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Epibenthic communities of sedimentary habitats in a NE Atlantic deep seamount (Galicia Bank)

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ABSTRACT

Galicia Bank is a deep seamount included as Site of Community Importance (SCI) in the Spanish Natura 2000 Network proposal. In the present study, epibenthic assemblages of sedimentary habitats have been described, together with the main environmental factor explaining species and communities distribution. Five epibenthic assemblages have been identified. Depth was the main factor explaining assemblage distribution, and the role of sediment type, water masses, and coral framework presence is also discussed. Three assemblages are located in the summit: the shallowest one (730–770 m), in the boundary between Eastern North Atlantic Central Water (ENACW) and Mediterranean Overflow Water (MOW) water masses is typified by ophiuroids and characterized by medium sands. The second assemblage (770–800 m) typified by the bivalve *Limopsis minuta* and the solitary coral *Flabellum chunii* correspond with medium sands and MOW core; and the third typified by the presence of cold-water coral communities dominated by *Lophelia pertusa* and *Madrepora oculata*, also on the MOW influence. In the border of the summit, in the bank break, an assemblage located in the range 1000–1200 m is dominated by the urchin *Cidaridiscus cidaris* and the sponge *Thenea muricata*. In the flat flanks around the bank, the deepest assemblage (1400–1800 m) is dominated by the holothurian *Benthogone rosea*, in a depth range dominated by the Labrador water (LSW) and in fine sands with highest contents of organic matter. Most of species appeared in a depth range smaller than 25% of total depth range sampled and in <10% of samples. Differential preference of species is evident in the different trophic guilds, with a higher dominance of filter-feeders in the summit and of deposit-feeders in the deepest assemblage, and have clear links with nutrient dynamics in the bank.

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1. Introduction

Seamounts comprise a unique deep-sea environment, usually described as hotspots of biodiversity and refuges of vulnerable fauna. Their special environmental conditions generate singular ecosystem functioning. Seamounts interacting with oceanic currents create flow complexities which include substantially enhanced currents, eddy formation and local upwelling (Boehlert and Genin, 1987). Eddies may become trapped over the seamounts and form closed circulation cells called Taylor columns which may have important effects upon pelagic and benthic ecosystems over seamounts, specifically on nutrients dynamics. Topographic-induced nutrient retention and resuspension allow the presence of well-developed communities of vulnerable

filter-feeders (cold-water corals, sponges) and their accompanying fauna (Genin et al., 1986; Boehlert and Genin, 1987; Rogers, 1994; Flach et al., 2002; Tempera et al., 2012).

Deep seamount communities typically include slow-growing, long-living organisms that are sensitive to mechanical disturbance (Schlacher et al., 2013). This is one of the main reasons to consider seamounts as highly vulnerable, together with the wide range of pressures which can potentially affect them. As part of the necessary effort to preserve these deep-sea ecosystems, the Spanish government has named eleven off-shore areas as Sites of Community Importance (SCI) under the Habitat Directive (Council Directive 92/43/EEC). These areas were shortlisted based on previous knowledge and their priority features studied within the research project INDEMARES (EC contract LIFE 07/NAT/E/000732) and will become Special Areas of Conservation (SACs) upon the development of management plans and the agreement of the European Commission. The main objective of the project

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INDEMARES was to provide the necessary information to establish a network of representative Marine Protected Areas (MPAs) in Spanish waters.

Galicia Bank (GB) is the deepest SCI of the Spanish proposal. This area was considered relevant for research in the framework of the INDEMARES project because of the presence of well-developed and conserved priority habitats such as *Lophelia* and *Madrepora* communities and black and bamboo coral aggregations (Duineveld et al., 2004; Somoza et al., 2014), some of which are catalogued as vulnerable (OSPAR, 2008; Annex I Habitat Directive, 92/43/EEC). Most of the 800 major seamounts catalogued in the North Atlantic occur in high seas (Gubbay, 2003). GB is not that kind of seamount, showing several singularities due to its proximity to the continent, its deep summit (Surugiu et al., 2008) and its location on the confluence of water masses and currents (Cartes et al., 2014).

Seamounts provide a variety of environments resulting of a combination of sharp gradients of depth, slope, substrate type, water masses, currents, etc., which mirrors in the distribution of physical habitats and biotopes (i.a. Boehlert and Genin, 1987; Rogers, 1994; Tempera et al., 2012; Du Preez et al., 2016). Description of benthic biodiversity and habitat preference by deep-sea species is of great interest for the future monitoring on the effects of the GB SAC implementation. Such information is also important for the assessment of the Good Ecological Status in

several indicators of the Marine Strategy Framework Directive (MSFD) concerning habitats conservation, among them, typical species composition, multimetric indices and physical damage of habitats.

In this study we identified epibenthic assemblages dwelling on sedimentary habitats of GB, determine which environmental variables act as key factors explaining communities distribution, and describe the differential use of those habitats by GB deep-sea epibenthic species.

2. Material and methods

2.1. Study area

GB is an isolated non-volcanic seamount (Black et al., 1964), located 120 nautical miles west of the NW Spanish shoreline (Fig. 1). The outline of its summit is almost triangular-shaped, being 75 km long in NNE-SSW direction, 58 km wide in WNW-ESE direction, and with a total surface of 1844 km². Across its top surface, depths range from 600 m (to the SE) to >2000 m (to the W), showing a bank break (significant increase in slope) at around 1000–1400 m. Depth strata 1200–2000 m (called in this paper bank flanks) is a transitional area between summit and bank break characterized by a slight increase in slope.

In the northeastern Atlantic, GB is considered a “coastal” seamount, together with the Ampere, Gorringe, Josephine and Seine banks, in

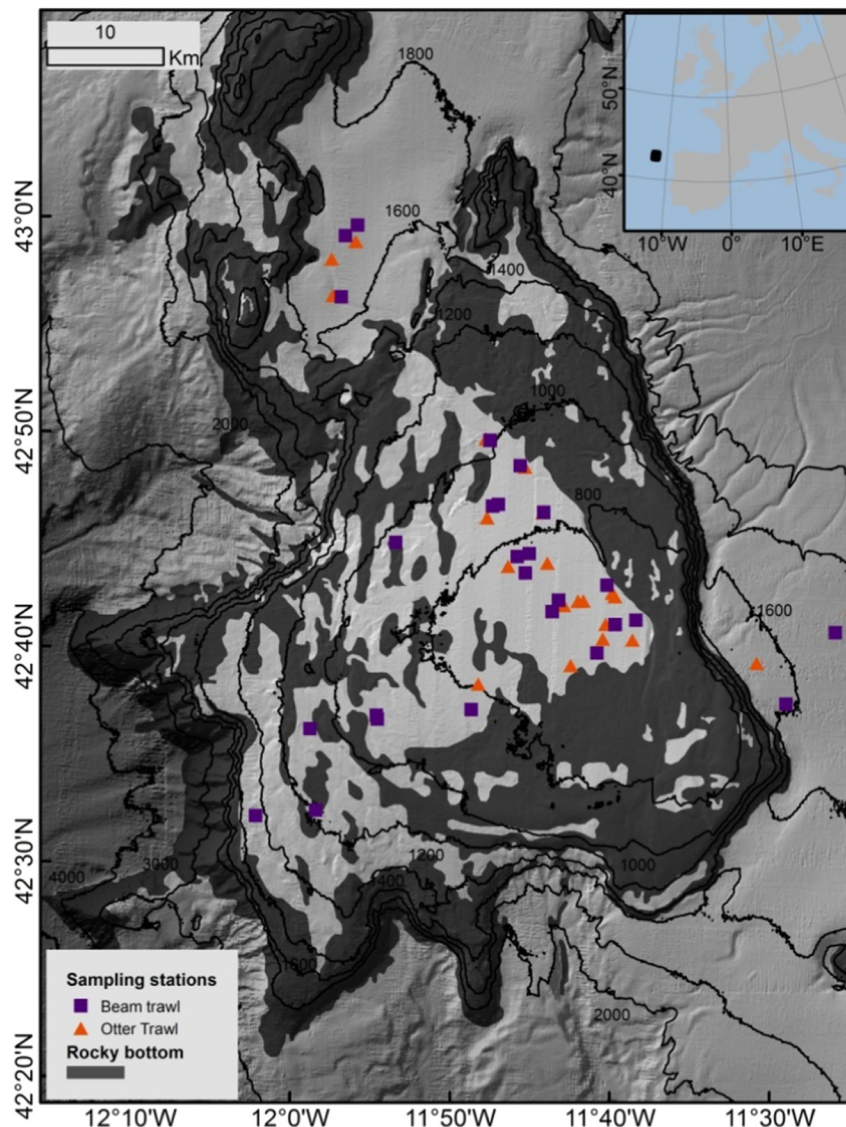


Fig. 1. Study area and sampling stations. Bathymetry from the Spanish EEZ Project (multibeam bathymetry).

contrast with oceanic seamounts, including the Atlantis, Hyeres, Irving, Meteor and Plato banks located in high seas (Gofas, 2007; Surugiu et al., 2008). Nevertheless, some results on inter-seamount faunal similarity highlight the differentiation of GB due to its isolated northern position and deep plateau (Surugiu et al., 2008).

