



Demersal and epibenthic communities of sedimentary habitats in the Avilés Canyon System, Cantabrian Sea (NE Atlantic)

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ABSTRACT

The aim of this study was to describe the epibenthic and demersal communities of the Avilés Canyon System (ACS) in relation to the environmental variables that characterize their biotope. ACS (Cantabrian Sea, NE Atlantic) was recently included in the Natura 2000 network as a Site of Community Importance (SCI). Data of faunal biomass derived from 6 surveys carried out using beam trawl and otter trawls in 2009 and 2010 within INDEMARES and ERDEM projects. Data were divided into two groups to obtain information about the two ecological compartments: benthic and demersal. The total number of species used in this analysis ascended to 116 in the case of benthic organisms and 110 in the case of demersal. Hierarchical clustering analysis was applied to obtain groups of samples similar in terms of species composition for the two ecological components. Depth was the main discriminating factor for grouping hauls, showing high consistency of bathymetric range independently from the compartment examined. Six groups were identified by depth as follows: medium shelf (~100–200 m), external shelf (~150–300m), shelf break (~300–400 m), upper-slope (~500–700 m), upper middle-slope (~700–1100 m), and lower-middle-slope (1200–1500 m). SIMPER analysis on biomass values was performed to determine the structure of the faunal assemblages observed for each group in both compartments. Using biomass values for the analysis allowed for the exploration of groups playing important roles in ecosystem functioning and energy fluxes taking place on the sedimentary bottom of this SCI. Finally, CCA analysis revealed that the main environmental drivers were depth, broad scale bathymetric position index (BPI), near-bottom salinity, sedimentary type, and dynamics related variables (Q50 phy and So). This study gives an inventory of the soft bottom assemblages along a very wide depth range (100–1500 m) inside a SCI, linking both epibenthic and demersal communities with the biotope preferences. This study contributes to fundamental knowledge on soft-bottom communities as a pre-requisite, necessary for the next steps in terms of management framework in the SCI.

1. Introduction

The Avilés Canyon System (ACS) is located in NE Atlantic Waters (Cantabrian Sea, Bay of Biscay) and is a very complex ecosystem, constituted by three main canyons, La Gavieta, El Corbiro, and Avilés. In this area, structurally-controlled complex sedimentary and hydrodynamic processes take place (Gómez-Ballesteros et al., 2014; Álvarez et al., 2010; González-Quiros et al., 2004). The strong oceanographic

dynamics influence and control the sediment deposition and consequently boost the transport of the sediment finer fraction from the canyon heads (located in the continental shelf) to the Biscay Abyssal plain (about 4700 m depth). Marine canyons are known to be biodiversity hotspots and, in fact, this area was extensively studied within the projects LIFE + INDEMARES (2010–2015) and LIFE IP INTEMARES (2018–2024).

Previously, the COCACE project (1987–1988) studied benthic

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communities in the same area at the same depth range with different sampling methods (anchor dredge and epibenthic sled) (Louzao et al., 2010). Another study on epibenthic fauna (Serrano et al., 2006a, 2006b) included some samples collected by beam trawl in the ACS. Additionally, a general description of all the studies performed within the project LIFE + INDEMARES is available for this study area (Sánchez et al., 2014a, 2014b). Soft bottoms and their infauna assemblages have also been described (Lourido et al., 2014). More recently, an up-to date inventory on biodiversity has been published (Ríos and Sánchez, 2021), and some specific information, for example on sponge habitat, is available in SponGES Project (2016–2020) and in other studies (Rodríguez-Basalo et al., 2021).

The integrated project LIFE IP INTEMARES has the challenge of laying the foundations for effectively managing the marine areas within the Natura 2000 Network of protected areas and completing the work and progresses achieved within the framework of LIFE + INDEMARES project, which managed to take a major step in the designation of new areas. In this network, the ACS is known to show high biodiversity values (Sánchez et al., 2014b; Ríos and Sánchez, 2021) and was declared as Site of Community Importance (SCI) within the Nature 2000 network based on Habitat Directive 92/43/CEE (C.D. 1992). This declaration is the first step toward the protection and conservation of the marine natural resources which have to be followed by a management plan. Such plans shall fix the measure for sustainable usage of resources through a rational zonation which consider the presence and distribution of natural resources together with the socio-economic activities developed in the SCI (Sánchez et al., 2014b). The main purpose of declaring a SCI is to identify the presence of species and habitats of community interest. Then, in a second step, draft a management plan that regulates the activities within it, considering the stakeholders involved, especially in areas in which vulnerable habitats are present as the ACS. For these reasons, detailed studies are required in this area to reach a better understanding of the ecosystem functioning and achieve,

among other goals, the best management plan as possible. It is necessary to specifically analyse the communities that characterize these marine areas and the environmental factors on which they depend. All these actions are needed for attaining a sustainable use of the biological resources and to preserve biodiversity inside these areas.

The present study focused on i) a description of the soft bottom macro-epibenthic and demersal communities for the ACS and ii) the environmental factors within the available, which characterize these communities and determine their existence in the study area. Both focal points as part of the preliminary knowledge are necessary for reaching a good management of biological resources in the ACS.

2. Materials and methods

2.1. Study area

The area of the ACS is located in the Cantabrian Sea between latitude $43^{\circ} 13' N$ and $44^{\circ} 118' N$ and from $6^{\circ} 146' W$ to $5^{\circ} 118' W$ longitude (Fig. 1). This region is a complex zone which is part of the compressive continental margin north of the Iberian Peninsula (Gómez-Ballesteros et al., 2014). This area presents a canyon and valley system constituted by three main canyons of different morpho-structural characteristics which drive both water mass circulation and sedimentary processes in the area. The Aviles Canyon head is located 7 miles off the Spanish north coast, starting at $6^{\circ} 10' W$, and oriented on an oblique line at a depth from 140 m to 4750 m. In addition, a conspicuous morphologic feature (marginal shelf) called El Canto Nuevo is a horst (a raised fault block bounded by normal faults) in the outer continental margin and constitutes a sort of additional wall in the western margin of the Avilés Canyon. The sediment distribution in this area follows a grain size decrease from the continental shelf to the abyssal plain (Lourido et al., 2014). Sediment covers almost half the continental shelf of the SCI. The sedimentary surface in the ACS is very complex to explore with

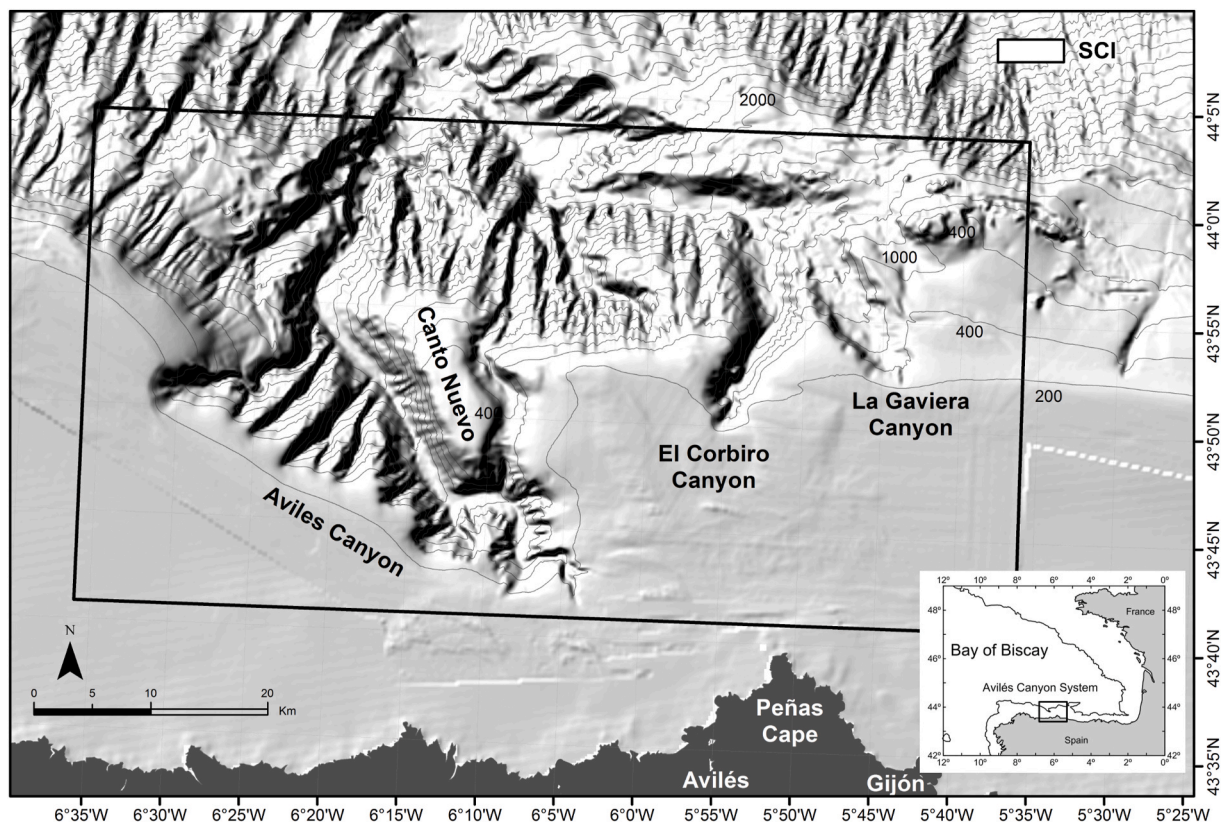


Fig. 1. Study area, SCI (Site of Community Importance) boundaries are indicated by solid black line.

extractive methods (i.e. bottom trawl hauls), due to geomorphological complexity described above, especially below 200 m deep. The three canyons boost sediment transport from continental margins to the abyssal plain (Gómez-Ballesteros et al., 2014) and they form a system that converges together in the abyssal plain.

The canyon system influences the water mass circulation in the area, generating a topographic effect with a particular hydrographic dynamic that strong influences mesoscale oceanographic processes forcing trophic pathways and fish larvae retention (Sánchez and Gil, 2000; González-Quirós et al., 2003, 2004; Gil, 2008). The water masses present in the study area act in different ways than of those which have been defined for the Eastern North Atlantic (see Van Aken, 2000a, 2000b; Lavin et al., 2006). From surface to bottom, the distribution comprises the Eastern North Atlantic Central Water (ENACW) that extends from the base of the winter mixed layer (200 m) to depths of around 500–600 m, the Mediterranean Outflow Water (MOW), found down to depths of about c.a. 1400 m (main core at 1000 m) (Iorga and Lozier, 1999); the Labrador Sea Water (LSW) which main core lies at 1800 m (Pingree, 1994; Paillet et al., 1998) and the North Atlantic Deep Water (NADW). Besides the large-scale mean flow, strong shelf and along-slope currents develop with a marked seasonal character and are strongly E-W polarized due to geostrophic topographic steering in the Aviles Canyon region (Pingree and Le Cann, 1990).

Other main factors that can influence soft bottom faunal assemblages, a part for the environmental conditions are anthropogenic pressures such as fishing activity that exists in the area (Punzón et al., 2016) and shipping (Borja et al., 2019), among others.

This canyon system is known to provide essential fish habitats (EFH) for important commercial species such as hake and monkfish (Sánchez and Gil, 2000; Sánchez and Olaso, 2004), as well as habitats for some species of cetaceans (Llavona et al., 2011), Chondrichthyes (Rodríguez-Cabello et al., 2013), and benthic habitats-forming species (Louzao et al., 2010; Rodríguez-Basalo et al., 2021).

