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Habitat characteristics as determinant of the structure and spatial distribution of epibenthic and demersal communities of Le Danois Bank (Cantabrian Sea, N. Spain)

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Abstract

The purpose of this paper is to detect and describe general trends in the spatial distribution of epibenthic and demersal communities of Le Danois Bank (El Cachucho) in relation to the environmental variables that characterize their habitat by means of multivariate ordination. Data were derived from two multidisciplinary surveys carried out in October 2003 and April 2004 included in the ECOMARG project. The surveys were focused on the study of the physical scenario, including both geological (seabed characterization from bathymetry and backscatter data) and hydrographic features, and the different compartments of the benthic fauna (endobenthic, epibenthic, suprabenthic and demersal communities). For the present study, epibenthos and demersal species were sampled using two different gears, a 3.5 m beam trawl and a Porcupine 39/52 type *baca* otter trawl respectively. The total species richness combining both samplers ascended to 221, including 71 species of fishes, 65 crustaceans, 35 molluscs, 29 echinoderms, 10 cnidarians and 5 sponges.

Multivariate methods were used for the study of the characteristics of communities and habitats. Hierarchical cluster analysis was applied to calculate and visualize similarities between samples in terms of species composition. To assess the amount of variation of faunal densities related to a set of eight environmental variables, a redundancy analysis (RDA) was used. The set of environmental variables used were: depth, near-bottom temperature and salinity, sedimentary typology (dry weight percentages of coarse sands, medium and fine sands, silt and organic matter) and seafloor reflectivity. Using the spatial distribution of the ranges of depth and seafloor reflectivity that characterize the habitats of the faunal assemblages we defined the spatial distribution of the different communities.

The multivariate analysis of 18 beam-trawl samples and 15 otter trawl samples showed the existence of 4 main assemblages associated with the more characteristic habitats of the area. The *Callogorgia–Chimaera* community live mainly in the areas at the top of the Bank (425–550 m depth), where the sediment coverage is lower and there exists a high presence of rocky outcrops. The

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Gryphus–Galeus community were found in the areas at the top of the Bank covered by medium and fine sand sediments with low organic matter content. The *Phormosoma–Trachyrincus* community live on the sedimentary terraces that characterize the Bank break (550–800 m) and the *Pheronema–Deania* community occupy all the deeper (800–1050 m) sedimentary grounds of the inner basin.

Keywords: Le Danois Bank; Benthic communities; Demersal communities; Cantabrian Sea; Deep-sea; Faunal assemblages; Spatial distribution; Habitat characteristics

1. Introduction

The “El Cachucho” Bank was known to Spanish fishermen in the first years of the twentieth century. At that time, the Bank was probably covered by three-dimensional well-developed habitats, since a large specimen of cold water coral *Lophelia pertusa* was caught by a Spanish trawler on the Bank in 1918 (Santander Maritime Museum collections). Following the 1934–1939 surveys on board the RV *Président-Théodore-Tissier*, Le Danois introduced the Bank to the scientific community and made the first descriptions of biological communities (Le Danois, 1948). Later, the geological studies made by French researchers came out in the seventies (Boillot and D’Ozouville, 1970; Boillot et al., 1970, 1971; Boillot and Malod, 1988) and most recently studies of seismic depth (ESCI, 1995). At the end of the seventies the French RV *Thalassa* made a sampling survey in the Bank but only some results on polychaetes were published (Amoureux, 1974). The multidisciplinary French project BIOGAS also studied samples obtained in the abyssal plain surrounding the Bank (Laubier and Monniot, 1985), and more recently the Council of Rural Means and Fisheries of the Principality of Asturias carried out biological samplings with traps and some experimental trawls in 1988 and 1989, which provided qualitative information on the presence of some species of fish and invertebrates in the area (Alcázar et al., 1992). In summary, the biological communities of the Bank were barely known in spite of forming part of the Spanish EEZ and being subject to fishing activities.

No regular fishery is currently operating in Le Danois Bank. Only a few vessels (4–6) work sporadically using gillnets and targeting monkfish (*Lophius* spp.), or long lines targeting *Beryx* spp., forkbeard (*Phycis blennoides*) and red sea-bream (*Pagellus bogaraveo*). In the past, a high fishing pressure existed, mainly by fisheries targeting red sea-bream in the seventies and eighties, and also by gillnets up to 2002. To date, it has been impossible to obtain a historical record of the landings coming from the Bank due to the absence of geographically referenced information with enough precision to estimate the catches from such a relatively small area. According to the information available at present, no stable trawl fishery works in the Bank except some exploratory hauls or sporadic activities. The sudden increase in trawling activities on bottoms of greater depth, due to the drastical fall in the abundance of target species in the continental shelf (hake, Norway lobster, anglerfishes and megrims) and their possible impacts on the delicate benthic communities of the Bank, led to the necessity to carry out a research project that allowed the collection of the information needed to define appropriate management measures for this particular ecosystem.

During the years 2003 and 2004 the Bank was studied by the ECOMARG project, focusing mainly on the benthic-demersal ecosystem (http://www.ecomarg.net/). In its initial stage, the project looked at the physical scenario through morpho-sedimentary and bathymetric characteristics, and the study of the dynamic and characteristics of the water masses. In a second phase, the project focused on the fauna, with an integrated study of the three main benthic compartments: endobenthos, epibenthos and suprabenthos. The trophic ecology of the dominant species of fish and crustaceans will be used to estimate the energy flows, the consumption and the niche overlap among high level trophic groups. All this information, together with the study of the impact of the fisheries working in the area, will be integrated in a trophodynamic mass-balance model (Ecopath). This methodological approach offers a holistic view of ecosystem variability, its communities and the distribution of fishing resources. Finally, it can also be an efficient tool for the management of the Bank. Trophodynamic modeling allows us to explain and synthesize the characteristics of the ecosystem, to compare it with others similar and to try to predict the consequences of possible management measures that could be adopted in this remarkable area.

Deep-sea habitats are considered exceptional ecosystems from a biodiversity perspective, harbouring singular trophic webs. With the exception of hydrothermal vents, deep-sea ecosystems depend on the import of energy from outside to maintain those trophic webs. In these environments two major pathways of energy are recognized: vertical flux from the euphotic zone (sea snow) and advective flux from the adjacent continental shelf via bottom nepheloid layers and submarine canyons (Sorbe, 1999). Both pathways are relevant in Le Danois Bank due to the topographic effects on primary production, its location on the path of slope currents and the vicinity of Lastres and Llanes canyons.

Moreover, the deep-sea is now the ultimate target of industrial fisheries looking for new resources following the depletion of shelf fish species. Therefore, deep-water fish stocks and habitats may be at serious risk due to their high vulnerability and low resilience to over-exploitation (Morato et al., 2006). For all these reasons, knowledge on the structure and dynamics of deep-sea communities is now of great importance.

The purpose of this paper is to detect and describe general trends in the spatial distribution of the epibenthic and demersal communities of Le Danois Bank and surrounding area in relation to the environmental variables that characterize their habitat by means of multivariate analysis. Also, since the dynamic of the Cantabrian Sea ecosystems is strongly determined by seasonality (OSPAR, 2000), this study includes the temporal effects on the results.

2. Material and methods

2.1. Study area

Le Danois Bank (Le Danois, 1948), locally known by fishermen as 'El Cachucho' (the local name of *Beryx decadactylus*) fishing ground, is a marginal shelf located in the Cantabrian Sea at 5°W longitude and 44°N latitude (Fig. 1). In plan view the Bank is convex southward for a length of about 72 km in an east–west direction and about 15 km wide from north to south; it has an almost flat surface with a minimum depth of 424 m, and is separated at 25 km from the Cantabrian Sea continental shelf by a deeper inner basin (Montadert et al., 1974). This structure infers to be a "horst" type, which presents an elongated form in an E–W direction and great dissymmetry between its northern and southern flanks. The northern side of Le Danois Bank has a pronounced continental slope with a relief of 3600 m, its base located at a depth of 4400 m. In the space of only a few miles the depth changes from 500 m at the top of the Bank to over 4500 m at the Biscay abyssal plain, as observed by Malod and Vanney (1980) and Malod et al. (1980) aboard the French submersible Cyana. This indicates that the slope consists of a succession of cored cliffs. The southern side shows a relatively smooth link to the inner basin by a saddle that descends eastward from a depth of 800 m to 2000 m. The top of Le Danois Bank presents a scarce unconsolidated sediment cover and so there are many highly reflective rocky outcrops that make biological sampling difficult. Nevertheless, the inner basin has a relevant sedimentary coverage that includes sediment drifts emplaced under current flows, suggesting a very different dynamic to that of the top of the Bank (Ballesteros et al., 2006). Along the south side of the saddle in the middle of the Inner Basin is Lastres Canyon, which forms a stretch of the continental shelf bordering the Bank. This is one of the main characteristics responsible for the scarce sedimentary coverage in this area of the Cantabrian Sea, since it is an important route by which sediments are carried from the continental shelf to the deepest seafloor of the Bay of Biscay (Ballesteros et al., 2006).

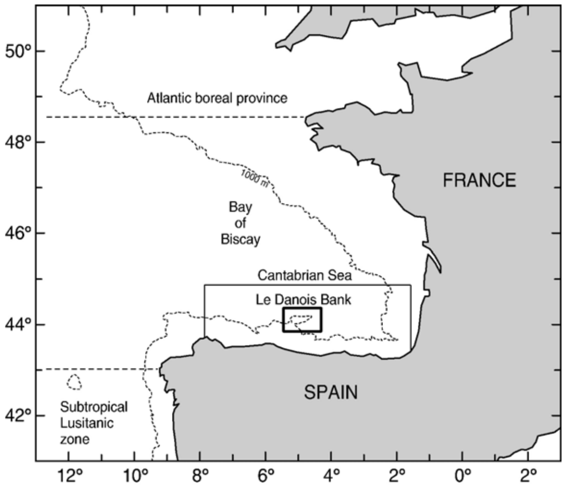

Fig. 1. Location of Le Danois Bank in the OSPAR Warm Lusitanean subprovince (Bay of Biscay) and limits of the surrounding biogeographic regions.

From the hydrographic point of view, Le Danois Bank is located at the depth that corresponds to the area of transition between the masses of North Atlantic central water (NACW, up to 500 m, where there is relatively minimal salinity), and the saline Mediterranean Outflow Water (MOW, whose main nucleus is between 800 and 1100 m depth). The latter is characterized by high oxygen and low nutrient content (oligotrophic). The area of the continental slope of the Cantabrian Sea seems to be in general critical to the mixing of water masses through isopycnals, which is why the topographic anomaly formed by Le Danois Bank favours the mixing of these water masses (Fiuza et al., 1998; Van Aken, 2000). The topographical effects of the Bank on the general current dynamic of the Cantabrian Sea, predominantly in a W–E direction, as in the case of the slope current (winter poleward current) or the Mediterranean water flow, have a very important role in sedimentation processes and the systems of production of the ecosystem. The current regime reaching the Bank is more intense than if it were a seamount in the open ocean. Alterations in the general flow may generate phenomena of vertical transport and mixing of the water masses and may determine the productivity of the area and its surroundings. The data set from CTD obtained during the two surveys carried out in the ECOMARG project supporting this study showed that the Bank induces a distortion in the isopycnals at the level of the waters of the thermocline and affects the Mediterranean water flow, which leads us to assume that currents are more intense (Ruiz-Villarreal et al., 2006).

Seasonal atmospheric cycle and meteorological conditions have a strong influence in the Cantabrian Sea and a typical seasonal cycle of hydrographic features in the area has been described (OSPAR, 2000; Lavin et al., 2006). The production of the area is greatly influenced by seasonal coastal upwelling (spring and summer) and hydrographic mesoscale activity along the northwestern shelf break. This is a consequence of winter fluxes from the warm poleward current (also known as the "Navidad Current"), which results in a convergent front at the boundary between coastal and oceanic waters (OSPAR, 2000; Sánchez and Gil, 2000). These produce a regular pattern of hydrographic conditions throughout the year characterized by winter mixing and summer stratification, with phytoplankton blooms occurring during the transition periods. The onset of the spring bloom occurs with remarkable regularity in March–early April when seasonal re-stratification begins and consequently the mixed layer becomes shallower than the critical depth at which phytoplankton growth exceeds mortality and respiration, according to Sverdrup's classical mechanism. From May onwards, chlorophyll drops sharply, and the lowest values are observed in summer when water column stratification prevents nutrient supply to the photic layers (Lavin et al., 2006). From the information obtained from satellite images (from http://reason.gsfc.nasa.gov/Giovanni), the periods of highest production over Le Danois Bank do not seem to differ greatly from what occurs throughout the Cantabrian Sea area (Fig. 2). Regarding the present study, of the two periods in which the two surveys were carried out, one corresponds to a phase of low production and the other to one of high primary production, which is important to consider when interpreting the results. Zooplankton biomass also shows a cyclical seasonal pattern with maximum values usually in spring, which corresponds to, but lags behind, the pulse of phytoplanktonic production and the beginning of the heating of the water column starts (Lavin et al., 2006). This seasonal pattern has a significant effect on the dynamics of the ecosystem.

