Bathyal infaunal communities from a deep seamount (Galicia Bank, northeast Atlantic)

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Summary: Seamounts are isolated topographic elevations rising steeply from the ocean floor that are characterized by high spatial heterogeneity and topographic complexity. They offer a large number of microhabitats that favour faunal diversity as well as fish feeding and spawning grounds. Though there is increasing research interest in seamounts, it is most often focused on studying large suspension feeders or fish populations, while the infauna is usually neglected. In this paper, we studied the infaunal macrobenthic diversity and distribution of sedimentary habitats on the Galicia Bank (northwest Iberian peninsula), as well as their links with the environment. We sampled 28 sites (683–2274 m depth) and identified more than 1300 specimens from 182 taxa, mostly polychaetes (67% of the total). Sediments were mainly sandy (medium, fine and very fine sands) with low levels of organic matter. We found three major macrobenthic assemblages through multivariate analyses: A, with medium depths and the lowest abundances; B, the shallowest, with medium sands and intermediate abundances; and C, the deepest and most diverse with the finest sediments. Depth, mud content and median grain size were best related to macrofauna distribution patterns, separating shallow environments with medium sands from deeper ones with finer sediments.

Keywords: benthic infauna; soft bottom; Galicia Bank; seamount; deep sea; northeast Atlantic.

Comunidades batiales infaunales de una montaña submarina (Banco de Galicia, Atlántico nororiental)

Resumen: Las montañas submarinas son elevaciones topográficas aisladas que se elevan abruptamente desde el fondo oceánico y se caracterizan por una alta heterogeneidad espacial y complejidad topográfica. Ofrecen un gran número de microhábitats que favorecen la diversidad faunística, así como las zonas de alimentación y desove de los peces. A pesar del creciente interés de la investigación sobre las montañas submarinas, la mayoría de las veces se centra en el estudio de grandes suspensívoros o en las poblaciones de peces, y no tiene en cuenta la infauna. En este trabajo se estudia la diversidad macrobentónica de la infauna y la distribución de los hábitats sedimentarios del Banco de Galicia (Noroeste Ibérico), así como su relación con el ambiente. Se muestrearon 28 estaciones (683-2274 m de profundidad) y se identificaron más de 1300 especímenes pertenecientes a 182 taxones, en su mayoría poliquetos (67 % del total). Los sedimentos fueron principalmente arenosos (arenas medias, finas y muy finas), con bajos niveles de materia orgánica. A través de análisis multivariantes se encontraron tres grandes agrupaciones macrobentónicas: A, de profundidades medias y las abundancias más bajas; B, con las profundidades más someras, arenas medias y abundancias intermedias; y C, la más diversa, la más profunda y con los sedimentos más finos. La profundidad, el contenido en fango y el tamaño medio de grano fueron las variables que mejor se relacionaron con los patrones de distribución de la macrofauna, separando los ambientes poco profundos con arenas medias de los más profundos con sedimentos más finos.

Palabras clave: infauna bentónica; fondos blandos; Banco de Galicia; montaña submarina; aguas profundas; Atlántico Nororiental.

INTRODUCTION

Seamounts, underwater mountains or isolated topographic elevations rising steeply from the ocean floor, have summits at least 100 m above the deep-sea floor (hills <500 m; knolls >500 m; and seamounts >1000 m from the seafloor; Yesson et al. 2011). The total number of deep-sea seamounts is still uncertain, and the studies show great differences in global estimates (Morato et al. 2013). However, seamounts cover a significant portion of the seafloor, forming one of the largest ocean biomes (Rogers 2018) and showing high spatial heterogeneity and topographic complexity (Rogers 2004). Seamounts offer a variety of environments by combining strong gradients of depth, slope, substrate type, water masses, currents, etc., which are reflected in the physical habitat and biotope distribution (Boehlert and Genin 1987, Rogers 1994). The seamount relief is an obstacle to currents, creating local upwellings and closed circulation cells known as Taylor columns (Boehlert and Genin 1987, White et al. 2007). These are related to the arrival of nutrient-rich deep water, which leads to increased productivity in the upper seamount regions (Rogers 2004) and has a functional role in increasing local food supply, erosion and sediment deposition (Rogers 1994). Seamounts also provide essential ecological habitats, thus affecting faunal diversity, offering a large number of microhabitats with particular hydrographic, productivity and substratum characteristics (Ramírez-Llodra et al. 2010), as well as suitable habitats for fish feeding and spawning grounds (Wessel et al. 2010).

Despite the remoteness of deep-sea seamounts and the challenge of accessing them, current knowledge of them is increasing thanks to a reduction in the technical limitations to the exploration of deep-sea environments (Rowden et al. 2010), and research attention is focusing particularly on ecosystem ecology and hydrography (Davies et al. 2015). Accordingly, seamounts seem not to be ecologically isolated habitats because, though they differ in structure (González-Irusta et al 2021), their communities may harbour comparable assemblage compositions to those of adjacent areas (Consalvey et al. 2010, Clark et al. 2012). However, some sampling efforts have inaccurately reported high levels of endemism (Clark et al. 2012, De Forges et al. 2000).

Seamount research is often biased to study fishes or large suspension feeders, such as corals and sponges. Thus, soft-bottom infauna remains poorly studied in comparison with hard bottom biota (Bongiorni et al. 2013, Chivers et al. 2013, Rogers 2018), despite playing a key role in plankton/benthos interactions and being a fundamental food source for pelagic organisms such as fish (Sautya et al. 2011).

The present paper focused on the Galicia Bank seamount (northwest coast of Spain), which was included in the ninth update of the Sites of Community Importance for the Atlantic Biogeographical Region list in November 2015, as part of the necessary efforts to preserve this deep-sea ecosystem. Also, it is one of the areas under evaluation for habitat monitoring in the European Union Marine Strategy Framework Directive (2008/56/CE). The benthic and pelagic ecosystems of the seamount and the physical processes supporting them, together with its geology and geophysics, were the focus of the INDEMARES (LIFE+) project "Inventory and designation of marine Natura 2000 areas in the Spanish sea" (www.indemares.es; EC contract LIFE 07/NAT/E/000732). Its main objective was to identify, protect and conserve valuable areas under the Habitats Directive, providing the necessary information to establish a network of representative marine protected areas in Spanish waters. Framed within this multidisciplinary investigation, this paper specifically deals with the benthic macroinfauna.

