lepidion lepidion</i>	24.81
<i>Nezumia aequalis</i>	34.96
<i>Mora moro</i>	42.63
<i>Notacanthus bonaparte</i>	49.71
<i>Etmopterus spinax</i>	56.42
<i>Epigonus telescopus</i>	62.18
<i>Phycis blennoides</i>	67.66
<i>Lophius piscatorius</i>	73.1
<i>Trachyscorpia cristulata echinata</i>	78.24
<b>Seamount summit with coral</b>	
<i>Hoplostethus mediterraneus</i>	13.44
<i>Lepidion lepidion</i>	24.51
<i>Nezumia aequalis</i>	34.02
<i>Notacanthus bonaparte</i>	42.74
<i>Mora moro</i>	51.01
<i>Deania profundorum</i>	57.54
<i>Scymnodon ringens</i>	63.68
<i>Etmopterus spinax</i>	69.8
<i>Epigonus telescopus</i>	74.47
<i>Trachyscorpia cristulata echinata</i>	78.49
<b>Seamount break</b>	
<i>Hoplostethus mediterraneus</i>	16.09
<i>Lepidion lepidion</i>	29.19
<i>Trachyscorpia cristulata echinata</i>	41.25
<i>Alepocephalus bairdii</i>	52.63
<i>Mora moro</i>	63.23
<i>Nezumia aequalis</i>	73.82
<i>Epigonus telescopus</i>	83.38
<b>Seamount flanks</b>	
<i>Coelorinchus labiatus</i>	15.3
<i>Coryphaenoides guentheri</i>	28.06
<i>Alepocephalus bairdii</i>	39.54
<i>Rouleina attrita</i>	49.31
<i>Conocara macropteryum</i>	56.79
<i>Apristurus aphyodes</i>	63.49
<i>Etmopterus princeps</i>	69.91
<i>Synaphobranchus kaupii</i>	76.16

ment or turnover ( $\beta\text{SIM} = 0.71$ ), while changes in species richness were responsible to a lesser extent ( $\beta\text{SNE} = 0.06$ ). Total  $\beta$  diversity was higher between the seamount flank assemblage and the rest of the

assemblages, and its different species composition was also mostly explained by the replacement of species ( $\beta\text{SIM} > 0.69$  in all cases). The importance of the turnover effect can also be observed in the indicator values analysis (Table 4). From the 75 fish species considered in the specificity analyses, 37 were found to be 'group-specific'. The seamount flank assemblage showed the highest number of 'group-specific' species (19 species), followed by the continental slope assemblage (10 species). The 2 seamount summit assemblages showed intermediate values, with 3 species for the seamount summit with coral assemblage and 4 for the other summit assemblage. Finally, the seamount break assemblage exhibited the lowest number of fish fauna significantly associated with the assemblage, with only 1 species (*Aphanopus carbo*) from the several which form the assemblage being 'group-specific'. Three species (*Cataetix alleni*, *Entelurus aequoratus* and *Guttigadus latifrons*) were associated with the seamount summit with coral assemblage ( $A = 1$ ), although 2 of them (*E. aequoratus* and *G. latifrons*) had a p-value  $> 0.05$  (0.058 and 0.068, respectively).

### 3.3. Depth CoG and CWMD values

To better understand the effect of the 2 main biodiversity environmental drivers (depth and distance to coast), species were ordered by their depth CoG (Fig. 5). Species absent on the seamount but present on the continental slope were clearly defined by a shallow CoG, ranging from 200 to 500 m. Of the 20 shallowest species, 9 were absent in our otter trawl samples from the GB (including *Merluccius merluccius*, *Lepidorhombus boscii*, *Galeus melastomus* and *Helicolenus dactylopterus*). Species present in both GB and continental slope samples showed a wider range of CoG values, ranging from 200 to 1700 m depth, although most had values shallower than the 1000 m depth according to limitations on continental slope samples. Finally, species detected only on the GB had the deepest CoG, with values ranging from 750 to 1750 m depth. Fig. 5 also shows 2 clear transition zones (at  $\approx 900$  and  $\approx 1500$  m) according to the species bathymetry distribution, allowing the differentiation of 3 groups of species. It is important to highlight that all samples deeper than 900 m were located in the GB; therefore, the absence of deep species from the continental slope is not indicative of the absence of these species in this area but is an artefact of sampling limitations. For the same reason, the CoGs of these species are probably biased