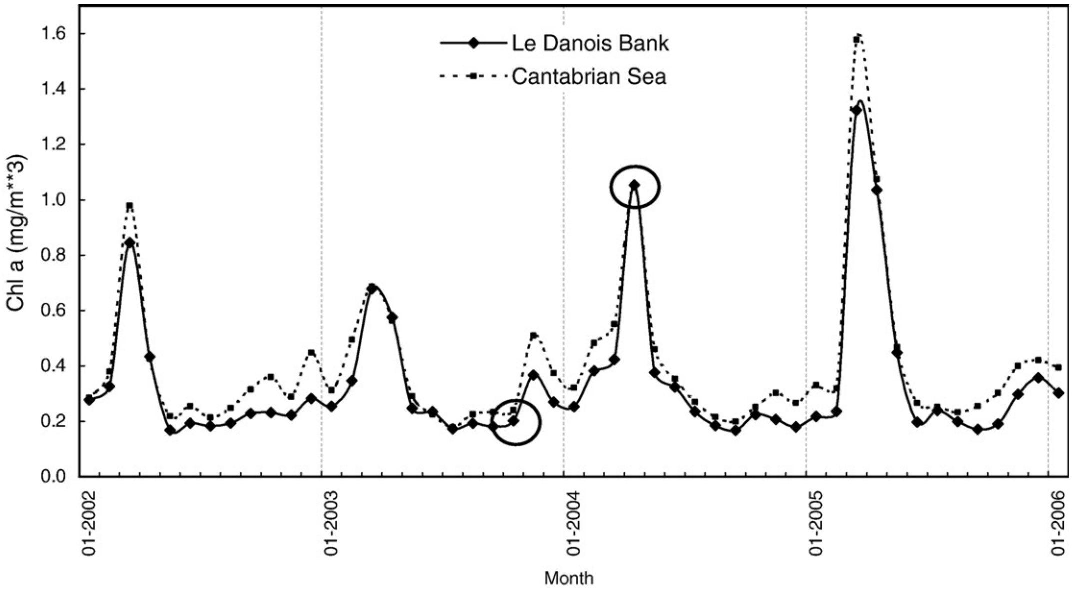

Fig. 2. Historical series of chlorophyll_a concentration (mg/m^3) monthly average, taken from satellite imagery (from http://reason.gsfc.nasa.gov/Giovanni/), on Le Danois Bank zone — 3600 km^2 and over all the Cantabrian Sea area — 54,345 km^2 (see reference rectangles on Fig. 1). Circles show the periods when the two surveys of this study were carried out.

2.2. Sampling and data sets

Data were derived from two multidisciplinary surveys carried out in October 2003 and April 2004 on board the RV *Vizconde de Eza*. The surveys were focused on the study of the physical scenario, including both bathymetry and hydrographic features, and the different compartments of the benthic fauna (endobenthic, epibenthic, suprabenthic and demersal communities). The bathymetry and backscatter (the intensity of sound reflected from the seafloor, know as reflectivity) data were obtained using a Simrad EM-300 multibeam echosounder. Backscatter maps were derived using software tools for processing data to get a reflectivity mosaic 1-metre pixel resolution. Textural classification was used to classify the mosaic into three distinct bottom types. Images from a photogrammetric sled, bathymetry data, sedimentary samples, and the backscatter were integrated to describe the geological aspect of the habitat.

In order to obtain better information on interspecific relationships among these different compartments of the ecosystem, the strategy was followed of using the same stations for the different sampling systems. This allowed us to jointly analyse the databases of the corresponding communities in the same spatial context of the ecosystem. Sediments and endobenthos samples were collected using a box corer (0.25 m^2 effective sampling area), the suprabenthic fauna was sampled using a suprabenthic sled and the benthopelagic plankton was sampled with a WP2 net type. Particle size analysis of sediments was performed by a combination of dry sieving and sedimentation techniques (Buchanan, 1984). Organic matter in the sediment was estimated as weight loss of dried (100 °C, 24 h) samples after combustion (500 °C, 24 h). For the present study, epibenthos and demersal species (Benthic Boundary Layer megafauna) were sampled using two different gears, a small beam trawl (Serrano et al., 2006) and a Porcupine 39/52 type *baca* otter trawl (ICES, 2003) respectively. The beam-trawl horizontal opening was of 3.5 m and the vertical opening of 0.6 m (mesh size of 10 mm). Beam trawls lasted 15 min on the bottom at a mean speed of 2.5 knots. *Baca* otter trawl mesh size was of 90 mm along the net but with a 20 mm liner inside the cod end. The groundrope was of synthetic wrapped wire core double coat so as to avoid damage on the rough grounds of Le Danois Bank. The horizontal opening was of 18.5 ± 1.3 m and the vertical opening of 3.14 ± 0.20 m. The sampling unit was a 30-minute haul, all carried out in daytime at a speed of 3.5 knots. Both trawl gears were monitored using Scanmar net sensors. The mean swept area, used to obtain the standardized biomass (g ha^{-1}) and abundance (n ha^{-1}) indices, was 3494 m^2 in beam trawls and 57,461 m^2 in *baca* otter trawls.

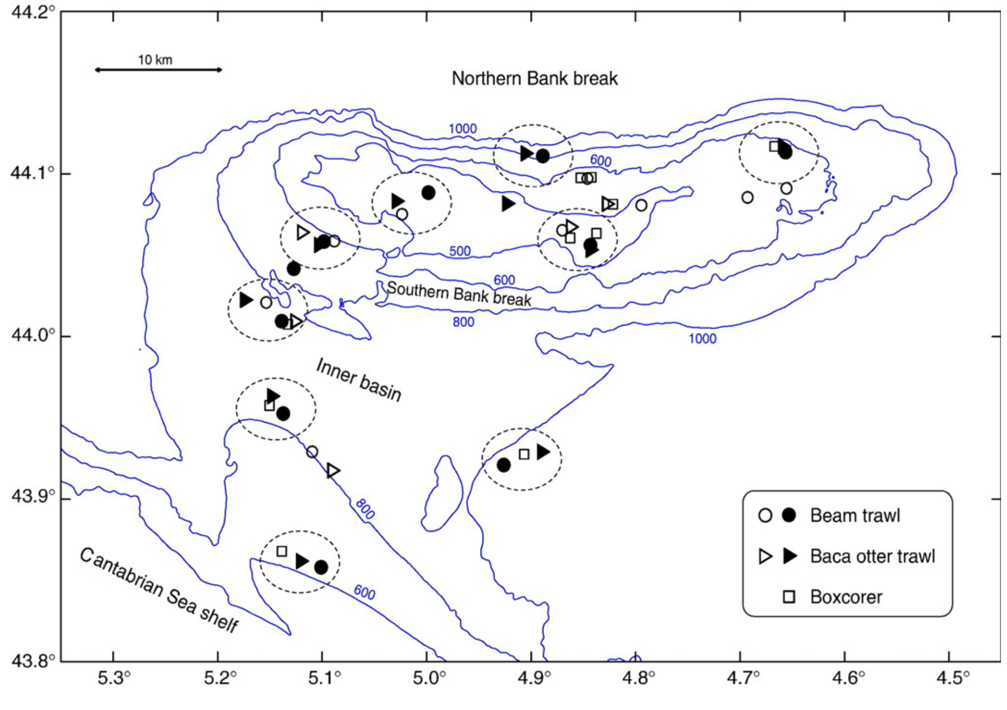

Fig. 3. Map showing the study area and the multidisciplinary sampling stations used in this study (only beam trawl and *baca* otter trawl for fauna and box corer for sediments characteristics). Empty symbols corresponds to autumn 2003 survey and filled symbols to spring 2004 survey.

The number of individuals and the wet weight of each species were obtained from each sample. A total of 18 valid hauls (8 autumn + 10 spring) were made using beam trawl and 15 with *baca* trawl (5 autumn + 10 spring). Fig. 3 shows the location of the hauls made with these two samplers during the autumn (October 2003) and spring (April 2004) surveys.

2.3. Data analysis

Biomass and abundance indices from both gears were standardized to a common sampled area (ha = 10,000 m^2) using the swept area methodology. In the original survey design, the study area was divided following a bathymetric criterion: the upper part of Le Danois Bank (400–700 m) was identified as Stratum 1, and the inner basin (701–1100 m) corresponded to Stratum 2. In a first step analysis, data were pooled for these two depth intervals and the ecological parameters of species richness, biomass (kg ha^{-1}), abundance (n ha^{-1}) and diversity (Shannon–Wienner indices in biomass and number) were calculated.

Hierarchical cluster analysis using the Bray–Curtis index (Clarke and Warwick, 1994) and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) as the aggregation algorithm were applied to calculate and visualize similarities between samples in terms of species composition. The biomass data were transformed by log $(1+x)$ to minimize the influence of extreme values and zeros. For this analysis, species poorly represented (less than 0.1% of total catches) were rejected with the aim of reducing the percentage of zeros in the matrix. The contribution of each species to the similarity of the cluster groups of samples was determined using the SIMPER (similarity percentages) routine (Clarke and Warwick, 1994). Values of 18 hauls and 112 species from beam-trawl samples and 15 hauls and 140 species from *baca*-trawl samples were used for this analysis. In order to eliminate the effect of the greater coverage of stations during the spring survey, in the study of the dissimilarities between seasons the data from hauls that did not have a corresponding equivalent haul in autumn, i.e. those made at greater depth and those that were closest to the Cantabrian Sea continental shelf, were not used (Fig. 3).

To assess the amount of variation in faunal densities related to a set of habitat environmental characteristics, a redundancy analysis (RDA) was used (Ter Braak, 1996). Biomass matrices were also transformed by log $(1+x)$. Previous analysis of the main species showed a linear response in their abundance in relation to the environmental variables used, and so the use of the RDA offers a greater percentage of the variance explained regarding the canonical correspondence analysis (CCA), which is more suitable when there is a unimodal response. The set of environmental variables used in RDA calculations comprised depth, near-bottom temperature and salinity (from CTD probe), and sedimentary characteristics determined at each multidisciplinary station using a box corer (Fig. 3). Sedimentary parameters used were dry weight percentages of coarse sand (GCS, >500 μm), medium and fine sands (MFS, 63–500 μm), silt (<63 μm) and organic matter (OM). Also, we used the values of seafloor reflectivity (from a multibeam echosounder, expressed in decibels — dB) as significant of sediment coverage and substrate hardness. The statistical significance of the direct method of ordination was obtained by the Monte-Carlo test using 999

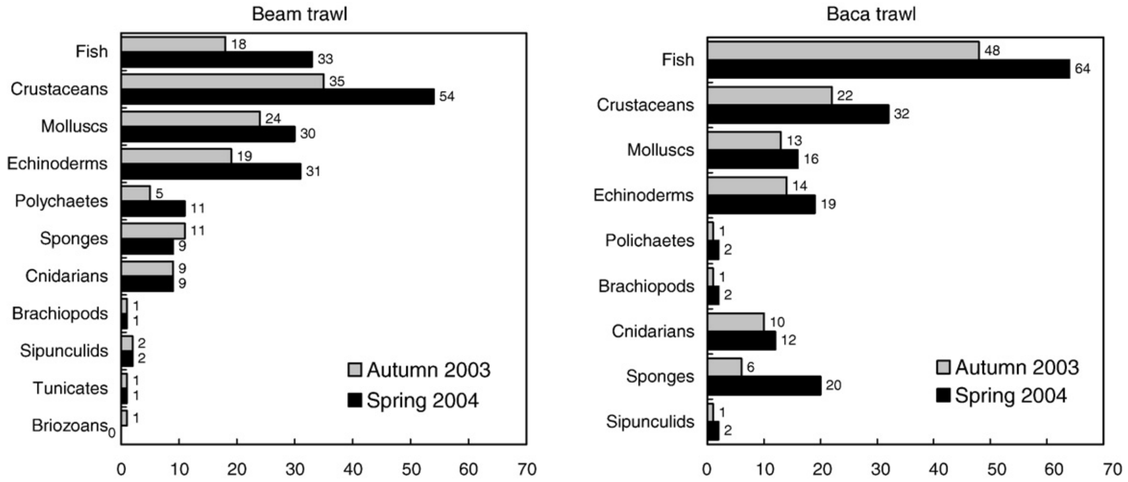

Fig. 4. Species richness by taxonomic group and season from beam trawl and *baca* otter trawl samples.

Table 1
Mean values of ecological indices by sampling gear, season and strata on Le Danois Bank

		S	SD_S	B	SD_B	N	SD_N	H'_B	$SD_{H'_B}$	H'_N	$SD_{H'_N}$
Beam trawl											
Autumn	Stratum 1	31.43	11.87	14.54	7.76	11,874.64	9843.73	2.58	0.65	2.09	0.84
	Stratum 2	34.00	24.04	7.33	9.96	586.72	696.05	2.58	0.65	4.13	0.74
Spring	Stratum 1	42.80	12.76	32.40	19.18	84,442.47	70,606.75	2.76	0.87	1.52	1.17
	Stratum 2	55.80	5.76	23.13	12.28	2262.16	1490.27	2.96	0.70	4.09	0.93
Baca trawl											
Autumn	Stratum 1	37.33	6.51	144.17	47.03	889.07	670.39	2.26	0.63	2.26	1.14
	Stratum 2	71.00	0.00	77.19	30.45	461.01	194.93	3.48	0.16	3.88	0.60
Spring	Stratum 1	43.33	5.50	43.44	31.51	315.92	265.92	2.73	0.34	2.96	1.00
	Stratum 2	57.75	15.97	58.59	18.69	473.50	548.91	3.57	0.17	3.56	0.79

Species richness (S), biomass (B, kg ha^{-1}), abundance (N, n ha^{-1}), diversity in biomass (H'_B) and number (H'_N) with their standard deviations (SD). Stratum 1: 450–700 m; Stratum 2:701–1050 m.

permutations under the reduced model. All the analyses were done using CANOCO software (Ter Braak and Smilauer, 2002). Environmental variables, samples and species relationships were displayed graphically as point-vector triplots. Points represent species code and samples (symbols + code), and vectors represent the