The Galicia Bank has probably been known by Galician fishermen for decades, but the scientific information on its biology and ecology is much more recent, likely due to its difficulty of access and depth (Gofas et al. 2021). However, it harbours a diverse soft-bottom megafauna including decapod crustaceans (Cartes et al. 2014), fish, corals and other habitat-forming organisms (Serrano et al. 2017a); a single study on the macroinfauna reports information only at family level (Lourido et al. 2019). The nutrient dynamics and the available trophic resources are predominantly pelagic, with the very reduced benthic compartment being conditioned by grain size and organic matter contents, which are driven by the strong currents dominating the area and its isolation from the mainland (Serrano et al 2017a).

The present paper studied the composition (diversity and abundance patterns), spatial distribution and community structure of the infaunal macrobenthic taxa of the Galicia Bank seamount, comparing them with those from surrounding areas of the North Atlantic and discussing their relationships with the prevailing environmental factors.

MATERIAL AND METHODS

Study area

The Galicia Bank, a non-volcanic coastal seamount located 120 miles off the northwest coast of Spain, has a total surface of 1844 km², is separated from the continental slope by a 2500 m deep channel, and is surrounded by deep abyssal plains: the Galicia Interior Basin (east), the Iberian Abyssal Plain (west) and the Biscay Abyssal Plain (north). Its summit is at 625 m depth (Serrano et al. 2017a) and its total extent is difficult to evaluate, because its eastern zone shows a very steep slope of bare rock with a 600 m peak and its northwest zone slopes from 800 m depth to the abyssal plain. The seamount is basically composed of basaltic lavas, with sediments of pelagic origin covering an uplifted oceanic crust (Ercilla et al. 2011) and showing small surface ripples in the shallow part, which are indicative of the high current velocities (5–30 cm.s⁻¹) (Flach et al. 2002, Duineveld et al. 2004). It is also characterized by its proximity to the continent, its deep summit, its isolated northern position, and its location at the confluence

of the dominant water masses and currents of the area (Surugiu et al. 2008, Serrano et al. 2017a).

In fact, the Galicia Bank is located in an upwelling area where the nutrient-rich waters over the bank give rise to high primary productivity. There are also complex water mass influences at different depths: the East North Atlantic Central Water from the surface to 500–600 m depth; the Mediterranean Water (MOW) progressing northwards from the Gulf of Cádiz along the western Iberian coasts and acting as a high salinity vein with a core at 1000 m depth; and the deeper Labrador Sea Water, spreading from the northwest with a local core at about 1800–1900 m (Cartes et al. 2014, Serrano et al 2017a).

The Galicia Bank sediments are overall sandy, with relatively homogeneous medium sands throughout the whole summit until 1000 m depth, followed by a bathymetric gradient towards fine and very fine sands at 1300 m depth. The sorting coefficient varied from moderate to moderately good down to 1600 m depth and from poor to bad at 1700 m depth (Serrano et al. 2017a). The organic matter content was 1.9% on average, with a maximum of 3.5% in the deepest areas.

Sample collection

Within the framework of the INDEMARES (LIFE+) project, two multidisciplinary surveys were carried out in summer on board the RVs *Thalassa* (2010) and *Miguel Oliver* (2011). Undisturbed samples were collected using a quantitative USNEL box corer (Hessler and Jumars 1974, Gage and Tyler 1991) of 0.09 m^2 (30×30 cm) with a subsample of 0.017 m^2 (17×10 cm) extracted for sediment analyses. Twenty-eight sampling stations were selected in low backscatter areas (i.e. soft sediments), as indicated by a multibeam echosounder, from 683 to 2274 m depth (Fig. 1) (see Lourido et al. 2019 for further details).

Infaunal samples were carefully sieved on board through a 0.5 mm mesh sieve using sea water. The retained material was anaesthetised with $MgCl_2$ and preserved with an 8% buffered formaldehyde seawater solution stained with Rose Bengal. All organisms recovered were sorted in the laboratory, identified to the lowest possible taxonomic level and preserved in 70% ethanol. Sipuncula and Nemertea were grouped as "others". All taxa were then assigned to five trophic categories: carnivores, surface-deposit feeders, subsurface-deposit feeders, suspension feeders and "remaining" (including omnivores, herbivores and scavengers).

Samples for sediment analyses were frozen on board to be later processed in the laboratory. Particle size was analysed through dry sieving for the coarse fraction (>62 μm) and by laser diffraction particle size analyser (Mastesizer 2000) for the finer fraction (<62 μm). The median grain size (Q_{50}) and sorting coefficient (S_0) (Trask 1932) were also determined. Organic matter contents were estimated as losses in weight of dried samples (100°C, 24 h) after combustion (500°C, 24 h) (Buchanan 1984).
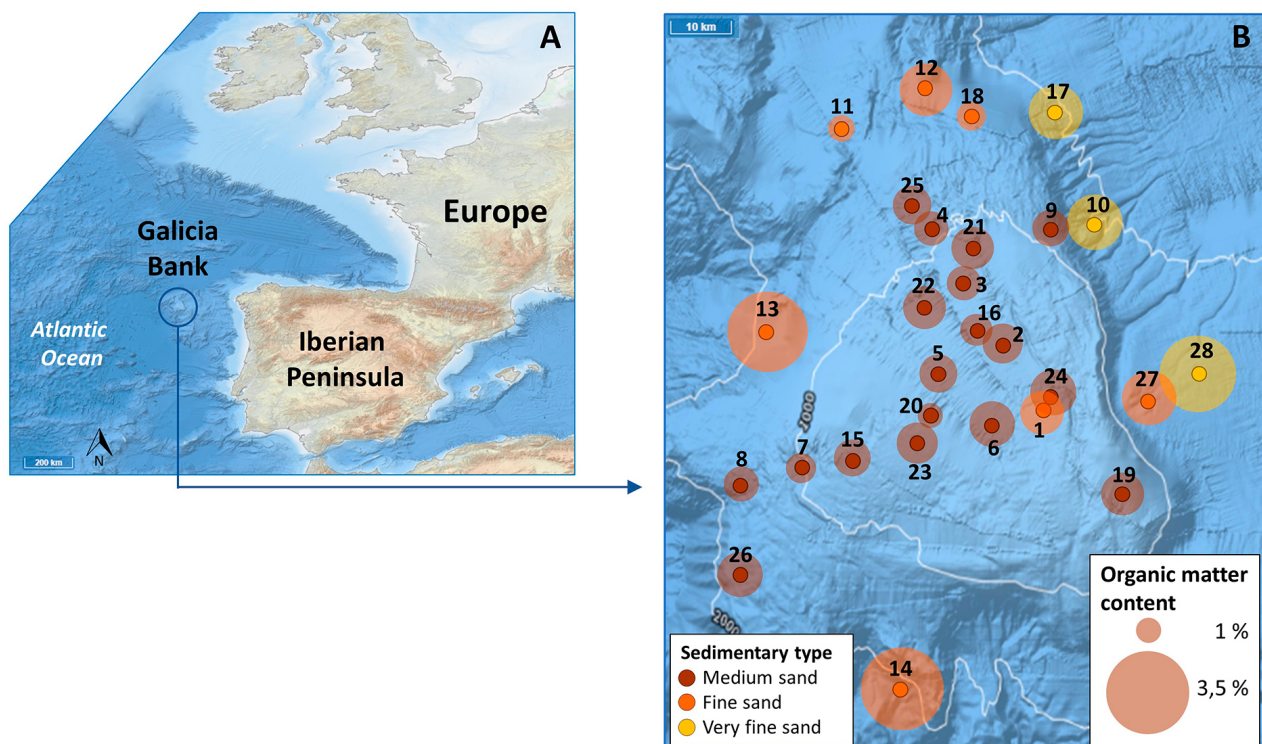