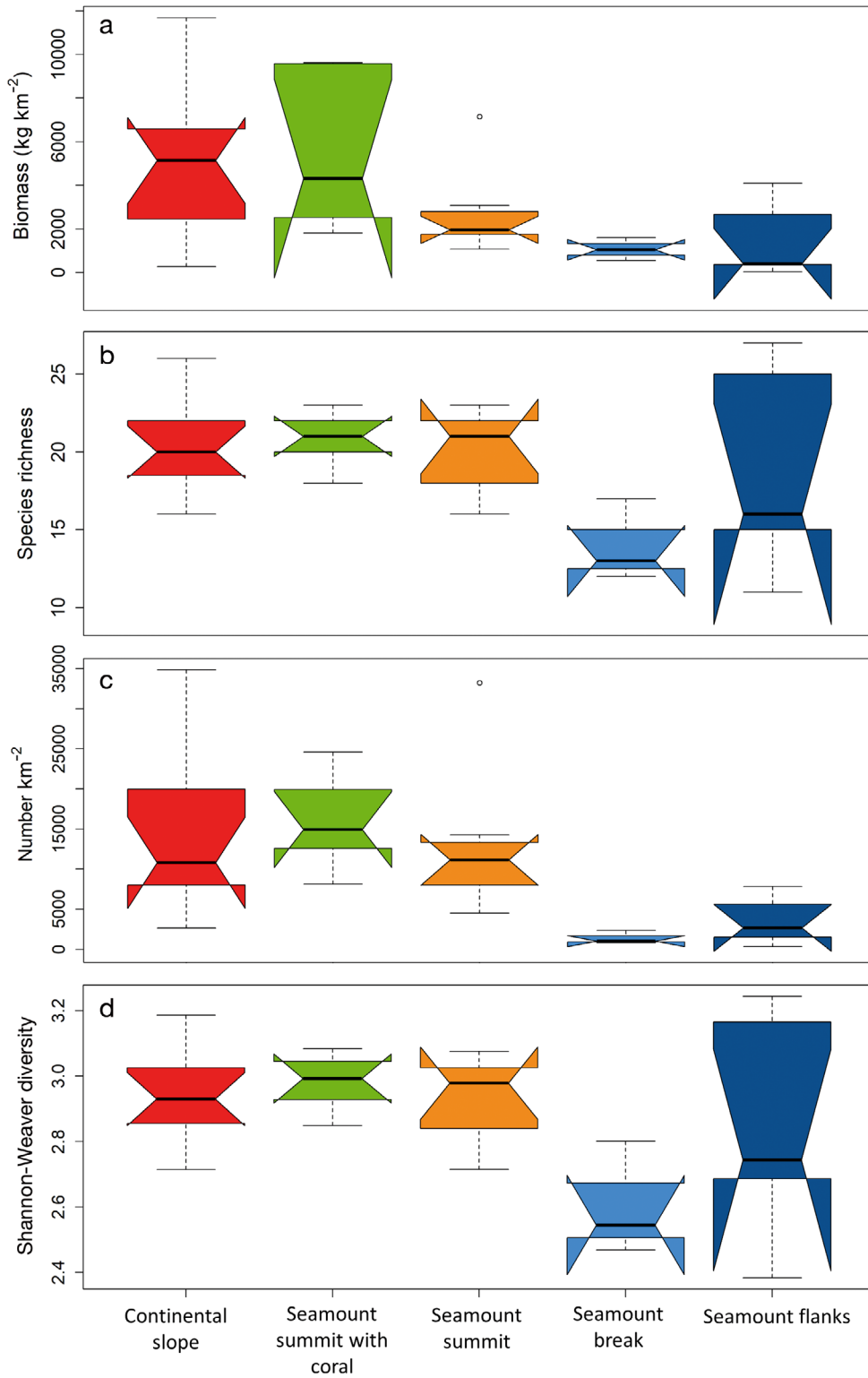


Fig. 4. Comparisons of fish assemblage characteristics: (a) biomass, (b) species richness, (c) density and (d) Shannon-Weaver diversity index ( $H'$ ). Colors represent otter trawl fish assemblages obtained from the cluster analysis. The boxes represent the interquartile range (IQR), the line is the median, and the notches are its confidence interval. The lines of the whiskers extend 1.5 IQR and outliers are identified as points beyond the whiskers

Table 3. Values of replacement or turnover ( $\beta$ SIM), changes in species richness ( $\beta$ SNE) and total  $\beta$  diversity ( $\beta$ SOR), for all the assemblages together and between assemblages

		Continental slope	Seamount summit with coral	Seamount summit	Seamount break
$\beta$ SIM (0.71)	Seamount summit with coral	0.571			
	Seamount summit	0.381	0.333		
	Seamount break	0.385	0.385	0.385	
	Seamount flanks	0.929	0.742	0.857	0.692
$\beta$ SNE (0.06)	Seamount summit with coral	0.028			
	Seamount summit	0.088	0.138		
	Seamount break	0.225	0.260	0.145	
	Seamount flanks	0.004	0.004	0.027	0.126
$\beta$ SOR (0.77)	Seamount summit with coral	0.60			
	Seamount summit	0.469	0.472		
	Seamount break	0.609	0.644	0.529	
	Seamount flanks	0.932	0.746	0.884	0.818

for the deepest species. To solve this limitation, we complemented the CoG values with data from OBIS (Table S2). The OBIS data were used to compute the preferred mean depth of fish regardless of sampling limitations. This value was then used to obtain the CWMD of all hauls carried out on the seamount summit (using hauls from both summit assemblages) and on the continental slope. Finally, the mean value for each assemblage of the difference