The great interest of GB is based on its location in the middle of main hydrographic drivers in the Atlantic Ocean. Surrounding GB, at depths sampled in this study (up to 1800 m), there are 3 water masses direct/indirectly related with the communities sampled: i) Eastern North Atlantic Central Water (ENACW) occupies the level of hydrographic structures found over the GB summit; ii) below ENACW and to ca. 1500 m, Mediterranean Outflow Water (MOW) characterized by an increase of salinity. MOW has a maximum core, with higher salinity and low-oxygen concentration at depths between 800 m and 1100–1200 m (Ambar and Howe, 1979; Iorga and Lozier, 1999; INDEMARES data). This water mass comes from the Strait of Gibraltar, and reaches velocities of 5–10 cm/s (Iorga and Lozier, 1999), and iii) below MOW, Labrador Sea Water (LSW) that moves southwards from northern latitudes to GB and has a core at 1800 m (Iorga and Lozier, 1999).

Data from INDEMARES project show that sediments on the GB are mainly composed of sands with low organic content. In general, medium sands dominate the summit of the bank, and finer sediments (fine and very fine sands) prevail in the deepest areas (below 1300 m deep), mainly in the northern and southern part of the bank. The sorting coefficient varies from moderate to moderately good down to 1600 m depth, but the selection is poor or bad in the deeper stations (from 1700 m depth). The organic matter content is low, especially in medium sands of the summit (1–2%), but also in the deeper fine and very fine sands (2–3.5%).

2.2. Biological samples

Data was obtained in three multidisciplinary surveys performed on GB in summers of 2009, 2010 and 2011 (Ecomarg0709; BanGal0810; BanGal0811). Megaepibenthic fauna was collected with two different sampling gears, beam trawl and otter trawl (GOC73), in sedimentary grounds. Beam trawls are optimal gear for collecting small epibenthic invertebrates. This sampling gear consists of two steel skids joined by a 3.5 m horizontal bar with a vertical opening of 1 m and mesh size of 10 mm. Trawling was carried out during 15 min at an average speed of 2 knots. The otter trawl used was a standardized GOC73 bottom trawl used in monitoring programs in the Mediterranean (Bertrand et al., 2002). It is a 2-warp trawl with two doors, 35.7 m headline length, 30 m bridles, a vertical height or opening of 2.7 m and 20 mm mesh at the codend. Haul duration was 45 min at 2.8–2.9 knots. Trawl openings were recorded by means of SCANMAR and Simrad ITI Trawl monitoring sensors mounted in the mouths of the trawls.

Faunal data from both samplers is quantitative and expressed in biomass (wet weight). During the three surveys, a total of 22 otter trawls and 26 beam trawls were carried out across the sedimentary grounds of the seamount from 650 to 1800 m deep (Fig. 1).

Sediments were collected with a USNEL box corer (Hessler and Jumars, 1974), a standard quantitative sampler, at the same station where trawls were performed. Temperature (T) and salinity (S) in the water column were measured during each haul using a CTD Seabird SBE-911 (only near-bottom T and S were used).

2.3. Epibenthic assemblages identification

In order to describe epibenthic assemblages, data from otter trawl and beam trawl were analysed by means of multivariate analysis. Those analyses were performed firstly for beam trawl and otter trawl data separately and secondly pooling together the two samplers, being the results very similar (same assemblages were obtained). Because of this, only pooled together results are explained in this paper. Pooling

of beam and otter trawl was performed through a standardization to a common area (kg/km²), obtaining a unique data matrix.

Within the INDEMARES project >800 species have been recorded in the Galicia Bank. Nevertheless, for all multivariate analyses, epibenthic invertebrate species matrix was reduced, considering only those species with a biomass >0.04% of the total biomass and a frequency of occurrence >5%, in order to reduce the variability in the matrix due to the high presence of zeros. The final set analysed consisted of 125 species (Annex 1).

This reduced matrix was log-transformed to minimize the effect of high values. To detect spatial patterns, a cluster analysis was applied using the Bray–Curtis similarity index. The distance matrix was processed with the UPGMA algorithm. Based on the groups obtained by cluster analysis, species responsible of intragroup similarity were identified using the SIMilarity PERcentage analysis (SIMPER). All these analyses were performed using PRIMER 6 package (Clarke and Warwick, 2001).

Differences between assemblages total biomass (kg/km²), species richness (number of species per sample) and Shannon diversity were determined using a Kruskal–Wallis one way ANOVA on ranks. When significant differences were detected, pairwise Dunn's tests were run to identify the assemblages responsible for such differences.

2.4. Environmental characterization of assemblages

Aiming to elucidate the effect of depth in the distribution of each species, the Center of Gravity (CoG: Stefanescu et al., 1992; Cartes et al., 2011) was estimated with the following equation:

$$CoG = \frac{\sum x_i * z_i}{\sum x_i}$$

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

Effect of environmental variables in the spatial distribution of assemblages was determined using canonical analysis, available with the CANOCO 4.5 package (ter Braak and Smilauer, 2002) performed on the same biomass matrix used in cluster analysis. Before the application of direct gradient (canonical) analysis, the length of gradient of the log-transformed biomass per sample of invertebrate species, was assessed by means of Detrended Correspondence Analysis. The resulting gradients were short (below 2.5SD units), and consequently a linear ordination method was used by applying Redundancy Analysis (RDA). The explanatory variables considered were depth, near-bottom temperature, near-bottom salinity, and sediment characteristics, including mean particle diameter (Q_{50}), sorting coefficient (S_0), weight percentage of gravel and coarse sands (>500 μ m), of medium, fine and very fine sands (63–500 μ m), and mud (<63 μ m), and weight percentage of organic matter. The weight of coral framework (dead and alive aggregations and reefs of cold-water corals) has been included in the analysis since it was described as determinant to benthic diversity in previous studies (Cartes et al., 2014). Three nominal (categorical) variables have been also included: water mass affecting the sample (ENACW, MOW, LSW), year and sampling gear (beam trawl, otter trawl). Particle size analysis of sediments was performed by a combination of dry sieving and sedimentation techniques (Buchanan, 1984). Organic matter in the sediment was estimated as weight loss of dry (100 °C, 24 h) weight after combustion (500 °C, 24 h).

The representativeness of the ordination analysis is given in terms of eigenvalues of the axes and variance explained by the biplots. The statistical significance was calculated with the Monte Carlo test (Verdonschot and Ter Braak, 1994) using 999 permutations under the reduced model. The significance of each environmental factor was tested by running the analysis with it as the variable and the other factors as covariables, and again calculated with the Monte Carlo test. Significance of groups obtained in the cluster analysis was also tested using the RDA model. Details of the model and procedure are described in Table 3.

RDA results are presented graphically in a bi-dimensional ordination diagram generated by biplot scaling focused on inter-species distances, in which species are represented by points and environmental variables by vectors. The arrows of the explanatory variables indicate the direction of maximum change of these variables across the diagram. The projection of species categories onto an arrow gives an approximation of their weighted averages related to the variable.

3. Results

3.1. Epibenthic assemblages

Five main clusters were found, assuming an uneven level of similarity in assemblage determination for description purposes, as shown in Fig. 2. Boundaries between clusters were detected at depths 770, 800, 1000 and 1200 m. First dichotomy splits the summit samples (737–1187 m) and those obtained in the deeper bank flank (1460–1809 m) at a level of 92% of dissimilarity. The first cluster groups samples of depths between 737 and 1187 m and the second, depths of 1460 to 1809 m, with a sampling gap between both. Sediment type seem to have a role in the clustering, since the cluster comprising samples from the seamount summit is characterized by medium sands and that with samples of the bank flanks, by fine and very fine sands. Distribution of cluster groups along the GB topography is shown in Fig. 3.

The following dichotomy (80% dissimilarity), within the bank summit cluster, forms two groups, one clustering shallower sites in the range 730–1000 m and one comprising deeper samples from depths between 1000 and 1187 m located in the bank break (BB). The group comprising shallower sites (730–1000 m) is further classified into three clusters after a first dichotomy (78%) around 770 m, and a second one (70%) around 800 m. This latter group can be easily identified with samples where cold-water coral reef was found. Gear used to obtain samples was not a decisive factor (except in cluster BB where otter and beam trawls are clustered separately).

SIMPER analysis (Table 1) highlights faunal differences between clusters and help to characterize the 5 assemblages identified:

- Bank Summit (BS₁) ophiuroid assemblage: shallowest samples (730–770 m) dwelled by a large biomass (1985 kg/km² of ophiuroids of the family Ophiacanthidae (*Ophiacantha densa*, *Ophiacantha* sp. and *Ophiomyces grandis*) and Amphiuroidae (*Amphiura grandisquama*), and by the solitary corals *Deltocyathus moseleyi* and *Flabellum chunii*, and the bivalve *Limopsis minuta*.
- Bank Summit (BS₂) *Limopsis* and *Flabellum* assemblage: samples in the range 770–800 m, similar to the BS₁, but without huge populations of ophiuroids. Typified by the small deep-sea bivalve *Limopsis minuta*, and the solitary coral *Flabellum chunii*, together with crawling crabs and shrimps.
- Bank Summit with CW coral reef (BS_{rf}), at depths ranging from 800 to 1000 m, covered by patches of cold-water coral colonies (*Lophelia pertusa* and *Madrepora oculata*, 315.5 and 306.0 kg/km² of live coral). Together with these two scleractinian species, typifying species are mostly sessile coral epibionts, such as the anthozoans *Acanthogorgia armata*, *Desmophyllum dianthus*, *Parantipathes* sp. and *Swiftia rosea*, the bivalves *Lima marioni* and *Asperarca nodulosa*, and crawling fauna such as different species of decapods crustaceans including *Munidopsis* spp. (most of which were *M. serricornis*), *Munida tenuimana* and *Bathynectes maravigna*.
- Bank Break (BB) *Cidaris* and *Thenia* assemblage: located in the range 1000–1200 m and dominated by the urchin *Cidaris cidaris* and the sponge *Thenia muricata* which explain together more than the 50% of the intragroup similarity. The seastar *Plinthasther dentatus* and the benthopelagic shrimps *Aristaeopsis edwardsiana* and *Systellaspis debilis* are secondary typifying species.
- Bank Flanks (BF) *Benthogone* assemblage: Deepest assemblage (1400–1800 m) clearly dominated by the holothurian of the order Elaspodida *Benthogone rosea* (628.2 kg/km²), accompanied by the leather urchin *Araeosoma fenestratum*, a very distinct arthropod fauna (the crab *Neolithodes grimaldii*,