Fig. 1. – Galicia Bank. A. Geographical location. B. Position of stations and spatial variability in sedimentary type and sediment organic matter (circle sizes are proportional to contents).

Statistical analyses

Total abundance, total number of species, Shannon diversity and Pielou evenness were estimated using the DIVERSE routine, based on a taxa per station data matrix. Multivariate analyses were performed on fourth-root transformed data to build a between-sample similarity matrix using the Bray-Curtis similarity. Group average clustering and non-metric multidimensional scaling (nMDS) were used to determine the faunal assemblages. The significance of the observed differences was tested by one-way analysis of similarity (ANOSIM) and the contribution of each individual taxa to the within-group similarity and between-group dissimilarity was examined with the similarity percentage routine (SIMPER). The possible relationships between environmental factors and macrobenthic structure was assessed by the BIO-ENV routine and by canonical correspondence analysis (CCA). CCA was also calculated for the dominant taxa, i.e. those representing ≤4% of total abundance following Field et al. (1982). The following abiotic variables were considered: water depth (m), total organic matter content (%), median particle diameter (Q_{50}; mm), sorting coefficient (S_0), and weight percentage of coarse sand (>500 μm), fine sand (62–500 μm) and mud (<62 μm), with all variables expressed in percentages being log (x + 1) transformed. Spearman rank correlations were used to examine relationships between abiotic and biotic variables.

Univariate and multivariate analyses were performed using the PRIMER v6.0 software routines (Clarke and Gorley 2006), except for the CCAs, which were done with the XLStat software (AddinSoft Inc., Ter Braak 1988), and the Spearman rank correlations, which were estimated with the SPSS 17.0 program (Sokal and Rohlf 1980).

RESULTS

Faunal composition

Our samples yielded 1397 individuals (19137 ind m^{-2}) from 182 taxa included in 87 families. Polychaetes accounted for 67.2% of the total, followed by molluscs (13.7%), echinoderms (9.5%), crustaceans (5.2%) and others (4.4%) (Fig. 2). Syllid and spionid polychaetes were the most abundant, whereas ampharetid and syllid polychaetes were the most species-diverse (Table 1). The most dominant taxa were *Aurospio dibranchiata* (10.0%), *Poecilochaetus* sp. (4.1%), *Limopsis cristata* (2.9%), *Thyasira succisa* (2.9%), *Glycera lapidum* (2.7%) and *Palposyllis prosostoma* (2.7%), which accounted for more than 25% of the total, and only the following taxa were present at more than a half of the stations: Nemertea (17), *Poecilochaetus* sp. (16), *Protodorvillea kefersteini* (16) and *T. succisa* (15).

Syllid and poecilochaetid polychaetes, ophiacanthid echinoderms and limopsid and thyasirid bivalves dominated the bank summit, while polychaetes clearly dominated the medium-depth stations (spionids, ampharetids and poecilochaetids) and deepest stations (spionids, glycerids, ampharetids, syllids, cirratulids and paraonids).

Infaunal assemblages

The cluster analysis distinguished three groups of stations at 25% similarity, which were confirmed by the nMDS and showed significant differences in faunistic composition (ANOSIM, global R=0.898, p=0.001): A (1311–1579 m depth), B (765–1092 m depth) and C (1477–2274 m depth) (Fig. 3A–B). Group A included three medium-depth stations with medium and fine sands and showed the lowest species richness and abun-
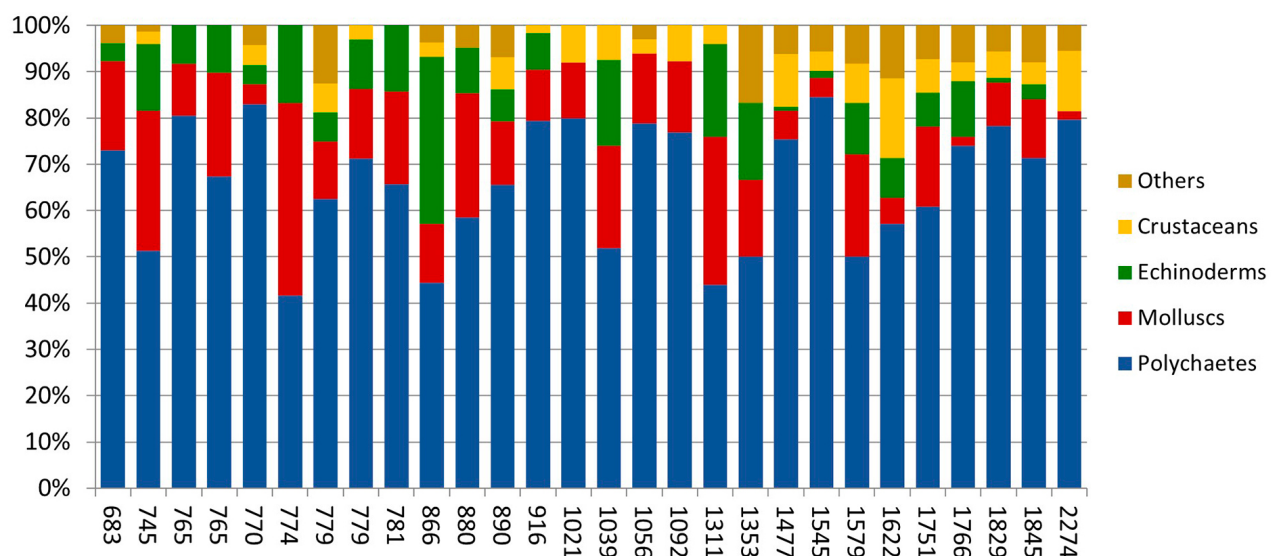

Fig. 2. – Relative abundance of the major macrofaunal taxa at each station of the Galicia Bank.