between the CWMD and the depth of each haul was computed (Fig. S1 in the Supplement). Values  $>0$  mean that in that haul, the CWMD was higher than the real depth; vice versa, negative values mean that in that haul, the CWMD was lower than the real depth. In both assemblages, the CWMD showed lower values than real depth (negative values), but these differences were significantly lower ( $p < 0.001$ , Kruskal-Wallis chi-squared = 9.25,  $df = 1$ ) in the continental slope than on the GB summit, showing that comparatively, the catch composition from the summit seamount has a higher abundance of species with deeper preferences than its equivalent from the continental slope.

#### 4. DISCUSSION

The GB hosts distinct and diverse demersal fish fauna with high  $\beta$  diversity across assemblages and clear differences between the GB summit and similar depths of the adjacent continental slope. Depth was

the main driver in separating the 5 assemblages at both locations, which is consistent with findings of similar studies on invertebrate assemblages of the GB (Cartes et al. 2014, Serrano et al. 2017a,b) and the closest continental slope (Serrano et al. 2008). Most of the observed differences were caused by species turnover between assemblages, mainly at depths of transition zones between water masses, which coincided with observed shifts in the CoG at 900 and 1500 m. Two assemblages from the seamount and one from the continental slope were located shallower than the first transition zone (900 m) in depths mainly affected by the Eastern North Atlantic Central Water mass. The seamount break assemblage was located in intermediate depths at the core of the Mediterranean Outflow Water mass