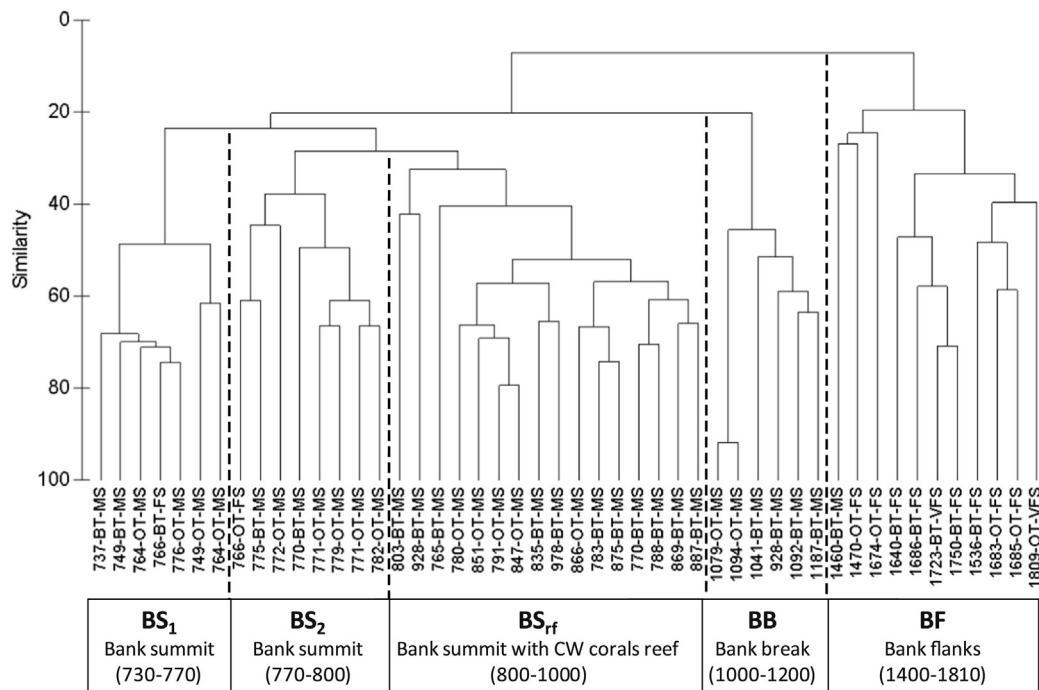


Fig. 2. Cluster analysis of similarity between samples using the Bray-Curtis index on log-transformed biomass values. Labels indicate depth (m), gear (BT - beam trawl, OT - otter trawl), and sediment type (MS - medium sands, FS - fine sands, VFS: very fine sands).

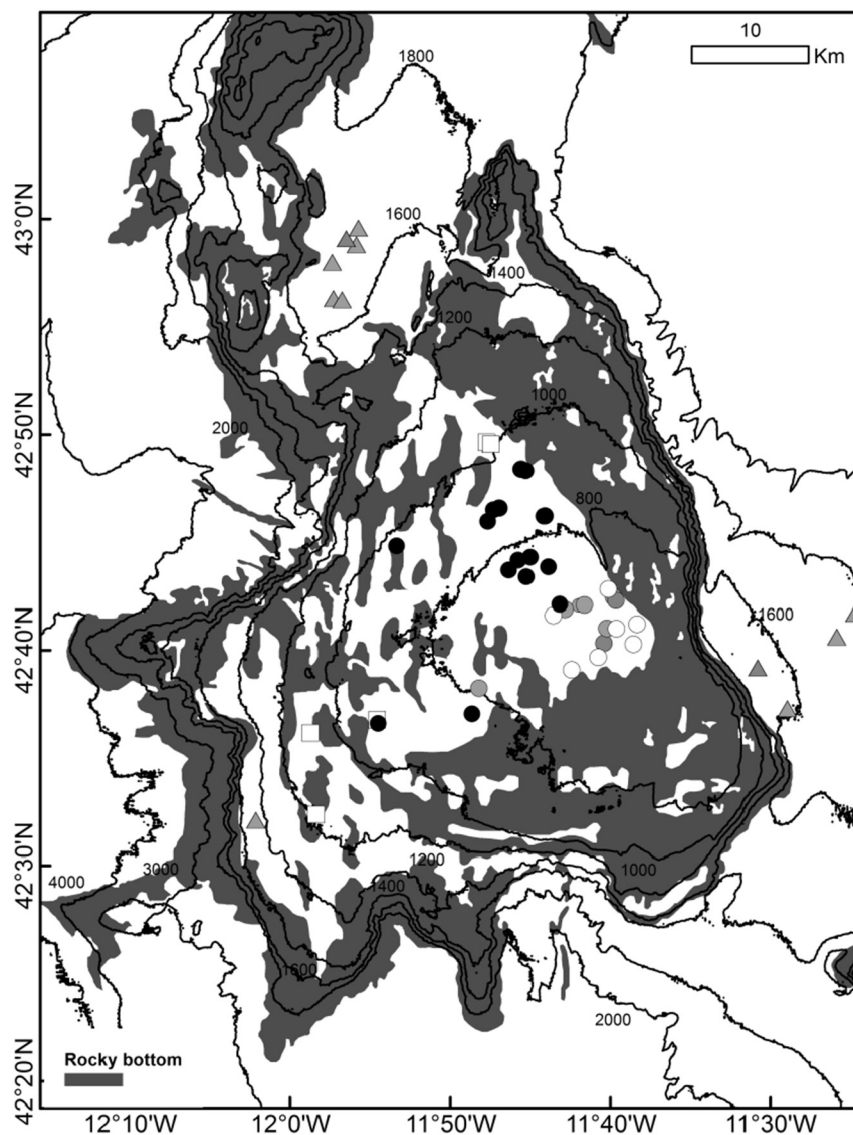


Fig. 3. Map showing the distribution of cluster groups. Symbols represent cluster groups of hauls (BS₁: white circles, BS₂: grey circles, BS₃: black circles, BB: white squares, BF: grey triangles).

Glyphocrangon longirostris or the giant sea spider *Colossendeis colossea*), the scaphopod *Fissidentalium capillosum*, and several anthozoans including the solitary coral *Stephanocyathus crassus*, the seapen *Umbellula* sp., the bamboo coral *Acanella arbuscula* and the gorgonian *Swiftia rosea*.

3.2. Patterns in bathymetric distribution of species

A generalized species substitution with depth has been found. From the 125 species analysed, the higher proportion (71 species, 56% of the total set) appeared in a depth range narrower than 25% of the total depth range sampled. A second group of 36 species (29% of total set) were distributed along 75% or more of the depth range explored.

Regarding frequency of occurrence (FO) from the total set only 7 species occurred in at least 50% of samples, whereas 53 species appeared in <10% of the samples (Annex 1).

Clear depth boundaries characterized by high species renewal or substitution of species can be observed after plotting species first appearance/disappearance vs. depth (Fig. 4). There is a sharp appearance of species between 700 and 900–1000 m, being the disappearance more progressive. Deeper than 1000 m, few species appeared for the first time or disappeared. The range 1200–1485 m shows a gap corresponding

with the slopes of the bank where no samples were obtained. In the 1485–1600 m stratum the number of species appearing and disappearing increases progressively, with a final plateau of appearance in the deepest samples, and the obvious sharp disappearance of remaining species.

These bathymetric boundaries are also evident in Fig. 5 where species CoG are plotted vs. depth. In this figure, a group of species is distributed with preference at depths shallower than 900 m, and another group shows its preferences for the 1400–1800 m depth range. Two ways of utilization of GB depth strata are also evident, with species with wide distribution ranges and species with small distribution ranges. In the summit the number of species with wide depth range of distribution is lower than in the deeper bank flanks.

Some genera are represented in GB with two species that show different ecology (Fig. 5). For example in the pairs *Polycheles typhlops*-*Polycheles laevis*, *Limopsis minuta*-*Limopsis cristata*, *Uroptychus rubrovittatus*-*Uroptychus concolor*, *Munida sarsi*-*Munida tenuimana*, the former species prefer clearly shallower depths (<1000 in *P. typhlops*, <800 in the rest), whereas the latter species of every pair have preference for deeper areas (>800 in *M. tenuimana*, and >1400 m in the others) (Fig. 5, Annex 1).

Epibenthic biomass per haul as a function of depth is shown in Fig. 6 and in Table 2. Biomass followed a U-shaped profile with depth and

Table 1
Cumulative contributions to the similarity (Cum. %) of epibenthic megafauna species by depth range obtained by SIMPER analysis. Cut-off at cumulative contributions of 75%.