2.2. Sampling methods, data treatment, and preliminary exploration

Samplings were performed in the ACS both inside and outside the SCI, the latter samplings in neighboring zones east of the SCI. For the present study, samplings were performed using 3 different gears within 2 different projects: one small beam trawl (Serrano et al., 2006a) and two different otter trawls, one (Bertrand et al., 2002) within the project INDEMARES and the other within the project ERDEM (for gear details see ICES, 2010). All the samplings were performed in 2010 and 2011. Data of beam trawl were gathered from the project INDEMARES (Sánchez et al., 2014b) and henceforth will be indicated as AV (Fig. 2a). Data of the otter trawl were gathered from two different projects, the first from INDEMARES (Sánchez et al., 2014b) henceforth AG (Fig. 2a), and the second from ERDEM survey (ICES, 2010), from now on DN (Fig. 2a). A total of 60 valid hauls (15 AV, 15 AG, and 30 DN) were performed (Fig. 2a). For the 3 samplings on board the vessels, the samples were sorted, identified, and wet weighted per each haul. Further identifications, when doubtful on board, were carried out later in the laboratory. Biomass data expressed as g per km² were obtained by standardizing each species wet weight per each haul by using mean swept area of each survey. Data on swept area were gathered using Scanmar net sensors (fishing line horizontal opening) for otter trawls gears. The mean swept areas, used to standardise biomass by surface results, were 0.003494 km² for AV, 0.0560345 km² for AG, and 0.0518805 km² for DN.

In order to focus exclusively on the species that constituted the main structure of soft bottom faunal assemblages, a pre-treatment of these matrices was applied consisting in filtering, and successively eliminate, all those species which:

- a) are considered rare (maximum 1 specimen for each type of gear)
- b) were classified at a higher taxonomic level than species

- c) not properly linked to sedimentary habitats (i.e., species typical of rocky beds)
- d) not properly linked with bottoms (classified as pelagic)

Finally, we filtered all those values for species detected as outliers in the weighted depth distribution obtained, as described by Stefanescu et al. (1992), Cartes et al. (2011), and Serrano et al. (2017). This latter step helped to better define the center of gravity (CoG) for each species, supporting in the task of defining the groups of species structuring both the epibenthic and demersal communities.

Analysis of species richness, percentage of biomass per taxonomic group, and percentage of biomass by ecological compartment was conducted using data from each sampler separately in order to explore the feasibility of analyse them, pooled or not. A preliminary analysis of the 3 sampler catches indicates that there are not important differences between the catch of the two otter trawls in terms of species composition, while evident differences have been observed for the beam trawl data. In the first case, both otter trawl gears targeted demersal species, while beam trawls caught more epibenthic organisms.

Therefore, all the following analysis were performed in terms of epibenthic fauna (data from beam trawl) and demersal fauna (data from the two otter trawls pooled).

2.3. Environmental variables

Environmental variables used to characterize each sampling station were obtained as follows:

- a) Bathymetry and its derivatives: A bathymetry layer of 200 m resolution was obtained from data set corresponding to two cruises (INDEMARES-AVILES 0410 and INDEMARES-AVILES 0511) carried out aboard the R/V Vizconde de Eza in the years 2010 and 2011 (Gómez-Ballesteros et al., 2014). From those data sets, we used the R package “raster” (Hijmans and Van Etten, 2011) to obtain depth (m) and all the other derivatives such as slope (degrees), roughness, bathymetric position index (BPI broad and BPI fine), expressed as an index of relative elevation of a point with respect to its neighboring, eastness, and northness (both latter derived from aspect). Values were thus associated to each haul.
- b) Water physical chemical variables: temperature at bottom in ° C degrees, and salinity at bottom in PSU. They were obtained by using a CTD profiler in each sampling station.
- c) Bottom sedimentary variables: Sediment parameters were inferred using data from an USNEL type boxcorer (Hessler and Jumars, 1974), which is widely employed in deep-sea benthic surveys (Gage and Tyler, 1991; Eleftheriou and Moore, 2005). Each sample covered an area of 0.09 m² on the bottom. A total of 57 stations at the ACS were sampled with this device (the position of these sampling stations are shown in Fig. 2b). Continuous variables used for each biological station were Q50 phi expressed as the main particle grain size, sorting coefficient (S₀) which was expressed as the interquartile range of the grain size and organic matter (OM) content of the sediments, in percentage (%), was estimated as weight loss of dried samples (100 °C, 24 h) after combustion (500 °C, 24 h). Additionally, a categorical variable was used for the sediment bottom type that was categorized into 5 classes: coarse sands (CS), medium sands (MS), medium and fine sands (MFS), fine sands (FS), and very fine sands and muds (VFSM) (Fig. 2b).

Preliminarily to data analysis, a linear regression with a Pearson correlation test was applied in order to explore the correlation between different environmental variables. After that, the variables which gave correlation over 0.7 were eliminated. The above-mentioned process was made in order to avoid overestimation of explained variance in the ensuing multivariate community structure analysis.

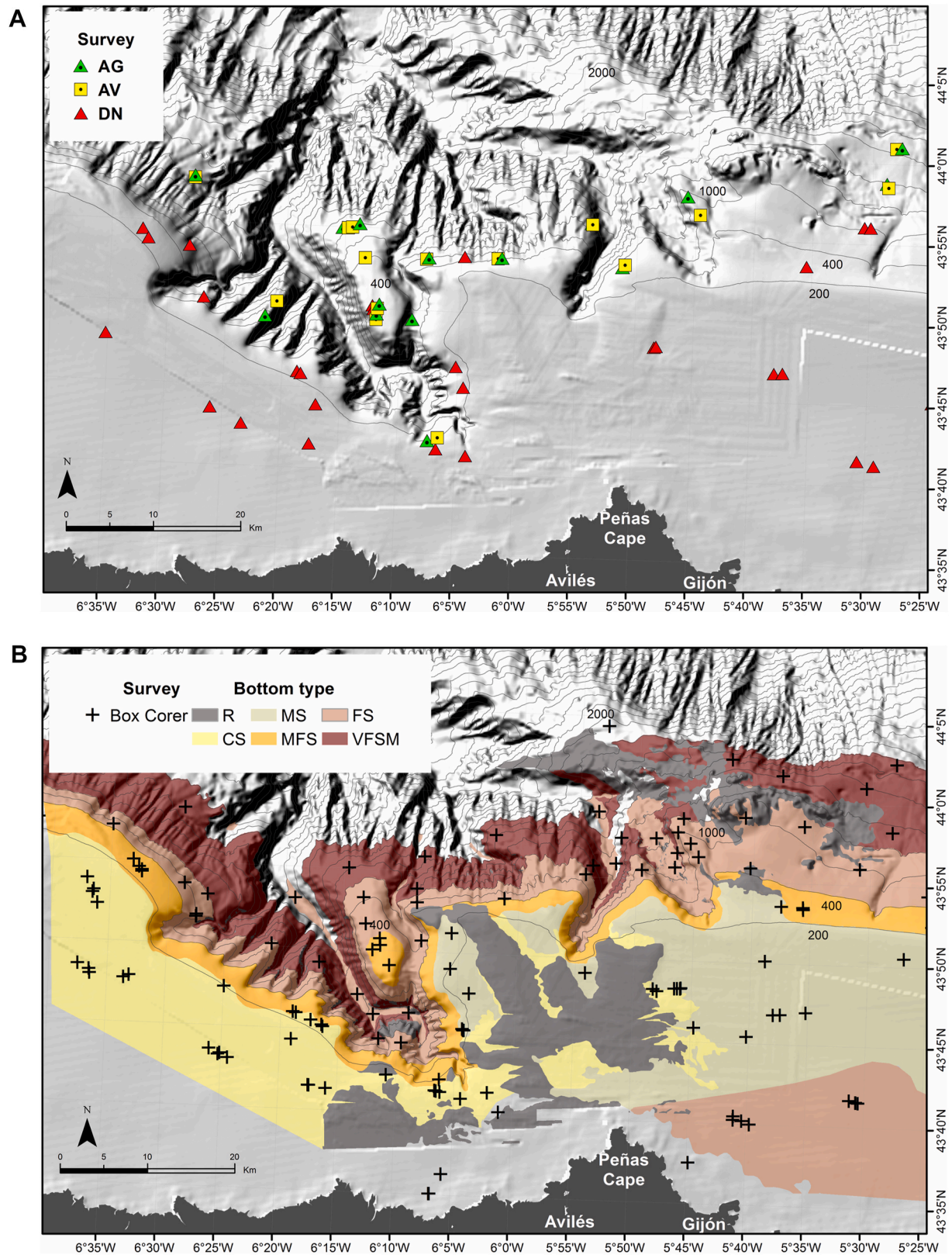


Fig. 2. Position of the sampling stations.

a) Biological samplings: yellow squares represents beam trawl hauls mean position. Triangles represents the two otter trawl samplings (red correspond to DN samples, pointed green correspond to AG). The point inside the symbols indicates samplings performed within the project INDEMARES.

b) Sedimentary samplings: black crosses represents the box-corer samples. R = rocky bottom; CS = coarse sands; MS = medium sands, MFS = medium and fine sands, FS = fine sands, and VFSM = very fine sands and muds.

2.4. Data analysis

Epibenthic (output of beam trawl samplings) and demersal (output of the otter trawls samplings) assemblages were determined through hierarchical classification method using R software package “vegan” (Oksanen et al., 2020). A distance matrix was constructed using the function “vegdist” of R software package “vegan” (Oksanen et al., 2020) by means of the Bray-Curtis coefficient by square-root transforming the biomass values. From the distance matrix, hauls were classified and ordered by cluster analysis (based on the group-average sorting algorithm).

In addition, the SIMPER (Similarity percentage breakdown) analysis (Clarke and Warwick, 1994) was applied to identify which species contributed most to the similarity within the group of different assemblages determined by the cluster analysis and to obtain their biomass within the assemblages.

Once assemblages for both epibenthic and demersal components were obtained, an exploration on the adequate ordination method was performed. The exploration consisted in performing detrended correspondence (DCCA) using the function “decorana” (Hill and Gauch, 1980) of the R package “vegan” (Oksanen et al., 2020) to assess the response of species to environmental gradients available. If the length of longest gradient calculated by using DCCA was larger than 4, using the unimodal constrained method was required (Lepš and Šmilauer, 2003). The unimodal methods always implicitly work with standardized data. Consequently, all environmental variables were standardized by making the mean equal to 0 and S.D. equal to 1 (i.e., scale into zero for mean and unit variance) by using the function “decostand” from the package vegan (Oksanen et al., 2020). It allowed for the ensuring that all the variables have similar weighting. The influences of high values (i.e., depth expressed in meters) are reduced and those of low values (i.e., percentage of organic matter in the sediment) are enhanced so that all have similar influence.

Hereafter, further selection was made based on an ANOVA test for significant variables (using R software package “Stats”) (Chambers and Hastie, 1992), to select only those variables which contribute most to explain the species distribution observed. The final set of variables obtained was used to perform a CCA (using R software package “vegan”) (Oksanen et al., 2020) for the two ecological compartments (epibenthic and demersal).

An ANOVA with 999 permutation test for significance of constrained axis was performed (using R software package “stats”) (Chambers and Hastie, 1992) for demonstrating the significance of the first two axis for both data sets (epibenthic and demersal).

Finally, the “envfit” function (using R software package “vegan”) (Oksanen et al., 2020) was used to compute analysis of variance tables for the fitted model obtained by CCA and get the p-value of correlation of each variable with overall species distribution. Significant predictors (p-values < 0.1), between those available, were used to explain the species distribution observed.

