Continental Shelf Research 29 (2009) 1174–1188

Contents lists available at ScienceDirect

Continental Shelf Research

journal homepage: www.elsevier.com/locate/csr

Photogrammetric quantitative study of habitat and benthic communities of deep Cantabrian Sea hard grounds

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ARTICLE INFO

Article history:
Received 20 June 2008
Received in revised form
21 November 2008
Accepted 1 December 2008
Available online 29 January 2009

Keywords:
Deep-sea benthic habitat
Epibenthic communities
Underwater photogrammetry
Cantabrian Sea
Le Danois Bank
El Cachucho

ABSTRACT

To study the highly complex deep-sea habitats of the Cantabrian Sea and their macro-epibenthic communities a new towed underwater sled was designed to carry out quantitative visual transects based on photogrammetric analysis. The main objective of the study was undertaken to provide a first approach for gaining a better understanding of the correlation between hard substrates, depth and ecology in this region; thereby enabling researchers to determine the extent to which benthic communities depend on physical factors.

The results were compared from two areas with different characteristics and methodological problems: one in the central Cantabrian Sea outer shelf (150 m depth), near the head of the Lastres Canyon, and another at the summit of the Le Danois Bank (555 m depth). Two image databases corresponding to two transects were analysed, with every photo being linked to a faunal list and a set of environmental variables. To assess the amount of variation in faunal densities related to the set of habitat environmental characteristics, a redundancy analysis (RDA) was used. The set of environmental variables comprised depth, temperature, salinity, substrate type and seafloor reflectivity. Using the hierarchical classification proposed by EUNIS, three habitats were identified from a Cantabrian Sea shelf visual transect: A4.12—Sponge communities on circalittoral rock (14.5% coverage), A5.35—Circalittoral sandy mud (56.8%) and A5.44—Circalittoral mixed sediments (28.7%). A typical community appeared on the rocky habitat, made up of yellow coral *Dendrophyllia cornigera* and the cup sponge *Phakellia ventilabrum*. On Le Danois Bank, three habitats were identified and the cnidarians (*Caryophyllia smithii* and *Callogorgia verticillata*) and the sponges (*Asconema setubalense*, *Aplysilla* sp., hexactinellids) characterized rocky habitats and patchy rock-sand habitats.

This study provided groundtruthing for the existing surficial seafloor features and very valuable information about the autoecology of sessile and vulnerable species, since the scale used was more appropriate for this kind of study than the macroscale of trawling, with several microhabitats being sampled in the same sample. Also, the use of this non-extractive methodology, which does not cause damage or alterations to benthic communities, is particularly necessary in vulnerable ecosystem studies and Marine Protected Areas monitoring.

1. Introduction

While commercially important groundfish have been extracted for centuries on the continental shelf, and for decades on the slope of the Cantabrian Sea, relatively little is known about benthic communities and their habitats in this region. Although Le Danois (1948) provided evidence that the deep-sea supported a variety of benthic fauna and began describing its regional distribution, attempts at habitat mapping were limited by the absence of bathymetric information. With only a basic knowledge of seafloor bathymetry coupled with information from biological samples, studies of the benthic fauna tended to focus on ecology (i.e. Olaso, 1990; Sánchez, 1993), biodiversity (i.e. Álvarez-Claudio, 1994; Altuna, 1995) or biogeography of certain taxa (i.e. Sánchez and Olaso, 1985; Sánchez et al., 2002; Reveillaud et al., 2008). More recently some studies have investigated the relationship between benthic communities and environmental variables, with the majority of these focusing on the sedimentary grounds of the shelf (Sánchez and Serrano, 2003; Serrano et al., 2006, 2007). Information on hard ground habitats and communities is therefore only available for relatively few areas, such as the Le Danois Bank (Sánchez et al., 2008).

The high primary production associated with the particular oceanographic features of the Cantabrian Sea, such as spring

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doi:10.1016/j.csr.2009.01.004

upwellings, the winter shelf break current or mesoscale eddies (OSPAR, 2000; Lavin et al., 2006; Gil, 2008) have made its fisheries very important historically. Due to the progressively scarce commercial species in the most accessible parts of the continental shelf and to the new technologies applied to vessels and their gears, these fisheries are gaining increasing access to rocky seabeds and to greater depths. Also, several areas of the Cantabrian Sea are essential fish habitats (EFH) for some commercial species (Sánchez et al., 2002). The Magnuson-Stevens Conservation and Management Act, amended in 1996, emphasized the need to characterize and protect these habitats, which are defined as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity". As a result of this requirement and the effort to move towards comprehensive ecosystem-based fisheries management, rebuilding plans for overexploited species must take habitat into consideration. Deep hard grounds on the canyon heads and slopes of the Cantabrian Sea are the spawning areas for the European hake (*Merluccius merluccius*) and recruitment processes have been described in the nearby muddy areas of the shelf associated with hydrographic drifts (Sánchez and Gil, 2000). In particular, the Le Danois Bank ecosystem is described as an essential fish habitat for the blue whiting (*Micromesistius poutassou*), the forkbeard (*Phycis blennoides*), the bluemouth (*Helicolenus dactylopterus*) and other species because spawners are very scarce on same depths of the nearby Cantabrian Sea shelf (Sánchez et al., 2008). In April 2008, these characteristics, together with the presence of threatened sessile species (cold-water corals, gorgonian forests, sponge aggregations, etc.) led the Spanish Ministry for the Environment to define Le Danois Bank as the first offshore Marine Protected Area (MPA) in Spanish waters (Heredia et al., 2008), and more recently it was integrated into the OSPAR Network of MPAs. There is now a great need to create new MPAs in order to comply with the EU Directives on Habitats, and study projects are underway to identify priority areas that will lead to the safeguarding of marine biodiversity and make it possible to sustain fisheries in the context of the ecosystem by means of appropriate management. In this context, there is a need to develop new surveillance methodologies which have minimum impact on these vulnerable ecosystems and, as such, provide information of species and habitat relationships.

Traditionally, extractive samplers (dredges, box-corer, beam trawl, otter trawl and other towed samplers) have been used to obtain abundance indices of the benthic and demersal species dwelling on soft bottoms. However, in some areas, where the presence of rocky outcrops hampers the use of these classical sampling methods and where habitats are biogenic and vulnerable, visual methods must be used, such as towed cameras (Rumohr, 1995; Williams and Leach, 1999; Kostylev et al., 2001), remotely operated vehicles (Trenkel et al., 2004; Lorance and Trenkel, 2006) or manned submersibles (Grassle et al., 1975; Uiblein et al., 2003). These systems are expensive and require sophisticated research vessels (dynamic positioning systems, multibeam echosounders, fibre optic umbilicals and specific winches, etc.) as well as a considerable number of back-up technicians to maintain and operate them. This means that only a small number of oceanographic research institutions are capable of studying deep hard ground ecosystems. In many cases, this methodology only provides qualitative or semi-quantitative information (photographs or video transects, etc.). Due to the high degree of observer subjectivity, data has very limited scope for statistical analysis which is consequently inadequate for comparing results from different ecosystems.

With the advent of multibeam technology (Kostylev et al., 2001; Kenny et al., 2003), marine benthic habitat mapping has entered into a new era of study. Although sonar techniques provide valuable information on seafloor morphology, they provide little information on the nature of the substrate and seafloor fauna due to scale limitations (Heezen and Hollister, 1971). Visual remote sensing methods, on the other hand, are able to provide an insight into biological considerations, but are restricted to non-turbid waters. These limitations highlight the need for new imaging methods that can provide data on the ecology of the deep-sea floor.

In an attempt to solve some of these problems, a new towed underwater photogrammetric sled was designed and the first results of the data collected are presented in this paper. Structure-forming invertebrates were the primary focus of this study, organisms consisting of mostly sessile and sedentary megafaunal invertebrates (mainly Porifera, Echinodermata and Cnidaria) that can significantly increase the complexity of physical habitats. Most of these species have been defined as threatened and/or declining by several conventions (OSPAR, 2003) and hence their study is of considerable importance.