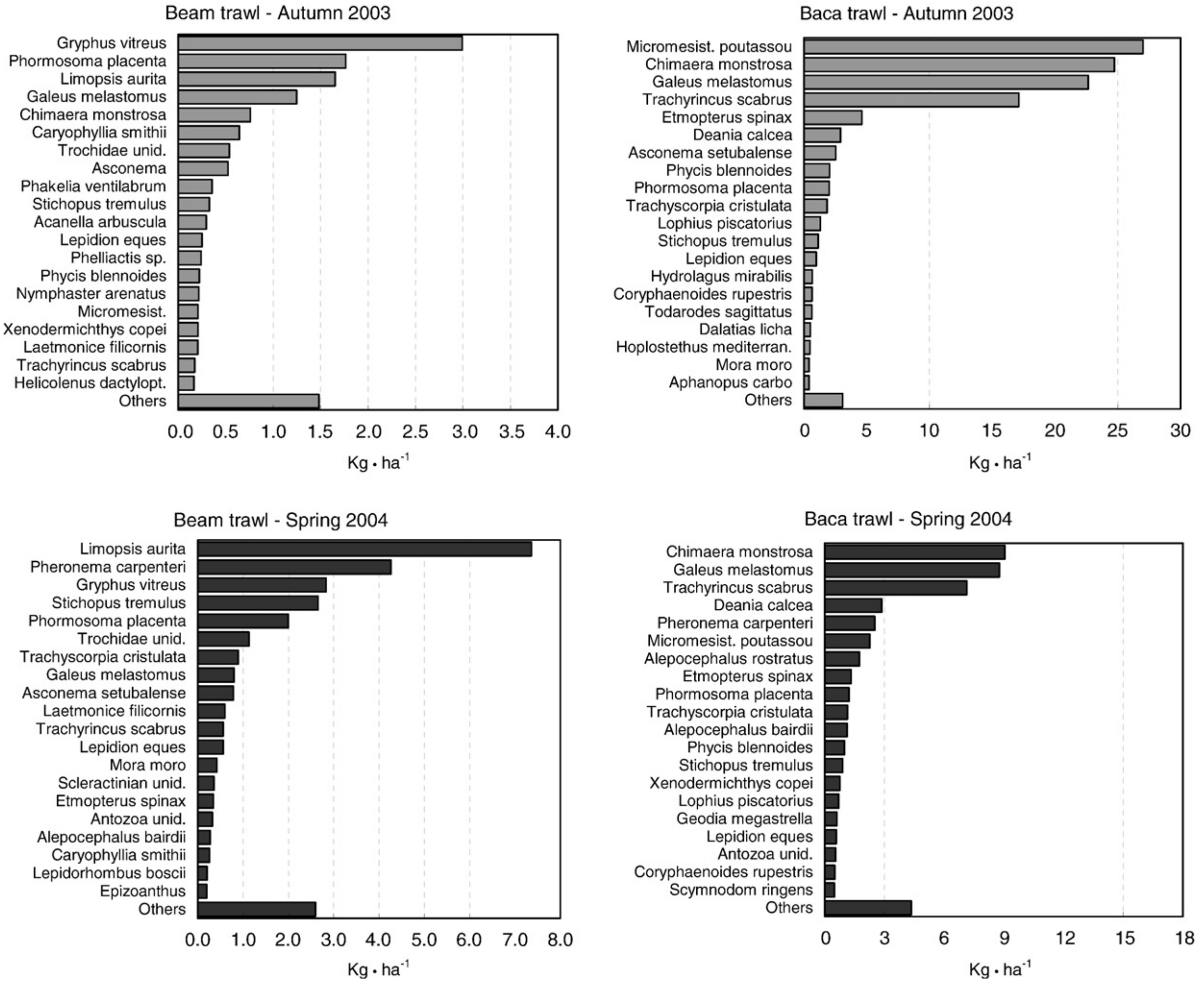

Fig. 5. Standardized biomass (wet weight) indices (kg ha^{-1}) of main species by season and gear.

direction of maximum changes of environmental variables.

A 1-way ANOVA was used to assess differences in species richness, biomass, abundance and species diversity in wet weight and numbers between assemblages resulting from the multivariate analysis. When significant differences were detected, a pairwise "a posteriori" Student–Newman–Keuls' test was run to identify the groups responsible for these differences.

3. Results

3.1. Species richness and taxonomic composition

A total of 181 species were identified from the beam-trawl catches, and 169 using the *baca* otter trawl. At present, the total richness combining both samplers ascends to 221, including 71 species of fishes, 65 crustaceans, 35 molluscs, 29 echinoderms, 10 cnidarians and 5 sponges. Appendix A shows the full list of species caught and identified to date with their standardized abundance (*n* ha^{-1}) and biomass (g ha^{-1}) indices. Fig. 4 presents the main differences in catchability between the two sampling systems used in this study. Those differences are related to the higher catchability of swimming and large-sized demersal and epibenthic species in the otter trawl, compared to the better sampling performance of beam trawl for flat and slow fish and for sessile and small-sized invertebrates. Therefore, communities sampled with the *baca* otter trawl were clearly dominated by fishes, while in beam-trawl sampling, smaller-sized communities of crustaceans, molluscs and echinoderms presented a higher number of dominant taxa. Species richness was greater in the spring survey than in that of autumn for both sampling systems, however this may be overestimated due to greater coverage in the 2004 survey (Fig. 3). Epibenthic communities of Stratum 2 (701–1050 m) are richer and more diverse than Stratum 1 (450–700 m) for both gears used and in both seasons (Table 1). The highest abundance and biomass indices were found in Stratum 1 for both sampling systems, although they were outstanding in spring for catches using beam trawl, and in autumn for those made with *baca* otter trawl.

3.2. Biomass and abundance

Beam-trawl catches in biomass and numbers were higher at the top of the Bank (Stratum 1) in both seasons,

Table 2
Species contribution of dissimilarity between seasons (autumn 2003 and spring 2004) from beam-trawl and *baca*-trawl samples (from Bray–Curtis analysis)

Species	*B* autumn	*B* spring	Dis	%Sp	%Cum
Beam-trawl samples	Average dissimilarity: 83.19				
Limopsis aurita	1543.22	8580.14	16.43	19.75	19.75
Gryphus vitreus	2789.07	3301.37	10.10	12.14	31.88
Stichopus tremulus	305.67	3093.59	7.43	8.94	40.82
Pheronema carpenteri	76.56	3352.89	6.89	8.28	49.10
Phormosoma placenta	1644.25	2208.36	5.66	6.81	55.91
Galeus melastomus	1163.42	931.31	4.08	4.90	60.81
Polymastidae unid.	487.98	914.14	2.76	3.31	64.12
Trochidae unid.	501.14	1313.11	2.75	3.31	67.43
Caryophyllia smithii	600.46	302.80	1.85	2.22	69.65
Chimaera monstrosa	706.93	86.15	1.76	2.12	71.77
Baca-trawl samples	Average dissimilarity: 63.68				
Chimaera monstrosa	24,660.97	12,275.04	11.92	18.71	18.71
Micromesistius poutassou	26,938.24	2754.16	11.85	18.60	37.31
Trachyrincus scabrus	17,064.65	6664.15	9.77	15.35	52.66
Galeus melastomus	22,573.29	12,030.26	8.93	14.02	66.68
Etmopterus spinax	4616.35	1825.59	2.84	4.45	71.14
Deania calcea	2916.76	3190.86	2.47	3.88	75.02
Pheronema carpenteri	2513.43	1210.89	2.04	3.21	78.23
Phormosoma placenta	2005.12	1655.91	1.36	2.13	80.36
Alepocephalus rostratus	374.31	1911.49	1.23	1.92	82.28
Trachyscorpia cristulata echinata	1834.29	1198.71	1.07	1.68	83.96

B: average biomass per season (g ha^{-1});. Dis: mean dissimilarity; %Sp: individual species contribution to total dissimilarity; %Cum: cumulative percentage of species contributions.

while in *baca* trawl the autumn catch at the top of the Bank exceeded that of Stratum 2. The spring *baca* catch of Stratum 2 was larger than at the top of the Bank (Table 1). In general terms and from beam-trawl catches, molluscs and brachiopods were most abundant in Stratum 1 and sponges and echinoderms in Stratum 2.

Fig. 5 shows the standardized biomass indices (kg ha^{-1}) of the twenty main species by gear and season. The brachiopod *Gryphus vitreus*, the sea urchin *Phormosoma placenta* and the bivalve *Limopsis aurita* were the three main epibenthic species found in autumn from beam-trawl samples. In this season, four demersal fish species make up 78% of biomass from *baca* catches: blue whiting (*Micromesistius poutassou*), *Chimaera monstrosa*, *Galeus melastomus* and *Trachyrincus scabrus*. During the spring survey and from beam-trawl samples, *L. aurita* and the sponge *Pheronema carpenteri* were the most important species in biomass. The high values of the sponge are a consequence of the better sampling coverage in the spring survey in the inner basin area, where there are aggregations of this species. *G. vitreus*, *Stichopus tremulus* and *P. placenta* also show high values of biomass in the spring season. From *baca*-trawl samples, three demersal fish species, *C. monstrosa*, *G. melastomus* and *T. scabrus* make up a total of 50.4% of biomass.

With respect to abundance of species of commercial interest in the area, only the presence of blue whiting, forkbeard (*P. blennoides*), monkfish (*Lophius piscatorius*), bluemouth (*Helicolenus dactylopterus*) and tornyhead (*Trachyscorpia cristulata echinata*) are worth mentioning. Also, the presence in Le Danois Bank of reproductive adults of some species (e.g. blue whiting, forkbeard, and bluemouth) is noteworthy, as they are very scarce in the Cantabrian Sea shelf. Also, the juveniles of four-spot megrim (*Lepidorhombus boscii*) are present in the upper plain of the Bank.

3.3. Seasonal differences

As described earlier, the processes of production in the area have a strong seasonal component (Fig. 2). To know which species contribute most to the differences between the catches of the two seasons of the year, the results of the Simper analysis are shown in Table 2. Regarding the epibenthic fauna caught using beam trawl, *L. aurita*, *G. vitreus*, *S. tremulus* and *P. carpenteri* make up almost 50% of the dissimilarity between the hauls made in both seasons of the year. These four species have a low trophic level since they are suspensivorous or detritivorous in their feeding habits and their greater values of biomass in spring may be

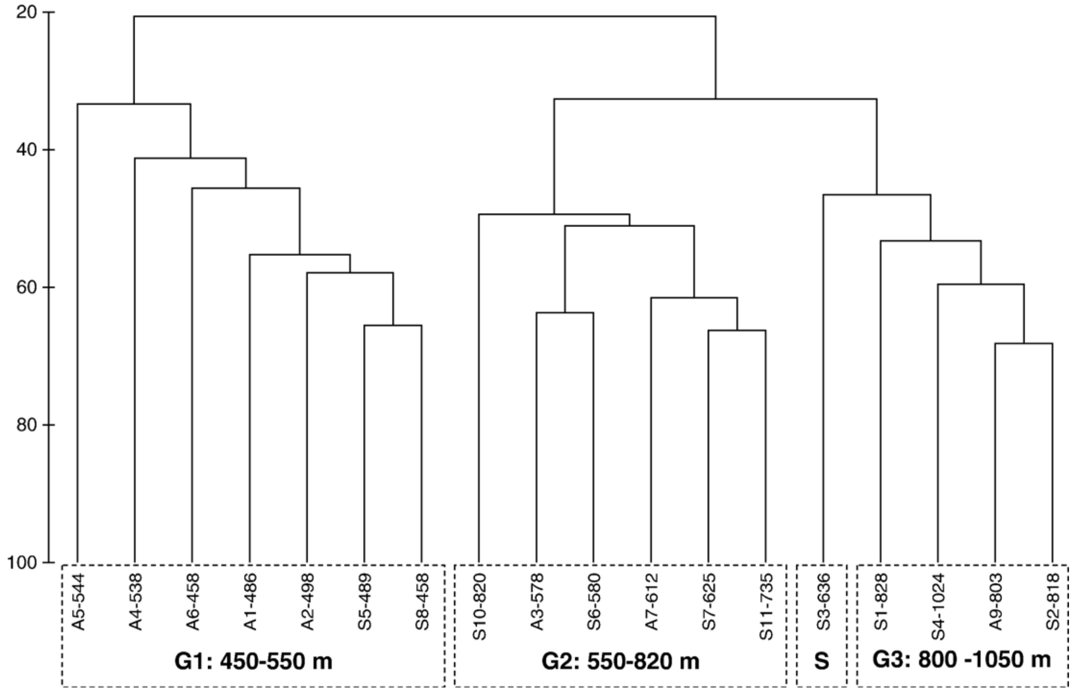

Fig. 6. Hierarchical cluster (Bray–Curtis) of beam-trawl samples. Labels indicate season (A — autumn, S — spring), sample number and depth (m). Main assemblages are defined by depth intervals and S is a sample carried out on Cantabrian Sea shelf slope.

significant of greater activity (or more accessibility) and growth of their populations in the season in which a greater quantity of food (POM, particulate organic matter) is available. From the information coming from the *baca* hauls the greatest differences between seasons are found in *C. monstrosa*, *M. poutassou*, *T. scabrus* and *G. melastomus*, which in total accumulate over 66% of dissimilarity (Table 2). Unlike what was shown for the epibenthic species caught with the beam trawl, in this case the differences between seasons are down to a higher presence of these demersal species in autumn. This greater accessibility of demersal fish in autumn is also reflected in Fig. 5.

3.4. Faunal assemblages

Cluster analyses show the existence of three main assemblages: Group G1 at the top of the Bank (450–550 m), Group G2 over the Bank break (550–800 m) and Group G3 in the inner basin (800–1050 m). The results are very similar for epibenthic communities (beam-trawl samples, Fig. 6) and for demersal communities (*baca*-trawl samples, Fig. 7). Group G1 is typified in epibenthic communities by the brachiopod *G. vitreus*, one unidentified gastropod of the family Trochidae and the bivalve *L. aurita* (38% of cumulative similarity) and by the fishes *C. monstrosa*, *G. melastomus* and *M. poutassou* in demersal communities (Table 3). Group G2 is typified in epibenthic communities by the sea urchin *P. placenta* and the polychaete *Laetmonice filicornis*, and by the demersal fishes *C. monstrosa*, *T. scabrus* and *G. melastomus*. Group G3 is characterized by the aggregations of the hexactinellid sponge *P. carpenteri* and the sea star *Psilaster andromeda*, and by the fish *T. scabrus*, *Deania calcea* and *T. cristulata echinata*. The seasonal effect is not relevant from this analysis and depth is the main environmental factor to define the main assemblages.