3. Results

3.1. General results on data preliminary exploration

Data exploration analysis revealed that no remarkable differences were observed for the two different otter trawl samplers in terms of species richness per taxonomic group (Fig. 3a), percentage of biomass of the catch compositions per taxonomic group (Fig. 3b), and of biomass percentage of organisms classified with regard to their ecological compartment (benthic, benthopelagic, or demersal) (Fig. 3c). Whilst differences have been observed between beam trawl samples and otter trawl samples (Fig. 3a, b, and 3c), in terms of species richness, beam trawl showed the highest values for invertebrates taxonomic groups such as Porifera, Sipuncula, Crustacea, and Mollusca, while lower for Chordata (Fig. 3a). The same results were observed in terms of biomass,

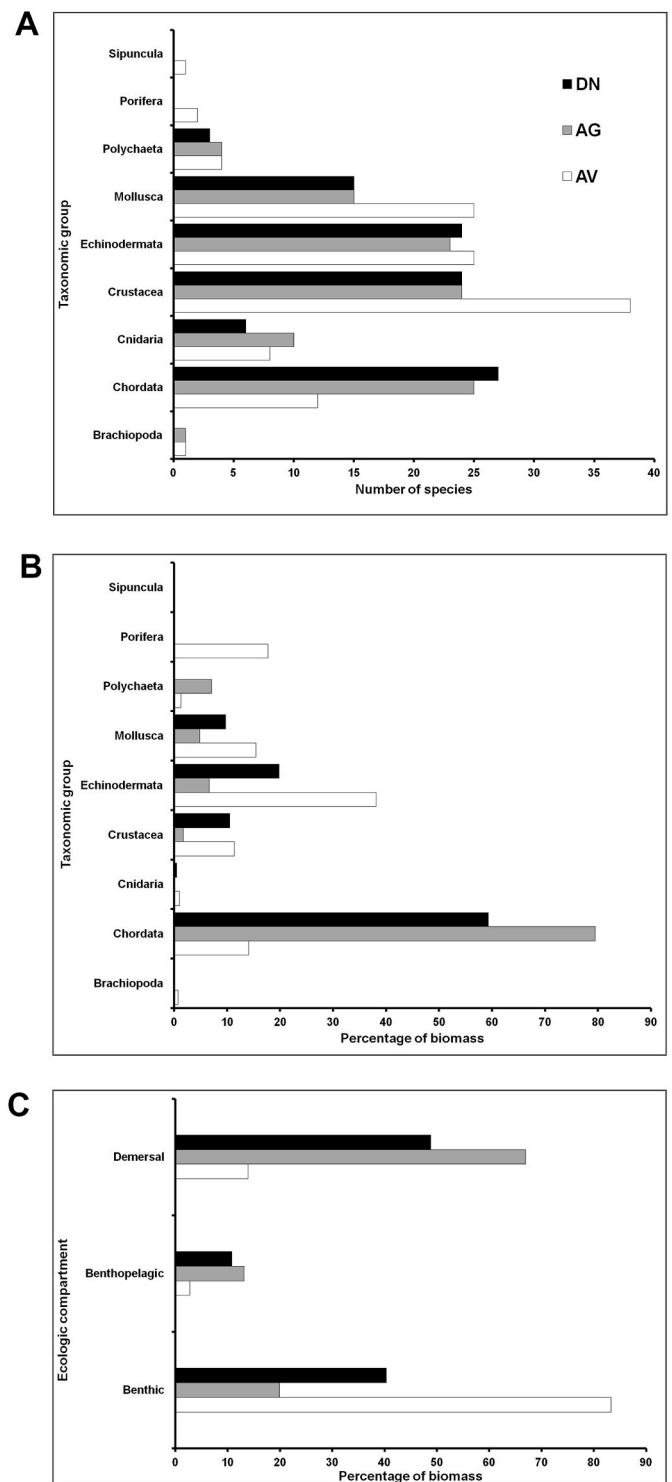


Fig. 3. Comparison of the samplers catch. AV (beam trawl): white boxes, AG (otter trawl): grey boxes, DN (otter trawl): black boxes, in terms of: a) Species richness, expressed as number of species per taxonomic group. b) Percentage of faunal biomass per taxonomic group. c) Comparison of percentage of faunal biomass per ecological data (benthic = fixed or free living on the bottom, demersal = free living close to the bottom, benthopelagic = benthic with the capability to move in the water column).

the chordates are much more present in the otter trawl samplers than in the beam trawl sampler (Fig. 3b). Additionally, the beam trawl sampler caught more benthic organisms than demersal (Fig. 3c). Moreover, the epibenthic fauna data obtained by beam trawl did not cover the entire

sampling depth range (c.ca 100–1500 m), as it covers only from 202 to 1473 m (Fig. 2a). The demersal fauna data obtained by the two otter trawls cover instead the entire sampling depth range (Fig. 2a).

Consequently, otter trawl samples were joined to gather results for the demersal component of the community, while beam trawl samples were used to get information about the epibenthic component of the community. The final species list consisted, after filtering, of 116 for AV (epibenthic) and 110 for AG and DN surveys joined together (demersal), respectively. The sampling systems used allowed for the covering of sedimentary bottoms from 100 m up to a depth of 1500 m inside the SCI of ACS.

3.2. Biological assemblages for epibenthic macrofauna (from beam trawl samples)

For the epibenthic data, cluster analysis shows the existence of 2 main groups of hauls (90% dissimilarity), structured by depth, for the shallow and deep with the break point located around 600 m depth (Fig. 4). Species groups are very heterogeneous and very diverse, being *Gracilechinus acutus* and *Marthasterias glacialis* the most important species in the shallower group and *Pheronema carpeni* the most important species in the deeper. More in detail, 5 subgroups at lower levels can be distinguished. These subgroups showed a clear bathymetric pattern (Supplementary Tables 1 and 2) and are described below.

- MS (Medium Shelf) c.ca 200 m depth: The most important species in terms of biomass were the echinoderms *G. acutus*, *M. glacialis*, and *Parastichopus regalis*, the mollusc *Astarte sulcata*, and the crustacean *Pagurus prideaux*. Together they constitute 90% of the total biomass for this bathymetric range (Supplementary Table 1).
- SB (Shelf Break) c.ca 300–400 m depth: This assemblage showed important decapod crustaceans as *Munida sarsi*, *Philocheirus echinulatus*, *Dichelopandalus bonnieri*, *Pagurus alatus*, *Pontophilus spinosus*, *Pandalina profunda*, *Goneplax rhomboides*, and *Solenocera membranacea*. The echinoderms *Ophiura ophiura*, second species in terms of biomass and *Astropecten irregularis* were also very important and together reached more than 15% of the cumulative biomass. Another important taxon represented in this group is Mollusca with the species *Eledone cirrhosa*, which is the most important species in terms of biomass, *Scaphander lignarius*, *Rossia macrosoma*, *Euspira fusca*, and *Neorossia caroli* (Supplementary Table 2a).

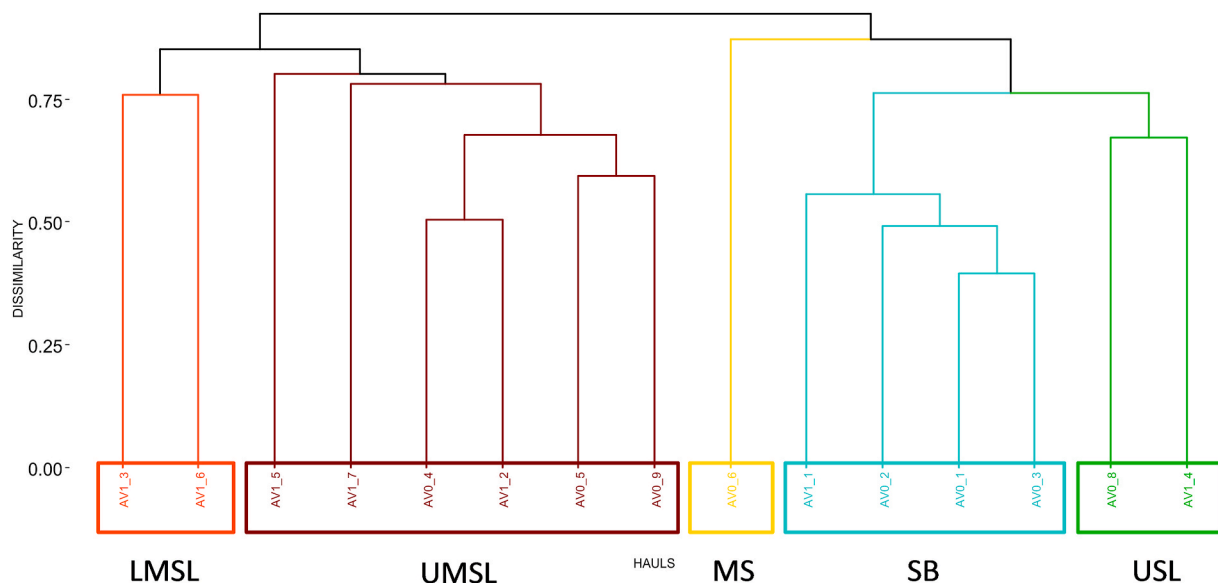


Fig. 4. Hierarchical cluster for benthic assemblages. Labels indicate hauls coded with survey, year 0: 2010 and 1: 2011. The part after the underscore indicate sample number. Groups were identified by depth (US ~200 m, SB ~300–400 m, USL ~500–600 m, UMSL ~600–1100 m, and LMSL ~1200–1500 m).

- USL (Upper Slope) c.ca 500–600 m depth: This assemblage is constituted as follows with 40% being crustaceans *Plesionika martia*, *D. bonnieri*, *Polychaetes typhlops*, and *Natatolana borealis* with *P. alatus* as the most important in terms of biomass; 25% by molluscs *Galeodea rugosa* and *Colus gracilis*, the first is the second most important species. Cnidarian was also represented by *Actinauge richardi* (10%) (Supplementary Table 2b).
- UMSL (Upper Middle Slope) c.ca 600–1100 m depth: The assemblage biomass is distributed among species as follows with echinoderms reaching 60% of cumulative biomass, being the most abundant *Phormosoma placenta*, *Nymphaster arenatus*, *Psilaster andromeda*, and *Araeosoma fenestratum*. Then crustaceans that reach 20% of biomass *P. typhlops*, *Pontophilus norvegicus*, *Parapagurus pilosimanus*, *P. alatus*, and *Munida tenuimana*. Molluscs were represented by *Limopsis aurita* and *Abra longicallus*, and lastly, the sponge *P. carpeni* (Supplementary Table 2c).
- LMSL (Lower Middle Slope) c.ca 1200–1500 m depth: This assemblage described the soft bottom middle slope domain and was composed mainly by the sponge *P. carpeni*. About one third of the similarity is due to the echinoderms *Zoroaster fulgens* and *Cidaris cidaris*. The brachiopod *Gryphus vitreus* was also present (Supplementary Table 2d).

3.3. Biological assemblages for the demersal community (from otter trawl samples)

Cluster analysis for the demersal assemblage (data from the two otter trawls) showed as in the case of the epibenthic assemblages a first main division between groups in the cluster (Fig. 5). This division remarks that continental shelf and shelf break assemblages were very different from the continental slope ones being the break point situated at 400 m depth, approximately. The species *Scylliorhinus canicula* represent the most important species for the shallower group, while *Galeus melastomus* and *Phycis blennoides* are the most abundant species in the deeper group. In detail, 6 subgroups were identified, 3 were observed in the continental shelf and in shelf break, and the other 3 subgroups along a depth gradient in the continental slope (Fig. 5).