The Cantabrian Sea (southern Bay of Biscay) is one of the most heterogeneous areas of the NE Atlantic, characterized by steep gradients sloping down from its narrow shelf (10–40 km wide), conspicuous submarine canyons (Aviles, Lastres, Llanes and Cap Breton canyons) and marginal shelf (Le Danois Bank). In addition, the occurrence of patchy distribution of rocky outcrops, and the great variety of sedimentary grounds raises the complexity and the boundary effects in the area (Sánchez and Serrano, 2003; Serrano et al., 2006; Sánchez et al., 2008). These characteristics made the study of highly complex habitats difficult, since it requires sampling at finer scales than is possible with classical methods. This study therefore provides the first quantitative analysis of benthic megafaunal communities of deep hard grounds within the Cantabrian Sea and Le Danois Bank. This research is also being conducted to provide a first approach for improving the understanding of the correlation between hard substrates, depth and ecology in this region; thereby enabling researchers to determine the extent to which benthic communities depend on physical factors.

2. Material and methods

This study is based on experiences during the TREBOL survey, carried out in April 2005, whose objective was to estimate the impact of trawl gear with rock-hopper as the fishing line over continental shelf hard grounds. The quantification of the impact on habitats with a biogenic structure (corals, sponges, etc.) needed the experimental approach of this survey, which gave rise to this first methodological approximation using non-destructive systems in the area. Also, the study was supported by data collected through the ECOMARG project carried out during 2003 and 2004. This project focused mainly on studying the Le Danois Bank benthic-demersal ecosystem by applying a multidisciplinary approach (www.ecomarg.net). The aim of the project was to study the physical scenario, including both bathymetry and hydrographical features, and the different compartments of benthic fauna (endobenthic, epibenthic, suprabenthic and demersal communities) in an attempt to describe the dynamics of this deep-sea ecosystem (Cartes et al., 2007a, b; Sánchez et al., 2008).

During the TREBOL survey, ten visual transects were undertaken with variable lengths over the seafloor, between 718 and 4816 m, and the number of valid pictures from each ranged between 216 and 440. In this study, only the dataset from two transects was analysed, one in the central Cantabrian Sea outer shelf, near the Lastres Canyon, and another near the summit of Le Danois Bank (Fig. 1), whose characteristics are shown in Table 1.

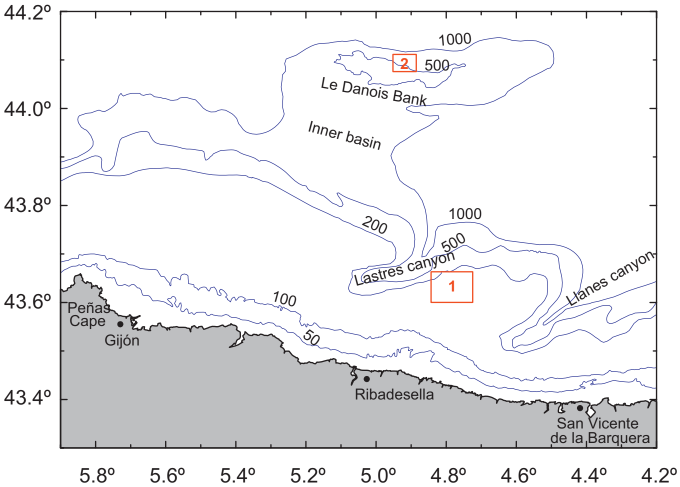

Fig. 1. Visual transect location on the Cantabrian Sea shelf (1) and on the Le Danois Bank (2).

Table 1
Characteristics of the two visual transects and the environmental variables shown with their standard deviations (SD).

	Cantabrian shelf	Le Danois Bank
Visual transect location start	43°38.4′N 4°44.8′W	44°05.8′N 4°55.5′W
Visual transect location end	43°37.1′N 4°48.2′W	44°05.9′N 4°55.2′W
Total images	432	216
Valid images	339	183
Time UTC	16:30–18:18	15:26–16:57
Photo time interval (sec)	15	20
Duration (min)	108	90
Track length (m)	2527.7	717.9
Mean speed (m/h)	1404.2	473.6
Mean distance between photos (m)	5.85±1.65	3.32±2.64
Maximum valid altitude (m)	4.81	8.32
Maximum area * photo (m^2)	12.47	18.23
Mean valid altitude (m)	2.87±0.63	3.15±1.32
Mean area covered by photo (m^2)	6.82±2.43	8.56±3.41
Environmental variables		
Depth limits	140–156	546–570
Mean bottom depth (m)	149.18±3.78	554.65±6.36
Mean reflectivity (dB)	−0.317±0.028	−0.165±0.018
Mean temperature °C	11.622±0.008	10.757±0.020
Mean salinity	35.543±0.002	35.453±0.004
Substrate surface (m^2)		
Very fine sands	1299.19	
Medium and fine sands		399.08
Mixed sediments	395.19	
Patchy sand and rock	186.15	1001.26
Patchy mixed sediments and rock	268.02	
Rock outcrops	164.52	166.97
Total area surveyed (m^2)	2313.06	1567.31

Both areas have predominant rocky grounds often buried by unconsolidated sediment coverage, due to the combined effects of the shelf break current and nearby topographic features (canyon head and pronounced slope).

2.1. Photogrammetric sled and visual transects

The system (Fig. 2) was designed at the IEO (Spanish Institute of Oceanography) Santander laboratory with the aim of sampling deep macro-epibenthic communities quantitatively in a cost-effective manner, in order to eliminate the need for high vessel performance or support from technicians. The system was equipped with a high-resolution digital still camera (10 million effective pixels) which was capable of taking exposures at constant pre-determined time intervals (normally every 10–15 s). In order to avoid problems associated with the accuracy of image calibration from photogrammetric analysis (Wolf, 1983; Kraus, 1993), the camera was fixed on a frame in a zenithal location (90° to the bottom). To increase the area covered by each image a wide angle lens (24 mm focal length, 60° underwater) was employed. The camera used an i-TTL synchronized strobe to illuminate the seafloor. Centrally aligned to the optical centre of the objective was a series of four powerful parallel red laser pointers, spaced at 40 cm, with the capability of a maximum projection of 8 m underwater in clear water conditions. It was also equipped with a Seabird CTD probe to characterize the oceanographic features (pressure, temperature and salinity) prevailing at each photographic site. The system was glide-towed at 2–6 m above the seabed at a speed of 0.5–1.5 knots. The distance to the bottom was controlled by digital signals from a precision altimeter (in cm), which transmitted data on distance between the sledge and the seabed/altitude to the research vessel in real time using an acoustic modem (Fig. 2) and it was then transferred via an RS-232 interface to a computer. Consequently, electrical or optical umbilicals requiring highly specialized winches were not needed, and the sled could be towed by a single steel wire hawser. To protect all the equipment from rough landings or onboard operations a strong steel frame supported the electronics, which was covered by fibreglass panels to avoid entanglement of overhanging objects. A float system in the upper part and heavy ballast in the lower part helped to maintain the stability of the sled and prevent, as far as possible, any pronounced swaying over the bottom that would later require important image rectification. Two rudders were located on the stern to ensure that the sled maintained the same direction during operation. The total weight of the system was approximately 350 kg and the total length was 280 cm. A near-vertical camera angle at a suitable stable distance from the seabed could be maintained only in calm waters. Imagery from rough seas was not possible using this system.

To monitor the sled flight over the seafloor during each transect an *ad hoc* software was created and all the information from each picture (UTC time, latitude, longitude, bottom depth, pressure, temperature, salinity, sled altitude, etc.) were compiled in the same database to allow for posterior analysis. The technical characteristics in combination with the image rectification and scaling processes applied to each picture (Fig. 3) defined the photogrammetric sled as a direct, quantitative sampling system.