In addition to these three assemblages that characterize the epibenthic and demersal communities in Le Danois Bank, the cluster analyses differentiated a station in each of the gears in the Cantabrian Sea shelf slope (marked with an ‘S’ in Figs. 6 and 7). At these stations, which are further from the Bank, we find species such as European hake (*Merluccius merluccius*) and *Xenodermichthys copei*. Moreover, in the case of *baca* another special haul was made in an area of very scarce sedimentary coverage over the top of the Bank (marked with an ‘R’ in Fig. 7). The greater presence of rocky outcrops in this area leads to the appearance of sessile organisms such as gorgonians (*Callogorgia verticillata*) and numerous species of sponges of the families Hexactinellidae and Geodidae, as well as a large biomass of *C. monstrosa*, which seems to be highly abundant in this type of rocky

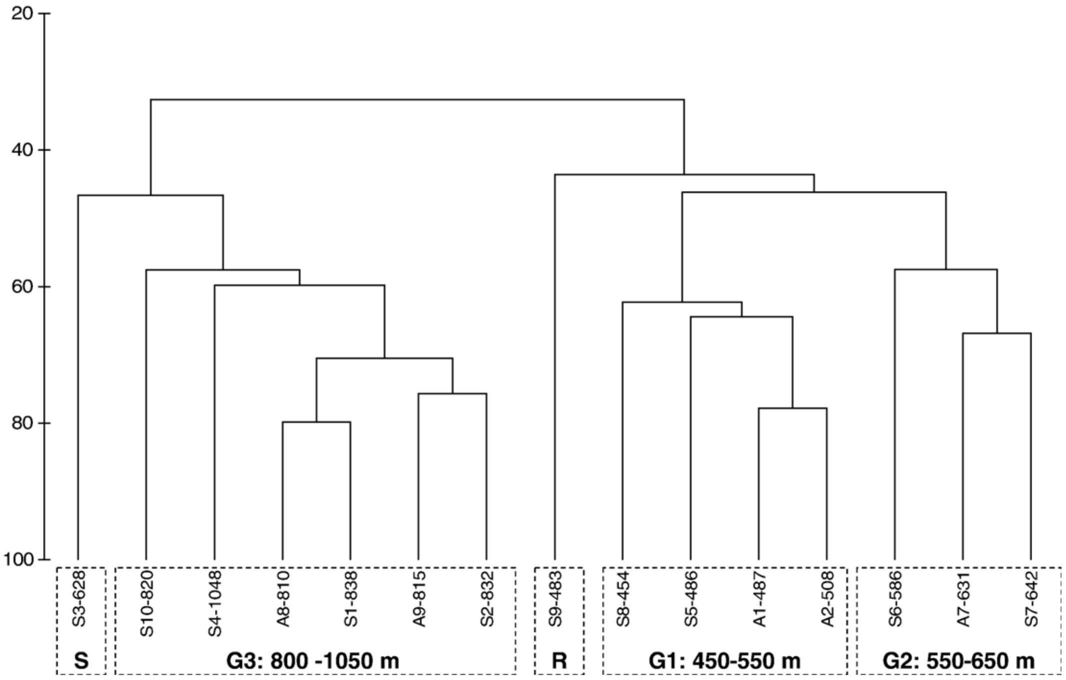

Fig. 7. Hierarchical cluster (Bray–Curtis) of *baca* otter trawl samples. Labels indicate season (A — autumn, S — spring), sample number and depth (m). Main assemblages are defined by depth intervals, R is a sample carried out on rocky grounds and S is a sample on Cantabrian Sea shelf slope.

Table 3
Main species contribution of assemblages of beam-trawl and *baca*-trawl samples (similarity percentages from Bray–Curtis)

Species	*B*	%Sp	%Cum
Beam-trawl samples			
Group G1: 450–550 m	Average similarity: 49.0		
Gryphus vitreus	6470.81	14.2	14.2
Trochidae unid.	666.29	12.2	26.4
Limopsis aurita	2593.02	11.9	38.3
Galeus melastomus	2486.26	10.5	48.8
Lepidorhombus boscii	459.93	9.9	58.7
Polymastidae unid.	1869.20	9.2	67.9
Pagurus alatus	215.51	5.2	73.1
Anapagurus laevis	42.36	3.1	76.2
Colus gracilis	65.83	3.0	79.2
Caryophyllia smithii	1084.72	2.7	81.9
Group G2: 550–820 m	Average similarity: 53.7		
Phormosoma placenta	2190.90	11.1	11.1
Laetmonice filicornis	1164.00	9.0	20.0
Mora moro	786.20	8.9	28.9
Trochidae unid.	1732.97	8.5	37.3
Gryphus vitreus	1639.38	8.5	45.8
Lepidion eques	523.18	8.4	54.2
Limopsis aurita	10,900.97	7.6	61.8
Polycheles typhlops	43.79	4.2	66.0
Pontophilus norvegicus	38.92	4.2	70.2
Colus gracilis	68.98	3.3	73.6
Group G3: 800–1050 m	Average similarity: 57.9		
Phormosoma placenta	1638.52	7.7	7.7
Lepidion eques	939.61	7.2	14.9
Psilaster andromeda	386.38	5.9	20.8
Munida tenuimana	192.90	5.4	26.1
Pheronema carpenteri	9924.16	5.0	31.1
Geryon trispinosus	178.59	4.5	35.6
Synaphobranchus kaupi	135.95	4.2	39.9
Phelliactis sp.	1193.76	4.2	44.1
Stichopus tremulus	2383.51	4.1	48.2
Pontophilus norvegicus	55.24	4.0	52.3
Baca-trawl samples			
Group G1: 450–550 m	Average similarity: 65.6		
Chimaera monstrosa	39,350.83	8.8	8.8
Galeus melastomus	31,508.59	8.6	17.4
Micromesistius poutassou	32,019.86	7.7	25.2
Etmopterus spinax	4788.90	6.8	32.0
Phycis blennoides	2525.02	6.8	38.7
Lepidorhombus boscii	547.47	5.6	44.3
Bathysolea profundicola	327.09	5.1	49.4
Leucoraja circularis	222.38	4.5	53.9
Stichopus tremulus	428.34	4.3	58.2
Phormosoma placenta	97.46	4.1	62.3
Group G2: 550–650 m	Average similarity: 60.6		
Chimaera monstrosa	13,064.81	7.7	7.7
Trachyrincus scabrus	19,822.14	7.3	15.0
Galeus melastomus	6777.64	7.3	22.3
Phormosoma placenta	2656.01	6.3	28.6
Phycis blennoides	1351.30	6.1	34.7
Micromesistius poutassou	8483.44	5.9	40.6
Trachyscorpia cristulata	1462.16	5.8	46.3
Mora moro	598.37	5.4	51.8
Hoplostethus mediterraneus	725.71	5.2	56.9
Opistoteuthis agassizii	226.54	5.1	62.0
Group G3: 800–1050 m	Average similarity: 64.3		
Trachyrincus scabrus	16,184.19	5.1	5.1
Deania calcea	7073.06	4.9	10.0
Galeus melastomus	8658.36	4.4	14.4
Trachyscorpia cristulata	2670.07	4.4	18.7
Alepocephalus rostratus	3194.60	4.2	23.0
Chimaera monstrosa	2356.29	4.1	27.1
Lepidion eques	1571.99	3.9	31.0
Phormosoma placenta	2246.39	3.9	34.8
Nezumia sclerorhynchus	409.32	3.4	38.2
Scymnodom ringens	799.76	3.3	41.5

B: average biomass (g ha^{-1}); %Sp: individual species contribution to total dissimilarity; %Cum: cumulative percentage of species contributions.

bottom with a relevant biogenic habitat. The structural complexity of this area and the presence of other typical species were studied in some dives carried out using a ROV and a photogrammetric sled.

To summarize this section, and taking into consideration the level of biomass and the contribution of typified species, we can denominate the community made up of Group G1 as *Gryphus–Galeus*, that formed by Group G2 as *Phormosoma–Trachyrincus* and that formed by Group G3 as *Pheronema–Deania*, for ease of identification. We will denominate the community that inhabits the rocky bottoms of the top of the Bank as *Callogorgia–Chimaera*, due to the abundance of these two species.

Table 4 summarizes the mean value of ecological parameters obtained for each group resulting from cluster analysis. No significant associations were found between biomass and abundance and the ecological indices. However, significant differences in species richness were detected in *baca* ($F=6.00$, $p=0.019$) and beam trawls ($F=9.32$, $p=0.003$), where group G3 presents a higher number of species than groups G1 and G2 in both gears. Likewise, regarding diversity in biomass for *baca* trawls, the three groups were significantly different from each other ($F=66.10$, $p<0.001$). Finally, beam-trawl diversity in numbers of G3 was significantly higher than G2 and G1 values ($F=7.67$, $p=0.006$).

3.5. Effects of habitat characteristics on communities structure

The particular characteristics of the study area determine that the set of environmental variables used

Table 4
Mean values of ecological indices by sampling gear and main assemblages resulting from cluster analysis

	Community	S	SD_S	B	SD_B	N	SD_N	H'_B	$SD_{H'_B}$	H'_N	$SD_{H'_N}$
Beam trawl											
Group G1	*Gryphus–Galeus*	31.00	10.88	20.09	10.22	23,156.84	22,763.74	2.54	0.63	2.06	0.78
Group G2	*Phormosoma–Trachyrincus*	42.33	10.63	26.16	18.95	57,775.24	77,831.65	2.79	0.76	1.97	1.56
Group G3	*Pheronema–Deania*	57.50	5.00	23.18	12.79	1572.70	685.43	3.09	0.99	4.49	0.69
Baca trawl											
Group G1	*Gryphus–Galeus*	39.75	7.97	115.95	54.87	755.82	619.58	2.12	0.27	2.39	0.95
Group G2	*Phormosoma– Trachyrincus*	42.00	5.29	68.45	54.41	308.67	294.05	3.00	0.08	3.41	0.40
Group G3	*Pheronema–Deania*	62.17	14.13	64.79	22.08	469.33	434.07	3.54	0.16	3.66	0.69

Species richness (S), biomass (B, kg ha^{-1}), abundance (N, n ha^{-1}), diversity in biomass (H'_B) and number (H'_N) with their standard deviations (SD).

in the analyses had a strong correlation with depth (Fig. 8). The two different seasons of the year in which the surveys took place do not appear to have had important consequences in the temperature and salinity of waters close to the bottom of this deep-sea ecosystem, the depth effect being the main conditioning factor (Fig. 8A and B). The extreme values of temperature were 9.70 and 11.08 °C, corresponding to the deepest area of the inner basin (1050 m) and to the shallowest part of the top of the Bank (450 m) respectively. Salinity varied between 35.56 and 35.80, reaching the highest values in the deep waters influenced by the Mediterranean water flow at over 800 m depth.

The top of the Bank presents very little unconsolidated sediment cover and so there are numerous rocky outcrops that make difficult both biological samplings and the use of the box corer to collect samples for sediment typology analysis. The references used to determine the sampling points were the seafloor reflectivity maps obtained from multibeam echosounder data. For this reason the granulometric characteristics obtained refer only to trawlable areas and do not reflect the extreme complexity of the habitats of the shallowest area of the Bank. Whatever the case, these areas present the highest percentages of GCS and MFS of the study area. The highest percentage of coarse sand (GCS) obtained was only 5.0%, whereas medium and fine sands (MFS) reached up to 86.22% (Fig. 8C).

The inner basin, meanwhile, presents greater structural homogeneity. Its relevant sedimentary thickness, which includes sediment drifts, indicating a very different hydrodynamic to that of the top of the Bank, mean the practical absence of rocky outcrops. In this area the highest percentages of silt (84.24%) and organic matter (7.00%) in the sediment are also found (Fig. 8D and E).

The seafloor reflectivity values at each sampling station varied between −40.0 dB in the most absorbent areas (strong sedimentary coverage) and −19.5 dB in the hardest (rocky seafloor). Fig. 8F shows a greater variability (therefore no significant correlation exists) in the values of reflectivity in depths shallower than 700 m, which correspond to the top and the break of the Bank due to their greater structural complexity.

Table 5 shows the mean values of environmental variables used to characterize the habitat of the main assemblages.

Using the set of eight environmental variables on multivariate ordination of beam-trawl data, the first two axes of the RDA plot explained 67.3% of variance of the species–environment relationship and 39.5% of the species data. The Monte-Carlo test indicated that all canonical axes together ($p = 0.001$) were significant. The RDA ordination plots show that the first discriminatory factor (axis 1) is strongly and positively correlated with depth (Fig. 9). All remaining variables show a higher correlation with axis 1 than with axis 2 (except seafloor reflectivity). These is due to the strong relationships between depth and the other variables. Therefore, none of the variables used in the analysis explain a significant percentage of axis 2 variability. The second discriminatory factor (axis 2) is negatively correlated with bottom reflectivity and with less weight with the increase of the sediment particle grain size. The sampling stations carried out at the top of the Bank were located in the habitat defined by warm and less salty waters with more MFS and GCS sediment typology (negatively correlated with axis 1). Species that appear in this habitat were the brachiopod *G. vitreus*, one unidentified gastropod of the family Trochidae, the bivalve *L. aurita* and four-spot megrim (*L. boscii*). Taking into consideration the EUNIS hierarchical habitat classification (Davies et al., 2004) this corresponded to the habitat type A6.31: Communities of bathyal detritic sands with [*G. vitreus*]. Under the opposing environmental conditions, reflected by deeper and salty grounds with sediments richer in organic matter and silt, appear the sampling stations of the inner basin. Species appearing in this habitat were the sponge *P. carpenteri*, the squat lobster *Munida tenuimana*, the sea star *P. andromeda* and the fishes *Lepidion*