According to SIMPER analysis, the species which most contributed to intragroup similarity for demersal community are reported (Supplementary Tables 3a–3f):

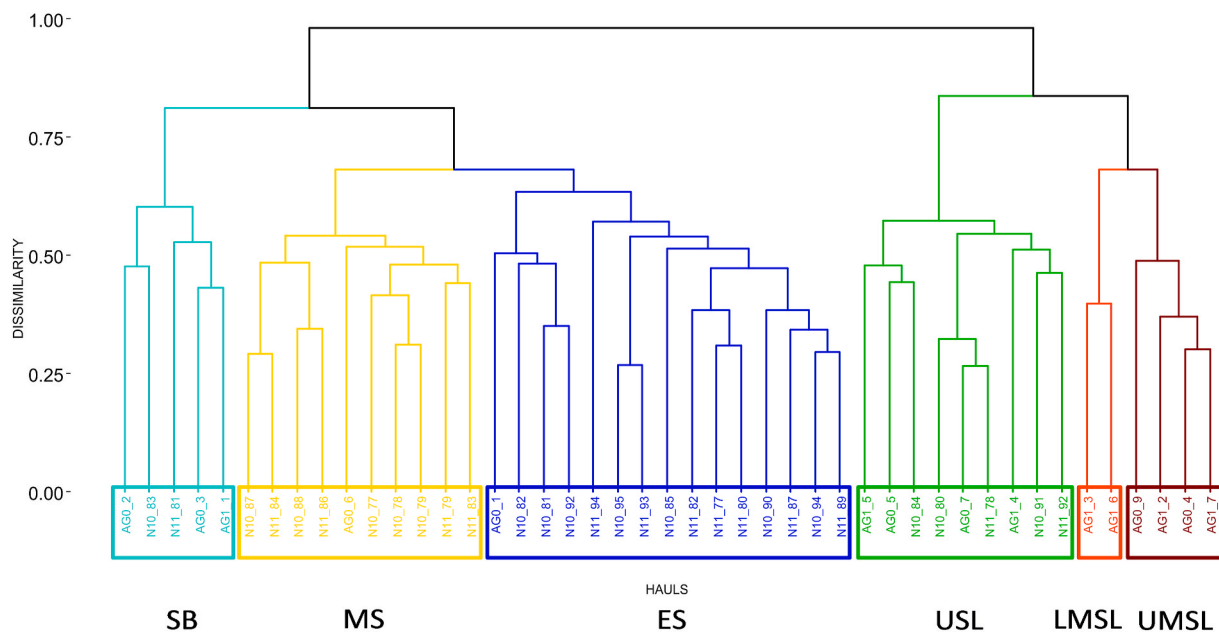


Fig. 5. Hierarchical clustering of the demersal assemblages. Labels indicate hauls coded with survey, year 0: 2010 and 1: 2011. The part after the underscore indicates sample number. Groups were identified by depth (US ~100–200 m, LS ~150–300 m, SB ~300–400 m, USL ~500–700 m, UMSL ~900–1100 m, and LMSL ~1200–1500 m).

- MS (Medium Shelf) c.ca 100–200 m depth: Mainly constituted by the elasmobranch *S. canicula*, followed by *Chelidonycis cuculus*. The only species that coincide with those observed for the beam trawl were *G. acutus* and *P. regalis* (Supplementary Table 3a).
- ES (External Shelf) c.ca 150–300 m: Mainly constituted by *S. canicula* but accompanied by other fish species such as *Lepidorhombus boscii* and *Lepidorhombus whiffiagonis*, and some benthic species like *M. sarsi*. (Supplementary Table 3b).
- SB (Shelf Break) 300–400 m depth: Main species are teleostean fishes like the Macrouridae *Coelorrinchus caelorhincus*, the flatfish *L. boscii*, *Microchirus variegatus*, and the chondrichthyes *G. melastomus* (Supplementary Table 3c). The cephalopod *E. cirrhosa* and *R. macrosoma* and the decapod crustacean *M. sarsi* have been observed. This latter, together with *E. cirrhosa*, showed the greatest biomass values (Supplementary Table 3c).
- USL (Upper Slope) c.ca 500–700 m depth: Most important species were *G. melastomus*, *P. blennoides*, *Chimaera monstrosa*, and *Etmopterus spinax*. These species were accompanied by the octopod *Opisthoteuthis agassizii* followed in importance by the Chondrichthyes *Deania profundorum* and fishes like *Hoplostethus mediterraneus*, *Lepidion lepidion*, and *Nezumia aequalis* (Supplementary Table 3c).
- UMSL (Upper Middle Slope) 900–1100 m depth: Clearly dominated by *Trachyrincus scabrus*, *Deania calcea* (Chondrichthyes), and *Alepocephalus rostratus* which represents almost two thirds of the percentage of biomass of the species collected in these samples (Supplementary Table 3e). There is no match with the same depth group for benthic species (Supplementary Table 2c).
- LMSL (Lower Middle Slope) 1200–1500 m depth: Mainly constituted by *A. rostratus* and *Alepocephalus bairdii* which are the 56% of the total biomass collected (Supplementary Table 3f). The most important benthic species was the sponge *P. carpenteri* (Supplementary Table 3f).

These subgroups showed bathymetric boundaries were very similar to those observed for the epibenthic ones sampled by beam trawl (Figs. 4 and 5).

3.4. Link with environmental variables used

The environmental variables that were considered widely varied (Supplementary Table 4). Multiple regression analysis performed showed the existence of significant correlations in both data sets. The variables which were strongly correlated were temperature to depth, roughness to slope, and organic matter to sorting coefficient. Being the most obvious, the decrease of temperature in water column with depth, temperature was not used in the calculation of CCA. We have obtained a pool of 6 continuous variables: depth, BPI broad, salinity, organic matter content in sediments (% OM), main particle size (Q50 phi), and sorting coefficient (S_0). Finally, we considered the categorical variable bottom type (surface sediments) (Fig. 2b).

3.4.1. Links with environment for epibenthic community

The length of the gradient detected with DCCA was 5.852, consequently CCA was applied (unimodal constrained method). CCA ordination applied for epibenthic community accounted for 70.4% of total inertia (Supplementary Table 5). The first two axes of the CCA plot explained 44.6% of variance of the species-environment relationship and 47.5% of the species data (Fig. 6). These species already showed in the SIMPER analysis (Supplementary Tables 1 and 2) and have an intimate link with the biotope (bottom and water characteristics).

An ANOVA test for significance of constrained axis has been performed, demonstrating the significance for the first two axes (Supplementary Table 6). Significant environmental factors for the first axis were depth, salinity, and MFS; significant environmental factors for the second axis were BPI broad, Q50 phi, and FS (Table 1).

As shown in Fig. 6, an arc Guttman effect has been observed since length gradient is very large, beta diversity of species observed between different biotopes is very large due to the wide depth range (200–1500 m) with a certain variety of characteristics also within the same depth ranges. The Guttman effect occurs because the mean values of the most significant variable on the first axis (depth) are correlated with the maximum values of BPI (on the shelf break) on second axis of the biplot (Fig. 6). Only two species do not fall in the arc form because they showed extreme values for their depth distribution (one of the discriminant factors playing a role in determining first ordination axis), *Hyalinoecia*

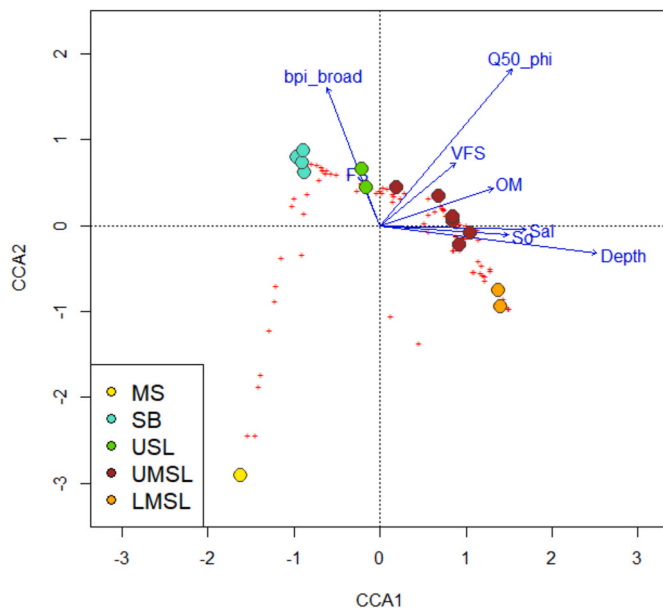


Fig. 6. Canonical Correspondence Analysis (CCA) for benthic assemblages (sampling AV performed with beam trawl). Ordination of hauls and environmental variables used were depth, BPI broad, bathymetric position index broad, salinity (Sal), organic matter (OM) content in sediments, Q50_phi, median of the grain size, sorting coefficient (S₀) expressed as interquartile distance of the grain size distribution. Categorical variable bottom type was defined as follows: fine sands (FS), and very fine sands (VFS). Assemblages of sampling stations from Fig. 4 are indicated with coloured points: yellow (US: upper shelf), turquoise (SB: shelf break), green (USL: upper slope), brown (UMSL: upper middle slope), orange: (LMSL: lower middle slope).

Table 1

Results of the CCA analysis to find significant environmental variables for the epibenthic community (beam trawl samplings). CCA1: Contribution of the environmental variables for the first constrained axis. CCA2: Contribution of the environmental variables for the second constrained axis. r²: correlation between the environmental variables and the ordination system selected by CCA. Pr (>r): p-value for each variable with overall species distribution. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '.' 1.

Environmental variable	CCA1	CCA2	r ²	Pr (>r)	Significance level
Depth	0.9922	-0.1245	0.9633	0.001	***
bpi_broad	-0.3578	0.9337	0.4416	0.040	*
Sal	0.9996	-0.0280	0.4309	0.083	.
OM	0.9501	0.3118	0.2845	0.188	
Q50_phi	0.6443	0.7647	0.8424	0.001	***
So	0.9973	-0.0733	0.3331	0.126	
VFS	0.7687	0.6395	0.1939	0.303	
FS	-0.3884	0.9214	0.0414	0.962	
CS	-0.4875	-0.8730	0.9666	0.062	.

tubicola a polychaete and *Stichastrella rosea* a starfish (Fig. 6) observed at a very wide depth range.

3.4.2. Links with environment for demersal community

The length of the gradient obtained with DCCA was 7.719, also in this case a unimodal multivariate method was applied. CCA ordination applied for the demersal component (AG and DN samplers) accounted for 51.2% of total inertia (Supplementary Table 7). The first two axes of the CCA plot explained 50.4% of variance of the species-environment relationship and 36% of the species data (Fig. 7) (Supplementary Table 7).

An ANOVA test has been performed for demonstrating the significance for the first two axes (Supplementary Table 8). Significant

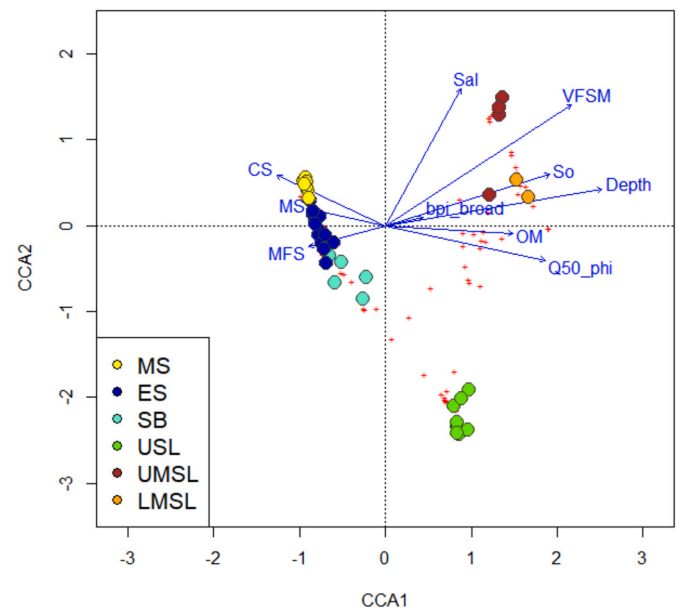


Fig. 7. Canonical Correspondence Analysis (CCA) for demersal assemblages (samplings AG and DN performed by otter trawls). Ordination of hauls and environmental variables used were depth, BPI broad, bathymetric position index broad, salinity (Sal), organic matter (OM) content in sediments, Q50_phi, median of the grain size, and sorting coefficient (S₀) expressed as interquartile distance of the grain size distribution. Categorical variable bottom types were defined as follows: coarse sands (CS), medium sands (MS), medium fine sands (MFS), fine sands (FS), and very fine sands and muds (VFSM). Assemblages of sampling stations from Fig. 5 are indicated with coloured points: yellow (US: upper shelf), blue (LS: lower shelf), turquoise (SB: shelf break), green (USL: upper slope), brown (UMSL: upper middle slope), orange: (LMSL: lower middle slope).

environmental factors for the first axis were depth, Q50 phi, OM, and S₀, while significant environmental factors for the second axis were salinity, VMFS, and CS (Table 2).

The results of the CCA for the samplings of the demersal compartment (otter trawls together) were very similar to those obtained for the beam trawl survey in terms of the influence of environmental variables considered on the groups of hauls (Fig. 7; Table 3).