The visual transect of the Cantabrian Sea outer shelf had a NW to SE orientation extending between 43°38.4′N to 43°37.1′N located on grounds between depths of 140–156 m (Fig. 4). From backscatter data, the values of reflectivity in the area studied were observed to be high, between −0.26 and −0.38 dB, which indicated thin sediment cover. From box-corer data, the sediments of the Cantabrian Sea shelf site were predominantly very fine sands with 8.5% organic matter (Serrano et al., 2006). Fauna inhabiting sedimentary grounds in the nearby area have been described as an outer shelf community in several studies (Olaso, 1990; Sánchez, 1993; Sánchez and Serrano, 2003), with different assemblages as a consequence of granulometric differences (Serrano et al., 2006).

Le Danois Bank is a marginal shelf located in the Cantabrian Sea at 5°W longitude and 44°N latitude (Le Danois, 1948), and is locally known as the "El Cachucho" fishing ground. The visual transect of Le Danois Bank was from 4°55.5′W to 4°55.1′W in a SW–NE direction, very close to the steepest northern slope, with a depth range from 546 to 570 m (Fig. 8). In general, this area had a medium backscatter level of between −0.12 and −0.20 dB, and

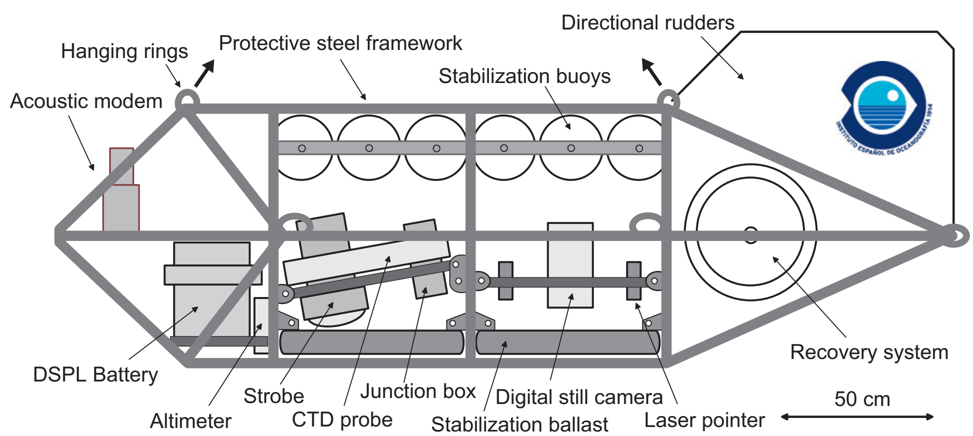

Fig. 2. Diagrammatic side-view of the TFS-2 photogrammetric sled showing the location of its main technical components.

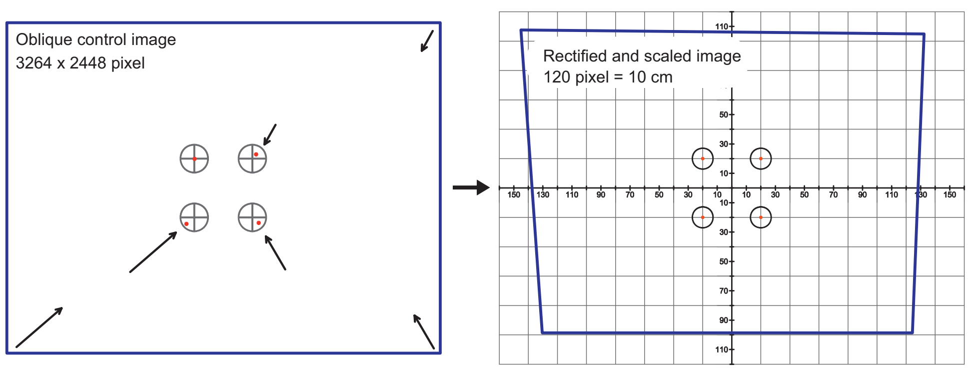

Fig. 3. Simplified scheme of image rectification and scaling processes. The coordinates estimated were used for resampling, surface calculations and for sizing species.

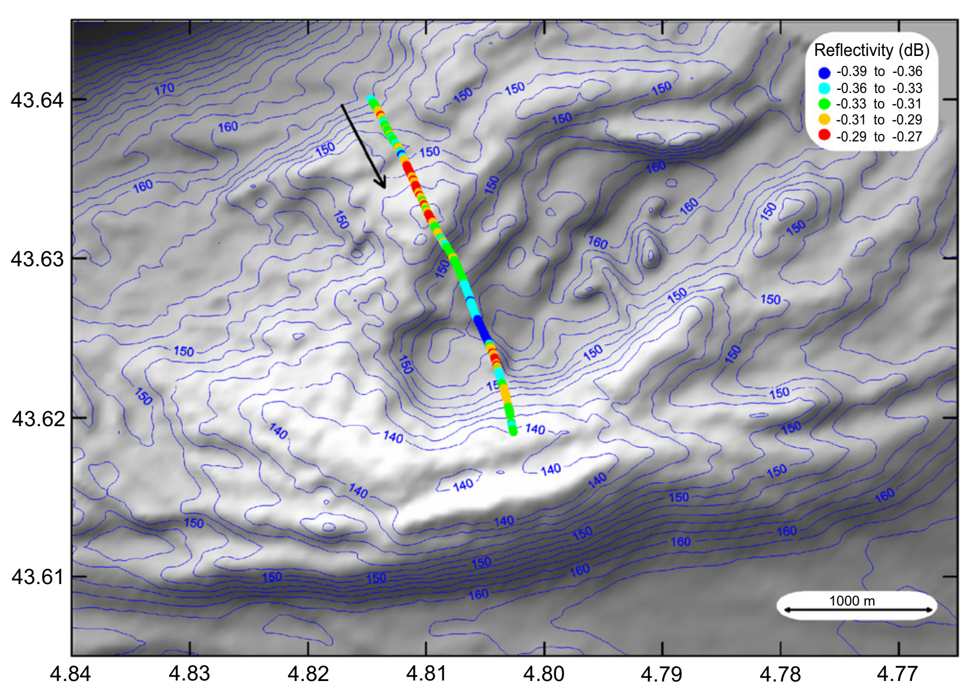

Fig. 4. Photogrammetric sled transect location on the Cantabrian Sea outer shelf. Depth (metre) and reflectivity (decibels) data were from multibeam backscatter.

was characterized by rocky bottoms with very scarce coverage of medium and fine sands, and 3.2% organic matter. The community that inhabits this area was described previously using a bottom trawl sampler as a "*Callogorgia-Chimaera* community" (Sánchez et al., 2008).

2.2. Data analysis

The geometrical location of the four laser dots in the centre of the field of view in each picture was used to correct the perspective (ground inclination in relation to picture plane) using photogrammetric techniques (Wolf, 1983; Kraus, 1993). The coordinates obtained using this method (image calibration and scaling) were used to resample each picture, resulting in rectified image pixel sizes representative of a specified distance over the ground (Fig. 3). The second step involved an estimation of the dimensions (surface, size or length) of the substrates or individual organisms on the seabed. Abiotic and biotic characteristics appeared in various combinations and it was important first to describe each of these separately in order to compile a comprehensive list of all characteristics seen on each photo. Such a classification scheme, which used various sets of data as layers in subsequent analyses, allowed an assessment of the relationships across several features at various levels of spatial resolution. Three main layers were defined for this analysis: substrate type (layer 1); species abundance (layer 2) and external features (layer 3). Substrates were used strictly from a geological point of view and only to describe the different geological and sedimentological characteristics of the seafloor (sand, mud, rocky outcrops, patchy sand and rock, sediment with current ripples, etc.). Layer 2 was composed of the density of different species and their size. Finally, layer 3 consisted of a pool of external features deposited on the seafloor, mainly anthropogenic impacts (lost gillnets, longlines, trawl damage, various types of rubbish, etc.).