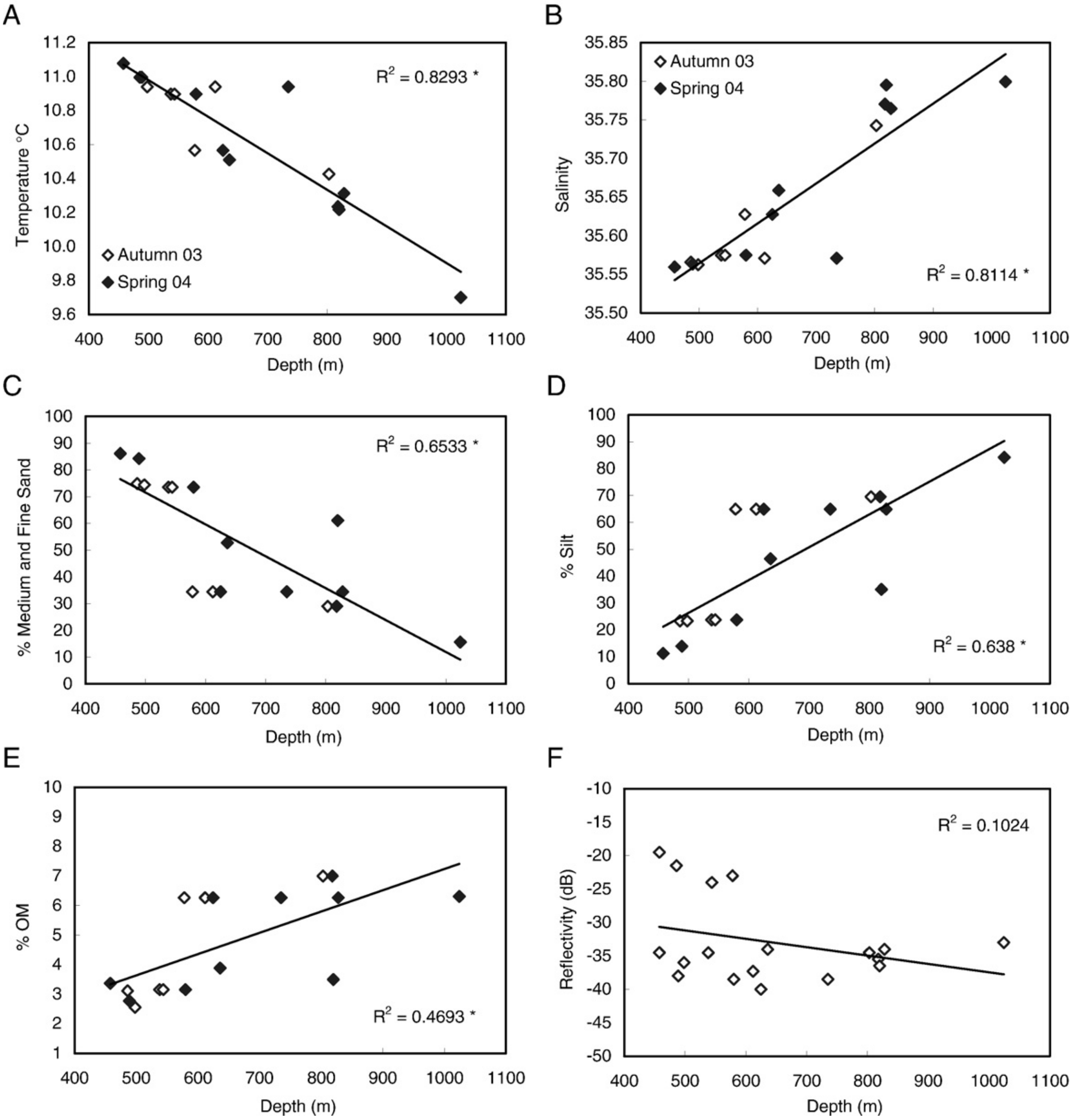

Fig. 8. Main environmental variables used in the RDA analysis of beam-trawl samples as a function of depth. A: near-bottom temperature; B: near-bottom salinity; C: medium and fine sands percentage; D: silt percentage; E: organic matter percentage and F: seafloor reflectivity. Asterisk marks significant Pearson correlation ($p < 0.005$).

eques and the deep-sea eel (*Synaphobranchus kaupi*). This corresponds to the EUNIS habitat type A6.621: facies with [*Pheronema grayi*]. Beam trawl is more efficient than *baca* trawl at capturing the deep-sea eel, due its smaller mesh size, but this species is probably more abundant in the study area than is reflected in the samples. The distribution of OM and the type of sediment (coarser on the top than deeper) explain the absence of decapod crustaceans linked to muddy sediments (e.g. *Nephrops norvegicus*, *Alpheus glaber*: Cartes et al., 2007a,b).

The sampling stations on the Bank break were positively correlated with axis 2. As is stated above, none of the environmental variables used seem to have a clear influence on the formation of this second discriminatory factor. This area of the Bank is characterized by a large slope (from 600 to 800 m depth) with relatively horizontal terraces with a certain sedimentary coverage where sampling is possible. Environmental factors not used in the analysis, such as a greater complexity of the habitat, the presence of

Table 5
Summary of environmental variables, mean values and their standard deviations (SD) that characterize the habitat of the main faunal assemblages

Assemblages	Group G1		Group G2		Group G3	
Environmental variable	Mean	SD	Mean	SD	Mean	SD
Depth (m)	491.50	29.95	645.40	81.10	863.60	91.62
Bottom temperature (°C)	10.99	0.07	10.73	0.26	10.19	0.27
Bottom salinity	35.57	0.01	35.62	0.07	35.77	0.02
% Gravel and coarse sand	2.24	0.43	1.48	1.29	1.15	1.08
% Medium and fine sand	79.37	5.88	46.07	17.85	31.18	12.59
% Silt	18.39	5.91	52.45	19.01	67.66	13.55
% Organic matter	3.03	0.31	5.26	1.50	6.29	1.04
Seafloor reflectivity (dB)	−31.25	7.50	−36.03	5.10	−34.25	1.40

currents or food availability, etc. are likely to have an influence on the structure of this community, inhabited by species such as the polychaete *L. filicornis*, the brittlestar *Ophiura albida* and the fish *Mora moro*. These environmental factors not used in this analysis may also be responsible for the great vertical dispersion

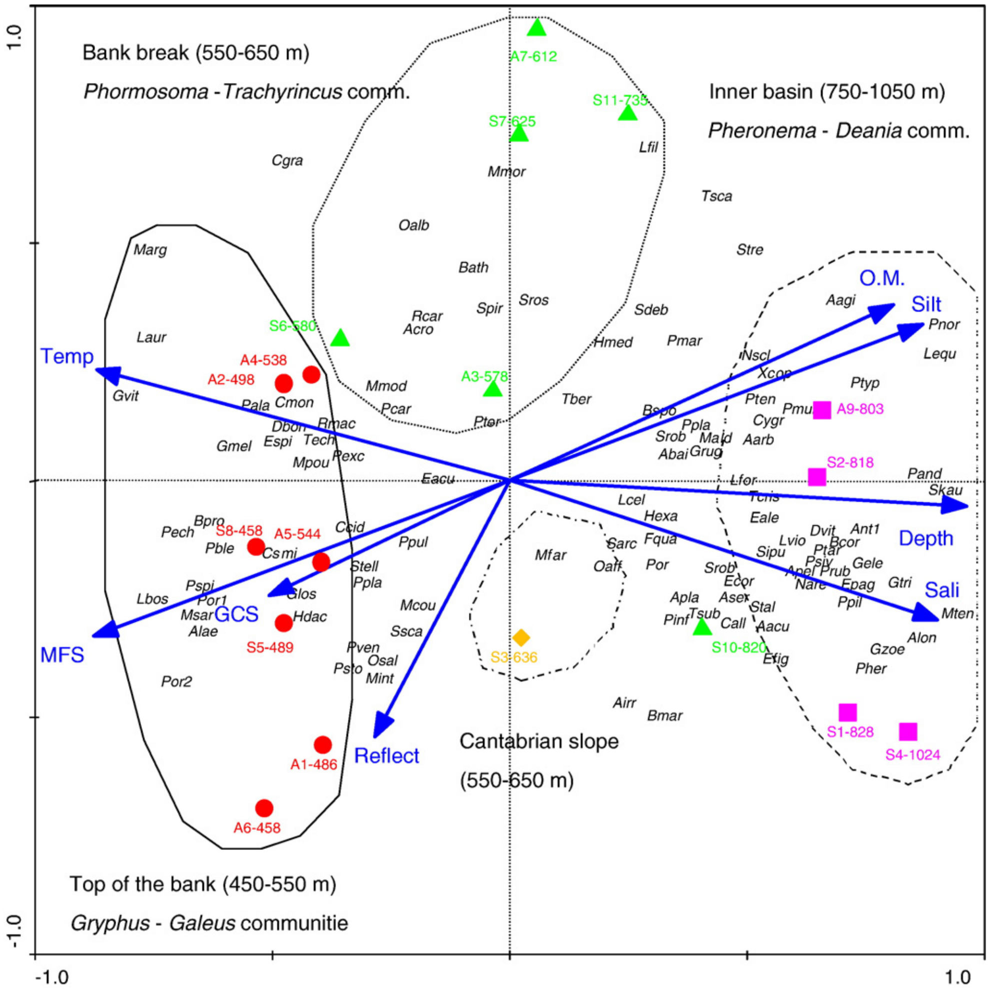

Fig. 9. RDA ordination triplot of axes 1 and 2 with environmental variables (arrows), species (code in italics) and beam-trawl samples (symbols with labels indicate season — A: autumn; S: spring, sample number and depth). Symbols show main assemblages: circles for G1, triangles for G2, squares for G3 and diamond for Cantabrian break shelf. Eigenvalues Ax1: 0.304, Ax2: 0.090; % variance explained of species–environment: 67.3.

(throughout axis 2) found at the stations of the two extreme habitats of the first discriminatory factor. Finally, the samples on the Cantabrian Sea shelf slope appear to be correlated with the increase in seafloor reflectivity in the negative segment of axis 2.

The first two axes of *baca* otter trawl RDA explained 66.1% of variance of the species–environment relationship and 49.5% of the species data. The Monte-Carlo test indicated that all canonical axes together ($p = 0.001$) were significant. Like the beam-trawl results, the RDA ordination plots of *baca* samples show that the first discriminatory factor (axis 1) has a strongly positive correlation with depth (Fig. 10). Axis 1 described a high percentage of variance (53.1%) since all variables showed a high correlation with this axis. Axis 1 contrasts the deepest samples from the inner basin (800–1050 m) with lower temperature and higher salinity, characterized by mud (silt) sediments with high organic matter content, to shallower samples from the top of the Bank (450–550 m) with higher temperature and lower salinity, characterized by a sediment composed of coarse, medium or fine sands of low organic content. At the top of the Bank habitat live flat fish such as megrim (*L. boscii*) and *Bathysolea profundicola* together with blue whiting, the bluemouth *H. dactylopterus* and the deep-water shark *Etmopterus spinax*. The demersal and megabenthic community of the inner basin is structured, from the distribution of species on the RDA ordination diagram (Fig. 10), by the sponge *P. carpenteri* and species of fish such as *Alepocephalus rostratus*, *Halargyreus johnsonii* and *Nezumia sclerorhynchus* and the deep-water sharks *Scymnodom ringens*, *D. calcea* and *Etmopterus pusillus*.

The clear discrimination between the top of Le Danois Bank and the deepest inner basin demersal communities is evident. At an intermediate location, the

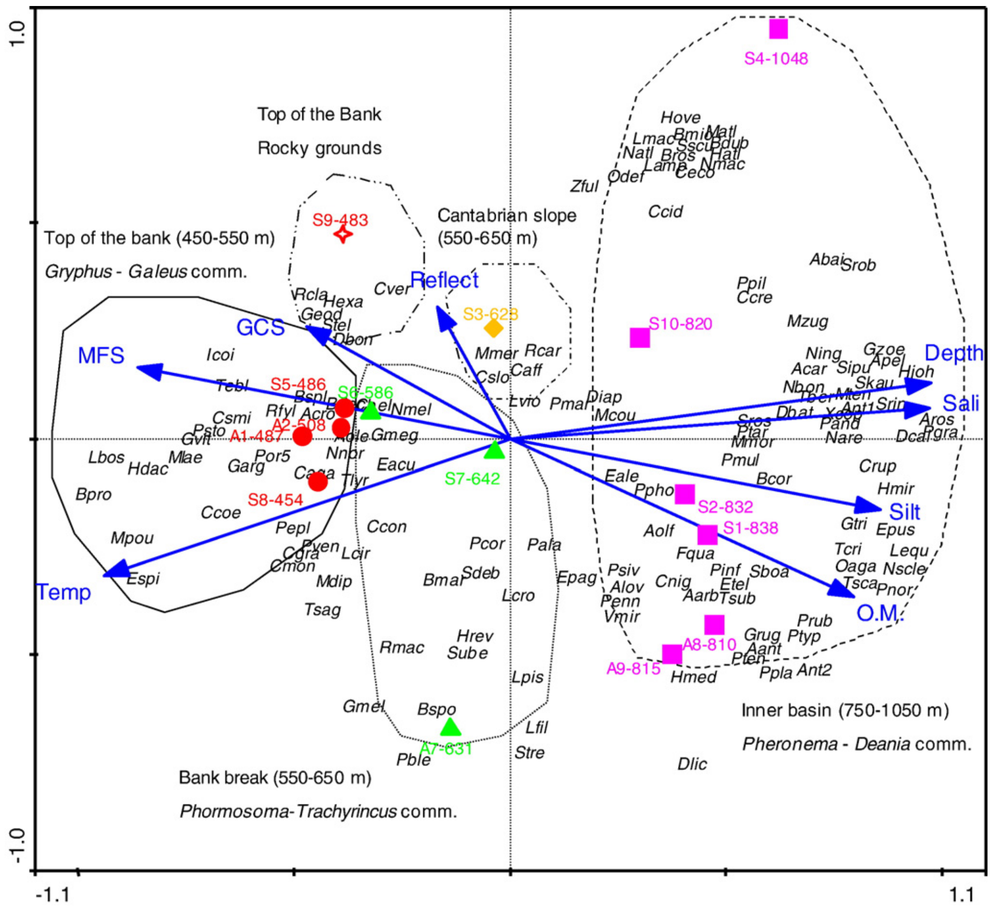

Fig. 10. RDA ordination triplot of axes 1 and 2 with environmental variables (arrows), species (italics) and *baca*-trawl samples (symbols with labels indicate season — A: autumn; S: spring, sample number and depth). Symbols show main assemblages: circles for G1, triangles for G2, squares for G3, star for rocky grounds and diamond for Cantabrian break shelf. Eigenvalues Ax1: 0.398, Ax2: 0.097; % variance explained of species–environment: 66.1.

Bank break samples are correlated negatively with axis 2. We have already said that this area is characterized by strong habitat complexity due to the presence of rocky outcrops between sedimentary grounds. On the contrary, Cantabrian Sea shelf slope stations (muddy grounds highly altered by fishing activities) and stations at the top of the Bank with rocky grounds showed positive correlations with axis 2 and high seafloor reflectivity.