between the first and second transition zones. This assemblage showed the lowest level of specificity, the lowest mean species richness and significantly lower densities than those recorded in other assemblages, indicating a scarcity of fauna that has also been observed in the invertebrate communities of the GB located in this water mass (Serrano et al. 2017a, Cartes et al. 2021). This same impoverishment has also been identified for the biological condition of benthopelagic shrimp and is likely connected with lower food availability at Mediterranean Outflow Water levels (Cartes et al. 2021). Finally, the seamount flanks assemblage (deepest assemblage) was found below the second transition zone, from near 1500 to 1800 m, in a seabed area affected by Labrador Sea Water. This assemblage showed the highest level of specificity and the highest value of total beta diversity when compared to other assemblages because of the high number of deep fish species (CoG deeper than 1500 m) found only in this assemblage.

##### 4.1. Differences between the GB summit and the closest continental slope

The fish assemblages found in the GB summit were different from the fish assemblages that inhabited the nearest continental slope even though all species found in the GB summit were also present on the continental slope. No fish species were unique to the

Table 4. A (specificity) and B (sensitivity) components of indicator values (IndVal) were calculated (De Cáceres et al. 2012). Only species that were significantly associated with assemblages ( $p < 0.05$ ) and whose A component (the probability that a sample belongs to the target assemblage) was higher than 0.5 were considered specific to an assemblage. Species with a p-value  $< 0.1$  but  $> 0.05$  are shown with an asterisk. Stat: square root of IndVal

Species	A	B	IndVal (%)	Stat	p
<b>Continental slope</b>					
<i>Bathysolea profundicola</i> *	1.000	0.364	36.4	0.603	0.065
<i>Coelorinchus caelorrinchus</i>	0.715	0.909	65.0	0.806	0.001
<i>Chimaera monstrosa</i>	0.839	1.000	83.9	0.916	0.001
<i>Galeus atlanticus</i> *	1.000	0.364	36.4	0.603	0.066
<i>Galeus melastomus</i>	1.000	1.000	100.0	1.000	0.001
<i>Helicolenus dactylopterus</i>	1.000	0.818	81.8	0.905	0.001
<i>Leucoraja circularis</i> *	1.000	0.364	36.4	0.603	0.070
<i>Merluccius merluccius</i>	1.000	0.545	54.5	0.739	0.011
<i>Molva macrophthalma</i>	1.000	0.727	72.7	0.853	0.002
<i>Trachyrincus scabrus</i>	0.681	0.909	61.9	0.787	0.001
<b>Seamount summit</b>					
<i>Chaunax pictus</i>	1.000	0.429	42.9	0.655	0.038
<i>Dalatias licha</i>	0.867	0.571	49.5	0.704	0.005
<i>Hymenocephalus italicus</i> *	0.529	0.571	30.2	0.550	0.101
<i>Neoscopelus microchir</i>	1.000	0.571	57.1	0.756	0.005
<b>Seamount summit with coral</b>					
<i>Cataetix alleni</i>	1.000	0.667	66.7	0.816	0.002
<i>Entelurus aequoreus</i> *	1.000	0.333	33.3	0.577	0.058
<i>Guttigadus latifrons</i> *	1.000	0.333	33.3	0.577	0.068
<b>Seamount break</b>					
<i>Aphanopus carbo</i>	0.692	0.667	46.1	0.679	0.018
<b>Seamount flanks</b>					
<i>Aldrovandia affinis</i>	1.000	0.400	40.0	0.632	0.032
<i>Aldrovandia oleosa</i>	1.000	0.600	60.0	0.775	0.008
<i>Apristurus aphyodes</i>	1.000	0.800	80.0	0.894	0.001
<i>Bathypterois dubius</i>	1.000	0.800	80.0	0.894	0.003
<i>Cataetix laticeps</i>	1.000	0.400	40.0	0.632	0.023
<i>Centroscymnus coelolepis</i>	1.000	0.400	40.0	0.632	0.023
<i>Coelorinchus labiatus</i>	0.847	1.000	84.7	0.920	0.001
<i>Conocara macropterum</i>	0.847	0.800	67.8	0.823	0.001
<i>Coryphaenoides guentheri</i>	1.000	1.000	100.0	1.000	0.001
<i>Coryphaenoides mediterraneus</i>	1.000	0.600	60.0	0.775	0.005
<i>Etmopterus princeps</i>	1.000	0.800	80.0	0.894	0.005
<i>Gadomus longifilis</i>	1.000	0.400	40.0	0.632	0.023
<i>Galeus murinus</i>	1.000	0.400	40.0	0.632	0.023
<i>Halosaurus macrochir</i>	1.000	0.400	40.0	0.632	0.032
<i>Hoplostethus atlanticus</i>	1.000	0.400	40.0	0.632	0.023
<i>Hydrolagus mirabilis</i>	1.000	0.400	40.0	0.632	0.032
<i>Polyacanthonotus rissoanus</i>	1.000	0.400	40.0	0.632	0.021
<i>Rajella bigelowi</i>	1.000	0.400	40.0	0.632	0.023
<i>Rouleina attrita</i>	1.000	0.800	80.0	0.894	0.003