Table 1. – Left, families accounting for more than 50% of all individuals; right, families accounting for more than 25% of all species.

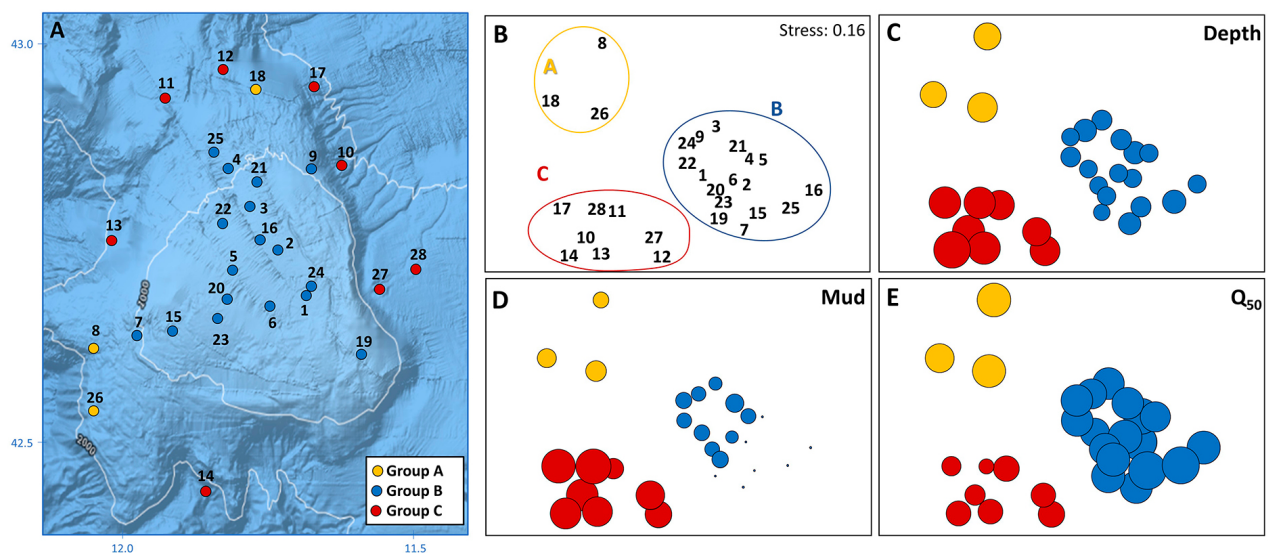| Families	Abundance (%)		Families	Species number	%
Spionidae	12		Ampharetidae	12	6.6
Syllidae	10.3		Syllidae	11	6
Ampharetidae	4.6		Onuphidae	8	4.4
Poecilochaetidae	4.1		Paraonidae	7	3.8
Cirratulidae	3.9		Spionidae	7	3.8
Paraonidae	3.6		Opheliidae	6	3.3
Limopsidae	2.9				27.9
Thyasiridae	2.9				
Glyceridae	2.7				
Sabeliidae	2.7				
Ophiacanthidae	2.6				
	52.3				

Fig. 3. – A. Geographical location of the sampling sites, showing the cluster analysis grouping. B. Non-metric multidimensional scaling ordination of sampling sites showing the cluster groups. Distribution of environmental variables in the ordination space. C. Depth. D. Mud. E. Median grain size (Q_{50}).

dance, being dominated by ophiuroids, ampharetids and gastropods. Group B included the shallowest stations with medium sands, moderate to moderate-well sorted sediments, the highest content of coarse sand and low organic matter content. The polychaetes *Poecilochaetus* sp. and *P. prosostoma*, the bivalves *L. cristata* and *T. succisa* and the ophiuroid *Ophiacantha* sp. were the most abundant taxa. Group C included the deepest stations, having fine and very fine sands and the highest mud and organic matter content and showing the highest species richness and abundance. The polychaete *A. dibranchiata* was the most abundant taxon.

The polychaetes *Poecilochaetus* sp. and *P. prosostoma*, and the bivalve *T. succisa* characterized the shallow Group B (Table 2, SIMPER, average similarity

=27.4%), while ampharetids, gastropods, ophiuroids and the holothuroid *Labidoplax buskii* characterized the medium-depth Group A (Table 2, SIMPER, average similarity =15.3%), and the polychaetes *A. dibranchiata* and *G. lapidum* and Nemertea characterized the deepest Group C (Table 2, SIMPER, average similarity =28.9%). The taxa most contributing to the dissimilarity between groups A and B (SIMPER, average dissimilarity =93.63%) and A and C (SIMPER, average dissimilarity =89.77%) were Ampharetidae spp., *Phascolion* sp. and *L. buskii*, while the taxa that most contributed to the dissimilarity between groups B and C (SIMPER, average dissimilarity =88.21%) were *A. dibranchiata*, *T. succisa*, *Poecilochaetus* sp., *P. prosostoma*, and *Syllis* sp. 1.

Table 2. – Cumulative contributions to the similarity (Cum. %, 50% cutoff) obtained by SIMPER analysis for the benthic infauna, according to the groups obtained in the cluster analysis.