It is important to emphasize in this analysis the low number of ubiquitous species (located near the centroid of the distribution), which means that the set of environmental variables used produces a strong discriminatory effect on the structure of communities.

3.6. Spatial distribution of communities

The multibeam mapping performed in the study area provides us with a 100% coverage of the seafloor and has the advantage that detailed cartography maps of the distribution of two of the environmental variables used in the analyses of the ordination are available: depth and seafloor reflectivity. Using the spatial distribution of the ranges of these two environmental variables characterizing the habitats of faunal assemblages we can define the spatial distribution of the main epibenthic and demersal communities of the Bank and surrounding area (Fig. 11).

The *Callogorgia–Chimaera* community lives mainly in the northern area of the top of the Bank, where the sediment coverage is lower, probably due to the strong shelf break current, and there is a high presence of rocky outcrops. The *Gryphus–Galeus* community (EUNIS habitat type A6.31) was found mainly on the southern area of the top of the Bank. The *Phormosoma–Trachyrincus* community lives on the sedimentary terraces that characterize the break of Le Danois Bank, both in the northern and in the southern area. The faunal assemblage with the largest distribution area is the *Pheronema–Deania* community (EUNIS habitat type A6.621), which occupies all of the deeper and muddy flat sedimentary grounds of the inner basin (Fig. 11). Finally, in the truncated slope of the near Cantabrian Sea shelf is the heavily-fished community, described in Sánchez (1993) and Sánchez and Serrano (2003), where the commercial species blue whiting, hake and Norway lobster live.

4. Discussion

The results of the present study highlight the importance of Le Danois Bank as an area with high

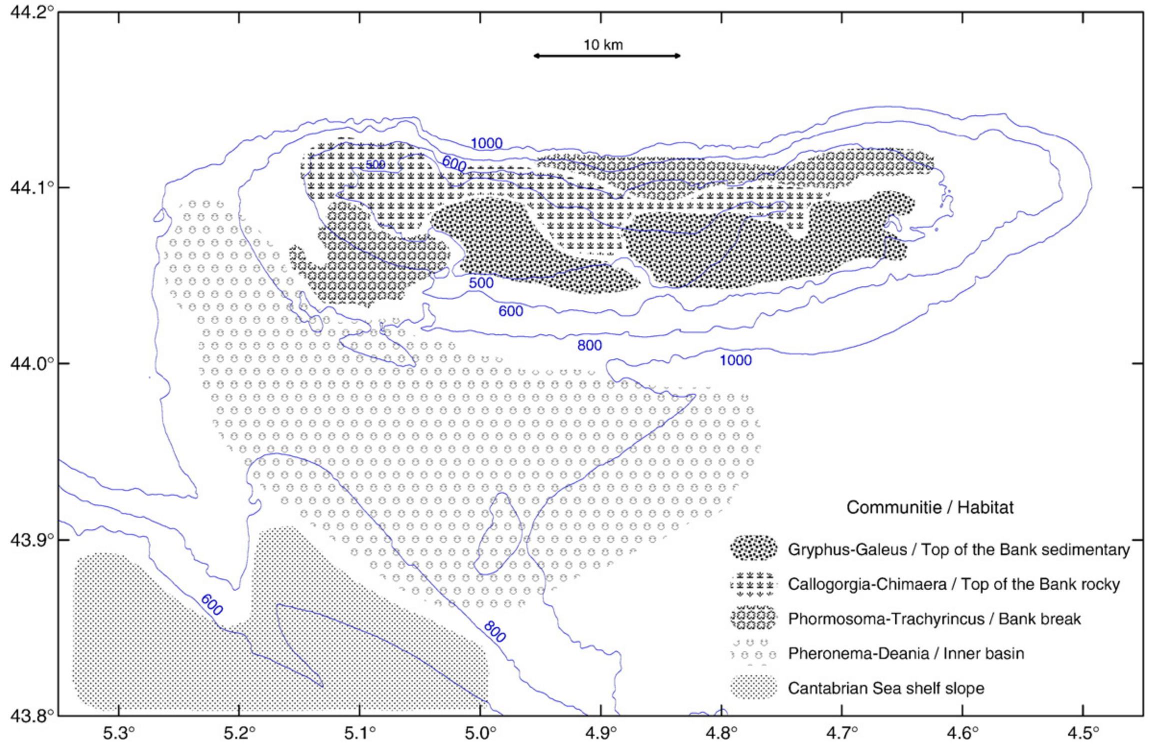

Fig. 11. Spatial distribution on main communities on Le Danois Bank study area based on seafloor reflectivity and depth characteristics of their habitat.

values of diversity. Communities dwelling in the Bank include species characteristic of seamount ecosystems (*Beryx* spp., *Hoplostethus* spp., *C. verticillata*, etc.) together with species of continental shelf (megrim, anglerfish, blue whiting, etc.), shelf break (*T. scabrus*, *L. eques*, etc.), and bathypelagic fauna (Alepocephalidae, *Pasiphaea* spp.). Both its proximity to the productive areas of the Cantabrian Sea and its location in an area of high water transport dynamics (shelf break current) contribute to the high level of food supply and consequently to the considerable values of biomass in relation to the near shelf area. When comparing the results from Le Danois Bank with their equivalents in depth in the Cantabrian Sea shelf (Sánchez et al., 2002) the large differences in biomass from Le Danois Bank mean catches are noteworthy. The Le Danois Bank catches are three times higher than those of the continental shelf. This could be a consequence of the noteworthy differences between the Le Danois Bank and the Cantabrian continental shelf ecosystem structure (Olaso, 1990; Sánchez, 1993; Sánchez and Serrano, 2003; Serrano et al., 2006) due to very different environmental scenarios. For example, the presence of two large canyons nearby (Lastres and Llanes canyons) may also influence the environmental conditions in the Le Danois Bank area, funneling a sediment and organic matter flux from the adjacent continental shelf (Sorbe, 1999; Canals et al., 2006). These geomorphological structures play an important role in the transport, erosion and deposition of sediment to the deepest seafloor (eroded by marine processes, wave erosion, current flows, mass wasting, etc.) and have been proved to be areas of high productivity (Monaco et al., 1990; in the Mediterranean Sea).

Nevertheless, fishing activity probably plays a significant role by disturbing ecosystems through top-down effects and increasing the proportions of r-strategy, small size and low longevity species as described in some areas (Olaso 1990; Jennings and Kaiser, 1998). According to our studies, no regular fishery is currently operating in the Bank. Only a few vessels work sporadically using gillnets or long lines and no stable trawl fishery works in the Bank, except some exploratory hauls or sporadic activities. In relation to the results obtained in this study, it seems likely that the higher fishing pressure that existed in the past had greater consequences on the abundance of vulnerable and low resilience sessile species, such as cold water corals, sponges and gorgonians. The presence in Le Danois Bank of large adults of some fish species (e.g. blue whiting, forkbeard, and bluemouth), which are very scarce at the same depths of the Cantabrian Sea shelf, is probably due to the lower degree of fishing activity in the Bank. Nevertheless, from a study of the dynamics of two communities characterised by different levels of fishing intensity, Blanchard (2001a) concluded that the effects of environmental perturbations (unpredictable mortalities) are more relevant on the structure and demography of fish communities than fishing pressure. The system adjusted to more environmental perturbations and inter-year variability (Bay of Biscay in the study) shows a high proportion of small-sized and *r*-strategy species than the more harvested system. Le Danois Bank is not likely to offer more environmental stability than the near Cantabrian Sea outer shelf. Habitat complexity, due to scarce sedimentary coverage and the low bottom trawl disturbance, probably plays an important role in structuring the communities of the Bank by increasing the presence of large fish species. Kaiser et al., 1999 demonstrated that deep-water communities with sessile epifauna had some slow-growing species such as roundfish and small sharks that would be more vulnerable to fishing disturbance.

Canonical ordination shows depth to be the key factor structuring the Le Danois communities, as was also found in several deep-sea studies (Gordon et al., 1995, 1996; Moranta et al., 1998), Cantabrian Sea (Olaso, 1990; Sánchez, 1993; Sánchez and Serrano, 2003; Serrano et al., 2006) and Bay of Biscay (Blanchard, 2001b; Poulard et al., 2003). The remaining variables used in the analysis are strongly correlated with depth, except reflectivity, therefore contributing to the formation of axis 1 but, like depth, with little weight in axis 2. Only seafloor reflectivity seems to contribute to the second axis. This non-bathymetric second factor may be related to key factors such as habitat complexity and food availability, which probably play an important role in structuring the communities of the Bank (Cartes et al., 2007b). The use of redundancy analysis was determined by a better fit to a linear model than to a unimodal model of species–environmental variables relationship. This linear response is due to the particular characteristics of the study area, since it is the lower limit of distribution for many typical deep-water species of the continental shelf (blue whiting, forkbeard, monkfish, etc.), or on the other hand, the upper limit of distribution of the species inhabiting the continental slope (macrourids, deep-water sharks, etc.). Another relevant result of canonical analysis is the lack of ubiquitous species. This fact reflects how Le Danois communities are composed of stenotopic species more than eurytopic species. This fact may be a consequence of the location of the Bank in the extreme of gradients of two different environments, continental shelf break and slope, where more specialized species live.

Many years ago, and based on a very low number of sampling stations, Le Danois (1948) described in the first biological study of the area the presence of brachiopods at the top of the Bank and sponge aggregations (*Asconema setubalense*) in the inner basin, which is no mean feat given the great depths and the limitations of the sampling systems of the time. He also described the presence in the deepest areas of the Bank (800–1200 m) of the brittlestar *Brisingella coronata* and the deep-sea cucumber *Laetmogone violacea*, which present outstanding values of abundance in our study at these same depths (see Appendix A). Surprisingly, at the same time, he described the northern and southern slopes of the Bank covered by reefs of yellow corals (*Dendrophyllia cornigera*), a species which has not appeared in any of our samples and which is nevertheless only abundant in the rocky outcrops of the inner continental shelf (70-150 m depth) of the Cantabrian Sea. The absence of this species in the Cantabrian outer shelf is probably due to the lack of studies in rocky grounds, since *D. cornigera* has been found at 500 m depth (e.g. Álvarez-Pérez et al., 2005).

The sampling systems used in this study do not provide a full picture of the true scale of the communities of Le Danois Bank, since they do not allow access to the vertical walls of the Bank break nor to the numerous rocky outcrops in the area. Therefore, this study refers almost exclusively to the sedimentary grounds of the area. Some dives using a photogrammetric sled and a remote operated vehicle (ROV) on the rocky outcrops of the Bank suggest concentrations of the typical species of these bottoms, such as *B. decadactylus* (which gives its name to the fishing ground), red sea bream (*P. bogaraveo*) and the big red crab *Chaceon affinis*, whose true abundance is not reflected in the samplings obtained by trawl. At the same time, the existing *rasco* fishery in the area, a type of gillnet (Pereda et al., 1998), the target species of which is monkfish (*L. piscatorius*), would not be viable with the catches expected based on the estimations made from this study. Also, the abundance of some dominant species of the Bank, like the deep-sea eel (*S. kaupi*), was underestimated because the type of bottom trawl used only caught the largest specimens. Gordon and Mauchline (1996), using a semi-balloon trawl (OTSM), revealed that this species is the most abundant on the slopes of the North Atlantic. The affinity of the red crab *C. affinis* for deep rocky bottoms means that in the results of our studies it is not well represented, but some previous exploratory experiences by means of traps (Alcázar et al., 1992) and data from trawlers (Sánchez and Olaso, 1985) showed a higher presence of this species.

The influence of surface productivity on deep-sea megafauna is poorly understood in the area. Pelagic production and its arrival, as phytodetritus, on the sea floor is one of the most important sources of organic matter in Le Danois Bank (Cartes et al., 2007a). The top of the Bank has a greater number of suspensivorous species (brachiopods, molluscs, cnidarians, etc.) than the inner basin. This is probably due to the greater dynamics of horizontal transport motivated by the topographic effects of the Bank over the shelf break current, which has been detected in our surveys by the isopycnal transformations (Ruiz-Villarreal et al., 2006). This increases the speed of the current, limits the presence of sedimentary coverage and facilitates the necessary presence of rocky outcrops for the sessile organisms of great bearing like the community characterized by the gorgonians *C. verticillata*, which also includes large-sized Geodidae and Hexactinellidae sponges. These suspension feeders require a higher rate of marine snow supply and their biomass and productivity depend positively on water dynamics. On the contrary, the inner basin shows strong sedimentary processes and the high level of organic matter seems to make it a suitable habitat for detritus feeders like echinoderms (*S. tremulus*, *L. violacea*) and dense sponge aggregations of *P. carpenteri*. In the Porcupine Seabight, Rice et al. (1990) suggest that *Pheronema* aggregations occur close to, but not within, regions of the upper continental slope where the bottom topography enhances the near-bottom current velocities, but may nevertheless be dependent upon the re-suspended or undeposited organic matter carried there from these regions.

The seasonal fall of phytodetritus to the seabed of Le Danois Bank provides an important input of energy derived from the high seasonal surface productivity of the Cantabrian Sea (see satellite data, Fig. 2), with a peak of Chl at the surface in April (where one of our cruises was performed). This peak may be important in zooplankton dynamics. Recent studies performed during this same project evidenced higher densities of decapod crustaceans in April (Cartes et al., 2007a) in comparison with autumn conditions, and the importance of euphausiids in the diet of small sharks inhabiting the top of the bank (Preciado et al., unpubl. data). The huge biomass of epibenthic filter-feeders has to be supported by marine snow. Studies in the Cantabrian Sea area indicate that a high percentage (80–90%) of the primary production is exported to the bottom as particulate organic matter (OSPAR, 2000). The impact of copepods, the main zooplankton group in biomass (Valdés and Moral, 1998; Sánchez and Olaso, 2004) on phytoplankton blooms is negligible in the Cantabrian Sea. The fate of the accumulated particulate carbon would be mostly determined by sedimentation and water dynamics (Barquero et al., 1998). The present study revealed that a number of phyla of epibenthic species of a low trophic level and with a greater dependence on POM supply are more abundant in spring. On the other hand and in general terms, the highest values of fish abundance appeared in the autumn survey. This is probably because a great number of these species spawn in this season in order to improve the survival of the larvae and juveniles in a more productive area than the deep-sea grounds (Gordon and Duncan, 1985, 1987). The higher abundance in spring of detritus feeders situated at low trophic levels (e.g. *S. tremulus*, *L. aurita*, etc.), may be caused by a feeding aggregation behaviour, as Cartes et al. (2007a) suggest occur in decapod crustaceans when analysing diets and stomach fullness. Evidence of deposition of phytoagreggates (Lampitt, 1985) and aggregations of holothurians in highly productive periods (Gage and Tyler, 1992; Billett et al., 2001) in neighbouring Atlantic areas have already been documented.