	Cum %
Average similarity: 57.2	
BS ₁ - Bank Summit (730–770 m)	
<i>Ophiacantha densa</i>	12.5
<i>Amphiura grandisquama</i>	24.6
<i>Ophiomyces grandis</i>	36.1
<i>Ophiacantha</i> sp.	46.7
<i>Limopsis minuta</i>	66.4
<i>Flabellum chunii</i>	74.5
<i>Deltocyathus moseleyi</i>	78.6
Average similarity: 51.3	
BS _{fr} - Bank Summit with coral reef (780–1000 m)	
<i>Lophelia pertusa</i>	12.7
<i>Madrepora oculata</i>	25.2
<i>Munida tenuimana</i>	37.4
<i>Acanthogorgia armata</i>	47.5
<i>Desmophyllum dianthus</i>	54.8
<i>Munidopsis</i> spp.	61.3
<i>Parantipathes</i> sp.	66.1
<i>Swiftia rosea</i>	69.6
<i>Lima marioni</i>	72.5
<i>Asperarca nodulosa</i>	74.8
<i>Bathynectes maravigna</i>	77.2
Average similarity: 30.35	
BB - Bank Break (1000–1200 m)	
<i>Cidaridius cidaris</i>	36.1
<i>Thenea muricata</i>	56.8
<i>Plinthasther dentatus</i>	69.5
<i>Aristaeopsis edwardsiana</i>	74.8
<i>Systellaspis debilis</i>	75.2
Average similarity: 40.5	
BS ₂ - Bank Summit (780–800 m)	
<i>Limopsis minuta</i>	30.3
<i>Flabellum chunii</i>	46.1
<i>Cancer bellianus</i>	59.7
<i>Chaceon affinis</i>	67.7
<i>Plesionika martia</i>	72.9
<i>Bathynectes maravigna</i>	75.1
Average similarity: 30.9	
BF - Bank Flanks (1400–1800 m)	
<i>Benthogone rosea</i>	26.4
<i>Neolithodes grimaldii</i>	36.8
<i>Araeosoma</i> spp.	43.1
<i>Stephanocyathus crassus</i>	49.0
<i>Colossendeis colossea</i>	53.5
<i>Glyphocrangon longirostris</i>	57.2
<i>Fissidentalium capillosum</i>	60.1
<i>Plinthasther dentatus</i>	62.7
<i>Flabellum chunii</i>	65.3
<i>Acanella arbuscula</i>	67.9
<i>Parapagurus pilosimanus</i>	70.4
<i>Umbellula</i> sp.	72.9
<i>Limopsis cristata</i>	75.2

highest biomass (Chi-sq. = 19.4, $p = 0.001$) was found at depths between 750 and 800 m, in the BS₁ ophiuroid assemblage, the second one in the range 1700–1800 m, due to the holothurians of BF. Around 900 m biomass was also relatively high, attributable to cold-water corals of the BS_{fr} assemblage.

Significant differences were also found in species richness (Chi-sq. = 22.3; $p < 0.001$) being BS_{fr} the richest assemblage, followed by BF and BS₁ (Table 2). BS₁ and BS_{fr} were the assemblages with a higher Shannon diversity (Chi-sq. = 22.3; $p < 0.001$, Table 2).

3.3. Effects of environmental variables on species and assemblages distribution

Environmental variables mean values between assemblages are summarized in Table 2. Greatest differences are in the substrate type

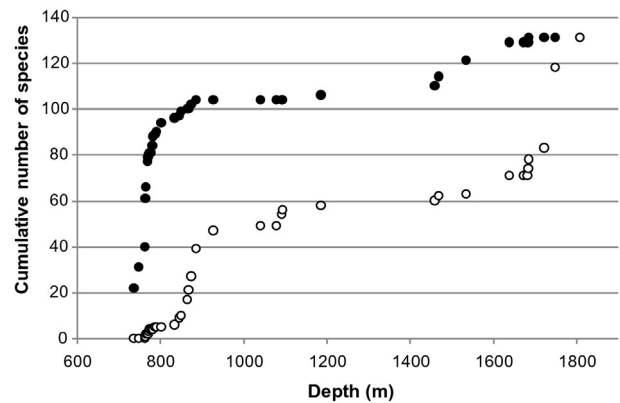


Fig. 4. Appearance (●) and disappearance (○) of accumulative number of species as a function of depth on the Galicia Bank. Sampling gap between 1200 and 1400 m depth.

between summit (medium sands) and flanks (fine and very fine sands with higher organic content).

Assemblages obtained by means of cluster analysis are also consistent in RDA, where environmental variables are included in the analysis. RDA results are listed in Table 3. The full model, which included all the variables and the factor “year” and “sampler” as covariables, was highly significant ($p = 0.001$) and explained almost 50% of the total variance. The RDA applied separately for each environmental factor included as a variable and the others as covariables showed that all of them were significant except temperature and year. Depth was the main factor affecting the species composition, accounting for 13.1% of the explained variance (EV). After depth, the factor “Coral” is the second key variable (9.3% EV) followed by sedimentary characteristics: the presence of coarse and medium sands (CS) and mud. These analyses did not detect significant variations in the species composition between the different surveys (years) and samplers. Using the RDA model on each cluster group as variable and all the environmental factors as covariables, all groups were significant (Table 3).

Fig. 7a shows the ordination of samples in relation to canonical axes (linear combination of environmental variables). Samples are distributed along two diagonal axes. The three summit assemblages are distributed along one of these axes (from the top left to the bottom right of the plot), with slight depth differences (730–800 m) and characterized all by medium sands with low organic content. BS₁ is located in the deepest limit of influence of the ENACW, whereas BS₂ and BS_{fr} are influenced by the MOW. The key factor segregating these three groups along this axis is coral reef presence, splitting clearly those samples where habitat is defined by CW coral. The other diagonal axis, perpendicular to the summit one, is clearly a depth gradient from the summit group, to the deepest assemblage (BF), with the BB assemblage in the middle. The BB assemblage is located in the areas where slope increases, near the bank break, and is still characterized by medium sands. Finally, the BF assemblage, at depths between 1400 and 1800 m, is typified by fine sands with a higher content of organic matter than the other assemblages. Distribution of cluster groups along canonical axis is in coherence with Fig. 2 and Fig. 3.

Fig. 7b shows the faunal differences between assemblages and is in coherence with the SIMPER results (Table 1). Autoecological information of the species inhabiting the different environments can be obtained by combining RDA and SIMPER results, and also bearing in mind the results on faunal renewal described in Section 3.2.

4. Discussion

4.1. Distribution of Galicia Bank epibenthic communities

Galicia Bank harbors a singular and characteristic diversity of environments. The combined effects of depth, slope, substrate type and

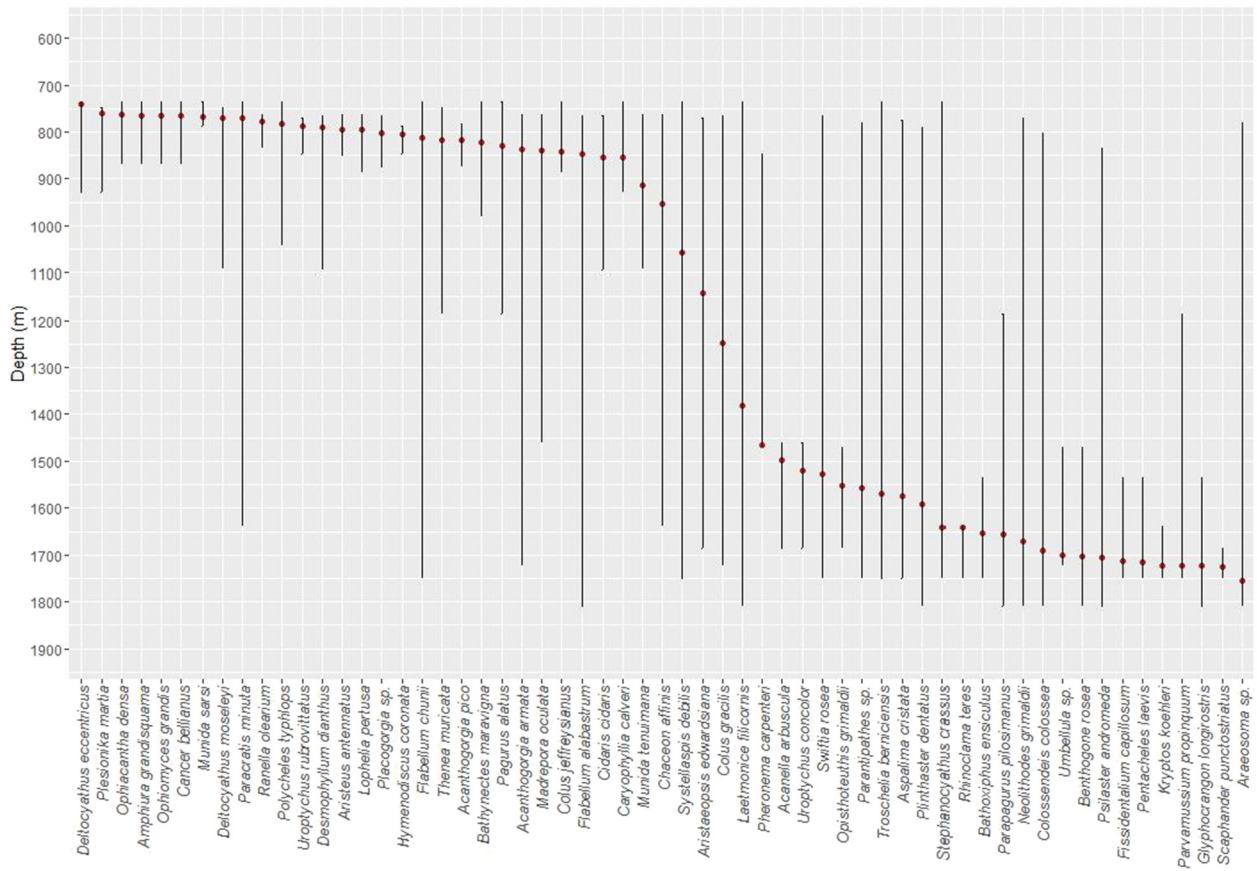


Fig. 5. Depth distribution of a selection of invertebrate species in the GB (more abundant plus more discriminant in analysis). Dots represent depth centre of gravity (CoG) and lines represent depth distribution range (maximum-minimum).

hydrographic gradients presumably shape habitats and communities distributions. Five epibenthic assemblages were identified in sedimentary habitats of the GB, typified by a fauna of deep sea invertebrates and characterized by different environmental conditions.