To investigate the habitat–species relationships the environmental characteristics obtained using other instruments, such as the CTD probe on the sled (water pressure, temperature and salinity) and hull-mounted multibeam echosounders (bathymetry and backscatter), were included in the analysis to detect their effects on habitat and community spatial distribution. The backscatter data were acquired simultaneously with the bathymetric data derived from a Simrad EM-300 multibeam echosounder, using software tools for processing data and obtaining a reflectivity mosaic with a 1 m pixel resolution. The values of seafloor reflectivity (expressed in decibels −dB) were an indicator of the sediment coverage thickness and substrate hardness, and provided sufficient basis for first-order seafloor classification based on the sediment lithology (Beyer et al., 2007). In addition, locations for surface sampling could be determined based on a backscatter map. To groundtruth the characteristics of sedimentary substrates (particle size and organic matter content) information was used from samples collected using a box-corer at the same locations from where the transects were taken (Serrano et al., 2006; Sánchez et al., 2008). Pictures from the photogrammetric sled, bathymetry data, sedimentary samples and the backscatter were integrated in order to describe geological aspects of the habitat.

During the image analysis, fish and invertebrates were recorded and identified to the lowest possible taxonomic level. The minimum size for the reliable identification of species when the distance of the sledge was approximately 2–4 m above the seafloor was approximately 10 mm (*Caryophyllia*, *Hymedesmia*, etc.), although reliable identification of individuals from larger taxa, such as sponges, required a laboratory microscope study. However, in many cases, individuals of some taxonomically difficult groups, such as sponges, sea-anemones, or bryozoans are often required to be identified at a relatively coarse spatial resolution, by truthing of the photographic material with direct sampling. An additional problem was the identification of several groups which needed direct examination of the specimen, such as hermit crabs (*Pagurus alatus*, *P. excavatus*, etc.) hidden in mollusc shells (*Colus*, etc.), echinoderms, polychaetes, etc. Small-sized species (<10 mm) that appeared with greater abundance and typified some of the biocoenosis (such as brachiopod grounds, *Gryphus vitreus*, and bivalve molluscs, *Limopsis aurita* on the Le Danois Bank; Sánchez et al., 2008) were not quantified in the photographic analysis due to their small size and high density. Only those species that were clearly identifiable at a minimum level of genera were considered in the analysis.

Species densities (number by hectare) vs. substrate type and standard deviations were calculated by dividing the number of individuals by the area of each substrate in the visual transect. 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). The set of environmental variables used in RDA calculations comprised depth, temperature, salinity, seafloor sediment lithology and reflectivity. The statistical significance of the direct method of ordination was obtained by the Monte-Carlo test using 999 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.

3. Results

In both visual transects the vessel drifted (subject to prevailing currents and winds), and so the mean speed and distance of each transect was different (Table 1). The optimal working height over the bottom for obtaining pictures valid for the analysis, i.e. those in which the four laser dots and species could be distinguished, was estimated at between 2 and 4 m. This varied depending on water clarity, so the mean height of the sled over the bottom for valid pictures was greater in clearer waters, such as occurred on the Le Danois Bank, where the maximum distance over the bottom at which the laser points could be distinguished was 8.3 m (area covered by the image 18.2 m^2). Working at the maximum operative height minimized the risk of impact with the bottom but prevented the identification of smaller species. In general, and in both areas, the number of species was low and the most abundant taxa were corals and sponges. From a total of 23 observed taxa in area 1 and 24 observed taxa in area 2, 13 and 16 were classified to species level, respectively.

3.1. Cantabrian Sea shelf transect

3.1.1. Habitat characterization

The images obtained showed that the study area was configured as a rocky seafloor with low sedimentary coverage. The transect, in a SSE direction, began to slope upwards in association with the head of the Lastres Canyon and reached a small flat area (144 m water depth). Next, the seafloor in this area was cut by a depression running in a NE–SW direction with a relief of 15 m. This basin had an elongated shape with its base at a depth of 155–165 m (Fig. 4). Seafloor reflectivity showed greater acoustic absorption in the upper flat area and was particularly less in the basin where the lowest backscatter value occurred. The presence of strong backscatter (−0.26 dB) at the slope in the topographically depressed area, indicated the presence of active seafloor currents which may have been guiding coarse material towards the depression where reflectivity values were lower (−0.36 dB). The greater hardness of the ground observed in slope areas was due to a lesser accumulation of sediments (Fig. 5). The seafloor in this area was classified into five prevailing substrate types from sands to rock outcrops (Table 1). Over half of the surface sampled (56.2%) appeared to be covered with a thin layer of fine sand, which showed abundant bioturbations (tracks, holes and burrows) and an absence of ripple-marks on the seabed. Certain areas (17%) were covered with mixed sediments of varying granulometry (medium and coarse sands, gravel, shells, etc). Owing to the high structural complexity of the seafloor and the scarce sedimentary coverage, there was a high percentage of mixed bottoms, among which were both types of sediments and rock outcrops. The rocky areas without sedimentary coverage appeared dispersed and associated with high relief outcrops and patchy high backscatter. The spatial distribution of these five substrates was extremely complex and patchy but, in general terms, the areas with high sediment coverage occurred at the start of the transect (canyon head) and in the basin (Fig. 5). These complex seafloor characteristics had important consequences for the results since the presence of sessile species could only be detected due to the small-scale spatial resolution of this type of sampling.

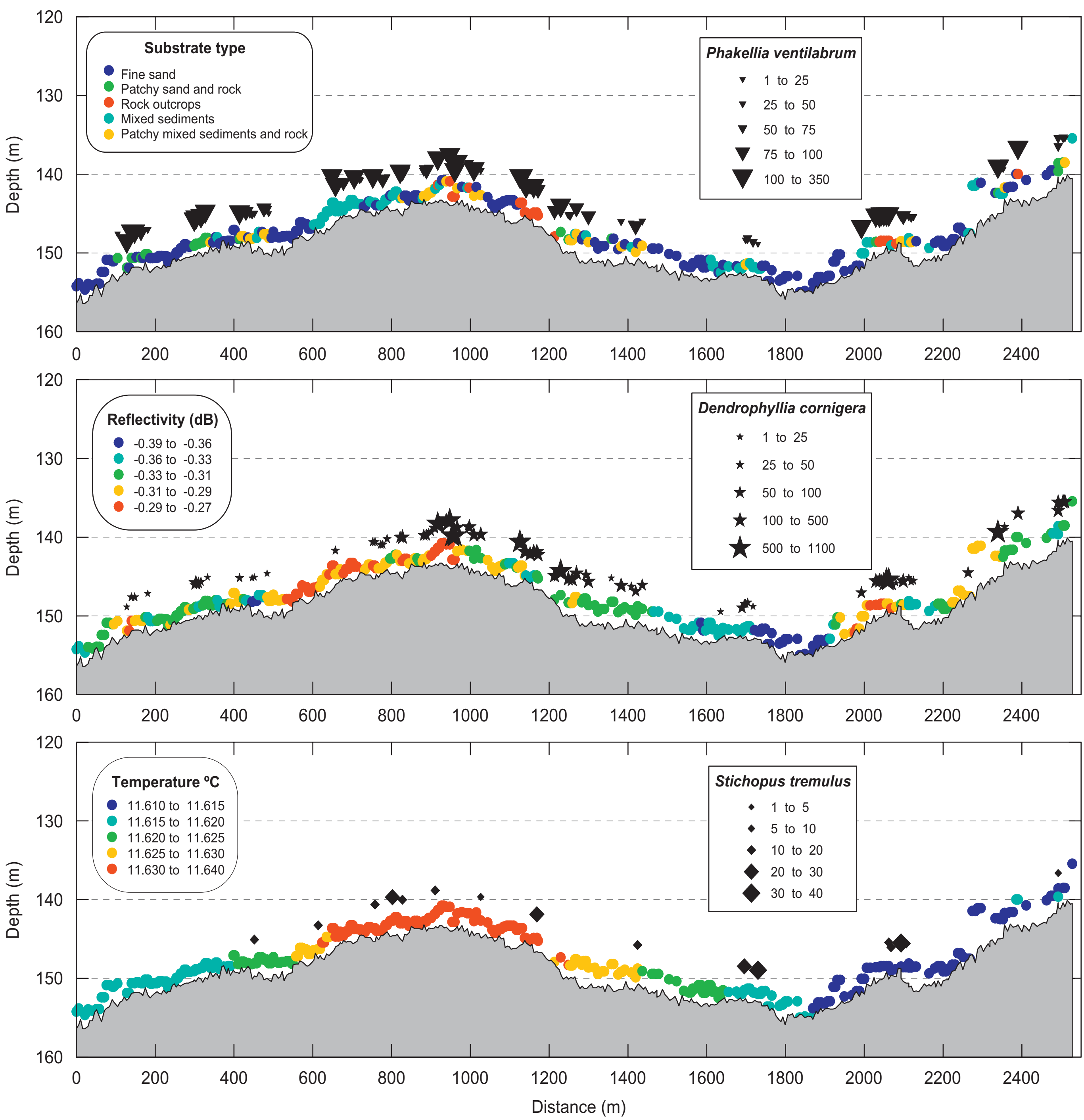

Fig. 5. Bottom depths (m), ground substrate types and species density (number × 100 m^2) at a microscale spatial distribution for the Cantabrian Sea shelf transect.