GB, in contrast to results obtained for other faunal groups (Cartes et al. 2014). The main difference between the study areas was the absence of species with shallow depth preferences at the GB summit, which were present on the continental slope (e.g. *Lepidorhombus boscii*, *Merluccius merluccius*, *Helicolenus dactylopterus*, *Molva macrophthalma*, *Galeus melastomus*). Although isolated adults of

some of these species have been observed on the GB, they are scarce in the area (Bañon et al. 2016). Depth is a proxy for other environmental variables such as pressure, temperature, light and food availability. All of these environmental factors associated with depth not only structure fish assemblages as previously described but can also influence fish populations by generating depth-related trends in size distribution such as the 'bigger-deeper' trend. Species showing this trend have a positive correlation between depth and size, with recruits and juveniles inhabiting the continental shelf or upper part of the slope. On the continental slope, seabed areas located at depths similar to the GB summit are available to direct migration of recruited or juvenile individuals from close and shallower seabed areas. These 'shallow-deep' migrations, which are characteristic in the life cycles of several species absent in our samples from the GB summit, such as *M. merluccius* (Woillez et al. 2007), *Lepidorhombus boscii* (Sanchez et al. 1998), *G. melastomus* (Morales-Nin et al. 2003) or *H. dactylopterus* (Santos et al. 2020), are not possible in the summit of an isolated seamount, such as the GB, where there are no nearby shallow seabed areas. Although isolated adults of some of these species have been found in the GB in previous works (Bañon et al. 2016), it is unlikely that these species can colonize the GB with stable populations because of the lack of proper habitats for juveniles, similar to what has been observed for the Rockall Plateau (Neat & Campbell 2011). The depth limit for recruitment imposed by the minimum seamount depth will be more likely to affect shallow

species than species with deeper preferences, explaining why most of the species only recorded on the continental slope had shallow depth niches.