Boundaries between GB assemblages found in the present study are in coherence with the depth-related Atlantic NE zonation studies, but taking

into account seamount topography, strong currents in the summit area and isolation from mainland as additional key factors. In most seamount studies, depth was the strongest environmental proxy for the community-structuring processes (McClain and Lundsten, 2014; Du Preez et al., 2016). Nevertheless, depth is a complex environmental factor which encompasses information of several variables such as near-bottom

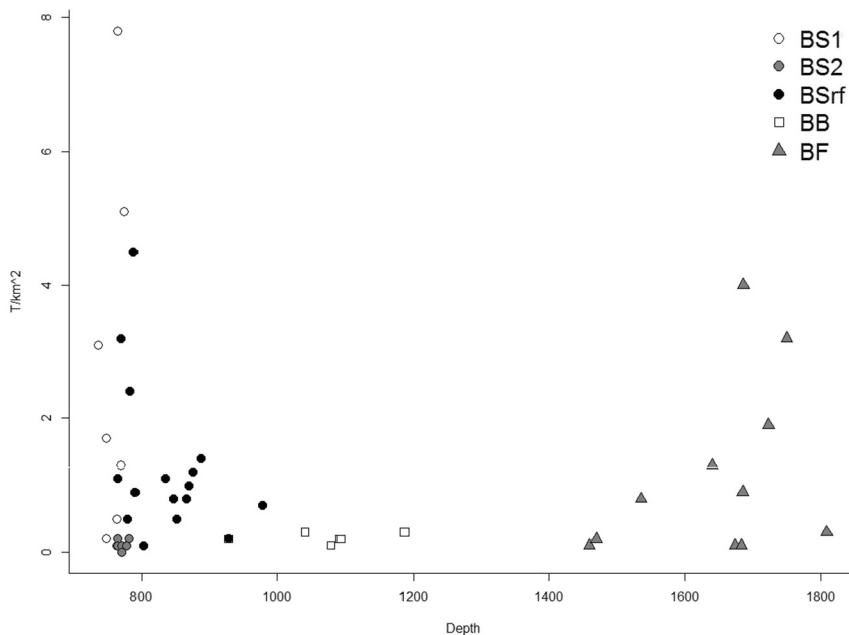


Fig. 6. Evolution of total biomass (1000 kg/km²) versus depth of samples (symbols representing cluster groups). Sampling gap between 1200 and 1400 m depth.

Table 2
Mean values and standard deviation by assemblage of environmental variables and ecological indices. T = bottom temperature, Sa = bottom salinity, type = sedimentary type (MS-medium sands, FS - fine sands, VFS-very fine sands), OM% = organic matter content, Q50, median particle diameter; S₀, sorting coefficient; CS, weight percentage of coarse and medium sands (>500 μm); FS = weight percentage of fine and very fine sands (63–500 μm); mud, percentage weight of mud (<63 μm); coral = weight of coral; S = species richness, W = biomass (T/km²), H' = Shannon diversity.

		Depth	T	Sa	Type	OM%	Q ₅₀	S ₀	CS	FS	Mud	Coral	S	W	H'
BS ₁	Mean	758.6	11.17	35.82	MS	1.85	295.5	1.45	17.03	82.07	0.91	0.0	20.86	2.81	1.92
	SD	13.7	0.16	0.09		0.22	30.9	0.06	4.24	4.21	0.50	0.0	3.58	2.75	0.45
BS ₂	Mean	771.4	11.16	35.83	MS	1.76	337.6	1.37	20.34	79.18	0.48	56.0	15.25	0.13	1.25
	SD	6.4	0.21	0.13		0.10	50.6	0.08	4.80	4.29	0.67	158.3	6.69	0.07	0.33
BS _{rf}	Mean	838.5	11.15	35.91	MS	1.56	308.5	1.36	15.05	84.37	0.57	574.2	28.63	1.29	1.85
	SD	61.0	0.15	0.11		0.19	34.36	0.05	5.19	5.18	0.67	605.3	7.86	1.16	0.30
BB	Mean	1070.2	10.84	35.94	MS	1.52	352.02	1.37	22.21	76.82	0.96	49.3	9.67	0.22	1.29
	SD	84.7	0.18	0.07		0.21	37.67	0.03	6.39	6.13	1.01	120.7	3.67	0.08	0.39
BF	Mean	1646.9	6.07	35.34	FS/VFS	2.72	179.15	1.99	5.68	81.96	12.36	0.0	22.64	1.17	1.26
	SD	112.4	0.57	0.10		0.87	65.01	0.85	3.81	15.46	17.19	0.0	9.76	1.34	0.70

temperature, water masses, substrate type and slope, all of them suitable to be key factors controlling species distribution. This “depth” regulated environment generates communities which were generally distributed as bands encircling the seamount, either on the summit or on the flanks (Du Preez et al., 2016). In a wider context, depth is also considered the main factor in deep-sea ecosystems, with a consistent reporting of bands with faunal boundaries at 500–700, 1000–1400 m, 1600–2000 m and 2500–3000 m (Gage, 1986; Gage et al., 2000; Howell et al., 2002; Olabarria, 2005; Howell, 2010; Cartes et al., 2014), in part coincident with boundaries found at GB for epibenthos.

An outstanding result of the present study is the evidence of how epibenthic species have a differential use of these environmental bands offered by the GB. There are a higher amount of species showing an estenobathyal response (low depth range, low FO) versus a small number of eurybathyal ones (wide depth range, high FO). This fact is in coherence with the results of Cartes et al. (2014) on GB decapods crustaceans who found a low percentage of species appearing along 75% or more of the depth range explored or occurring in at least 50% of samples.

In consonance with this, renewal of some species related to habitat partitioning was especially clear in some congeneric pairs of species with non-overlapping distribution in the bank: *Polycheles typhlops*,

Limopsis minuta, *Urophthychus rubrovittatus* and *Munida sarsi* prefer the shallower areas of the bank whereas *Polycheles laevis*, *Limopsis cristata*, *Urophthychus concolor*, and *Munida tenuimana* presented distributions on deeper bottoms (Fig. 7, Annex 1). Substitution of species that occupy a similar trophic niche, typically close species from a phylogenetic point of view, is a mechanism to avoid competence, and has been documented in oligotrophic areas, such as the deep Mediterranean (Cartes and Abelló, 1992; Cartes, 1993, 1998). GB has also some oligotrophic characteristics since epibenthic and endobenthic environments are impoverished (low mainland advection, strong summit currents, Duineveld et al., 2004; Surugiu et al., 2008) and near-bottom zooplankton is abundant (Papiol et al., 2014). In this sense, deposit feeders are less abundant than filter feeders in the GB summit and when occurring, in the depositional areas of the flanks, they are represented by rather K-strategists like the holothuroid *Benthoosema rosea* (see below).

4.2. Variables typifying communities and species distribution

The shallowest assemblage, with sediment mainly composed by medium sands and typified by ophiuroids (BS₁, 730–770 m) corresponds with the upper slope zone in the continental shelf, which ranges from the shelf slope break (depth of the seasonal thermocline) in the continent to the first faunal discontinuity, which in this region lies at approximately 750 m. The 750 m boundary is associated with the top of the permanent thermocline, the 10 °C isotherm, and the boundary between ENACW and MOW. Several assemblages similar to the BS₁ habitat have been described in the literature at similar depths. Moreover, besides coral and sponges, echinoderms were revealed as one of the key taxa typifying deep sea assemblages (Howell et al., 2002; Metaxas and Giffin, 2004). Metaxas and Giffin (2004) described dense beds of Ophiacanthidae (*Ophiacantha abyssicola*), in sedimentary areas of Nova Scotia, in depths similar to BS₁ on GB. Cherbonnier and Sibuet (1972) and Gage et al. (1983) described the bathymetrical preference of the species *Ophiomyces grandis* for the 200–700 m range. The spatial distribution of GB ophiuroids in an area of strong currents (presence of megaripples) could be a consequence of trophic-hydrographic drivers. Dense populations of *Ophiocten gracilis* able to intercept particles from near-bed flow (Gage, 1983), coincided with the slope current and largely disappeared at 1000 m at the Hebridan slope (Lamont and Gage, 1998; Gage et al., 2000). However, at those mainland continental slopes, macrobenthos at 700 m were represented not only by dense *Ophiocten gracilis*, but also by deposit feeder spatangoids urchins (Gage et al., 2000). The low contribution of deposit feeders at GB summit must be due to the low OM% (around 1.7%, Table 2) in this area compared with continental sedimentary slopes (e.g. in the Balearic Basin, muddy sediments has 4–8 OM%; Cartes et al., 2008, 2009). We argued above about the possible causes of this benthic organic impoverishment: strong currents winnowing organic material (Duineveld et al., 2004), together with an absence of advective inputs from mainland (Surugiu et al., 2008).