A comparative study among the different deep-sea fish assemblages of the Mediterranean and the Atlantic indicates that the biomass of fish increases towards the north, being lower in the Mediterranean and higher in Rockall Trough (Massutí et al., 2004). With respect to richness of fish the value found in Le Danois Bank (71 species) is greater than in the Mediterranean (43–47) and similar to Rockall Trough (80), with higher richness of fish in Porcupine Seabight (104). Nevertheless, this comparison is obviously dependent on the surface and bathymetric range of the studied area and sampling effort: the Porcupine values are based on a considerable sampling effort (twenty years and 214 bottom trawls) and a greater depth range (400–2000 m), and so the data of Le Danois Bank are underestimated.

As stated above, the low impact of the set of environmental variables in the second RDA discriminatory factor suggests the existence of other variables associated with the topographic complexity of the seabed habitat (biomass of sessile invertebrates, e.g.), water dynamics or food availability, not included in these analyses. This is a first contribution to the knowledge of abundance and biomass of deep-sea epifauna and their spatial distribution in Le Danois Bank and can be a potentially useful approach for understanding interspecific relationships. Biological factors such as resource availability, predator–prey relationships and interspecific competition may also play an important role in the local distribution pattern as has been described for some areas of the Atlantic (Macpherson and Roel, 1987; Merret, 1987; Mahault et al., 1990; Gordon et al., 1995) and these studies must be followed up. Finally, the combination of this information with the predator–prey relationships obtained from the analysis of stomach contents carried out during the surveys, and with the fisheries impacts information on the Bank will allow the development of a model of this singular deep-sea ecosystem. Due to the existence of a trophodynamic model of the Cantabrian Sea that includes fisheries impacts (Sánchez and Olaso, 2004; Sánchez et al., 2005), comparisons between both models will be possible, helping us to reach useful conclusions. All this information will allow us to draw up an integrated ecosystem assessment proposal or, depending on the characteristics and vulnerabilities of species and habitats, to define Le Danois Bank as a Marine Protected Area (MPA).

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Appendix A

Standardized biomass (g ha^{-1}) and abundance (*n* ha^{-1}) indices of total species from both gears (V = beam trawl and B = *Baca* otter trawl) and both surveys

Species	Biomass	Abundance	Gear
Fish			
Chimaera monstrosa	17,280.242	27.219	B
Galeus melastomus	14,962.713	34.815	B
Micromesistius poutassou	13,505.490	151.014	B
Trachyrincus scabrus	13,018.533	37.856	B
Etmopterus spinax	3952.939	24.918	B
Deania calcea	2207.096	1.084	B
Phycis blennoides	1497.049	4.773	B

Appendix A (*continued*)

Species	Biomass	Abundance	Gear
Paralepis coregonoides	0.159	0.026	B
Paraliparis membranaceus	0.159	0.026	B
Gonostoma bathyphilum	0.080	0.160	V
Hymenocephalus italicus	0.000	0.013	B
Ceratoscopelus maderensis	0.000	0.013	B
Borostomias antarcticus	0.000	0.007	B
Crustaceans			
Pagurus alatus	114.654	186.342	V
Munida tenuimana	55.698	32.833	V
Polycheles typhlops	41.090	16.520	V
Chaceon affinis	37.763	0.033	B
Geryon trispinosus	31.108	3.140	V
Parapagurus pilosimanus	30.927	4.293	V
Pontophilus norvegicus	30.641	56.588	V
Bathynectes maravigna	28.449	5.495	V
Gnathophausia zoea	17.152	41.302	V
Pagurus excavatus	16.027	10.112	V
Pasiphaea multidentata	14.210	3.855	V
Cancer bellianus	13.646	0.013	B
Anapagurus laevis	13.386	57.003	V
Dichelopandalus bonnieri	5.856	1.669	V
Meganyctiphanes norvegica	5.756	5.558	V
Pontophilus spinosus	4.679	23.326	V
Pasiphaea sivado	4.242	7.195	V
Pasiphaea tarda	3.875	3.140	V
Systellaspis debilis	3.549	5.406	V
Polybius henslowii	3.100	0.595	V
Plesionika martia	2.685	0.635	V
Acantephyra pelagica	2.584	2.347	V
Sergia robusta	2.380	0.893	B
Nephrops norvegicus	2.380	0.026	B
Aega sp.	2.210	1.391	V
Munida sarsi	1.969	12.759	V
Aristeus antennatus	1.428	0.033	B
Pagurus carneus	1.382	0.572	V
Philocheras echinulatus	1.317	5.916	V
Munida intermedia	1.145	0.094	V
Rochinia carpenteri	0.979	0.716	V
Scalpellum scalpellum	0.953	2.384	V
Cymonomus granulatus	0.930	7.275	V
Gennadas elegans	0.635	4.056	V
Sergestes arcticus	0.478	0.478	V
Nephropsis atlantica	0.476	0.086	B
Dorhynchus thomsoni	0.366	2.307	V
Ephirina figueirai	0.318	1.113	V
Monodaeus couchii	0.286	1.431	V
Eurynome aspera	0.238	1.193	V
Pandalina profunda	0.238	0.238	V
Psathyrocaris infima	0.212	0.953	V
Boreomysis tridens	0.206	1.591	V
Metacrangon jacqueti	0.180	0.358	V
Boreomysis arctica	0.175	0.796	V
Nematoscelis megalops	0.175	0.478	V
Stereomastis sculpta	0.159	0.020	B
Cirolana borealis	0.120	0.238	V
Liocarcinus depurator	0.120	0.238	V
Pagurus prideaux	0.120	0.238	V
Mysidetes farrani	0.103	0.796	V
Stylocheiron sp.	0.072	0.716	V

Appendix A (*continued*)

Species	Biomass	Abundance	Gear
Trachyscorpia cristulata echinata	1383.600	2.083	B
Lophius piscatorius	1008.346	0.225	B
Alepocephalus rostratus	799.219	2.711	B
Lepidion eques	655.306	9.414	B
Coryphaenoides rupestris	433.962	0.979	B
Alepocephalus bairdii	419.205	2.532	B
Hoplostethus mediterraneus	408.416	3.101	B
Mora moro	398.420	3.663	B
Hydrolagus mirabilis	328.922	0.622	B
Dalatias licha	307.502	0.245	B
Xenodermichthys copei	283.761	13.715	V
Chlorophthalmus agassizii	255.300	3.530	B
Aphanopus carbo	222.138	0.298	B
Scymnodom ringens	205.319	0.218	B
Lepidorhombus boscii	201.297	6.440	V
Helicolenus dactylopterus	188.085	0.335	V
Nezumia sclerorhynchus	174.061	2.764	B
Leucoraja circularis	152.323	0.159	B
Centroscymnus coelolepis	140.899	0.013	B
Bathysolea profundicola	112.814	2.102	B
Etmopterus pusillus	90.124	0.291	B
Synaphobranchus kaupi	45.017	7.355	V
Dipturus batis	37.605	0.053	B
Malacocephalus laevis	33.321	0.245	B
Conger conger	31.893	0.053	B
Molva dipterygia	31.099	0.066	B
Coelorhynchus coelorhynchus	19.834	0.238	B
Beryx splendens	18.723	0.040	B
Gadomus dispar	17.530	0.120	V
Beryx decadactylus	16.502	0.066	B
Halargyreus johnsonii	15.146	0.398	V
Epigonus telescopus	10.790	0.040	B
Centroscymnus crepidater	9.838	0.020	B
Centrolophus niger	8.886	0.013	B
Notacanthus bonapartei	6.664	0.112	B
Gadiculus argenteus	6.440	1.050	V
Nettastoma melanurum	5.871	0.013	B
Chauliodus sloani	5.804	0.160	V
Halosaurus ovenii	5.395	0.026	B
Hoplostethus atlanticus	4.919	0.007	B
Melanonus zugmayeri	4.601	0.086	B
Rajella fyllae	3.173	0.026	B
Nessorhamphus ingolfianus	2.856	0.026	B
Argyropelecus hemigymnus	2.516	2.799	V
Argyropelecus olfersii	2.384	1.631	V
Serrivomer beani	2.380	0.013	B
Stomias boa	1.269	0.046	B
Trigla lyra	0.952	0.026	B
Lampanyctus crocodilus	0.793	0.040	B
Raja clavata	0.793	0.013	B
Cataetyx alleni	0.635	0.318	V
Lampanyctus sp.	0.635	0.033	B
Bathypterois dubius	0.476	0.033	B
Leptoderma macrops	0.317	0.086	B
Bathytroctes microlepis	0.317	0.013	B
Neoscopelus macrolepidotus	0.317	0.007	B
Notoscopelus kroeyerii	0.160	0.160	V
Melagnostigma atlanticum	0.159	0.086	B

(continued on next page)

Appendix A (*continued*)

Species	Biomass	Abundance	Gear
Epimeria parasitica	0.060	1.193	V
Processa nouveli	0.057	0.094	V
Eucopia hansenii	0.054	0.635	V
Atelecyclus rotundatus	0.049	0.094	V
Ebalia nux	0.031	0.318	V
Calocarides coronatus	0.031	0.160	V
Phronima sedentaria	0.031	0.160	V
Galathea strigosa	0.023	0.238	V
Iphimedia obesa	0.023	0.238	V
Thysanopoda acutifrons	0.017	0.160	V
Calocaris macandreae	0.000	0.007	B
Molluscs			
Limopsis aurita	4017.436	17,794.219	V
Trochidae unid.	698.114	491.629	V
Todarodes sagittatus	396.833	0.767	B
Opistoteuthis agassizii	191.832	0.430	B
Bathypolipus sponsalis	114.044	0.993	V
Colus gracilis	46.812	22.418	V
Galeodea rugosa	37.207	0.478	V
Illex coindetii	31.099	0.093	B
Todaropsis eblanae	18.088	0.146	B
Antalis agilis	17.567	71.568	V
Cymbulia peroni	14.645	31.943	V
Modiolus modiolus	10.970	34.296	V
Arca tetragona	5.200	12.401	V
Troschelia berniciensis	4.611	0.558	V
Spirotropis monterosatoi	3.523	4.928	V
Glossidae unid.	3.506	6.511	V
Delectopecten vitreus	3.197	12.722	V
Octopus defilippi	3.015	0.013	B
Rossia macrosoma	2.267	0.358	V
Aporrhais serresianus	1.986	0.876	V
Lyonsia formosa	1.511	1.749	V
Histioteuthis reversa	1.111	0.053	B
Trophon echinatus	1.002	3.815	V
Abra alba	0.990	3.457	V
Abra longicallus	0.953	1.431	V
Argobuccinum olearium	0.793	0.026	B
Poromya granulata	0.621	0.716	V
Callumbonella suturale	0.381	0.286	V
Octopus salutii	0.381	0.094	V
Cuspidaria rostrata	0.349	0.876	V
Helicocranchia pfefferi	0.159	0.013	B
Cuspidaria cuspidata	0.094	0.238	V
Turritela communis	0.072	0.478	V
Sepietta oweniana	0.000	0.026	B
Emarginula crassa	0.000	0.013	B
Sponges			
Pheronema carpenteri	2307.687	7.393	V
Polymastidae unid.	801.128	4069.425	V
Geodia megastrella	453.161	0.040	B
Asconema setubalense manta	122.969	0.013	B
Phakelia ventilabrum	88.343	0.478	V
Stylocordyla borealis	14.794	13.618	V
Polychaetes			
Laetmonice filicornis	363.695	136.225	V
Aphrodite aculeata	0.836	1.869	V
Aponuphis bremmentii	0.011	0.478	V
Hyalinoecia tubicola	0.000	0.007	B

Appendix A (*continued*)

Species	Biomass	Abundance	Gear
Echinoderms			
Phormosoma placenta	1723.629	43.912	B
Stichopus tremulus	1445.455	7.115	V
Nymphaster arenatus	303.185	28.463	V
Psilaster andromeda	179.582	8.801	V
Laetmogone violacea	136.783	5.089	V
Echinus alexandrii	66.940	1.113	V
Brisingella coronata	59.943	1.989	V
Zoroaster fulgens	26.498	0.549	B
Peltaster placenta	21.262	0.317	B
Cidaris cidaris	10.472	0.278	B
Pontaster tenuispinus	9.141	2.665	V
Benthogone rosea	8.092	0.317	B
Pseudoporania stormii	6.488	0.094	V
Stichastrella rosea	6.305	1.846	V
Echinus acutus	5.916	2.481	V
Anseropoda placenta	4.293	0.796	V
Porania pulvillus	2.338	4.914	V
Ophiura albida	2.264	31.840	V
Echinocardium cordatum	1.986	1.909	V
Tethyaster subinermis	1.113	1.113	V
Leptometra celtica	1.082	2.290	V
Astropecten irregularis	1.065	0.255	V
Ypsiloturia talismani	0.584	4.373	V
Ophiura affinis	0.478	6.359	V
Ophiothrix fragilis	0.223	5.200	V
Asteronyx loveni	0.159	0.079	B
Echinocyamus pusillus	0.120	0.238	V
Leptosynapta inhaerens	0.060	0.120	V
Amphiura chiajei	0.011	0.120	V
Cnidarians			
Phelliactis sp.	463.732	11.926	V
Acanella arbuscula	381.050	3.815	V
Caryophyllia smithii	339.201	109.831	V
Epizoanthus paguriphilus	119.330	3.815	V
Pennatula rubra	16.617	4.928	V
Funiculina quadrangularis	2.988	3.815	V
Virgularia mirabilis	0.476	0.119	B
Parerythropodium coralloides	0.094	4.199	V
Lytocarpia myriophyllum	0.094	0.286	V
Pennatula phosphorea	0.000	0.007	B
Others			
Gryphus vitreus	2755.987	2653.240	V
Phascolion strombi	0.209	2.290	V

For species collected by both gears we show only the high value, assuming is the best sampler. Species are arranged by biomass level.