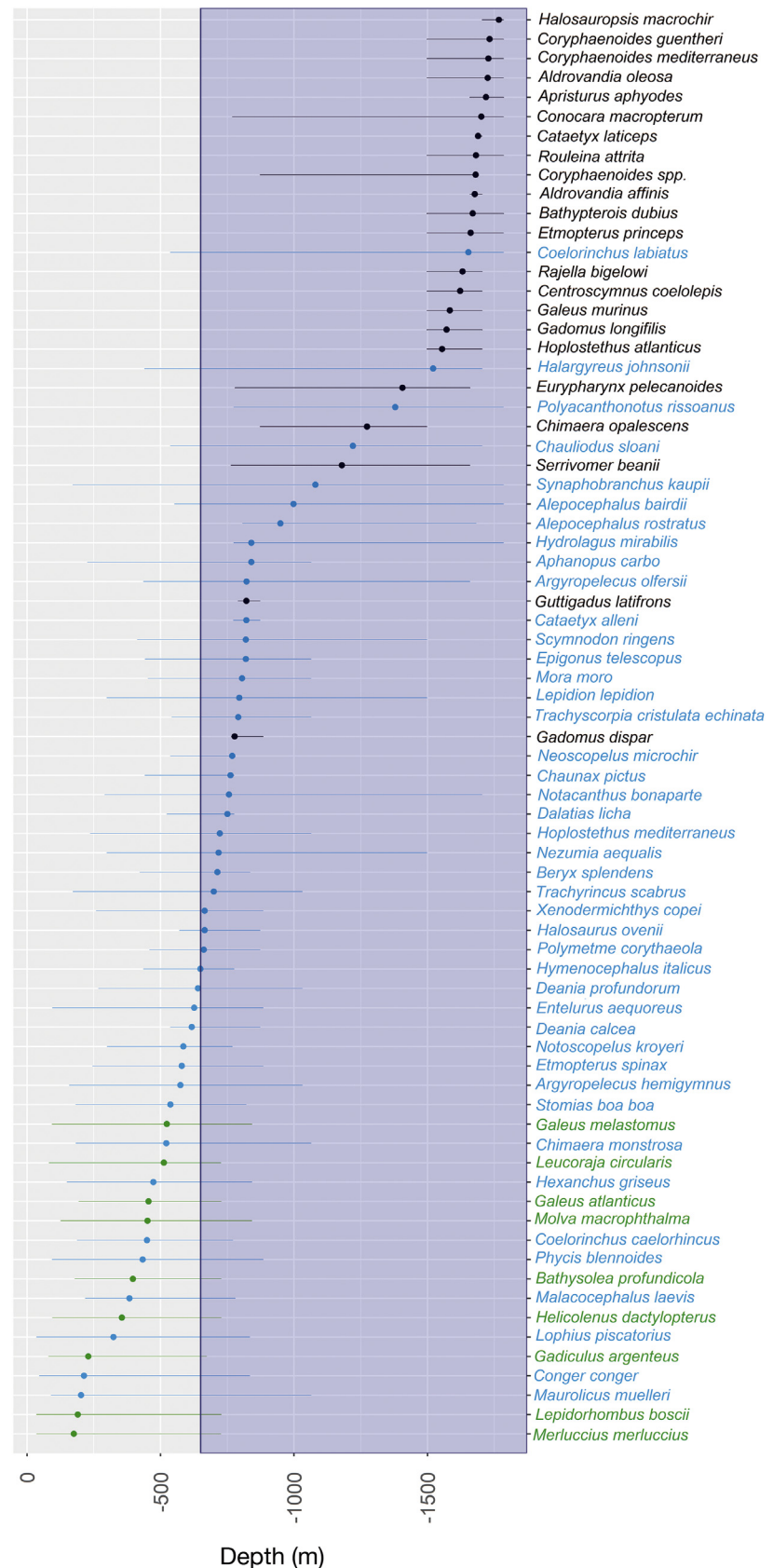
Interestingly, the absence of some of these species from the seamount did not generate a reduction in abundance, Shannon diversity or richness in the summit fish assemblages as observed in previous works (Neat & Campbell 2011, Porteiro et al. 2013). In fact,

species absent from the GB were replaced by species without these depth limitations (mainly species with deeper distributions), which explains the significantly deeper CMWDs observed in the summit samples than in those from the continental slope.