Table 3
Results of the redundancy analysis for the invertebrate species biomass matrix, showing the explained variance (EV) and the F-ratio for both the full model, which contains all the variables included in the model, and each individual variable after extracting the effect of the rest as covariables. Note that the sum of the EV for all variables is >100% due to the shared variance. The levels of significance of each explanatory variable are also shown (**p < 0.01, *p < 0.05 and -p > 0.05).

Effect	Covariable	EV	F-ratio	p-Value
<i>Variables included in the RDA</i>				
Full model	Sm, Y	48.5%	3.09	**
Depth (D)	Sm, Y, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	13.1%	7.46	**
Temperature (T)	Sm, Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	0.7%	0.89	-
Salinity (S)	Sm, Y, D, T, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	0.9%	1.73	*
Q ₅₀ (Q)	Sm, Y, D, T, S, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	2.0%	1.43	*
CS (G ₁)	Sm, Y, D, T, S, Q, G _{2,3} , O, S ₀ , Co, W _{1,2,3}	6.6%	5.17	**
FS (G ₂)	Sm, Y, D, T, S, Q, G _{1,3} , O, S ₀ , Co, W _{1,2,3}	5.9%	2.08	**
Mud (G ₃)	Sm, Y, D, T, S, Q, G _{1,2} , O, S ₀ , Co, W _{1,2,3}	7.8%	6.85	**
OM% (O)	Sm, Y, D, T, S, Q, G _{1,2,3} , S ₀ , Co, W _{1,2,3}	1.9%	7.61	**
Sorting coef. (S ₀)	Sm, Y, D, T, S, Q, G _{1,2,3} , O, Co, W _{1,2,3}	2.5%	3.58	*
Coral (Co)	Sm, Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , W _{1,2,3}	9.3%	5.17	**
ENACW (W ₁)	Sm, Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{2,3}	2.8%	1.98	**
MOW (W ₂)	Sm, Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,3}	4.5%	5.18	**
LSW (W ₃)	Sm, Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2}	6.8%	7.55	**
Year (Y)	Sm, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	0.7%	0.98	-
Sampler (Sm)	Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	1.5%	2.61	*
<i>Variables not included in the RDA</i>				
Cluster BS ₁	Sm, Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	6.1%	4.63	**
Cluster BS ₂	Sm, Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	2.5%	2.69	**
Cluster BS _{rf}	Sm, Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	7.3%	6.99	**
Cluster BB	Sm, Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	3.7%	3.42	**
Cluster BF	Sm, Y, D, T, S, Q, G _{1,2,3} , O, S ₀ , Co, W _{1,2,3}	7.5%	7.89	**

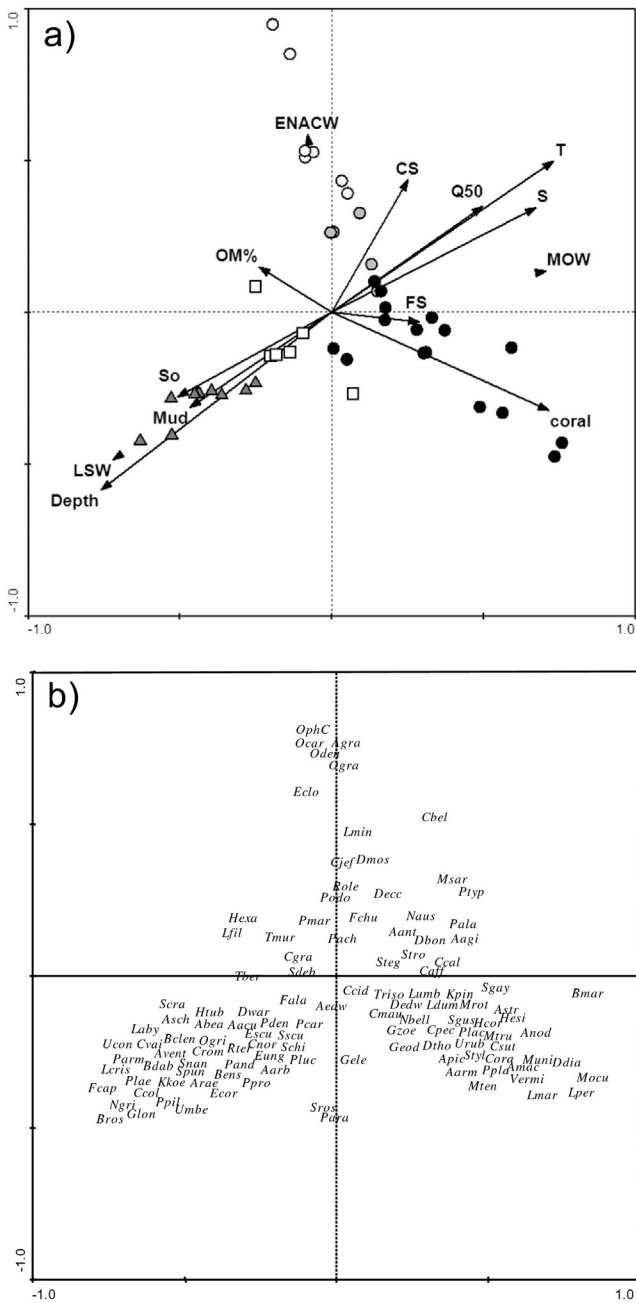


Fig. 7. RDA biplots. a) Environmental variables versus hauls. Symbols represent cluster groups of hauls (BS₁: white circles, BS₂: grey circles, BS_{rf}: black circles, BB: white squares, BF: grey triangles). Q₅₀, median particle diameter; S₀, sorting coefficient; CS, weight percentage of coarse and medium sands (>500 μm); FS = weight percentage of fine and very fine sands (63–500 μm); mud, percentage weight of mud (<63 μm); OM%, weight percentage of organic matter. b) Species. Areas represent groups of hauls. Species codes are in Annex 1.

Some *Ophiacantha* species can act as deposit feeder or suspension feeder depending of resource availability (Gallagher et al., 1998), while *Amphiura* are suspension feeders (Loo et al., 1996) recycling sinking particulate material (marine snow). The depleted δ¹³C signal found for GB ophiuroids at BS₁ (−22.7‰, authors unpub. data), more depleted than the lowest values found in other areas for deep mesopelagic zooplankton (−21.76‰, Fanelli et al., 2011), suggest they are suspension feeders (e.g. *Amphipholis squamata*) which main food source must be marine snow generated by zooplankton over GB summit. Over GB summit near-bottom zooplankton reached relatively high biomass (5.2 gWW/1000 m³, Papiol et al., 2014), being the only food source for epibenthos and fish (Preciado et al., 2016).

BS₂ is an assemblage located in medium sands, deeper than the area of distribution of dense populations of ophiuroids and shallower than cold-water coral reef, and characterized for the small bivalve *Limopsis minuta* and the solitary coral *Flabellum chunii*. The OM in BS₂ decreased probably due to higher hydrodynamism associated with steeper slope at BS₂ stations. The fall of ophiuroids could be also due to such presumable higher disturbance, more than to the decrease of OM. A regime of strong bottom currents favors coarser sediments and low benthos biomass, as happens at the shelf break over Hebridan slope (Gage et al., 2000) or in the Balearic Islands for hyperbenthic peracarids (Cartes et al., 2008). At these more disturbed levels ophiuroids are practically absent.

On the GB at 800 m the BS_{rf} assemblage appears (*Lophelia* and *Madrepora* reef on medium sands, 800–1000 m). This zone, defined in the continent as the upper bathyal zone, ranges from the first faunal discontinuity to the second, which in this region is broadly defined as 750–1100 m (Howell et al., 2010). The 1100 m boundary is associated with changes in slope gradient, current speed, and food supply, which on the GB corresponds to the beginning of the summit break. Sánchez et al. (2014) described that the presence of living cold-water reefs is directly related to a high-energy environment at depths between 700 and 1200 m, between the lower boundary of ENACW and the core of MOW, in a depth range that matches the water density range σ_θ = 27.35–27.65 kg m⁻³ that has been identified as the limit range for cold-water coral distribution in the North Atlantic. BS_{rf} presented significantly highest values of species richness and diversity. Cold-water corals form complex three-dimensional structures that support a diverse macro- and mega-faunal community, by enhancing habitat complexity and heterogeneity, and providing attachment substrate, shelter, feeding, spawning and nursery areas for fish and invertebrate species (Henry and Roberts, 2007; Buhl-Mortensen et al., 2010).

Seamount conditions favor the presence of sessile-vulnerable filter-feeder species such as corals and sponges (Auster et al., 2005; Samadi et al., 2007; Rowden et al., 2010). Sessile filter feeders rely on currents to provide nutrition as well as to remove sediments that may smother them. Consequently, they are usually associated with strong current velocities or unique current patterns such as recirculation gyres, which in turn are indicative of increased concentrations of particles (Moore and Bullis, 1960, Tendal, 1992). GB cold-water coral reefs are located in areas of stronger hydrodynamism such as megaripple sandy areas of the summit and southern slope facing northward currents (Prieto et al., 2013).