3.1.2. Habitat–species associations

The most abundant species on fine sandy grounds were the sea pen *Funiculina quadrangularis* (77 specimens/ha) and sea urchins *Echinus acutus* and *Spatangus purpureus*, together with some flat fishes (*Arnoglossus* sp., *Lepidorhombus whiffiagonis* and *Microchirus variegatus*). In the areas covered by mixed sediments of varying granulometry, the previously described species appeared together with some other sessile organisms (*Parazoanthus*, *Phakellia*) attached to the elements of the larger facies, such as shell remains and cobbles. In these mixed sediments, the sea cucumber (*Stichopus tremulus*) was particularly abundant with densities close to 230 specimens/ha. On the seafloors where rocky outcrops abounded to a greater or lesser extent, with scarce or null sedimentary coverage, a typical community appeared, made up of yellow coral *Dendrophyllia cornigera* and the cup sponge *Phakellia ventilabrum*, which strongly coincided in the same places (Fig. 5). The densities of these two species could be very high in areas where there were rocky outcrops, and they were usually accompanied by the gorgonian coral *Acanthogorgia* sp.

Fig. 6 shows the habitat preferences of species identified. Sessile species showed a clear preference for rocky outcrops or mixed bottoms of sand and rock. It is noteworthy that the yellow coral clearly dominated over the sponge in rocky areas without nearby sediments, whereas *Phakellia* showed greater tolerance of the presence of sediment. The sea cucumber (*Stichopus tremulus*), mean length 32.3 cm (Table 2), was observed to be a eurioic

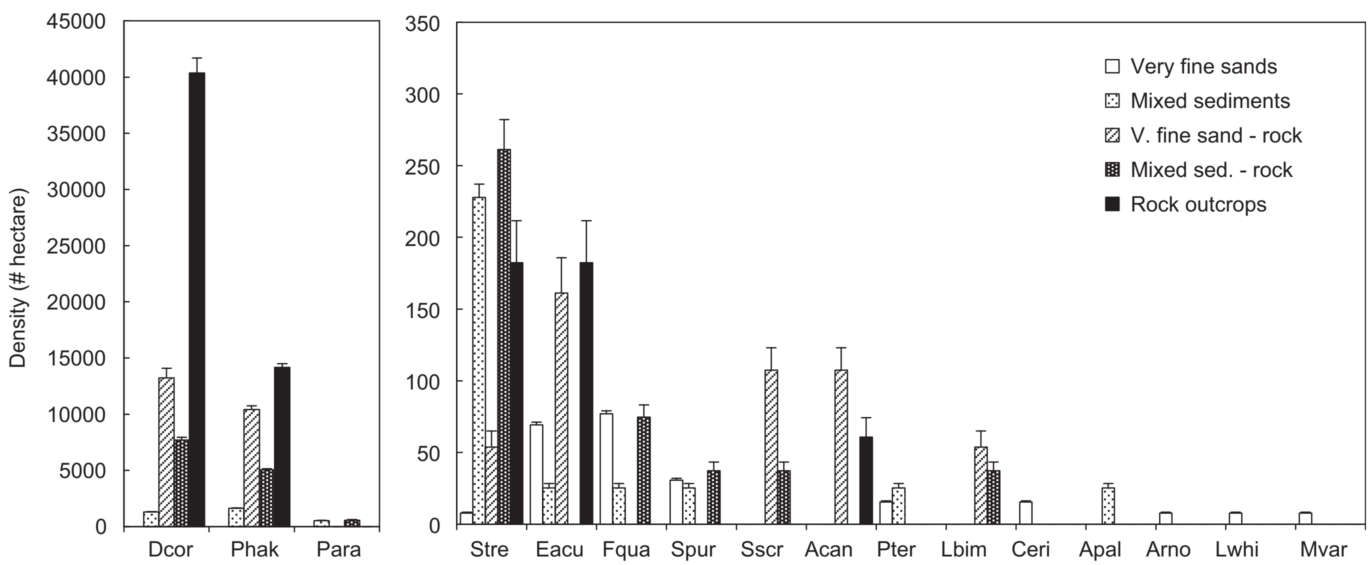

Fig. 6. Species mean densities (number/hectare) by substrate type shown with their standard deviation (SD) for the Cantabrian shelf transect. Species codes are in Table 2.

Table 2
Species codes, mean densities (number/hectare) and mean size (cm) shown with their standard deviation (SD) by study area.

Cantabrian Sea shelf					Le Danois Bank				
Code	Species	Density	SD	Mean size	Code	Species	Density	SD	Mean size
Apal	*Acantholabrus palloni*	4.3	0.2	15.72	Bdec	*Beryx decadactylus*	38.3	1.1	26.8 ± 2.8
Arno	*Arnoglossus* sp.	4.3	0.2	16.27	Hdac	*Helicolenus dactylopterus*	6.4	0.5	17.4
Lbim	*Labrus bimaculatus*	8.6	0.3	14.2 ± 5.2	Skau	*Synaphobranchus kaupi*	31.9	1.0	23.4 ± 3.7
Lwhi	*Lepidorhombus whiffiagonis*	4.3	0.2	23.6	Muni	*Munida* sp.	82.9	2.1	
Mvar	*Microchirus variegatus*	4.3	0.2	13.9	Bmar	*Bathynectes maravigna*	12.8	0.6	9.7 ± 5.3
Sscr	*Scorpaena scrofa*	13.0	0.4	49.8 ± 4.6	Lcel	*Leptometra celtica*	12.8	1.0	
Eacu	*Echinus acutus*	69.2	1.1	9.6 ± 0.4	Phor	*Phormosoma placenta*	102.1	1.9	11.4 ± 1.9
Stre	*Stichopus tremulus*	90.8	1.3	32.3 ± 1.0	Pora	*Porania* sp.	31.9	1.2	11.4 ± 1.7
Spur	*Spatangus purpureus*	25.9	0.6	10.0 ± 0.5	Sros	*Stichastrella rosea*	51.0	1.3	7.8 ± 4.4
Fqua	*Funiculina quadrangularis*	56.2	1.0	22.1 ± 2.5	Stre	*Stichopus tremulus*	19.1	0.8	28.4 ± 12.8
Phak	*Phakellia ventilabrum*	2706.4	17.6	7.6 ± 0.2	Pelt	*Peltaster placenta*	19.1	0.8	7.8 ± 1.1
Dcor	*Dendrophyllia cornigera*	5045.3	46.3	7.4 ± 0.2	Scle	*Anthomastus grandiflorus*	25.5	1.1	
Ceri	*Cerianthus* sp.	8.6	0.3		Csmi	*Caryophyllia smithii*	2054.5	17.3	2.2 ± 0.8
Para	*Parazoanthus axinellae*	160.0	3.5		Cver	*Callogorgia verticillata*	82.9	1.8	76.7 ± 32.6
Acan	*Acanthogorgia* sp.	13.0	0.4		Hexa	Hexactinellid sponge	274.4	4.0	30.2 ± 16.2
Pter	*Pteroides griseus*	13.0	0.4		Aset	*Asconema setubalense*	31.9	1.0	14.6 ± 6.0
					Pach	*Pachastrella monilifera*	153.1	3.3	22.9 ± 10.6
					Prob	*Phakellia robusta*	102.1	2.4	27.2 ± 6.2
					Hyme	*Hymedesmia paupertas*	567.9	7.0	
					Aply	*Aplysilla sulfurea*	950.7	12.1	
					Pcon	*Paratimea constellata*	76.6	3.3	
					Ceri	*Cerianthus* sp.	63.8	1.7	
	Species richness	16				Species richness	22		