The most important difference observed with the epibenthic assemblages was the lack of significance of the BPI broad variable (see Table 3 for a synthetic comparison). Additionally, in this case, a marked arc

Table 2

Results of the CCA analysis to find significant environmental variables for the demersal community (baca otter trawl samplings). CCA1: Contribution of the environmental variables for the first constrained axis. CCA2: Contribution of the environmental variables for the second constrained axis. r²: correlation between the environmental variables and the ordination system selected by CCA. Pr (>r): p-value for each variable with overall species distribution. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '.' 1.

Environmental variable	CCA1	CCA2	r ²	Pr (>r)	Significance level
bpi_broad	0.9729	0.2312	0.0318	0.606	
Depth	0.9821	0.1883	0.9475	0.001	***
Sal	0.5120	0.8589	0.4620	0.001	***
OM	0.9995	-0.0298	0.3152	0.002	**
Q50_phi	0.9844	-0.1757	0.5123	0.001	***
So	0.9507	0.3100	0.5776	0.001	***
CS	-0.9216	0.3879	0.2716	0.007	**
MS	-0.9825	0.1861	0.1184	0.118	
MFS	-0.9612	-0.2756	0.1194	0.139	
FS	-0.9612	-0.2756	0.1194	0.139	
VFSM	0.8426	0.5384	0.9751	0.001	***

Table 3
Main environmental link for the 6 main assemblages identified with cluster and SIMPER analysis.

Group	Epibenthic species (SIMPER)	Accompanying Demersal species (SIMPER)	Mean depth (mean \pm sd) (m)	Main environmental links for epibenthic community (H = high, M = medium, L = low)	Main environmental links for demersal community (H = high, M = medium, L = low)	Sediment type
MS	<i>G. acutus</i> <i>M. glacialis</i> <i>P. regalis</i>	<i>S. canicula</i> <i>C. cuculus</i>	157 \pm 37	L depth L Q50phy L OM	L depth L Q50phy L OM	CS/MS
ES	n. a.	<i>L. boscii</i> <i>L. whiffagonis</i> <i>M. sarsi</i> (epibenthic)	211 \pm 64	L depth L Q50phy L OM	L depth L Q50phy L OM	MS/FS
SB	<i>E. cirrhosa</i> <i>O. ophiura</i> <i>M. sarsi</i>	<i>C. caelorhincus</i> <i>M. variegatus</i> <i>G. melastomus</i>	394 \pm 63	H BPI broad L So	L So L Salinity	FS
USL	<i>P. alatus</i> <i>G. rugosa</i> <i>A. richardi</i>	<i>G. melastomus</i> <i>C. monstrosa</i> <i>P. blennoides</i> <i>E. spinax</i>	572 \pm 60	MH BPI broad M Q50phy M Salinity	M Q50phy M Salinity	FS
UMSL	<i>P. placenta</i> <i>A. fenestratum</i> <i>N. arenatus</i> <i>P. andromeda</i>	<i>A. rostratus</i> <i>T. scabrus</i> <i>D. calcea</i>	920 \pm 173	H depth H Salinity H OM	H depth H Salinity H OM	VFSM
LMSL	<i>P. carpenteri</i> <i>Z. fulgens</i>	<i>A. rostratus</i> <i>A. bairdii</i>	1362 \pm 151	H depth L BPI broad H So	H depth H So H Q50phy H OM	VFSM

effect had been observed because of the extremely large gradient and very large beta-diversity between sites (Fig. 7). The most important variation is due to the species that characterize the hauls and their groups (Table 3). As already evidenced by the SIMPER results, benthic assemblages (collected by beam trawl) (Supplementary Tables 1 and 2) have a more intimate link with the biotope (bottom and water conditions) and could be considered the most representative of the community because of their scarce mobility (Table 3). Table 3 reported the main environmental variables characterising the assemblages observed.

4. Discussion

Our study on soft bottom substrate inside this SCI is useful in the definition of an appropriate management plan, considering that, for reaching this goal, provide an inventory as complete as possible of the organisms living in these zones is needed. It focused on the study of species assemblages (epibenthic and demersal) and their environmental preferences as a first step to understand the system functioning. Additionally, the use of different samplers in the same area allowed for obtaining an up-to-date snapshot of the communities (epibenthic and demersal) characterising the soft bottoms in the ACS. This study revealed a particularly complete view of the fauna inhabiting the soft bottom inside the SCI, since it comprise not only epibenthic megafauna, but also nektonic coexisting species. In general, we can confirm that the otter trawl samplers gives more results in term of nektonic demersal assemblages compared with beam trawl samplers which give more information in terms of epibenthic assemblages. These results on the information of the biological data gathered from each sampler coincide with those obtained by other authors for both type of samplers (Kaiser et al., 1994 for beam trawl; Castro et al., 2012 and Stergiou et al., 2003 for otter trawls).

Although the mixture of epifaunal assemblages with the demersal ones, which showed a greater spatial range, makes the discussion of the results challenging, we decided to discuss the interpretation of the environmental variables influencing both assemblages together. Taking into account that the samplings for AV (beam trawl focused on epibenthic fauna) and AG hauls (focused on demersal fauna) were performed practically at the same location, using different tools for almost the whole depth range (200–1500 m c.ca) and that the environmental factors influencing both epibenthic and demersal assemblages were similar, we consider this decision justified.

The species of the epibenthic fraction of the population have a more intimate link with the biotope (bottom and water conditions) and could be considered the most indicative of the community because of their null or scarce mobility, while the demersal species have to be considered as associated fauna since they have the ability to move between different zones (Sunday et al., 2015). In this work, a lower level of variance was explained for demersal data than that explained for the epibenthic assemblages. Consequently, we consider demersal assemblage less linked to the environmental variables at our disposal than the epibenthic assemblage. Demersal community was composed of fish mainly, describing this data together with the benthic is very important because of the spatial-temporal coexistence showed. Their coexistence make possible their biological interactions (e.g., in terms of predatory control) (Villéger et al., 2017) or competition for the same resources.

Additionally, as part of the same project, data from infauna have already been published for the same area (Lourido et al., 2014) making these characterizations practically complete for soft bottoms in the SCI. Finally, the choice of working with biomasses, instead of numbers, gives a more realistic image of what species are the most important for ecosystem dynamics (Grime, 1998). Depth played a very important role in the segregation of the assemblages observed. Bathymetric differentiation of benthic communities is commonly observed (Carney, 2005; Gage and Tyler, 1991), and has already been described in the Cantabrian Sea (e.g., Sánchez and Serrano, 2003; Serrano et al., 2006a, 2006b; Sánchez et al., 2008). Particularly, in the same study area, it has been observed that benthic faunal assemblages were principally structured by depth (Louzao et al., 2010). The same patterns have been observed for the infauna in the same area (Lourido et al., 2014), depth and sediment type seems to be the main factors structuring these assemblages. As underlined by Ciercoles et al. (2018), this is probably due to the response of organisms in combination with several changes in various environmental variables which vary with depth (e.g., physical chemical variables of the water column, food availability, and sediment characteristics) and finally ecological interspecific interactions which could determine the bathymetric ranges of some species (Snelgrove and Butman, 1994; Cartes et al., 2004; Martins et al., 2014). Other factors played an important role in assemblage definition such as bottom type and other sedimentary variables that indirectly indicate hydrodynamics of the area. The most important remarks are about not so obvious variables (e.g., lowest values of S_0 indicate very constant transportation of sediments while high S_0 indicates not constant depositional movements,

for example due to the presence of turbidity currents). This is typical of geologic formations like the canyons in which strong hydrodynamic events take place periodically (Gómez-Ballesteros et al., 2014).

Hydrodynamics have been considered as the ultimate factor, not only affecting the spatial distribution of different sediment types but also the associated benthic organisms (Nowell, 1983; Jumars and Nowell, 1984; Nowell and Jumars, 1984; Butman, 1987a, 1987b; Miller and Sternberg, 1988). Finally, BPI broad resulted significant for the epibenthic fauna, whilst almost irrelevant in the case of demersal community. This makes sense considering that this variable discriminates if the haul was performed in a concave, convex, or in a flat area, which is more important for those species with reduced or no mobility, whilst it has less for the nektonic species. Swimming ability had positive relationships with ecological generalism (Sunday et al., 2015). Actually, the constrained variance explained for demersal species, with better swimming ability, is lower than that explained for the benthic community, in which most organisms are sessile or have reduced movement. Five main assemblages for the benthic data and six main assemblages for demersal data were observed. Two allocated in the continental shelf, of which just the upper one for the benthic community, and both (upper and lower) for the demersal community. Another one is present mainly in the marginal continental shelf of El Canto Nuevo (shelf break assemblage) for both biological components. Finally, the other 3 assemblages in the continental slope (upper, upper middle, and lower middle), for both biological components, followed a bathymetric pattern. These results are in accordance with those already observed by Louzao et al. (2010).

MS assemblages: Beginning from the shallower bottoms sampled, we found the continental shelf community at depths between 100 and 300 m. In this zone, two assemblages were identified, the first by the coarsest sediments and by low values of Q50 phi which indicated flattened areas in which transport of sediment is not very energetic in both cases (beam trawl and otter trawl samplings). The most important epibenthic species in this group were *P. regalis*, *M. glacialis*, and *G. acutus*, the latter known to be very abundant at this depth range in the Cantabrian Sea fishing grounds and to prefer coarse sediments (González-Irusta et al., 2012). Nevertheless, no reference was found about the preference of *G. acutus* for flattened and low energy transport environment as it was observed in our work.

The species characterising these assemblages do not coincide with those observed by Louzao et al. (2010) at the same depth range, probably because of the differences in the samplers used by these authors (anchor dredge and epibenthic sledge) and also because of the sampling location (they sampled also on rocky bottoms). Swimming species observed were *S. canicula*, *L. boscii*, and *L. whiffagonis* are by definition more ubiquitous since their ability to move gives them more dispersal capacity and a more generalist ecological behaviour (Sunday et al., 2015). Specifically, *S. canicula* is well known to have wide depth range and aggregate behaviour (Rodríguez-Cabello et al., 2004). Both *Lepidorhombus* species inhabit these soft grounds, although it is known that *L. boscii* has a wider distribution and depth range, while *L. whiffagonis* occupies shallower waters (Sánchez et al., 1998).

ES assemblage: It was not observed in epibenthic assemblage due to the lack of samples in this bathymetric range, differently from what observed later for the demersal assemblages. Thus, the second assemblage observed for the continental shelf came out exclusively from data of otter trawls and revealed practically the same fish species as the shallower one. This assemblage differs from the MS above all for the smaller sediment grain size that clearly does not influence the distribution of the demersal species. In this assemblage, it also appeared that some benthic species differ from the MS e.g. *M. sarsi* an opportunistic benthic decapod crustacean which appears predominantly at depths of between 200 m and 500 m (Freire et al., 1992). This species has a burrowing behaviour (Fariña et al., 1997) and a preference for medium fine sands (Serrano et al., 2006a).

SB assemblages: At depth of about 300–400 m, they presented preferences by MFS and FS, low OM levels and low values of S_0 which

indicate constant transportation of the sediments. Moreover, there were high values of BPI broad in the case of epibenthic community, indicating that this group prefers to stay in convex zones like the top of the El Canto Nuevo marginal shelf or on the edge of the canyons. The most important epibenthic species for this group was *E. cirrhosa*. This species has a wide bathymetric range, but Lauria et al. (2016) found an optimum at 300 m depth and a presence in soft bottoms as observed in our results, while Giordano et al. (2010) found it at a shallower depth. Additionally, the scarce hydrodynamics that are indicated by the constant transportation processes is preferred by the demersal octopods. In fact, the currents are expected to have the strongest effects on pelagic species like squid rather than in demersal species like octopods (Coelho, 1985). Another important species in this assemblage is *O. ophiura*, that is typically found on soft bottoms (Fell, 1966) with a wide depth range (0–685 m) (Koukouras et al., 2007). *M. sarsi* also played an important role. In this case, the main benthic species structuring the assemblage do not coincide with those described by Louzao et al. (2010) in the same area, probably for the reasons exposed above. The results partially coincide with those observed by Serrano et al. (2006a) which observed other ophiuroid together with *M. sarsi* in the Cantabrian Sea at a similar depth range and for similar sediment type.