In the outer part of the summit, the bank break (BB) assemblage was found. This area corresponds with the limit between the upper and the mid bathyal zone, and is typified by the urchin *Cidaris cidaris* and the sponge *Thenea muricata*. This assemblage is characterized by a different relief and a higher slope, with patches of medium sands surrounded of rocky outcrops. Flow acceleration on upper flanks of seamounts may lead to low sedimentation, hence a higher presence of rock (Boehlert and Genin, 1987) and low OM (1.66%) in the sediments. This habitat is located in the area of influence of the core of MOW (Iorga and Lozier, 1999; Cartes et al., 2014). MOW influence, characterized by higher S and T (Iorga and Lozier, 1999; Fig. 7) of the water mass, coincided in its core distribution with a general impoverishment of fauna (emptiness of species observed in RDA plot with MOW) and of biomass (Fig. 6). This faunistic belt had the lowest diversity in GB and it is, in this sense, similar to the shelf slope break of continent areas (Gage et al., 2000; Cartes et al., 2008), located at shallower depths (150–300 m).

The deepest assemblage, BF, located on the bank flanks beside GB covered by sediments with a high content of mud, and typified by the holothurians *Benthogone rosea*, correspond with the mid bathyal zone, which in this region lies between 1100 and 1800 m. In the BF there was a significant increase in OM% (mean = 1.80%), especially in the deepest areas (reaching 3.2–3.5% in the deepest samples). The 1800 m boundary is associated with the bottom of the permanent thermocline, the 4 °C isotherm and the boundary between MOW and LSW, which could cause changes in food supply and the increase in OM% (Howell

et al., 2010). Higher OM% likely favored the dominance of *B. rosea*, which is a deposit feeder that seems to couple its biological cycle to spring phytodetritus inputs in the Atlantic. Still, OM% values in the sediments were below those found on mainland slopes. *Benthogone rosea* have large eggs that develop into a juvenile without a larval stage (Hudson et al., 2004), so it is a K-strategist species probably adapted to depths with low trophic resources. At 1500–1800 m, coinciding with the depth occupied by BF assemblage, slow-growing lithodids were the dominant decapods among epibenthic invertebrates (Cartes et al., 2014). Lithodids also have life history adaptations (prolonged brooding of embryos, delayed age at maturity (Thatje, 2004) of a K-strategist.

As conclusion, results in the present study show that epibenthic species in this deep seamount are in general controlled by the same factors

than other deep sea ecosystems, mainly depth and substrate type, but also by other seamount-related environmental characteristics such as the influence of different water masses, the low OM% in sediments, attributable to strong currents and mainland isolation, and sea floor inclination. All this factors explain changes in epibenthic biomass.

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Annex 1. List of species analysed. Code = abbreviature used in the RDA biplots, Min Z and Max Z = minimum and maximum depth (m), cogZ = centre of gravity for depth, % range Z = percentage of total depth where this species appear, FO% = frequency of occurrence

Code	Species	Taxon	Min Z	Max Z	cogZ	% range Z	FO%
Aarb	<i>Acanella arbuscula</i>	Cnidaria Anthozoa	1460	1685	1498.2	21.0	8.3
Aarm	<i>Acanthogorgia armata</i>	Cnidaria Anthozoa	764	1723	837.7	89.5	25.0
Apic	<i>Acanthogorgia pico</i>	Cnidaria Anthozoa	783	875	818.7	8.6	6.3
Avent	<i>Aegiochus ventrosa</i>	Crustacea Isopoda	1536	1750	1669.7	20.0	6.3
Amac	<i>Alpheus macrocheles</i>	Crustacea Decapoda	765	928	792.5	15.2	22.9
Aacu	<i>Amphissa acutecostata</i>	Mollusca Gastropoda	749	1723	1713.6	90.9	6.3
Agra	<i>Amphiura grandisquama</i>	Echinodermata Ophiuroidea	737	869	764.8	12.3	18.8
Asch	<i>Anatoma schioettei</i>	Mollusca Gastropoda	803	1750	1564.0	88.3	6.3
Aagi	<i>Antalis agilis</i>	Mollusca Scaphopoda	737	1640	867.1	84.2	29.2
Abea	<i>Aphrocallistes beatrix</i>	Porifera Hexactinellida	803	1750	1258.9	88.3	6.3
Arae	<i>Araeosoma</i> sp.	Echinodermata Echinoidea	780	1809	1755.8	96.0	8.3
Aedw	<i>Aristaeopsis edwardsiana</i>	Crustacea Decapoda	771	1685	1141.0	85.3	22.9
Aant	<i>Aristeus antennatus</i>	Crustacea Decapoda	764	851	794.0	8.1	12.5
Anod	<i>Asperarca nodulosa</i>	Mollusca Bivalvia	765	1460	862.2	64.8	31.3
Astr	<i>Astroporina</i> undet.	Porifera Demospongia	764	1470	825.2	65.9	22.9
Bens	<i>Bathoxiphus ensiculis</i>	Mollusca Scaphopoda	1536	1750	1654.0	20.0	10.4
Bmar	<i>Bathynectes maravigna</i>	Crustacea Decapoda	737	978	821.4	22.5	52.1
Bros	<i>Benthogone rosea</i>	Echinodermata Holothuroidea	1470	1809	1704.3	31.6	20.8
Bdab	<i>Boretrophon dabneyi</i>	Mollusca Gastropoda	1640	1750	1731.0	10.3	6.3
Bclen	<i>Brocchinia cf. clenchi</i>	Mollusca Gastropoda	1686	1809	1739.0	11.5	6.3
Cmau	<i>Calliostoma maurolici</i>	Mollusca Gastropoda	770	772	771.2	0.2	6.3
Cvai	<i>Calliotropis vaillanti</i>	Mollusca Gastropoda	1640	1750	1727.2	10.3	6.3
Csui	<i>Callumbonella suturalis</i>	Mollusca Gastropoda	765	928	807.3	15.2	14.6
Cbel	<i>Cancer bellianus</i>	Crustacea Decapoda	737	866	766.3	12.0	45.8
Ccal	<i>Caryophyllia calveri</i>	Cnidaria Anthozoa	737	928	855.8	17.8	14.6
Caff	<i>Chaceon affinis</i>	Crustacea Decapoda	764	1640	954.5	81.7	37.5
Ccid	<i>Cidaris cidaris</i>	Echinodermata Echinoidea	766	1094	855.7	30.6	33.3
Cirr	<i>Cirripedia</i> undet.	Crustacea Cirripedia	772	1640	1339.6	81.0	14.6
Crom	<i>Cirsonella romettensis</i>	Mollusca Gastropoda	1640	1750	1747.0	10.3	6.3
Ccol	<i>Colossendeis colossea</i>	Pycnogonida	803	1809	1691.2	93.8	16.7
Cgra	<i>Colus gracilis</i>	Mollusca Gastropoda	765	1723	1248.4	89.4	25.0
Cjef	<i>Colus jeffreysianus</i>	Mollusca Gastropoda	737	887	841.4	14.0	6.3
Cora	<i>Coralliophila</i> sp.	Mollusca Gastropoda	765	875	786.5	10.3	10.4
Crin	<i>Crinoidea</i> undet.	Echinodermata Crinoidea	887	1750	1512.6	80.5	8.3
Cpec	<i>Cryptolaria pectinata</i>	Cnidaria Hydrozoa	766	866	822.6	9.3	10.4
Cnor	<i>Cymonomus normani</i>	Crustacea Decapoda	1460	1640	1545.3	16.8	6.3
Dwar	<i>Dacrydium wareni</i>	Mollusca Bivalvia	851	1750	1601.4	83.9	6.3
Decc	<i>Deltocyathus eccentricus</i>	Cnidaria Anthozoa	737	928	741.0	17.8	18.8
Dmos	<i>Deltocyathus moseleyi</i>	Cnidaria Anthozoa	749	1092	769.6	32.0	25.0
Ddia	<i>Desmophyllum dianthus</i>	Cnidaria Anthozoa	765	1094	790.4	30.7	29.2
Dbon	<i>Dichelopandalus bonnieri</i>	Crustacea Decapoda	771	847	781.6	7.1	14.6
Dedw	<i>Diodora edwardsi</i>	Mollusca Gastropoda	780	887	869.1	10.0	6.3
Dtho	<i>Dorhynchus thomsoni</i>	Crustacea Decapoda	743	1640	1008.4	83.7	27.1
Ecor	<i>Ennucula corbuloides</i>	Mollusca Bivalvia	1640	1750	1726.2	10.3	6.3
Epiz	<i>Epizoanthus</i> sp.	Cnidaria Anthozoa	765	1723	828.7	89.4	37.5
Eclo	<i>Ergasticus clouei</i>	Crustacea Decapoda	737	766	768.3	2.7	8.3
Ehan	<i>Eucopeia unguiculata</i>	Crustacea Lophogastrida	803	1750	1279.4	88.3	27.1
Escu	<i>Eucopeia sculpticauda</i>	Crustacea Lophogastrida	1460	1536	1492.3	7.1	8.3
Enor	<i>Eumice norvegica</i>	Annelida Polychaeta	765	887	825.9	11.4	29.2
Fcap	<i>Fissidentalium capillosum</i>	Mollusca Scaphopoda	1536	1750	1713.3	20.0	12.5
Fala	<i>Flabellum alabastrum</i>	Cnidaria Anthozoa	766	1809	846.2	97.3	14.6
Fchu	<i>Flabellum chunii</i>	Cnidaria Anthozoa	737	1750	813.5	94.5	64.6
Gele	<i>Gennadas elegans</i>	Crustacea Decapoda	770	1750	1132.2	91.4	37.5
Geod	<i>Geodia</i> sp.	Porifera Demospongia	770	869	787.2	9.2	14.6
Glon	<i>Glyphocrangon longirostris</i>	Crustacea Decapoda	1536	1809	1723.9	25.5	16.7