species, capable of colonizing different habitat types due to its mobility. At a lesser extent, the urchin *Echinus acutus* also appeared in all habitats (except mixed sediments-rock), but preferred rocky outcrops. On the contrary, other species absent on rocky outcrops predominated in mixed sand-rock (mainly roundfish such as *Scorpaena scroffa*, *Labrus bimaculatus*, *Acantholabrus palloni*) or in sand habitats (mainly flatfish such as *Arnoglossus* sp., *Lepidorhombus whiffiagonis* and *Microchirus variegatus*).

Using the set of nine environmental variables with multivariate ordination of transect data, the first two axes of the RDA plot explained a high value of variance (99.9%) for the species–environment relationship and 57.4% for the species data. The Monte Carlo test indicated that all canonical axes together ($p = 0.001$) were significant. The RDA ordination plots showed that the first discriminatory factor (axis 1) was strongly correlated with seafloor characteristics, negatively correlated with sedimentary areas (sand) and positively with rocky areas and, consequently, with seafloor reflectivity (Fig. 7). Hydrographical variables showed a higher correlation with axis 2 due to the strong relationships between depth and the other two variables: the second discriminatory factor (axis 2) was negatively correlated with temperature and salinity, and positively with depth.

Presence of rock in this area was a discriminating factor, but there was low discrimination between sandy and mixed sediment habitats. In other words, the fauna from rock, patchy sand and rock, and patchy mixed sediments and rock were clearly separated, whereas sand and mixed sediment samples were not separated by the analysis. These differences were a consequence of the specificity of species which inhabited each environment. In the triplot (Fig. 7), most species were located near the centroid and showed a low preference for one of the sedimentary habitats. On the contrary, rocky habitats were inhabited by some specialist species. Two sessile species showed higher discrimination for these environments: the sponge *Phakellia ventilabrum* and the coral *Dendrophyllia cornigera*. Autoecological conclusions of both species can be extracted from this analysis. The coral showed a clear preference for rocky outcrops without sediments, whereas the sponge was related to rocky habitats located close to muddy-sandy habitats. However, both species were associated to the rocky or mixed rock-sand communities where they coexisted with a higher or lower predomination of one or the other (Fig. 7).

According to the hierarchical classification of habitats proposed by EUNIS (Davies et al., 2004), three habitats were identified: A4.12—sponge communities on circalittoral rock (14.5% coverage), A5.35—circalittoral sandy mud (56.8%) and A5.44—circalittoral mixed sediments (28.7%). However, these classifications were relatively general and did not really identify the particularities of the habitats and biocoenosis observed in visual sampling.

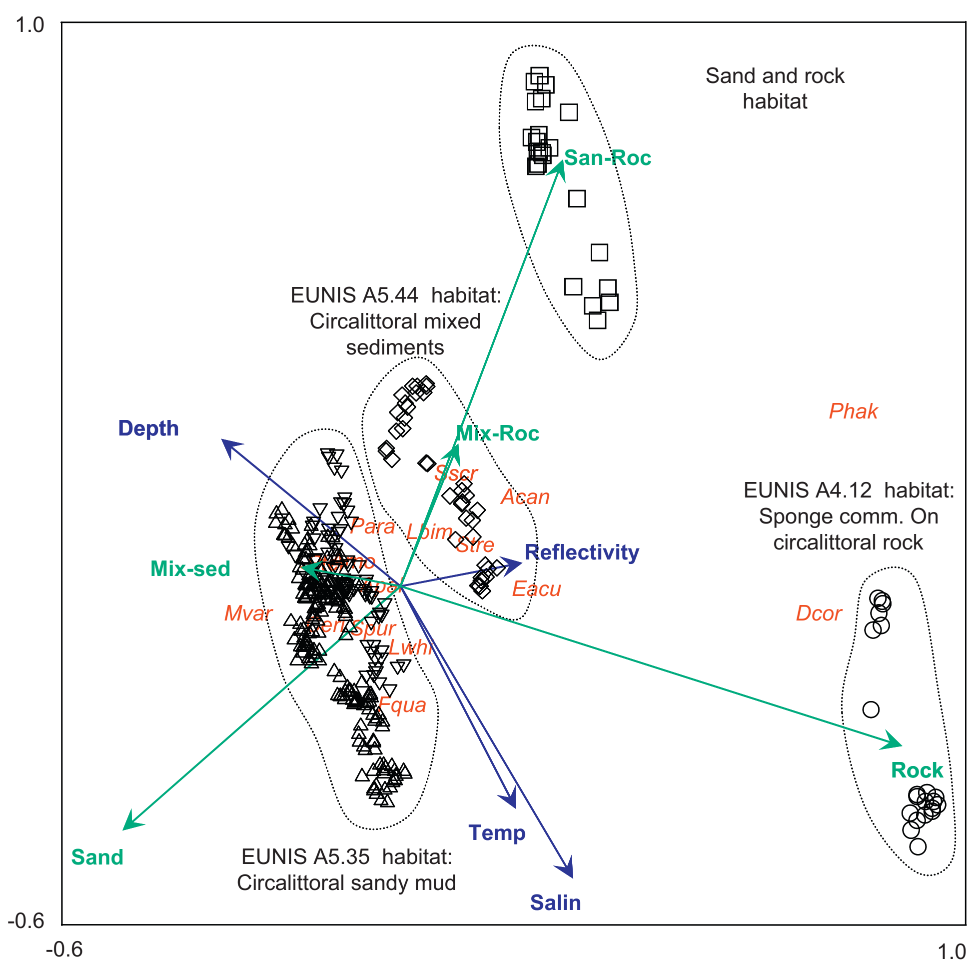

Fig. 7. Cantabrian Sea shelf RDA ordination triplot of axis 1 and 2 with environmental variable contributions (arrows), photographic samples (symbols), and species (italics). Photographic sample groups identify the different habitats.

3.2. Le Danois Bank transect

3.2.1. Habitat characterization

The path of the transect did not have a constant direction, since it was altered by a local current that carried the vessel northwards to a deeper area of the slope (Fig. 8). This had consequences for sampling since the instability of the sled prevented a suitable height from being maintained, which was necessary so that the laser points and species could be seen correctly, thus reducing the number of valid images (Table 1). Principally, as in the continental shelf transect, the seafloor observed in this area showed very low sedimentary coverage. The transect, in a SW–NE direction, began to slope downwards and the structure of the seafloor was less complex than that of the shelf area. The north side of Le Danois Bank in this area was from a depth range 525–600 m and the transect was located at a depth of approximately 546–570 m (Fig. 9). In general, the seabed had a uniform backscatter as imaged on the echosounder backscatter imagery, and was characterized by a single type of sandy sediment that covered the bedrock to a greater or lesser extent. The backscatter level in the area varied from the highest value (−0.16) to the lowest (−0.18), with the mean values of bottom reflectivity being higher than transect 1, mainly due to the thinness of sedimentary coverage. The change in backscatter levels between both areas indicated changes in sediment properties which could have been related to down-slope currents and sediment transport. As a result, a large part of the surface observed (63.9%) was made up of mixed bottoms of sand and rock (Table 2), and a quarter of the area studied was totally covered by sand. From the analysis of box-corer samples collected during the ECOMARG surveys (Sánchez et al., 2008) the granulometric characteristics of this bottom were identified. Variability in sediment lithology was observed within the two chosen areas. The percentage of coarse sand (GCS) obtained was only 2.24%, whereas medium and fine sands (MFS) reached up to 79.37% with 18.39% silt. The organic matter content was very low (3.03%). This habitat would occupy a high percentage of the surface studied since it would include all the sandy bottoms plus a high proportion of patchy sand and rock bottoms.