Fish species typical of this group appeared also in deeper hauls characterized by other environmental variables. Consequently, we can consider them ubiquitous species on soft bottoms. These species are *L. boscii*, *M. variegatus*, and *C. caelorrhincus*, although the latter is caught up to 1250 m, it is commonly found at 200–500 m (Cohen et al., 1990). *L. boscii*, which has a commercial value is known to be distributed at this depth range on shelf break. Furthermore, it seems that *L. boscii* is present on all the soft bottoms of the continental shelf both in Cantabrian Sea (Sánchez, 1994; Sánchez et al., 1995) and in other areas (Sartor et al., 2002).

USL assemblages: Corresponding to hauls performed between 500 and 600 m depth, for the epibenthic fauna it extends until 700 m for the demersal fauna. These assemblages showed preferences for mixed sediments with high values of Q50 phi (highly energetic movement of sediments produced by typical poleward slope currents, as demonstrated by Pingree and Le Cann (1990). Preference for high values of BPI broad has been observed only for epibenthic fauna indicating the affinity of these organisms for convex zones. Unlike the shelf break, this group showed preference for high hydrodynamic conditions. The typical epibenthic species of this group is *P. alatus*, although it is important to remark that its higher biomass values is due to a bias in weighting this species with the shell (obviously not produced by this organism). So in terms of biomass, the most important species in the epibenthic upper slope group is *G. rugosa*. This gastropod was found to dominate the same bathymetric range with high slope values in the Alboran Sea (Ciercoles et al., 2018).

Other species included in this group are crustaceans (*P. martia*, *D. bonnieri*, *P. typhlops*, and *N. borealis*), cnidarians (*A. richardi*), and mollusks (*C. gracilis*). *A. richardi* is known to be widely distributed in the Cantabrian Sea at this depth strata (Serrano et al., 2006a). Serrano et al. (2017) found that *C. gracilis* showed similar environmental preferences. All the former species seem to be able to adapt to instable sedimentary environments. In the present study, we hypothesized the presence of strong currents to explain these environmental conditions. Another important species in terms of biomass was *O. agassizii*. This species depends principally on zoobenthos for their food supply, as well as the bivalve *Limopsis* sp. (Villanueva and Guerra, 1991) which is a highly abundant species in this and adjacent depth strata (present work; Louzao et al., 2010) highlighting the link in terms of ecological interactions.

G. melastomus was the most important representative for the demersal assemblage in this group. Pennino et al. (2013) underlined that the presence of this species in the Mediterranean Sea was linked to the same bathymetric range and areas of strong slope, compatible with the environmental condition preferences observed in our work. Furthermore, other elasmobranch species that were observed in this group (i.e.,

Etmopterus spinax) already demonstrated to have the same environmental preferences as *G. melastomus* (Pennino et al., 2013).

UMSL assemblages: Upper middle slope was identified at 700–1100 m depth. In this zone, it was observed that the Mediterranean outflow water (MOW) had high values of salinity (see González-Pola et al., 2012; Sánchez et al., 2014a, 2017) and a high content of organic matter in the sediment due to the contourite depositional system generated by along-slope sedimentary processes (Van Rooij et al., 2010). The sediment dominant was very fine sand (VFS) with high S_0 values which indicates non-constant movements of sediments. It is known that near the upper or lower boundary of the MOW, enhancement of the bottom-current velocity by internal tides and waves occurs (Van Rooij et al., 2010; Hernández-Molina et al., 2016). Epibenthic community, showed a preference for low values of BPI broad which represented the concave areas where turbidity currents could occur (Sánchez et al., 2014a).

Benthic species that characterize this area the most were the sea urchin *P. placenta*, an omnivorous urchin (Serrano et al., 2011; Stevenson and Rocha, 2013). The dominance of deposited organic matter feeding echinoderms in deeper areas of the slope have already been described (e.g., Sibuet, 1977; Thurston et al., 1994; Iken et al., 2001; Cartes et al., 2009). Another echinoderm, the starfish *N. arenatus*, was important as it is a common scavenger (Costa et al., 2015). In general, organisms living at such depths rely their existence directly or indirectly on the high organic matter content of the sediment in which they live, this content is the engine for a secondary trophic chain alimented by the detritus of the primary food chain of the shallower photic zone (Cartes et al., 2007). Most of the organic material derived from shallower zones primary productivity is transported to the ocean-floor (Gooday and Turley, 1990). Bacteria and protozoa (flagellates and foraminifers) rapidly colonize and multiply on phyto-detritus, while large deposit feeding animals ingest it (Gooday and Turley, 1990), thus recycling the organic matter and providing energy to feed the deep trophic web like that observed in this stratum.

Other organisms that play an important role at this depth are *P. carpenteri* a hexactinellid which is the most important structuring species in the deepest assemblage observed. Further, *L. aurita* plays an important role in terms of biomass, this result is in accordance with what was previously observed by Louzao et al. (2010). It is a semi-infaunal, or sessile fauna anchored to sediment particles and is a filter feeding organism which has been indicated as a habitat structuring species for offshore detrital bathyal bottoms (Gofas et al., 2014).

Demersal species characteristics at this depth describes the nektonic fraction of the assemblage as composed by the fish *A. rostratus* and *A. bairdii* and the chondrichthyan *D. calcea*, which are known to be deep sea distributed. *A. rostratus* has been reported to be very abundant in the middle slope in the Mediterranean basin (Moranta et al., 1998). Alepocephalidae prey mainly on myctophiid fishes and the crustacean *Pasiphaea multidentata* (Esmark, 1866). Sedimented globigerinids with other prey (siphonophores, tunicates, and copepods) contribute less mass to its diet (Modica et al., 2014) which makes them not strictly rely on epibenthic fauna observed at the same depth and, consequently, being an important link in the connection between shallower and deep assemblages.

LMSL assemblages: These epibenthic assemblages inhabiting the sedimentary bottoms in this SCA is the deepest identified, living between 1200 m and 1500 m depth and located at the basement of the canyon. It showed preference for the lowest values of BPI broad and high values of the sorting coefficient (S_0). Preference for high values of sorting coefficient means a high heterogeneity of the sediment and so indicating a non-constant action in the transportation process. This is typical of geologic formations like canyons in which strong hydrodynamic events take place periodically (Gómez-Ballesteros et al., 2014). Additionally, this heterogeneity in sediments could be due to near-bottom currents described on ACS occurring at each tidal cycle (Sánchez et al., 2014a).

The most important species for this deepest assemblage was *P. carpenteri*, a hexactinellid nest sponge. It is probably the most important porifera structuring soft bottom benthic community in the Cantabrian Sea. In fact, it has been reported that it forms large aggregations at temperate latitudes (Rodríguez-Basalo et al., 2021). Its importance is probably amplified in ACS because in it, these sponges represent a unique enclave because they are usually concentrated on continental margins (Rodríguez-Basalo et al., 2021). Their presence in ACS is propitiated by high re-suspension levels, providing an increased food supply and silicate availability for this important structuring species (Rodríguez-Basalo et al., 2021; Rice et al., 1990).

Other important species in this group were the epibenthic *Z. fulgens* a brittle star which shows a generalist infaunal predation behaviour (Gale et al., 2013). The other structuring species are *G. vitreus* a soft bottom filter feeding brachiopod and the sea urchin *C. cidaris*, which has scarce mobility and opportunistic feeding strategies relying on deep sea corals and other organisms, including detrital organic matter contained in the sediment, foraminifera, fragments of hydroids, crinoids, carrier crabs, and sponge materials (Stevenson and Rocha, 2013).

The feeding strategy of these abundant species in terms of biomass indicate that this deep assemblage depends energetically from the production of the shallower part of the ecosystem, constituting an important connection ring in the recycling of matter in this highly productive canyon system.

In the case of demersal assemblage, as already explained, BPI broad does not play an important role. The nektonic fraction of the assemblage, as composed by the fish *A. rostratus* and *A. bairdii*, as in the case of the upper level and also include the chondrichthyan, *C. monstrosa*, which is known to be deep sea distributed.

Furthermore, as explained some species as for example *H. tubicola* does seem to belong to none of assemblages observed, the reason may encounter an explanation in the fact that recently other authors have discovered the presence of another very similar species of the same genus (*H. robusta*) in the same study area that is deep distributed (Arias and Paxton, 2022).

In conclusion, the present work shared results of the sedimentary macrofaunal assemblages of the SCI and neighboring of the ACS. The links with some environmental variables available have been interpreted. Nevertheless, there are other factors such as fishing activities that play an important role in determining these assemblages (Collie et al., 2000). These aspects are important when considering that certain fishes and Chondrichthyes observed, especially those found in shallower depth strata, have commercial value.

In fact, in all the area, but especially in the shallower zone (i.e., sedimentary continental shelf and shelf break), professional fishing activity is carried out, mainly by bottom otter trawling and bottom pair trawling (Punzón et al., 2016). In these layers, the assemblages observed are not “pristine” due to fishing activity that actuates like a top-down control, removing repeatedly and unselectively commercial fish species together with non-target species and epibenthic organisms. These pressures surely had an effect both on the quantity and type (i.e., species) of organisms observed. In fact, we have observed a predominance in these shallower assemblages of species like *G. acutus*, *M. sarsi*, and *O. ophiura*. That species has already been observed as abundant in trawled bottoms (Kaiser et al., 1998; Serrano et al., 2006a; Fariña et al., 1997). This may be due to their resistance to trawling pressure, as *M. sarsi* is extremely resistant to trawling due to its burrowing capability (Hudson and Wigham, 2003), while *O. ophiura* can autogenerate missing arms (Lindsay, 2010). Others, like *G. acutus*, have a scavenging feeding behaviour and take advantage of the trawled grounds due to the fishing discards (Lejeune et al., 2022).

Highlighting both benthic and demersal components for the soft bottoms in this highly productive canyon system, this study is the first step toward the elaboration of a management plan for sustainable usage of the resources through a rational zonation of the SCI in the ACS.

CRediT authorship contribution statement

Larissa Modica: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Cristina Rodríguez-Cabello:** Formal analysis, Data curation, Conceptualization. **Augusto Rodríguez-Basalo:** Data curation. **Pilar Ríos:** Data curation. **Alberto Serrano:** Supervision. **Santiago Parra:** Supervision, Data curation. **María Gómez-Ballesteros:** Supervision, Funding acquisition. **Beatriz Arrese:** Data curation. **Francisco Sánchez:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2022.107966>.