	Cum %		Cum %
Average similarity: 27.40		*Average similarity: 28.90*	
Group B (765-1092 m)		Group C (1477-2274 m)	
Poecilochaetus sp. Claparède in Ehlers, 1875	7.6	*Aurospio dibranchiata* Maciolek, 1981	23.2
Palposyllis prosostoma Hartmann-Schröder, 1977	12.8	*Glycera lapidum* Quatrefages, 1866	29.4
Limopsis cristata Jeffreys, 1876	17.9	Nemertea spp.	32.8
Thyasira succisa (Jeffreys, 1876)	23	Ampharetidae spp. Malmgren, 1866	35.5
Ophiacantha sp. Müller & Troschel, 1842	27.9	*Syllis* sp. Lamarck, 1818	38.1
Protodorvillea kefersteini (McIntosh, 1869)	31.8	Ostracoda spp. Latreille, 1802	40.5
Syllis sp. 1 Lamarck, 1818	35.6	Cirratulidae spp. Ryckholt, 1851	42.6
Jasmineira caudata Langerhans, 1880	39.1	*Spiophanes* sp. Grube, 1860	44.8
Ophiomyces grandis Lyman, 1879	42.5	*Parexogone wolfi* (San Martín, 1991)	46.8
Synelmis sp. Chamberlin, 1919	44.8	*Antalis agilis* (M. Sars, 1872)	48.6
Amphiura chiajei Forbes, 1843	47	*Aricidea* sp. Webster, 1879	50.4
Aglaophamus malmgreni (Théel, 1879)	49		
Eurysyllis tuberculata Ehlers, 1864	50.9		
Average similarity: 15.33			
Group A (1311-1579 m)			
Ampharetidae sp. Malmgren, 1866	36.71		
Labidoplax buskii (MacIntosh, 1866)	51.47		

Relationship between biotic and environmental variables

The number of individuals per station ranged from 82 ind m^{-2} (1353 m depth, west part of the seamount) to 1822 ind m^{-2} (866 m depth, near the bank top), and the number of taxa per station ranged from 6 (1353 m depth, medium sand, west part of the seamount) to 49 (1751 m depth, very fine sand, east part of the seamount) (Table 3). The highest and lowest diversity were observed at medium sand stations from the bank top (station 24, 745 m depth, H'=5.1 bits; station 16, 774 m depth, H'=2.5 bits) (Table 3, Fig. 4).

Total macrofaunal abundance was positively correlated with depth ($p < 0.05$) and mud ($p < 0.01$), and negatively with median grain size and coarse sand ($p < 0.01$). Depth was correlated positively with mud and organic matter ($p < 0.01$) and negatively with median grain size ($p < 0.05$).

Polychaetes were correlated positively with mud ($p < 0.01$) and negatively with median grain size ($p < 0.05$), while crustaceans were correlated positively with depth and mud ($p < 0.01$) and negatively with median grain size ($p < 0.01$) and coarse sand ($p < 0.05$). The others were correlated positively with depth ($p < 0.05$) and mud and negatively with median grain size and coarse sand ($p < 0.01$), whereas echinoderms were correlated negatively with total organic matter ($p < 0.05$) and molluscs showed no significant correlation.

Depth, mud content and median grain size were the major structuring factors of the benthic community (BIO-ENV, $\rho_w = 0.596$) and showed the highest correlations when considered separately (depth, $\rho_w = 0.540$; mud, $\rho_w = 0.456$; Q_{50}, $\rho_w = 0.374$). In the nMDS, the stations were distributed from left to right following increasing values of median grain size and decreasing depths and mud (Fig. 3C–E).

Axes I and II were the most important in the CCA (variance = 47.59%). Group C stations were distributed along axis I negative sector, showing the deepest and muddy bottoms, whereas Group B stations appeared distributed along axis I positive sector, and Group A stations were intermediate between those of groups B and C (Fig. 5A). The taxon distribution in the CCA (variance of axis I and II = 59.20 %) was consistent with the SIMPER results, showing clear differences between the bank top (Group B, medium sands) and the deeper stations (Group C, fine sand flanks with the highest organic matter) (Fig. 5B).

Trophic structure

Carnivores dominated the assemblages at the bank top (mobile species with no organic matter requirements), while surface-deposit feeders increased their abundance with depth, where the lower hydrodynamics favoured the deposit of organic matter they require. Carnivores accounted for more than 30% of total abun-

Table 3. – Summary of biotic and physical characteristics of the assemblages derived from the cluster analysis (mean with standard deviation and range of values).

Group (st.)		Depth (m)	Sediment type	TOM (%)	Q_{50} (mm)	S_0	CS (%)	FS (%)	Mud (%)	S	N (ind.m^{-2})
A (8, 18, 26)	Mean	1414 ± 144.1	MS (2st.)-FS (1st.)	1.5 ± 0.3	0.30 ± 0.04	Mod.-ModW	10.4 ± 6.1	87.6 ± 6.3	2.0 ± 0.8	15 ± 9	306 ± 208
	Range	1311-1579		1.2-1.9	0.24-0.32		3.6-15.3	82.0-94.3	1.2-2.8	6-24	82-493
B (1, 2, 3, 4, 5, 6, 7, 9, 15, 16, 19, 20, 21, 22, 23, 24, 25)	Mean	859 ± 125.5	MS(16st.)-FS(1st.)	1.6 ± 0.2	0.31 ± 0.05	Mod.-ModW	16.9 ± 6.4	82.5 ± 6.3	0.6 ± 0.6	22 ± 11	586 ± 406
	Range	765-1092		1.1-2.0	0.24-0.40		10.1-29.3	70.7-88.8	0-1.8	7-49	164-1822
C (10, 11, 12, 13, 14, 17, 27, 28)	Mean	1764 ± 245.4	FS(5st.)-VFS(3st.)	2.6 ± 0.8	0.15 ± 0.05	Mod.-Poor-Bad	4.9 ± 2.3	75.0 ± 13.0	20.2 ± 14.2	32 ± 9	1033 ± 418
	Range	1477-2274		1.1-3.5	0.07-0.20		1.9-7.7	51.3-90.9	2.7-46.3	20-49	479-1562