#### 4.2. Effect of cold-water corals on GB summit fish fauna

The presence of cold-water coral patches (*Desmophyllum pertusum* and *Madrepora oculata*) on the GB summit was the third main driver structuring the studied fish assemblages. The differences between both summit assemblages (with and without corals) were related to small differences in species composition and species abundance. The coral assemblage hosted twice the number of rare species (only found in 1 sample) than the other summit assemblage, probably indicating a higher total richness and diversity of this assemblage although there were no significant differences in the mean richness or diversity by haul. Three species (*Cataetix alleni*, *Guttigadus latifrons* and *Entelurus aequoreus*) sampled on more than one occasion were observed only on the seamount summit with coral assemblage. *G. latifrons* has been previously observed to be strongly associated with cold-water corals, together with species of the genus *Gaidropsarus* (*G. argentatus* and *G. granti*, Söffker et al. 2011, Linley et al. 2017, Bello 2018). Two spe-

Fig. 5. Depth distribution of fish species. Dots represent depth centre of gravity (CoG) and lines represent depth distribution range (maximum–minimum). Green represents species present only on the continental slope, blue indicates species present on both Galicia Bank (GB) and the continental slope, and black represents species only detected on the GB. The purple rectangle shows GB depths. Note that the deepest sample from the continental slope was 798 m



cies of this genus (*G. granti* and *Gaidropsarus* sp.) were also found in samples with coral in this work. To our knowledge, no previous works have described the specific attachment of *E. aequoreus* or *C. alleni* to cold-water corals, although 2 individuals of *C. alleni* were recently caught in a haul with abundant living and dead cold-water coral in Porcupine Bank (Bañón et al. 2020). Furthermore, 1 adult female *C. alleni* carrying well-developed embryos was caught in 2020 in a bamboo coral field (RECOMARES0320 cruise, Balearic Basin). Despite these observations, caution is necessary before cataloguing a species as being coral associated. The finding of certain species only caught in hauls with the presence of cold-water corals is potentially interesting for future works on the association between fish fauna and cold-water corals, but without more data, it is not possible to draw solid conclusions. Other species identified as typical of the assemblage seamount summit with coral (*Mora moro*, *Epigonus telescopus*, *Nothacanthus bonaparte*) have been described as typical of cold-water coral habitats but not specific to them (Söffker et al. 2011, Linley et al. 2017), which explains their presence as characteristic species in both summit assemblages. Finally, some species usually abundant in cold-water coral reefs of the European slope, such as *Galeus melastomus*, *Helicolenus dactylopterus* or *Chimaera monstrosa* (D'Onghia et al. 2012, Kutti et al. 2014, Linley et al. 2017) were absent from the GB summit and were scarce within the whole GB (Bañón 2016, Bañón et al. 2016). These specificities in the fish fauna of the cold-water corals of the GB confirm the importance of macro- and mesoscale diversity drivers (such as depth or distance to shallow habitats) in the formation of coral-reef fish communities (Auster 2007). It is important to note that these differences were observed under certain limitations, including no previous knowledge of cold-water coral distribution (which would require a specific sampling design), geolocation error associated with the sampling gear (which can merge in the same sample areas with and without coral) and proximity between samples with and without coral. A more specific approach with more appropriate sampling gears (e.g. non-destructive, fine-scale visual methods) is needed to confirm the results obtained in this work. Despite these limitations, our study offers results that coincide with previous studies that describe cold-water coral reefs as hot spots of biodiversity, potentially hosting specific fauna such as *G. latifrons* or other *Gaidropsarus* species (Ross & Quattrini 2007, Söffker et al. 2011, D'Onghia et al. 2012, Linley et al. 2017).

### 4.3. Other factors

Of course, other factors in addition to the drivers already described can also play an important role in structuring the analysed fish communities. Fishing pressure is quite different between the continental slope and the GB, although at the analysed depth (>650 m), it is low at both sites. Historically, the GB has experienced low fishing pressure (Bañón et al. 2016), in part because of the scarcity of some important commercial species (e.g. *Merluccius merluccius*, *Lepidorhombus boscii*, *Helicolenus dactylopterus*) described in this work. Therefore, although hidden impacts of fishing on the fish fauna of the continental slope are not discarded, the main observed differences in this work in the fish fauna of both areas are not a consequence of differences in fishing pressure but rather an explanation for them.