References

- Álvarez, I., Gómez-Gesteira, M., de Castro, M., Gómez-Gesteira, J.L., Dias, J.M., 2010. Summer upwelling frequency along the western Cantabrian coast from 1967 to 2007. *J. Mar. Syst.* 79, 218–226. <https://doi.org/10.1016/j.jmarsys.2009.09.004>.
- Arias, A., Paxton, H., 2022. Life History and Reproductive Traits of the East Atlantic Deep-Sea Quill Worm *Hyalinoecia Robusta* Southward, 1977 (Annelida: Onuphidae). *Estuarine, Coastal and Shelf Science*, 107850.
- Bertrand, J., Gil de Sola, L., Papaconstantinou, C., Relini, G., Souplet, A., 2002. The general specifications of the MEDITS surveys. *Sci. Mar.* 66, 9–17.
- Borja, A., Amouroux, D., Anschutz, P., Gómez-Gesteira, M., Uyarra, M.C., Valdés, L., 2019. The Bay of Biscay. In: *World Seas: an Environmental Evaluation*. Academic Press, pp. 113–152.
- Butman, B., 1987a. The effect of winter storms on the bottom. Chap.11. In: Backus, R.H. (Ed.), *Georges Bank*. MIT Press, Cambridge, pp. 74–77.
- Butman, B., 1987b. Physical processes causing superficial-sediment movement. Chap. 13. In: Backus, R.H. (Ed.), *Georges Bank*. MIT Press, Cambridge, pp. 147–162.
- Carney, R.S., 2005. Zonation of deep biota in continental margins. *Oceanogr. Mar. Biol. Annu. Rev.* 43, 211–278.
- Cartes, J.E., Maynou, F., Moranta, J., Massuti, E., Lloris, D., Morales-Nin, B., 2004. Patterns of bathymetric distribution among deep-sea fauna at local spatial scale: comparison of mainland vs. insular areas. *Prog. Oceanogr.* 60, 29–45. <https://doi.org/10.1016/j.pocean.2004.02.001>.
- Cartes, J.E., Huguet, C., Parra, S., Sánchez, F., 2007. Trophic relationships in deep-water decapods of Le Danois bank (Cantabrian Sea, NE Atlantic): trends related with depth and seasonal changes in food quality and availability. *Deep Sea Res. Oceanogr. Res. Pap.* 54, 1091–1110.
- Cartes, J.E., Maynou, F., Fanelli, E., Romano, C., Mamouridis, V., Papiol, V., 2009. The distribution of megabenthic, invertebrate epifauna in the Balearic Basin (western Mediterranean) between 400 and 2300 m: Environmental gradients influencing assemblages composition and biomass trends. *J. Sea Res.* 61, 244–257.
- Cartes, J.E., Mamouridis, V., Fanelli, E., 2011. Deep-sea suprabenthos assemblages (Crustacea) off the Balearic Islands (western Mediterranean): mesoscale variability in diversity and production. *J. Sea Res.* 65, 340–354.
- Castro, J., Marín, M., Pérez, N., Pierce, G.J., Punzón, A., 2012. Identification of métiers based on economic and biological data: the Spanish bottom otter trawl fleet operating in non-Iberian European waters. *Fish. Res.* 125, 77–86.
- Chambers, J.M., Hastie, T.J., 1992. *Statistical Models in S*. Wadsworth & Brooks/Cole.
- Ciércoles, C., García-Ruiz, C., Aguilar, M.G., Gutiérrez, J.M., López-González, N.M., Recuero, J.U., Ruiz, J.L.R., 2018. Molluscs collected with otter trawl in the northern Alboran Sea: main assemblages, spatial distribution and environmental linkage. *Mediterr. Mar. Sci.* 19, 209–222.
- Clarke, K.R., Warwick, R.M., 1994. *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*. Natural Environmental Research Council, UK.
- Coelho, M.L., 1985. Review of influence of oceanographic factors on cephalopod distribution and life cycles. *NAFO Scientific Council Studies* 9, 47–57.
- Cohen, D.M., Inada, T., Iwamoto, T., Scialabba, N., 1990. *FAO species catalogue. Gadiform fishes of the world (order gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date*. Rome: Fao Fish. Synop. 10, 442, 125, Rome. FAO.
- Collie, J.S., Hall, S.J., Kaiser, M.J., Poiner, I.R., 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. *J. Anim. Ecol.* 69, 785–798.
- Costa, P.A.S.D., Mincarone, M.M., Braga, A.D.C., Martins, A.S., Lavrado, H.P., Haimovici, M., Falcão, A.P.D.C., 2015. Megafaunal communities along a depth gradient on the tropical Brazilian continental margin. *Mar. Biol.* 11, 1053–1064.
- C.D. 92/43/EEC, of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Off. J. L* 206, 22/07/1992 P. 0007– 0050.
- Eleftheriou, A., Moore, D.C., 2005. *Macrofauna techniques*. Chap.5. In: Eleftheriou, A., McIntyre, A. (Eds.), *Methods for the Study of Marine Benthos*. Blackwell Scientific Publications, Oxford, pp. 160–228.
- Fell, H.B., 1966. The ecology of Ophiuroids. In: Booloottan, R.A. (Ed.), *Physiology of Echinodermata*. Interscience Publ., NY, pp. 129–143.
- Freire, J., González-Gurriarán, E., Olaso, I., 1992. Spatial distribution of *Munida intermedia* and *M. sarsi* (Crustacea: Anomura) on the Galician continental shelf (NW Spain): application of geostatistical analysis. *Estuar. Coast Shelf Sci.* 35, 637–648. [https://doi.org/10.1016/S0272-7714\(05\)80044-7](https://doi.org/10.1016/S0272-7714(05)80044-7).
- Gage, J.D., Tyler, P.A., 1991. *Deep-sea Biology: a Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, UK, p. 504. <https://doi.org/10.1017/CBO9781139163637>.
- Gale, K.S., Hamel, J.F., Mercier, A., 2013. Trophic ecology of deep-sea Asteroidea (Echinodermata) from eastern Canada. *Deep Sea Res. Oceanogr. Res. Pap.* 80, 25–36. <https://doi.org/10.1016/j.dsr.2013.05.016>.
- Gil, J., 2008. Macro and mesoscale physical patterns in the Bay of Biscay. *J. Mar. Biol. Assoc. U. K.* 88, 217–225.
- Giordano, D., Busalacchi, B., Bottari, T., Perdichizzi, F., Profeta, A., Perdichizzi, A., Pirrera, L., Modica, L., Rinelli, P., 2010. Population dynamics and distribution of *Eledone cirrhosa* (Lamarck, 1798) in the southern Tyrrhenian sea (central mediterranean). *Cah. Biol. Mar.* 51, 213–227.
- Gofas, S., Salas, C., Rueda, J.L., Canoura, J., Farias, C., Gil, J., 2014. Mollusca from a species-rich deep-water *Leptometra* community in the Alboran Sea. *Sci. Mar.* 78, 537–553.
- Gómez-Ballesteros, M., Druet, M., Muñoz, A., Arrese, B., Rivera, J., Sánchez, F., Cristobal, J., Parra, S., García-Alegre, A., González-Pola, C., Gallastegui, J., Acosta, J., 2014. Geomorphology and sedimentary features of the Avilés canyon system. Cantabrian sea (Bay of Biscay). *Deep Sea Res. Part II* 106, 99–117. <https://doi.org/10.1016/j.dsr2.2013.09.031>.
- González-Irusta, J.M., Punzón, A., Serrano, A., 2012. Environmental and fisheries effects on *Gracilechinus acutus* (Echinodermata: Echinoidea) distribution: is it a suitable bioindicator of trawling disturbance? *ICES J. Mar. Sci.* 69, 1457–1465.
- González-Pola, C., del Río, G.D., Ruiz-Villarreal, M., Sánchez, R.F., Mohn, C., 2012. Circulation patterns at le Danois bank, an elongated shelf-adjacent seamount in the Bay of Biscay. *Deep Sea Res. Oceanogr. Res. Pap.* 60, 7–21.
- González-Quirós, R., Cabal, J., Álvarez-Marqués, F., Isla, A., 2003. Ichthyoplankton distribution and plankton production related to the shelf break front at the Avilés Canyon. *ICES J. Mar. Sci.* 60, 198–210. [https://doi.org/10.1016/S1054-3139\(03\)00009-2](https://doi.org/10.1016/S1054-3139(03)00009-2).
- González-Quirós, R., Pascual, A., Gomis, D., Anadón, R., 2004. Influence of mesoscale physical forcing on trophic pathways and fish larvae retention in the central Cantabrian Sea. *Fish. Oceanogr.* 13 (6), 351–364. <https://doi.org/10.1111/j.1365-2419.2004.00295>.
- Gooday, A.J., Turley, C.M., 1990. Responses by benthic organisms to inputs of organic material to the ocean floor: a review. *Phil. Trans. Roy. Soc. Lond. Math. Phys. Sci.* 331, 119–138.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910.
- Hernández-Molina, F.J., Serra, N., Stow, D.A.V., Llave, E., Ercilla, G., Van Rooij, D., 2016. Along-slope oceanographic processes and sedimentary products around the Iberian margin. *Geo Mar. Lett.* 31, 315–341. <https://doi.org/10.1007/s00367-011-0242-2>.
- Hessler, R.R., Jumars, P.A., 1974. Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Res.* 21, 185–209.
- Hill, M.O., Gauch, H.G., 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42, 47–58.
- Hijmans, R.J., Van Etten, J., 2011. Raster: geographic analysis and modeling with raster data. R Package 9–67. R Package Version 1.
- Hudson, I.R., Wigham, B.D., 2003. In situ observations of predatory feeding behaviour of the galatheid squat lobster *Munida sarsi* using a remotely operated vehicle. *J. Mar. Biol. Assoc. U. K.* 83, 463–464.
- ICES, 2010, 22–26 March 2010. *Manual for the International Bottom Trawl Surveys in the Western and Southern Areas*. Addendum 2 to the Report of the International