3.2.2. Habitat–species associations

The general pattern was similar to that found on the Cantabrian shelf with cnidarians and sponges characterizing rocky habitats and patchy rock and sand habitats. Nevertheless, in contrast to the Cantabrian shelf these species were always more abundant on rock than on patchy sand and rock. Table 2 shows the mean densities and mean sizes of the species visualized in the transect. The two most abundant species showed the same pattern, with the maximum presence on rock, intermediate presence on patchy sand and rock substrate, and absent from exclusively sandy habitats. These species were the coral *Caryophyllia smithii* and the encrusting sponge *Aplysilla sulfurea*. The other most abundant species were sponges (*Hymedesmia paupertas*, unidentified Hexactinellids and *Pachastrella monilifera*).

Fig. 9 shows the greater presence of the coral *Caryophyllia smithii* in rocky and steeper areas, partly coinciding with the distribution (scarcer) of the gorgonian *Callogorgia verticillata*. The cup sponge (*Asconema setubalense*) was only present in the last part of the visual transect. In contrast to sampling from the Cantabrian Sea continental shelf, the habitat with the greatest density of identified species in this deep ecosystem was the rocky habitat (Fig. 10). Larger species found in the area were gorgonians (*C. verticillata*), which grew up to 122 cm in width, and hexactinellid sponges (Table 2). Some species seemed to prefer habitats with sediment coverage, and were absent on rocky outcrops, such as benthophagous fishes *Beryx decadactylus*, *Synaphobranchus kaupi*, and *Helicolenus dactylopterus*, the deposit-feeder *Stichopus tremulus*, and the sponge *Paratimea constellata*. On the other hand, the crinoid *Leptometra celtica* only appeared in rocky habitats. The only species present in both study areas was

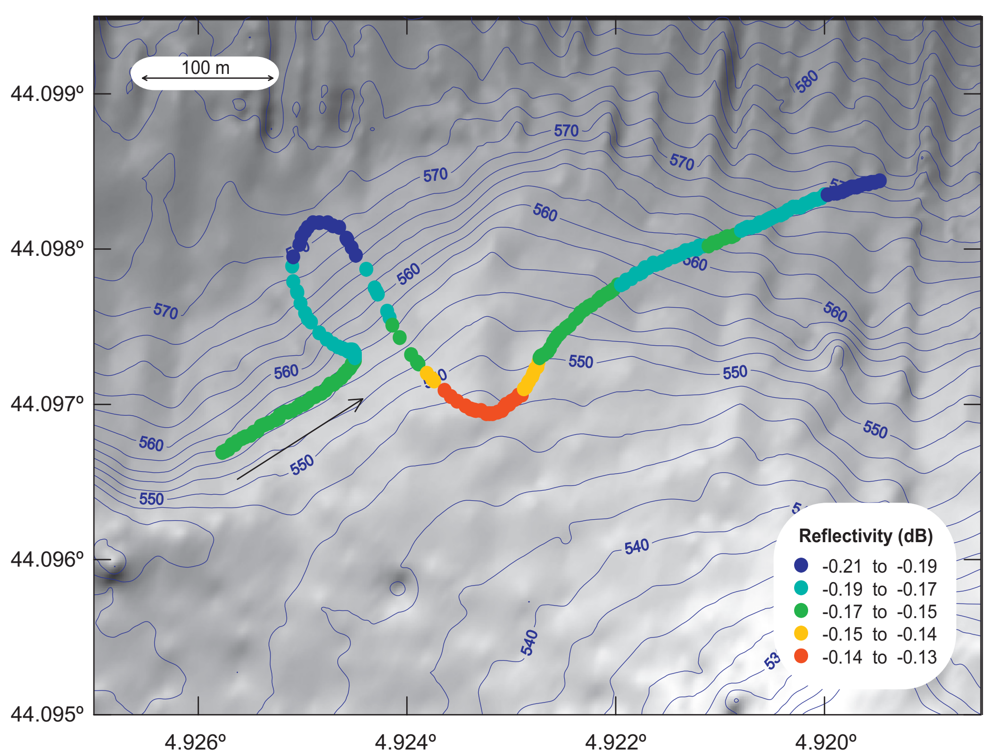

Fig. 8. Photogrammetric sled transect location on the Le Danois Bank. Depth (metre) and reflectivity (decibels) data were from multibeam backscatter.

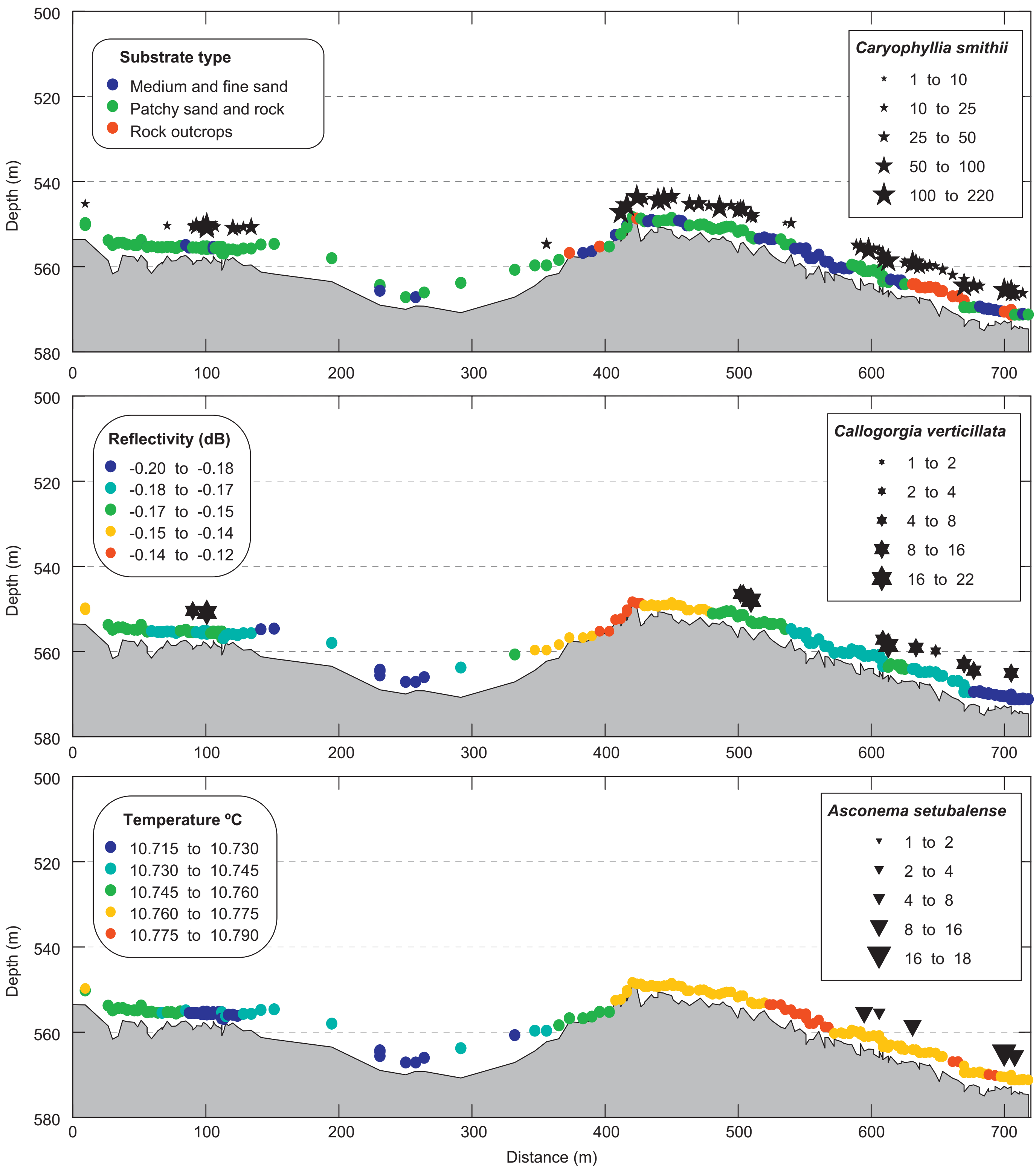

Fig. 9. Bottom depths (m), ground substrate types and species density (number*100 m^2) at a microscale spatial distribution for the Le Danois Bank transect.

the sea cucumber *Stichopus tremulus*, although they seemed to be smaller-deeper (Table 2).