Notes: TOM, total organic matter; Q_{50}, mean grain size; S_0, sorting coefficient; Mod, moderate sorted; ModW, moderate-well sorted; CS, coarse sand; FS, fine sand; MS, medium sand; VFS, very fine sand; N, infaunal abundance; S, number of species; st., number of stations these values were based on.
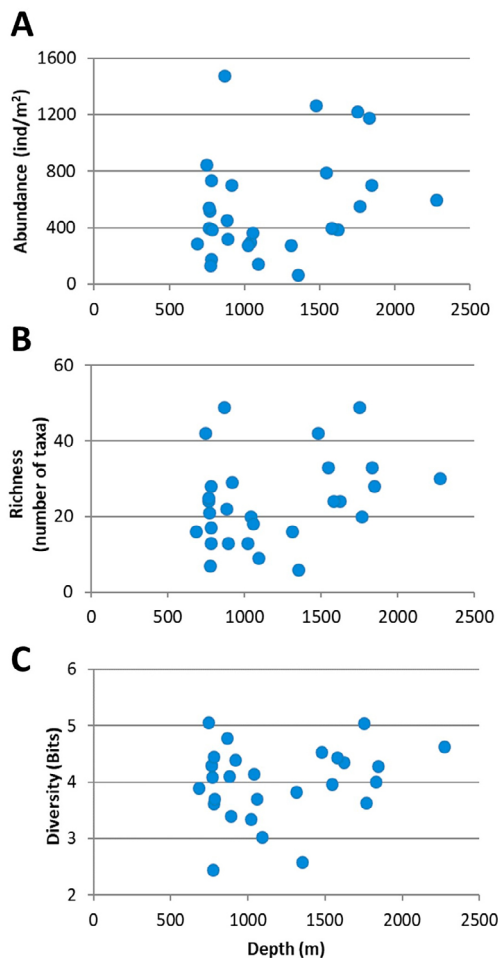

Fig. 4. – Bathymetric changes in macrofaunal descriptors: A. Density; B. Taxon richness; C. Diversity.

dance on average, but their number decreased from 42% under 1000 m depth to 21% at more than 1500 m depth. In contrast, the abundance of deposit feeders increased with depth, with topography (from 41% at the summit, <1000 m depth) to 62% on the flanks (deep stations, >1500 m) and with granulometry, being positively correlated with mud content (p<0.05). Moreover, surface-deposit feeders dominated at 14 stations (7%–68%), carnivores at 9 (8%–75%), and suspensivores (0%–33%), subsurface-deposit feeders (0%–50%) and remaining (0%–35%) at only one (Fig. 6).

DISCUSSION

Seamounts offer a variety of habitats and environmental conditions to benthic fauna, alternating between hard substrates and soft sediments (Clark et al. 2010). Although there are no identical seamounts, their tops are usually characterized by bioclastic sands and their slopes by basalts with sponges and corals (Somoza et al. 2014), while the accumulated sands and muds are the perfect habitat for small invertebrate organisms such as polychaete annelids, bivalve molluscs, ophiuroids and crustaceans (Rogers 2004).

On the Galicia Bank, sediment grain size decreases with depth, with medium sands characterizing most stations at the bank summit, and fine and very fine sands dominating at the deeper stations, as reported for other deep-sea areas (Levin and Gooday 2003, Thistle 2003, Louzao et al. 2010). In general, the energy of ocean currents and waves decreases from shallow to deeper waters, therefore favouring settling of smaller particles mainly in the less energetic, deeper waters (Karl 2006). The organic matter was low in all our samples (1.1%–3.5%), but the highest values occurred
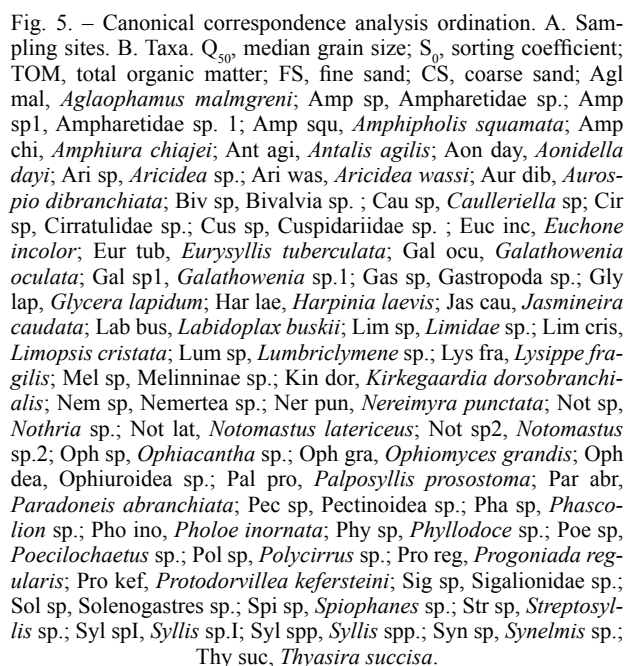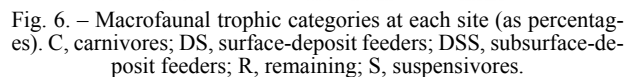
on the bank flanks, likely due to the strong currents winnowing organic particles (Duineveld et al. 2004), plus a lack of advective input of organic matter from the continental shelf (Surugiu et al. 2008).

Fig. 6. – Macrofaunal trophic categories at each site (as percentages). C, carnivores; DS, surface-deposit feeders; DSS, subsurface-deposit feeders; R, remaining; S, suspensivores.

Macrofaunal abundances also tend to decrease with depth in many deep-sea environments (Thistle 2003) such as the Gay Head-Bermuda transect (Hessler and Sanders 1967), the northeast Atlantic Goban Spur (Flach et al. 2002), the northwest Atlantic (Levin and Gooday 2003) and the Gulf of Mexico (Thistle 2003). On seamounts, the particular composition of substrata, often varying along summits, flanks and ridges, combined with other environmental parameters (such as depth) allow each structure to host particular assemblages (Rogers 2018). On the Galicia Bank, this is reflected in a bathymetrical increase in macrofaunal abundance. On seamounts, depth is not a linear factor but depends on topography, with the nature of the substratum, the slope and the exposure to currents likely influencing the faunal distribution at smaller scales (Clark et al. 2010, Yesson et al. 2011). Mud content often tends to increase with depth, as in the northeast Atlantic Senghor Seamount, where this is likely associated with an increasing organic matter availability (Chivers et al. 2013). Therefore, macrofaunal abundances may be favoured by the slope habitat heterogeneity but hindered by the strong bottom currents at the summit (Duineveld et al. 2004, Levin and Thomas 1989).