- Bottom Trawl Surveys Working Group. ICES CM 2010/SSGESST, Lisbon, Portugal, p. 58, 06.
- Iken, K., Brey, T., Wand, U., Voigt, J., Junghans, P., 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Prog. Oceanogr.* 50, 383–405.
- Iorga, M.C., Lozier, M.S., 1999. Signatures of the Mediterranean outflow from a North Atlantic climatology. *Diagnostic velocity fields*. *J. Geophys. Res.* 104, 26011–26029.
- Jumars, P.A., Nowell, A.R.M., 1984. Effects of benthos on sediment transport: difficulties with functional grouping. *Continent. Shelf Res.* 3, 115–130.
- Kaiser, M.J., Rogers, S.I., McCandless, D.T., 1994. Improving quantitative surveys of epibenthic communities using a modified 2 m beam trawl. *Mar. Ecol. Prog. Ser.* 106, 131–138.
- Kaiser, M.J., Edwards, D.B., Armstrong, P.J., Radford, K., Lough, N.E.L., Flatt, R.P., Jones, H.D., 1998. Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES J. Mar. Sci.* 55, 353–361.
- Koukouras, A., Sinis, A.L., Bobori, D., Kazantzidis, S., Kitsos, M.S., 2007. The echinoderm (Deuterostomia) fauna of the Aegean Sea, and comparison with those of the neighbouring seas. *J. Biol. Res.* 7, 67–92.
- Lauria, V., Garofalo, G., Gristina, M., Fiorentino, F., 2016. Contrasting habitat selection amongst cephalopods in the Mediterranean Sea: when the environment makes the difference. *Mar. Environ. Res.* 119, 252–266.
- Lavin, A., Valdes, L., Sánchez, F., Abaunza, P., Forest, A., Lazure, P., Jegou, A.M., Boucher, J., 2006. The Bay of Biscay: the encountering of the ocean and the shelf. In: Robinson, Brink (Ed.), *The Sea, 14B*. Harvard University Press, The Global Coastal Ocean, pp. 935–1002.
- Lejeune, B., Mouchet, M.A., Mehault, S., Kopp, D., 2022. Gut content metabarcoding reveals potential importance of fisheries discards consumption in marine fauna. *Can. J. Fish. Aquat. Sci.* 99, 1–10.
- Leps, J., Šmilauer, P., 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge university press, p. 269.
- Lindsay, S.M., 2010. Frequency of injury and the ecology of regeneration in marine benthic invertebrates. *Integr. Comp. Biol.* 50, 479–493.
- Lourido, A., Parra, S., Sánchez, F., 2014. A comparative study of the macrobenthic infauna of two bathyal Cantabrian Sea areas: the le Danois bank and the Avilés canyon system (S Bay of Biscay). *Deep Sea Res. Part II* 106, 141–150. <https://doi.org/10.1016/j.dsr2.2013.09.039>.
- Louzagó, M., Anadón, N., Arrontes, J., Álvarez-Claudio, C., Fuente, D.M., Ocharan, F., Anadón, A., Acuña, J.L., 2010. Historical macrobenthic community assemblages in the Avilés Canyon, N Iberian Shelf: baseline biodiversity information for a marine protected area. *J. Mar. Syst.* 80, 47–56. <https://doi.org/10.1016/j.jmarsys.2009.09.006>.
- Llavona, A., Martínez-Cedeira, J., Covelo, P., Morales, X., Dios, J.J., Bracali, V., Pérez, P., García, J.A., Santos, L., López, A., 2011. Indemares project: identification of special areas of conservation for cetaceans at the “Galician bank” and “Aviles canyon” (Atlantic and Cantabrian Sea) for Natura for Natura 2000. In: *Abstracts 25th Conference of the European Cetacean Society*, Cádiz, 208.
- Martins, R., Sampaio, L., Quintino, V., Rodrigues, A.M., 2014. Diversity, distribution and ecology of benthic molluscan communities on the Portuguese continental shelf. *J. Sea Res.* 93, 75–89.
- Miller, D.C., Sternberg, R.W., 1988. Field measurements of the fluid and sediment dynamic environment of a benthic deposit feeder. *J. Mar. Res.* 46, 771–796.
- Modica, L., Cartes, J.E., Carrassón, M., 2014. Food consumption of five deep-sea fishes in the Balearic Basin (western Mediterranean Sea): are there daily feeding rhythms in fishes living below 1000 m? *J. Fish. Biol.* 85, 800–820.
- Moranta, J., Stefanescu, C., Massutí, E., Morales-Nin, B., Lloris, D., 1998. Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian basin, western Mediterranean). *Mar. Ecol. Prog. Ser.* 171, 247–259.
- Nowell, A.R.M., 1983. The benthic boundary layer and sediment transport. *Reviews of Geophysics. Phys. Oceanogr.* 21, 1181–1192. <https://doi.org/10.1029/RG021i005p0118>.
- Nowell, A.R.M., Jumars, P.A., 1984. Flow environments of aquatic benthos. *Annu. Rev. Ecol. Systemat.* 15, 303–328. <https://doi.org/10.1146/annurev.es.15.110184.001511>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2020. *Vegan: Community Ecology Package*. R Package Version 2, pp. 5–6, 2019.
- Paillet, J., Arhan, M., McCartney, M.S., 1998. Spreading of Labrador Sea water in the Eastern North Atlantic. *J. Geophys. Res.* 103, 10223–10239. <https://doi.org/10.1029/98JC0026>.
- Pennino, M.G., Muñoz, F., Conesa, D., López-Quílez, A., Bellido, J.M., 2013. Modeling sensitive elasmobranch habitats. *J. Sea Res.* 83, 209–218. <https://doi.org/10.1016/j.seares.2013.03.005>.
- Pingree, R.D., 1994. Winter warming in the southern Bay of Biscay and Lagrangian eddy kinematics from a deep-drogued Argos buoy. *J. Mar. Biol. Assoc. U. K.* 74 (1), 107–128. <https://doi.org/10.1017/S0025315400035700>.
- Pingree, R.D., Le Cann, B., 1990. Structure, strength and seasonality of the slope currents in the Bay of Biscay region. *Journal of the Marine Biological Association of the United Kingdom* 70, 857–885. <https://doi.org/10.1017/S0025315400059117>.
- Punzón, A., Arronte, J.C., Sánchez, F., García-Alegre, A., 2016. Spatial characterization of the fisheries in the Avilés canyon system (Cantabrian Sea, Spain). *Cienc. Mar.* 42, 237–260.
- Rice, A.L., Thurston, M.H., New, A.L., 1990. Dense aggregations of a hexactinellid sponge, *Pheronema carpenteri*, in the Porcupine Seabight (northeast Atlantic Ocean), and possible causes. *Prog. Oceanogr.* 24, 179–196.
- Ríos, P., Sánchez, F., 2021. Informe sobre el estado actual de conocimiento de la biodiversidad del LIC-ESZZ12003 “SISTEMA DE CAÑONES SUBMARINOS DE AVILÉS”. In: *Fundación Biodiversidad del Ministerio de Agricultura, Alimentación y Medio Ambiente*, p. 110.
- Rodríguez-Basalo, A., Prado, E., Sánchez, F., Ríos, P., Gómez-Ballesteros, M., Cristobo, J., 2021. High resolution spatial distribution for the hexactinellid sponges *Asconema setubalense* and *Pheronema carpenteri* in the Central Cantabrian Sea. *Front. Mar. Sci.* 8, 612761. <https://doi.org/10.3389/fmars.2021.612761>.
- Rodríguez-Cabello, C., Sánchez, F., Fernández, A., Olaso, I., 2004. Is the lesser spotted dogfish (*Scyliorhinus canicula*) population from the Cantabrian Sea a unique stock? *Fish. Res.* 69, 57–71. <https://doi.org/10.1016/j.fishres.2004.04.002>.
- Rodríguez-Cabello, C., Pérez, M., Sánchez, F., 2013. New records of chondrichthyans species caught in the Cantabrian Sea (southern Bay of Biscay). *J. Mar. Biol. Assoc. U. K.* 93, 1929–1939.
- Sánchez, F., 1994. Campaña de evaluación de recursos pesqueros Demersales 0991, 155. *Informes Técnicos del Instituto Español de Oceanografía*, p. 51.
- Sánchez, F., Gil, J., 2000. Hydrographic mesoscale structures and Poleward Current as a determinant of hake (*Merluccius merluccius*) recruitment in southern Bay of Biscay. *ICES J. Mar. Sci.* 57, 152–170.
- Sánchez, F., Serrano, A., 2003. Variability of groundfish communities of the Cantabrian Sea during the 1990s. *ICES (Int. Counc. Explor. Sea) Mar. Sci. Symp.* 219, 249–260.
- Sánchez, F., Olaso, I., 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem. *Ecol. Model.* 172, 151–174. <https://doi.org/10.1016/j.ecolmodel.2003.09.005>.
- Sánchez, F., De la Gándara, F., Gancedo, R., 1995. Atlas de los peces demersales de Galicia y el Cantábrico. Otoño 1991–1993. *Publicaciones Especiales del Instituto Español de Oceanografía* 20, Madrid, p. 100. Ministerio de Agricultura, Pesca y Alimentación.
- Sánchez, F., Pérez, N., Landa, J., 1998. Distribution and abundance of megrim (*Lepidorhombus boschii* and *Lepidorhombus whiffiagonis*) on the northern Spanish shelf. *ICES J. Mar. Sci.* 55, 494–514.
- Sánchez, F., Serrano, A., Parra, S., Ballesteros, M., Cartes, J.E., 2008. Habitat characteristics as determinant of the structure and spatial distribution of epibenthic and demersal communities of Le Danois Bank (Cantabrian Sea, N. Spain). *J. Mar. Syst.* 72, 64–86.
- Sánchez, F., González-Pola, C., Druet, M., García-Alegre, A., Acosta, J., Cristobo, J., Parra, S., Ríos, P., Altuna, A., Gómez-Ballesteros, M., Muñoz-Recio, A., Rivera, J., Díaz del Río, G., 2014a. Habitat characterization of deep-water coral reefs in La Gavierra canyon (Avilés canyon system, Cantabrian Sea). *Deep Sea Res. Part II* 106, 118–140. <https://doi.org/10.1016/j.dsr2.2013.12.014>.
- Sánchez, F., Gómez-Ballesteros, M., González-Pola, C., Punzón, A., 2014b. Sistema de cañones submarinos de Avilés. *Proyecto LIFE +INDEMARES*. In: *Fundación Biodiversidad del Ministerio de Agricultura, Alimentación y Medio Ambiente*, p. 114.
- Sánchez, F., Rodríguez-Basalo, A., García-Alegre, A., Gómez-Ballesteros, M., 2017. Hard-bottom bathyal habitats and keystone epibenthic species on le Danois bank (Cantabrian Sea). *J. Sea Res.* 130, 134–153.
- Sartor, P., Sbrana, M., Ungaro, N., Marano, C.A., Piccinetti, C., Manfrin, G.P., 2002. Distribution and abundance of citharus linguatula, *Lepidorhombus boschii* (Risso, 1810) and *Solea vulgaris* (Osteichthyes, Pleuronectiformes) in the Mediterranean Sea. *Sci. Mar.* 66, 83–102.
- Serrano, A., Sánchez, F., García-Castrillo, G., 2006a. Epibenthic communities of trawlable grounds of the Cantabrian Sea. *Sci. Mar.* 70, 149–159.
- Serrano, A., Sánchez, F., Preciado, I., Parra, S., Frutos, I., 2006b. Spatial and temporal changes in benthic communities of the Galician continental shelf after the Prestige oil spill. *Mar. Pollut. Bull.* 53, 315–331.
- Serrano, A., Sánchez, F., Punzón, A., Velasco, F., Olaso, I., 2011. Deep sea megafaunal assemblages off the northern Iberian slope related to environmental factors. *Sci. Mar.* 75, 425–437. <https://doi.org/10.3989/scimar.2011.75n3425>.
- Serrano, A., Cartes, J.E., Papiol, V., Punzón, A., García-Alegre, A., Arronte, J.C., Ríos, P., Lourido, A., Frutos, I., Blanco, M., 2017. Epibenthic communities of sedimentary habitats in a NE Atlantic deep seamount (Galicia Bank). *J. Sea Res.* 130, 154–165. <https://doi.org/10.1016/j.seares.2017.03.004>.
- Sibuet, M., 1977. Repartition et diversité des Echinoderms (Holothurides- Astérides) en zone profonde dans le Golfe de Gascogne. *Deep Sea Res.* 24, 549–563. [https://doi.org/10.1016/0146-6291\(77\)90527-6](https://doi.org/10.1016/0146-6291(77)90527-6).
- Snelgrove, P.V., Butman, C.A., 1994. Animal-sediment relationships revisited: causes versus effect. *Oceanogr. Mar. Biol. Annu. Rev.* 32, 111–177.
- Stefanescu, C., Lloris, D., Rucabado, J., 1992. Deep-living demersal fishes in the Catalan Sea (western Mediterranean) below a depth of 1000 m. *J. Nat. Hist.* 26, 197–213.
- Stergiou, K.I., Machias, A., Somarakis, S., Kapantagakis, A., 2003. Can we define target species in Mediterranean trawl fisheries? *Fish. Res.* 59, 431–435.
- Stevenson, A., Rocha, C., 2013. Evidence for the bioerosion of deep-water corals by echinoids in the Northeast Atlantic. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* 71, 73–78. <https://doi.org/10.1016/j.dsr.2012.09.005>.
- Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., Edgar, G.J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R.A., Smale, D.A., Fulton, E.A., Feng, M., Radford, B.T., Thompson, P.A., Bates, A.E., 2015. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol. Lett.* 18, 944–953. <https://doi.org/10.1111/ele.12474>.
- Thurston, M., Bett, B., Rice, A., Jackson, P., 1994. Variations in the invertebrate abyssal megafauna in the North Atlantic ocean. *Deep Sea Res. Oceanogr. Res. Pap.* 41, 1321–1348. [https://doi.org/10.1016/0967-0637\(94\)90100-7](https://doi.org/10.1016/0967-0637(94)90100-7).
- Van Aken, H.M., 2000a. The hydrography of the mid-latitude Northeast Atlantic Ocean. Part I: the deep water masses. *Deep Sea Res. Oceanogr. Res. Pap.* 47, 757–788. [https://doi.org/10.1016/S0967-0637\(99\)00092-8](https://doi.org/10.1016/S0967-0637(99)00092-8).

- Van Aken, H.M., 2000b. The hydrography of the mid-latitude Northeast Atlantic Ocean. Part II: the intermediate water masses. *Deep Sea Res. Oceanogr. Res. Pap.* 47, 789–824. [https://doi.org/10.1016/S0967-0637\(99\)00112-0](https://doi.org/10.1016/S0967-0637(99)00112-0).
- Van Rooij, D., Iglesias, J., Hernández-Molina, F.J., Ercilla, G., Gomez-Ballesteros, M., Casas, D., Llave, E., De Hauwere, A., Garcia-Gil, S., Acosta, J., Henriot, J.-P., 2010. The le Danois contourite depositional system: interactions between the mediterranean outflow water and the upper cantabrian slope (north Iberian margin). *Mar. Geol.* 274, 1–20. <https://doi.org/10.1016/j.margeo.2010.03.001>.
- Villanueva, R., Guerra, A., 1991. Food and prey detection in two deep-sea cephalopods: *Opisthoteuthis agassizi* and *O. vossi* (Octopoda: Cirrata). *Bull. Mar. Sci.* 49, 288–299.
- Villéger, S., Brosse, S., Mouchet, M., Mouillot, D., Vanni, M.J., 2017. Functional ecology of fish: current approaches and future challenges. *Aquat. Sci.* 79, 783–801. <https://doi.org/10.1007/s00027-017-0546-z>.