The environmental conditions of sedimentary habitats differ between the GB and the continental shelf. The GB summit is characterized by organic-poor (1.5–1.7%) middle sands (with high percentages of sand and coarse sand) of pelagic/biogenic origin with a low development of the endobenthic compartment (Cartes et al. 2014, Serrano et al. 2017a,b), whereas the continental slope fishes dwell among very fine sands (with a high percentage of mud) with a higher organic content (3%), advective inputs from the mainland and well-developed endobenthic communities. The low dominance of endobenthic species on the GB summit is especially adverse for benthos feeders (with inferior mouths), which might explain the low densities observed for some of these species (e.g. *Phycis blennoides*, *Trachyrincus scabrus*, *Chimaera monstrosa*). On the other hand, GB species have a higher dominance of plankton and/or suprabenthic feeders with terminal or sub-terminal (protractile in some cases) mouths. Macrozooplankton, micronekton and mesobathypelagic shrimps constituted the main prey for fish in the GB food chain (Peciado et al. 2017). While at the summit we found plankton feeders belonging to mesopelagic Myctophiformes (Myctophidae, *Neoscopelus microchir*), the clearest trend for the seamount flank assemblages was the diversification of the Alepocephalidae (*Alepocephalus* sp., *Rouleina attritta*, *Conocara macropterum*). At these depths, coinciding with the lowest organic matter content in sediments, species in this family mainly prey on gelatinous zooplankton, which are well distributed in the North Atlantic at these depths (900–1500 m; Hargreaves et al. 1984). These observations suggest an important role of the pelagic food chain for seamount-dwelling fish, as previously

reported by other studies (Porteiro & Sutton 2007, Genin & Dower 2008, Preciado et al. 2017).

To our knowledge, this is the first time that the lack of species from the continental slope on a seamount summit has been related with a higher relative abundance of deeper species in its fish communities. This trend has important implications in terms of the vulnerability of these communities to global warming and other anthropogenic pressures. If the trend observed in the GB summit is common to other seamounts with similar summit depths and distance to shallow seabed areas, these assemblages will be more sensitive to warming than their equivalents on continental slopes because the species that form them will have preferences for deeper (and therefore in many cases, colder) habitats. Furthermore, the replacement of cold-water species by species with warmer and shallower affinities predicted for the demersal communities of the continental slope (Punzón et al. 2016, 2021) will work differently on the seamount summit where there are no close shallow seabed areas. In the same way, the biological traits of deep species (long-lived, late maturation) will make these assemblages more sensitive to anthropogenic pressure, a feature accentuated by the isolated nature of these areas that prevent recolonization. It is important to note that despite the efforts made to sample the GB, the work is restricted to one seamount with limitations in terms of the number of samples and seasonality. Thus, caution is needed in interpreting the results of this work and its potential implications. Further studies are necessary to verify the results and to investigate whether the observed trends are present at other seamounts.

#### 4.4. Conclusions

Our work shows that in the GB, the composition of the communities at the top of the seamount is driven by its lack of connectivity with shallower seabed areas, which makes recruitment of species spending early life stages in shallow waters difficult. These connectivity limitations restrict the populations of several species with bigger–deeper trends, but do not affect biodiversity of these communities because they are replaced by species with deeper niches. Because of this, seamount communities at the top have comparatively deeper preferences than their equivalents (at the same depth) in continental areas. Since the lack of nearby shallow seabed areas is a common feature of isolated seamounts, we hypothesize that this characteristic observed at the top of the GB could be present in other seamount summits under

similar conditions. A higher relative abundance of deeper species in the fish communities of the seamount summits as observed in this work can have an important impact on the biological traits of the species in these communities, increasing their vulnerability to warming temperatures and anthropogenic impacts since deep species usually have cold-water preferences, are long-lived and mature late.

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