Among macrofaunal organisms, polychaetes are the most abundant deep-sea taxon (Gage and Tyler 1991, Grassle and Maciolek 1992, Ramírez-Llodra et al. 2010), including seamounts (Surugiu et al. 2008), where they may represent more than 50% of the abundance (Gillet and Dauvin 2000, Glover et al. 2002). The Galicia Bank was no exception (Table 4). Molluscs also occurred at all depths, representing more than 10% of the total on the Galicia Bank (Table 4), with bivalves being the most numerous (63.5% of the molluscs). All remaining taxa represented less than 10% of the abundance.

Spionid, cirratulid and paraonid polychaetes typically dominate deep-sea bottoms, often contributing up to 25% of all species and individuals in slope or abyssal environments (Schüller and Ebbe 2007). Polychaetes are also dominant on seamounts, being particularly represented by Paraonidae, Cirratulidae, Sabellidae, Syllidae and Ampharetidae (Rogers 1994), in agreement with our results (Table 4). However, abundances

Fig. 5. – Canonical correspondence analysis ordination. A. Sampling sites. B. Taxa. Q_{50}, median grain size; S_0, sorting coefficient; TOM, total organic matter; FS, fine sand; CS, coarse sand; Agl mal, *Aglaophamus malmgreni*; Amp sp, Ampharetidae sp.; Amp sp1, Ampharetidae sp. 1; Amp squ, *Amphipholis squamata*; Amp chi, *Amphiura chiajei*; Ant agi, *Antalis agilis*; Aon day, *Aonidella dayi*; Ari sp, *Aricidea* sp.; Ari was, *Aricidea wassi*; Aur dib, *Aurospio dibranchiata*; Biv sp, Bivalvia sp. ; Cau sp, *Caulleriella* sp; Cir sp, Cirratulidae sp.; Cus sp, Cuspidariidae sp. ; Euc inc, *Euchone incolor*; Eur tub, *Eurysyllis tuberculata*; Gal ocu, *Galathowenia oculata*; Gal sp1, *Galathowenia* sp.1; Gas sp, Gastropoda sp.; Gly lap, *Glycera lapidum*; Har lae, *Harpinia laevis*; Jas cau, *Jasmineira caudata*; Lab bus, *Labidoplax buskii*; Lim sp, *Limidae* sp.; Lim cris, *Limopsis cristata*; Lum sp, *Lumbriclymene* sp.; Lys fra, *Lysippe fragilis*; Mel sp, Melinninae sp.; Kin dor, *Kirkegaardia dorsobranchialis*; Nem sp, Nemertea sp.; Ner pun, *Nereimyra punctata*; Not sp, *Nothria* sp.; Not lat, *Notomastus latericeus*; Not sp2, *Notomastus* sp.2; Oph sp, *Ophiacantha* sp.; Oph gra, *Ophiomyces grandis*; Oph dea, Ophiuroidea sp.; Pal pro, *Palposyllis prosostoma*; Par abr, *Paradoneis abranchiata*; Pec sp, Pectinoidea sp.; Pha sp, *Phascolion* sp.; Pho ino, *Pholoe inornata*; Phy sp, *Phyllodoce* sp.; Poe sp, *Poecilochaetus* sp.; Pol sp, *Polycirrus* sp.; Pro reg, *Progoniada regularis*; Pro kef, *Protodorvillea kefersteini*; Sig sp, Sigalionidae sp.; Sol sp, Solenogastres sp.; Spi sp, *Spiophanes* sp.; Str sp, *Streptosyllis* sp.; Syl spI, *Syllis* sp.I; Syl spp, *Syllis* spp.; Syn sp, *Synelmis* sp.; Thy suc, *Thyasira succisa*.

Table 4. – Summary of deep-sea polychaete and mollusc abundances. A, Ampharetidae; Am, Amphinomidae; C, Cirratulidae; Ch, Chrysopetalidae; D, Dorvilleidae; Eu, Eunicidae ; F, Flabelligeridae; G, Glyceridae; M, Maldanidae; N, Nereididae; O, Opheliidae; Or, Orbiniidae; On, Onuphidae; Pa, Paraonidae; Ph, Phyllodocidae; Pl, Pilargidae; Po, Poecilochaetidae; Ps, Pisionidae; Sa, Sabellidae; Sp, Spionidae; Sy, Syllidae.

Study area	Reference	Polychaete abundances	Best represented polychaete families
Galicia Bank (Galicia seamount, Spain)	This study	67.2%	Sp (12%), Sy (10%), A (5%), Po (4%), Pa (4%), C (4%)
Senghor Seamount (northeast Atlantic)	Chivers et al. 2013		Sy (34%), Sp (10%), C (13%), Ch (7%), Sa (5%)
Continental slope off the eastern seaboard of the USA	Gage and Tyler 1991	45%	Am, Pa and Sp
Central Pacific abyss	Glover et al. 2002		C (17%), Sp (17%), Pa (17%), Sa (10%), Sy (10%)
Gay Head–Bermuda transect	Levin and Gooday 2003	34%–84%	A, M, Pa, Ph, Sp, Sy
Cape Hatteras and Charleston Bump	Levin and Gooday 2003	50%	
North Atlantic Bight margin and Mid-Atlantic Bight margin	Levin and Gooday 2003	44%–47%	C, D, Pa, Sp
Porcupine Abyssal Plain	Levin and Gooday 2003	35%	Sp (25%), C (22%), Sa (10%), O (8%), Pa (8%)
Tagus Abyssal Plain	Levin and Gooday 2003	58%	C (24%), Sp (17%), Pl (11%), O (11%), Pa (9%)
Madeira Abyssal Plain	Levin and Gooday 2003	49%	Sa (24%), F (20%), Pa (16%), Sp (8%), Ps (6%)
Horizon Guyot and Magellan Rise cap (central Pacific seamounts)	Levin and Thomas 1989	54%	Pa, C, Sa, A, Sy
16 deep seamounts in the East Pacific	Levin and Thomas 1989	58%	Pa, C, Sa, Sy, A
Region of the Subtropical Front, Chatham Rise, New Zealand	Probert et al. 2009		Sp (15%), Pa (13%), C (9%), Sy (7%), Or (6%)
Mid-Atlantic Ridge, North Atlantic Ocean	Shields and Blanco-Pérez 2013	60%	Sp (>40%), C, Sy, G
Northeast Atlantic seamounts	Surugiu et al. 2008	78.4%	On (27%), Sy (18%), Eu (16%), Am (11%), N (6%)