Annex 1 (continued)

Code	Species	Taxon	Min Z	Max Z	cogZ	% range Z	FO%
Gzoe	<i>Gnathophausia zoea</i>	Crustacea Lophogastrida	749	1809	996.8	98.9	75.0
Hesi	Hesionidae undet.	Annelida Polychaeta	765	887	827.8	11.4	18.8
Hexa	Hexactinellida undet.	Porifera Hexactinellida	749	1674	1499.0	86.3	29.2
Htub	<i>Hyalinoecia tubicola</i>	Annelida Polychaeta	1470	1809	1716.8	31.6	8.3
Hcor	<i>Hymenodiscus coronata</i>	Echinodermata Asteroidea	788	847	805.9	5.5	8.3
Kpin	<i>Kirchenpaueria pinnata</i>	Cnidaria Hydrozoa	765	866	788.2	9.4	8.3
Kkoe	<i>Kryptos koehleri</i>	Mollusca Gastropoda	1640	1750	1723.1	10.3	8.3
Lfil	<i>Laetmonice filicornis</i>	Annelida Polychaeta	737	1809	1382.1	100.0	16.7
Ldum	<i>Lafoea dumosa</i>	Cnidaria Hydrozoa	765	866	789.1	9.4	10.4
Lmar	<i>Lima marioni</i>	Mollusca Bivalvia	765	1640	845.8	81.6	39.6
Lcris	<i>Limopsis cristata</i>	Mollusca Bivalvia	775	1750	1574.6	91.0	12.5
Lmin	<i>Limopsis minuta</i>	Mollusca Bivalvia	737	1640	770.4	84.2	31.3
Lper	<i>Lophelia pertusa</i>	Cnidaria Anthozoa	764	887	794.7	11.5	31.3
Lumb	<i>Lumbrineris</i> sp.	Annelida Polychaeta	765	887	883.2	11.4	8.3
Laby	<i>Lyonsiella abyssicola</i>	Mollusca Bivalvia	1640	1750	1703.0	10.3	6.3
Mocu	<i>Madrepora oculata</i>	Cnidaria Anthozoa	764	1460	840.8	64.9	37.5
Mtru	<i>Megerlia truncata</i>	Brachiopoda	765	875	828.8	10.3	12.5
Mrot	<i>Modeeria rotunda</i>	Cnidaria Hydrozoa	765	866	789.1	9.4	10.4
Msar	<i>Mumida sarsi</i>	Crustacea Decapoda	737	788	769.0	4.8	29.2
Mten	<i>Mumida tenuimana</i>	Crustacea Decapoda	764	1092	915.0	30.6	33.3
Muni	<i>Munidopsis serricornis</i> & spp.	Crustacea Decapoda	770	887	840.4	10.9	29.2
Nbell	<i>Narella bellissima</i>	Cnidaria Anthozoa	866	1092	948.3	21.1	6.3
Naus	<i>Nausithoe</i> sp.	Cnidaria Scyphozoa	737	875	775.6	12.9	12.5
Ngri	<i>Neolithodes grimaldii</i>	Crustacea Decapoda	770	1809	1670.9	96.9	16.7
Oden	<i>Ophiacantha densa</i>	Echinodermata Ophiuroidea	737	869	764.0	12.3	18.8
OphC	<i>Ophiacantha</i> sp.	Echinodermata Ophiuroidea	737	775	763.8	3.5	16.7
Ogra	<i>Ophiomyces grandis</i>	Echinodermata Ophiuroidea	737	869	765.2	12.3	18.8
Ocar	<i>Ophiura carnea</i>	Echinodermata Ophiuroidea	737	865	763.8	11.9	16.7
Ogri	<i>Opisthoteuthis grimaldii</i>	Mollusca Cephalopoda	1470	1685	1551.6	20.1	6.3
Pach	<i>Pachastrellidae</i> undet.	Porifera Demospongia	764	978	880.1	20.0	6.3
Pala	<i>Pagurus alatus</i>	Crustacea Decapoda	737	1187	829.1	42.0	52.1
Para	<i>Parantipathes</i> sp.	Cnidaria Anthozoa	780	1750	1557.8	90.5	37.5
Ppil	<i>Parapagurus pilosimanus</i>	Crustacea Decapoda	1187	1809	1655.1	58.0	16.7
Ppro	<i>Parvamusium propinquum</i>	Mollusca Bivalvia	1187	1750	1723.5	52.5	6.3
Ppla	<i>Peltaster placenta</i>	Echinodermata Asteroidea	783	1041	842.6	24.1	12.5
Parm	<i>Petalophthalmus papilloculatus</i>	Crustacea Mysida	1536	1750	1672.4	20.0	8.3
Pcar	<i>Pheronema carpenteri</i>	Porifera Hexactinellida	847	1470	1465.6	58.1	4.2
Phyl	<i>Phyllodocidae</i> undet.	Annelida Polychaeta	783	887	838.2	9.7	8.3
Plac	<i>Placogorgia</i> sp.	Cnidaria Anthozoa	765	875	803.5	10.3	8.3
Pmar	<i>Plesionika martia</i>	Crustacea Decapoda	749	928	759.9	16.7	33.3
Pden	<i>Plinthaster dentatus</i>	Echinodermata Asteroidea	791	1809	1591.6	95.0	37.5
Podo	<i>Podospongia</i> sp.	Porifera Demospongia	749	1750	771.5	93.4	6.3
Plae	<i>Polycheles laevis</i>	Crustacea Decapoda	1536	1750	1716.2	20.0	18.8
Ptyp	<i>Polycheles typhlops</i>	Crustacea Decapoda	737	1041	783.4	28.4	50.0
Pluc	<i>Propeamusium lucidum</i>	Mollusca Bivalvia	1536	1686	1611.2	14.0	6.3
Pand	<i>Psilaster andromeda</i>	Echinodermata Asteroidea	835	1809	1705.3	90.9	6.3
Role	<i>Ranella olearium</i>	Mollusca Gastropoda	764	835	778.0	6.6	12.5
Rter	<i>Rhinoclama teres</i>	Mollusca Bivalvia	1640	1750	1642.0	10.3	6.3
Spun	<i>Scaphander punctostriatus</i>	Mollusca Gastropoda	1686	1750	1725.7	6.0	6.3
Schi	<i>Schizopathes</i> sp.	Cnidaria Anthozoa	887	1686	1409.3	74.5	6.3
Sgay	<i>Sertularella gayi</i>	Cnidaria Hydrozoa	765	866	789.1	9.4	10.4
Sipu	<i>Sipunculidae</i> undet.	Sipunculida	749	1750	1655.9	93.4	18.8
Sgus	<i>Spondylus gussonii</i>	Mollusca Bivalvia	765	887	817.5	11.4	14.6
Steg	<i>Stegopoma</i> sp.	Cnidaria Hydrozoa	765	866	790.6	9.4	8.3
Scra	<i>Stephanocyathus crassus</i>	Cnidaria Anthozoa	737	1750	1640.9	94.5	27.1
Snan	<i>Stereomastis nana</i>	Crustacea Decapoda	1640	1750	1714.9	10.3	12.5
Sscu	<i>Stereomastis sculpta</i>	Crustacea Decapoda	875	1640	1476.0	71.4	6.3
Sros	<i>Stichastrella rosea</i>	Echinodermata Asteroidea	765	1092	847.3	30.5	27.1
Styl	<i>Stylasteridae</i> undet.	Cnidaria Hydrozoa	770	887	796.2	10.9	10.4
Sros	<i>Swiftia rosea</i>	Cnidaria Anthozoa	765	1750	1527.6	91.9	54.2
Syll	<i>Syllidae</i> undet.	Annelida Polychaeta	875	887	882.5	1.1	6.3
Sdeb	<i>Systellaspis debilis</i>	Crustacea Decapoda	737	1750	1057.0	94.5	81.3
Tere	<i>Terebellidae</i> undet.	Annelida Polychaeta	766	1092	792.3	30.4	12.5
Tmur	<i>Thenea muricata</i>	Porifera Demospongia	749	1187	818.0	40.9	31.3
Triso	<i>Trisopathes</i> sp.	Cnidaria Anthozoa	851	1809	902.3	89.4	8.3
Tber	<i>Troschelia berniciensis</i>	Mollusca Gastropoda	737	1750	1570.6	94.5	12.5
Umbe	<i>Umbellula</i> sp.	Cnidaria Anthozoa	1470	1723	1701.7	23.6	12.5
Ucon	<i>Uropyichus concolor</i>	Crustacea Decapoda	1460	1686	1520.3	21.1	10.4
Urub	<i>Uropytychus rubrovittatus</i>	Crustacea Decapoda	770	847	787.2	7.2	18.8
Vermi	<i>Vermiliopsis</i> sp.	Annelida Polychaeta	766	978	828.8	19.8	20.8

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