References

Alcázar, J.L., González, P., Fernández, C.L., García, L., Rucabado, J., Lloris, D., Castellón, A., 1992. Prospecciones Pesqueras en Aguas Profundas. (Sector VIIIc — ICES). Rec. Pesqueros de Asturias, no. 6 (128 pp.).

Álvarez-Pérez, G., Busquets, P., De Mol, B., Sandoval, N.G., Canals, M., Casamor, J.L., 2005. Deep-water coral occurrences in the Strait of Gibraltar. In: Freiwald, A., Murray Roberts, J. (Eds.), Cold-

Water Corals and Ecosystems. (Erlangen Earth Conference Series). Springer-Verlag, Berlin Heidelberg, pp. 207–221.

Amoureux, L., 1974. Annelides polychetes du banc Le Danois. Bol. R. Soc. Esp. Hist. Nat., Secc. Biol. 72, 101–127.

Ballesteros, M., Acosta, J., Muñoz, A., Rivera, J., Sánchez, F., 2006. Estudio morfoestructural de "El Cachucho" (Le Danolis Bank) basado en batimetría multihaz. Proyecto ECOMARG. 5ª Asamblea Hispano-Protuguesa de Geodesia y Geofisica. ISBN: 84-8320-373-1.

Barquero, S., Cabal, J.A., Anadon, R., Fernandez, E., Varela, M., Bode, A., 1998. Ingestion rates of phytoplankton by copepod size fractions on a bloom associated with an off-shelf front off NW Spain. J. Plankton Res. 20 (5), 957–972.

Billett, S.M., Bett, B.J., Rice, A.L., Thurston, M.H., Galéron, J., Sibuet, M., Wolff, G.A., 2001. Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). Prog. Oceanogr. 50, 325–348.

Blanchard, F., 2001a. Una approche de la dynamique des peuplements de poissons démersaux exploités: analyse comparée de la diversité spécifique dans le golfe de Gascogne (océan Atlantique) et dans le golfe du Lion (mer Méditerranée). Aquat. Living Resour. 14 (2001), 29–40.

Blanchard, F., 2001b. The effect of fishing on demersal fish community dynamics: an hypothesis. ICES J. Mar. Sci. 58, 711–718.

Boillot, G., D'Ozouville, L., 1970. Etude structurale du plateau continental nord-espagnol entre Aviles et Llanes. C.R. Acad. Sci. Fr. T.270 D, 1865–1868.

Boillot, G., Dupeuble, P.A., Le Lann, F., D'Ozouville, L., 1970. Etude stratigraphique des terrains affleurants sur le plateau continental nord-espagnol entre Aviles et Llanes. C.R. Acad. Sci. Fr. T.3 D, 78–80.

Boillot, G., Dupeuble, P., Lamboy, M., d'Ozouville, L., Sibuet, J.C., 1971. Structure et histoire géologique de la marge continentale au Nord de l'Espagne (entre 4° et 9° W). Histoire Structural du Golfe de Gascogne. Tome, 2, V.6, pp. 1–52.

Boillot, G., Malod, J., 1988. The north and northwest Spanish continental margin: a review. Rev. Soc. Geol. Esp. 1 (3–4), 295–316.

Buchanan, J.B., 1984. Sediment analysis. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the Study of Marine Benthos. Blackwell Scientific Publications, Oxford, pp. 41–65.

Canals, M., Puig, P., Durrieu, X., Heussner, S., Palanques, A., Fabres, J., 2006. Flushing submarine canyons. Nature. 444, 354–357.

Cartes, J.E., Huguet, C., Parra, S., Sanchez, F., 2007a. 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., Part 1 54, 1091–1110.

Cartes, J.E., Serrano, A., Velasco, F., Parra, S., Sanchez, F., 2007b. Community structure and dynamics of deep-water decapod assemblages from Le Danois Bank (Cantabrian Sea, NE Atlantic): Influence of environmental variables and food availability. Prog. Oceanogr. 75, 797–816.

Clarke, K.R., Warwick, R.M., 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory (144 pp).

Davies, C.E., Moss, D., Hill, M.O., 2004. EUNIS habitat classification revised 2004. Report of European Environment Agency (EEA). European Nature Information System (EUNIS) (306 pp).

ESCI, 1995. In: Santanach, P. (Ed.), Estudios sismicos de la corteza iberica. Rev. Soc. Geol. Esp., vol. 8, p. 4.

Fiuza, A., Hamann, M., Ambar, I., Díaz del Rio, G., González, N., Cabanas, J.M., 1998. Water masses and their circulation off western Iberia during May 1993. Deep-Sea Res., Part 1, Oceanogr. Res. Pap. 45, 1127–1160 (1998).

Gage, J.D. and Tyler, P.A., 1992. Deep Sea Biology: A Natural History of Organisms at the Deep-Sea Floor. Ed. Cambridge University Press, 495 pp.

Gordon, J.D.M., Duncan, J.A.R., 1985. The biology of fish of the family Moridae in the deep-water of the Rockall Trough. J. Mar. Biol. Assoc. U.K. 65 (2), 475–485.

Gordon, J.D.M., Duncan, J.A.R., 1987. Aspects of the biology of *Hoplostethus atlanticus* and *H. mediterraneus* (Pisces: Berycomorphi) from the slopes of the Rockall Trough and the Porcupine Sea Bight (North-Eastern Atlanthic). J. Mar. Biol. Assoc. U.K. 67 (1), 119–133.

Gordon, J.D.M., Mauchline, J., 1996. The distribution and diet of the dominant, slope-dwelling eel, *Synaphobranchus kaupi*, of the Rockall Trough. J. Mar. Biol. Assoc. U.K. 76 (2), 493–503.

Gordon, J.D.M., Merret, M.R., Haedrich, R.L., 1995. Environmental and biological aspects of slope dwelling fishes of the north Atlantic. In: Hopper, A.G. (Ed.), Deep Water Fisheries of the North Atlantic Oceanic Slope. Kluwer Academic Publisher, Dordrecht.

Gordon, J.D.M., Merrett, N.R., Bergstad, O.A., Swan, S.C., 1996. A comparison of the deep-water demersal fish assemblages of the Rockall Trough and Porcupine Seabight, eastern North Atlantic: continental slope to rise. J. Fish Biol. 49 (Supplement A), 217–238 (1996).

ICES, 2003. Study group on survey trawl gear for the IBTS western and southern areas. ICES CM 2003/B:01 (19 pp).

Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. 34, 201–352.

Kaiser, M.J., Rogers, S.I., Ellis, J.R., 1999. Importance of benthic habitat complexity for demersal fish assemblages. Am. Fish. Soc. Symp. 22, 212–223.

Lampitt, R.S., 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. Deep-Sea Res. 32 (8A), 885–897.

Laubier, L., Monniot, C., 1985. Peuplements profonds du Golfe de Gascogne. Campagnes BIOGAS. IFREMER, Service Documentation-Publications, Brest (629 pp).

Lavin, A., Valdes, L., Sánchez, F., Abaunza, P., Forest, A., Boucher, J., Lazure, P., Jegou, A.M., 2006. In: Robinson, A., Brink, K. (Eds.), The Bay of Biscay: The Encountering of the Ocean and the Shelf, vol. 14. Harvard University Press, pp. 933–1001. chapter 24.

Le Danois, E., 1948. In: Payot (Ed.), Les Profondeurs de la Mer (Paris, 303 pp.).

Macpherson, E., Roel, B.A., 1987. Trophic relationship in the demersal fish community off Namibia. In: Payne, A.I.L., Gulland, J.A., Brink, K.H. (Eds.), The Benguela and Comparable Ecosystems. S. Afr. J. Mar. Sci., 5, pp. 585–596.

Mahault, M.L., Geistdorfer, P., Sibuet, M., 1990. Trophic strategies in carnivorous fishes: their significance in energy transfer in the deep-sea benthic ecosystem (Meriadzeck Terrace–Bay of Biscay). Prog. Oceanogr. 24, 223–237.

Malod, J.A., Vanney, J.R., 1980. Étude morphologique de la pente du Banc le Danois (marge continentale nord-Espagnole) d'apres un relevé bathymétrique au sondeur multifaisceaux et des observations en submersible Cyana2. Ann. Inst. Océanogr. 56, 73–83 (Pasris).

Malod, J.A., Boillot, G., Capdevilla, R., Dupeuple, P.A., Lepvrier, C., Mascle, G., Mueller, C., Taugourdeau-Lantz, J., 1980. Plongees en submersible au Sud de Golfe de Gascogne: stratigraphie et structure de la pente du Banc Le Danois. C.R. Somm. Soc. Geol. Fr. 3, 73–76.

Massutí, E., Gordon, J.D.M., Moranta, J., Swan, S.C., Stefanescu, C., Merret, N.R., 2004. Mediterranean and Atlantic deep-sea assemblages: differences in biomass composition and size-related structure. SCI. MAR. 68 (Suppl. 3), 101–115.

Merret, N.R., 1987. A zone of faunal changes in assemblages of abyssal fish in the eastern north Atlantic: a response to seasonality in production? Biol. Oceanogr. 9, 185–244.

Monaco, A., Courp, T., Heussner, S., Carbonne, J., Fowler, S.W., Deniaux, B., 1990. Seasonality and composition of particulate fluxes during ECOMARGE-I, western Gulf of Lions. Cont. Shelf Res. 10, 959–987.

Montadert, L., Winnock, E., Delteil, J.R., Grau, G., 1974. Continental margin of Galicia, Portugal and Bay of Biscay. In: Bueky, C.A., Drake, C.L. (Eds.), The Geology of Continental Margins. Springer-Verlag, pp. 323–342.

Moranta, J., Stefanescu, C., Massuti, 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.

Morato, T., Watson, R., Pitcher, T.J., Pauly, D., 2006. Fishing down the deep. Fish Fish. 7, 24–34.

Olaso, I., 1990. Distribución y abundancia del megabentos invertebrado en fondos de la plataforma Cantábrica. Publ. Espec. Inst. Esp. Oceanogr. 5 (128 pp).

OSPAR, 2000. Quality Status Report 2000: Region IV — Bay of Biscay and Iberian Coast. OSPAR Commission, London (134 pp).

Pereda, P., Punzón, A., Landa, J., 1998. The "rasco": a gillnet fishery for Anglerfish (*Lophius piscatorius* L., 1758 and *L. budegassa* Spinola, 1807) in the Cantabrian Sea (ICES Division VIIIc). ICES C.M. 1998/O:46 (12 pp).

Poulard, J.Ch., Blanchard, F., Boucher, J., Souissi, S., 2003. Variability in the demersal fish assemblages of the Bay of Biscay during the 1990s. ICES Mar. Sci. Symp. 219, 411–414.

Rice, A.L., Thurston, M.H., New, A.L., 1990. Dense aggregations of a hexactinellid sponge, *Pheronema carpentery*, in the Porcupine Seabight (northeast Atlantic Ocean), and possible causes. Prog. Oceanogr. 24, 179–196.

Ruiz-Villarreal, M., González-Pola, C., Sánchez, R., Plaza, F., Díaz del Río, G., Cabanas, J.M., González, N., Rodríguez, M., Alonso, J., Lavín, A., 2006. Recent observations of Mediterranean Water in the Bay of Biscay. In: Álvarez (Ed.), Oceanography of the Bay of Biscay, pp. 277–280.

Sánchez, F., 1993. Las comunidades de peces de la plataforma del Cantábrico. Publ. Espec. Inst. Esp. Oceanogr. 13 (137 pp).

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., Olaso, I., 1985. *Geryon affinis* Milne Edwards y Bouvier, 1984, en el Golfo de Vizcaya (Decapoda Brachyura). Bol. Inst. Esp. Oceanogr. 2 (1), 155–157.

Sánchez, F., Olaso, I., 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem. Ecol. Model. 172 (2004), 151–174.

Sánchez, F., Blanco, M., Gancedo, R., 2002. In: CYAN (Ed.), Atlas de los peces demersales y de los invertebrados de interés comercial de Galicia y el Cantábrico. Otoño 1997–1999. Inst. Esp. Oceanogr. (158 pp.).

Sánchez, F., Rodríguez-Cabello, C., Olaso, I., 2005. The role of elasmobranchs in the Cantabrian Sea shelf ecosystem and impact of the fisheries on them. J. Northwest Atl. Fish. Sci. 35, 467–480.

Sánchez, F., Serrano, A., 2003. Variability of groundfish communities of the Cantabrian Sea during the decade of the 1990s. ICES Mar. Sci. Symp. 219, 249–260.

Serrano, A., Sánchez, F., García-Castrillo, G., 2006. Epibenthic communities of trawlable grounds of the Cantabrian Sea. Sci. Mar. 70S1, 149–159.

Sorbe, J.C., 1999. Deep-sea macrofaunal assemblages within the benthic boundary layer of the Cap-Ferret Canyon (Bay of Biscay, NE Atlantic). Deep-Sea Res., Part 2, Top. Stud. Oceanogr. 46, 2309–2329.

Ter Braak, C.J.F., 1996. Unimodal Models to Relate Species to Environment. DLO-Agricultural Mathematics Group, Wageningen (266 pp).

Ter Braak, C.J.F., Smilauer, P., 2002. CANOCO reference manual and CanoDraw for Windows. User's guide (version 4.5). Microcomputer Power (Ithaca, NY, USA) (500 pp).

Valdés, L., Moral, M., 1998. Time series analysis of copepod diversity and species richness in the Southern Bay of Biscay (Santander, Spain) and their relationships with environmental conditions. ICES J. Mar. Sci. 55 (4), 783–792.

Van Aken, H.M., 2000. The hydrography of the mid-latitude Northeast Atlantic Ocean. II: the intermediate water masses. Deep-Sea Research (Part 1, Oceanographic Research Papers) [Deep-Sea Res. (1 Oceanogr. Res. Pap.)], vol. 47, no. 5, pp. 789–824 (May 2000).