Study area	Reference	Mollusc abundances
Deep sea (slopes and basins)	Gage and Tyler 1991	10%–15%
Cape Hatteras and Charleston Bump	Levin and Gooday 2003	16%
North Atlantic and Mid-Atlantic Bight margins	Levin and Gooday 2003	14%
Horizon Guyot and Magellan Rise cap	Levin and Thomas 1989	9% (cap sites) − 27% (perimeter site)

on the bank were low (19137 ind m^{-2}) compared with other deep-sea areas such as the Aviles Canyon System (56637 ind m^{-2}) (Lourido et al. 2023), probably because the bank is a deep, oligotrophic seamount with impoverished infaunal environments because of low mainland advection and strong summit currents (Duineveld et al. 2004, Surugiu et al. 2008). The 939 individuals from 33 polychaete families found on the bank resemble those on the northeast Atlantic Senghor Seamount (954/34) (Chivers et al. 2013) but were fewer than on the Condor Seamount (1541/32) (Bongiorni et al. 2013) and more than on the seamounts studied by Surugiu et al. (2008) (94–567/12–23). However, these authors used dredge and trawl samples and a relatively large mesh size, which may have biased their results, preventing comparisons.

Our results suggested the existence of three different infaunal assemblages on the Galicia Bank, being clearly different at the top than on the surrounding, deeper flanks. (1) The shallowest assemblage at the

bank summit (Group B, 765–1092 m depth) showed highly abundant thyasirid and limopsid bivalves, which are common or exclusive deep-sea taxa (Gage and Tyler 1991); ophiacantid ophiuroids occurred in an area with megaripples indicating strong currents, so their presence could be due to trophic-hydrographic drivers (Serrano et al. 2017a); syllids were the predominant polychaete family, as documented on the Condor Seamount, mainly at the summit (Bongiorni et al. 2013). (2) The deepest assemblage (Group C, 1477–2274 m depth) on the bank flanks was characterized by the dominance of the spionid polychaete *A. dibranchiata*, which accounted for 10% of the macrofauna, as shown for the NW Atlantic (Grassle and Maciolek 1992) and the Mid-Atlantic Ridge (Shields and Blanco-Pérez 2013); Spionidae, one of the most frequent polychaete families in deep-sea soft sediments (Glover et al. 2002, Shields and BlancoPérez 2013), may alternate between surface-deposit and suspension feeding, a competitive advantage that let them feed both in still waters and when current speed increases suspended food fluxes (Shields and Blanco-Pérez 2013). (3) The third assemblage (Group A,1311–1579 m depth) included stations with intermediate positions between the other two and was characterized by the presence of ampharetids, gastropods and ophiuroids.

The sedimentary habitats of the Galicia Bank showed four faunal assemblages defined by bathymetric, geomorphologic, granulometric, hydrographic dynamic and biological (including fishing impacts) data (Serrano et al. 2017b). Among them, "Summit Sands" matched with our Group B in both environmental characteristics and faunal composition, with highly abundant sand dwelling ophiacanthid (*Ophiacantha* sp.) and ophiohelid (*Ophiomyces grandis*) ophiuroids and limopsid bivalves (*Limopsis minuta* and *L. cristata*), while the deeper than 1400 m "Bank Flanks Sands" matched with our Group C. Depth and substrate type, together with depth-related water mass influences, were key factors in sedimentary habitats. This included seamounts, where depth was the strongest environmental proxy for the assemblage-structuring processes, giving rise to communities generally distributed as bands encircling the seamounts (Du Preez et al. 2016). These bands also occurred on the Galicia Bank, and this depth-related zonation was more evident on sedimentary than on rocky habitats (Serrano et al. 2017a). Therefore, depth, topography, current distribution (i.e. with the strongest ones in the summit area) and isolation from the mainland emerged as key factors controlling species distribution on the Galicia Bank.

Nevertheless, diversity was not correlated with depth, although a somewhat increasing trend could be observed. Many seamounts show a mid-slope peak (Cosson-Sarradin et al. 1998, Maciolek and Smith 2009, Probert et al. 2009), most likely being caused by factors other than depth, such as nutrient input, temperature, hydrostatic pressure and current dynamics (Gage and Tyler 1991) or by changes in sediment characteristics (Etter and Grassle 1992). On the Galicia Bank, diversity might be affected by the seamount morphol-

ogy, particularly the numerous slope microhabitats and the hostile summit environment. Accordingly, the shallowest summit stations of Group B differed in infaunal species composition from the deepest flank stations of Group C, a pattern resembling that of decapod crustaceans, which also showed a generalized bathymetric species substitution (Cartes et al. 2014).

The trophic structure also showed bathymetric patterns, with carnivores and filter feeders (e.g. ophiacanthids and limopsids) dominating the bank summit on the Galicia Bank, the latter taking advantage of the currents to feed on the more abundant suspended particles. In agreement with Probert et al. (2009), predators tended to be more abundant at shallower stations on the Galicia Bank, with their energetic profit decreasing with depth because of the amount of energy required to find their preys, which tend to be more distant in deeper environments (Thistle 2003). On the Galicia Bank, surface-deposit feeders increased their abundance with depth, showing maxima at the deepest part, as in the deep-sea Goban Spur transect (Levin and Gooday 2003). The organic matter reaching the deep sea is advantageously processed by deposit feeders (e.g. spionids, ampharetids, cirratulids or paraonids), which tend to be dominant in this environment (Thistle 2003).

CONCLUSIONS

Exploring seamount macroinfaunal assemblages provides key information that contributes to our understanding of the ecosystem distribution drivers. Therefore, our work provides an important environmental baseline information on the infaunal community of the Galicia Bank, while addressing the lack of studies on deep seamounts and the taxonomic bias towards larger animals. Our results agree with previous studies in showing that depth and substrate type combine with topography as the key factors driving the infaunal benthic community structure and distribution on the Galicia Bank.

DECLARATION OF COMPETING INTEREST

The authors of this article declare that they have no financial, professional or personal conflicts of interest that could have inappropriately influenced this work.

AUTHORSHIP CONTRIBUTION STATEMENT

Antía Lourido: Conceptualization; Data curation; Formal Analysis; Investigation; Methodology; Software; Visualization; Writing – original draft, review & editing.

Santiago Parra: Conceptualization; Data curation; Formal Analysis; Investigation; Methodology; Resources; Software; Supervision; Validation; Visualization; Writing – review & editing.

Alberto Serrano: Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing – review & editing.

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