Using the set of six environmental variables with multivariate ordination of transect data, the first two axes of the RDA plot explained a high proportion of the variance (95.4%) of the species–environment relationship and 19.1% of the species data. The Monte Carlo test indicated that all canonical axes together ($p = 0.001$) were significant. The RDA ordination plots showed that the first discriminatory factor (axis 1) was strongly correlated with seafloor lithology: positively correlated with the sandy areas and negatively with the rocky areas (Fig. 11). The second discriminatory factor (axis 2) was negatively correlated with

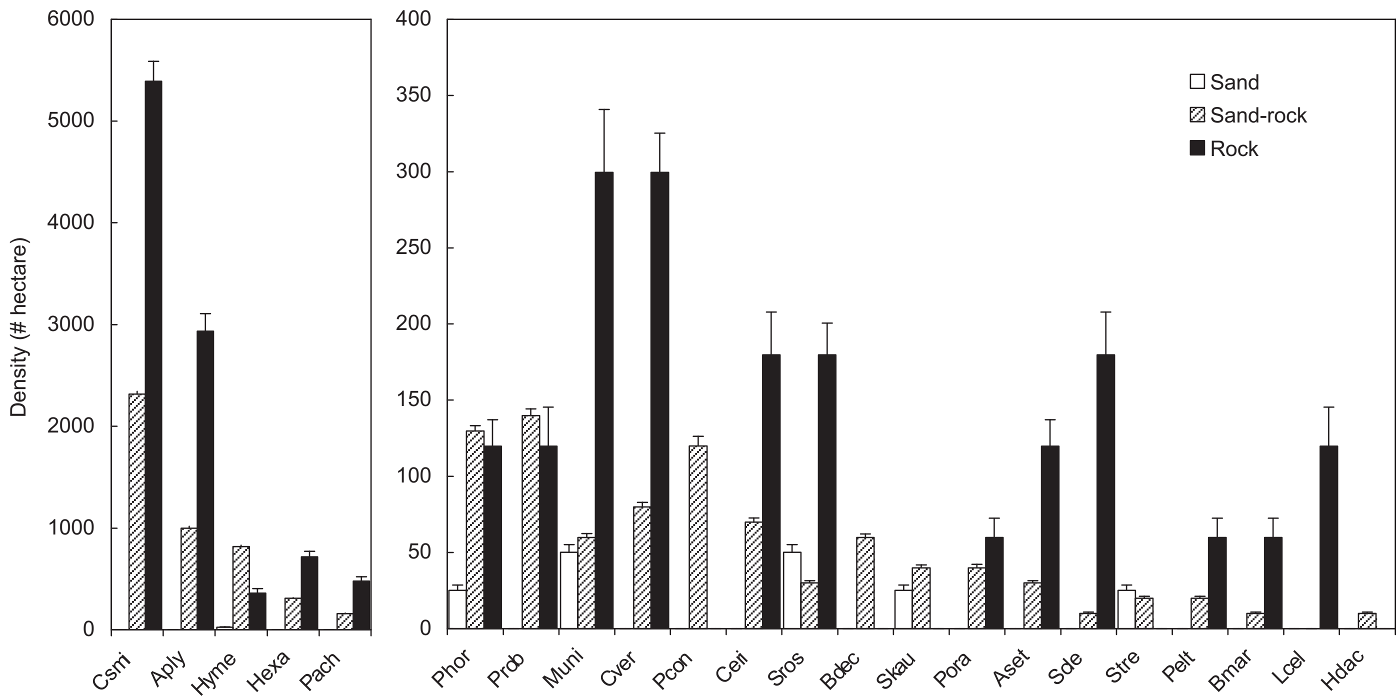

Fig. 10. Species mean densities (number/hectare) by substrate type shown with their standard deviation (SD) on the Le Danois Bank transect.

depth and salinity and positively with reflectivity, since highest reflectivity correspond to the shallower images of the transect (Fig. 8). Species ordination showed a concentration of species near the centroid but in the negative segment of axis 1. This was because only six species were present in the sandy habitat photographs and all but two of them were more abundant on rock or patchy sand and rock. The two most abundant species on sand (Table 2) were the holothurian *Stichopus tremulus* and the fish *Synaphobranchus kaupi*, both ubiquitous, which are located in Fig. 11 to the left of the species ordination. On the other extreme of the gradient, *C. smithii* and *A. sulfurea* were the species that tended most strongly toward rock habitats. The axis 2 (depth-salinity) gradient produced less species discrimination, with *Munida* spp, *A. sulfurea*, and the crinoid *Leptometra celtica* having higher affinity in shallower photographs, and *C. smithii*, the encrusting sponge *H. paupertas* and the cup sponge *Asconema setubalense* in deeper ones.

The community that lived in the sandy sediments of the Le Danois Bank was typified by the brachiopod *Gryphus vitreus* and the mollusc *Limopsis aurita*, which were visible in the images but uncountable due to their density and small size. This community typified the habitat according to the EUNIS classification, which was named A6.31—communities of bathyal detritic sands with [*Gryphus vitreus*]. Using this system of classification it can only be stated that the other two habitats observed would be included in the generically named A6.11—deep-sea bedrock, which indicates the absence of a more exact classification for the deep habitats in this area according to the EUNIS criteria.

Fig. 12 shows a characteristic view of the habitats and communities of the Le Danois Bank and their photogrammetric interpretation used to generate the data base sets. This image corresponds to a sand-rock boundary, where there is expected to be a change in hydrographical and topographical characteristics. Zooplankton feeders, such as the gorgonian *Callogorgia verticillata*, probably existed here, with the fan oriented to predominant currents in order to take trophic advantage of this microenvironment.

4. Discussion

4.1. Methodology

The methodology used in this study is a valuable tool to locate, characterize and provide high resolution information on habitat and macrobenthic species distribution in hard ground ecosystems. Also, the photogrammetric sled has advantages over manned submersibles and ROVs in that it is not subject to the same prohibitive costs. The high resolution of the still images is more valuable for this visual classification than video records since they include 20 times more information (one frame of a standard PAL video only has 0.4 Mpixels). In general terms, the zenithal view point is adequate to identify invertebrates (echinoderms, crabs, sponges, corals, etc.), the target species of this method, and flatfishes, although it is less adequate for roundfish. Also, species sizing from the zenithal view is possible for fish (total length), crabs (carapace width) or echinoderms (diameter) but it is impossible to determine the height of some sessile organisms, such as corals or sponges, for which only their width can be estimated. As the imagery is very oblique (typical in video transects from ROVs or submersibles), each image had to be strongly rectified to allow for scale changes. However, in contrast to the subjectivity of video strip transects, the photogrammetric sled is a real quantitative sampler.

Data from photographs provided the opportunity to explore relationships between community structure and a given set of environmental variables at various levels of spatial resolution, including the micro-scale, since within each individual photo there was a linked set of values for the different environmental variables. In contrast, samples from towed sampling gears (trawls and dredges) provide information about the fauna for the area of the seabed they are towed over. It may well be that such a sample could be comprised of animals from various habitat/community types, therefore, such data cannot be used to explore small-scale distribution patterns, nor to explore habitat–species interactions at small scales, such as microtopography, local hydrological

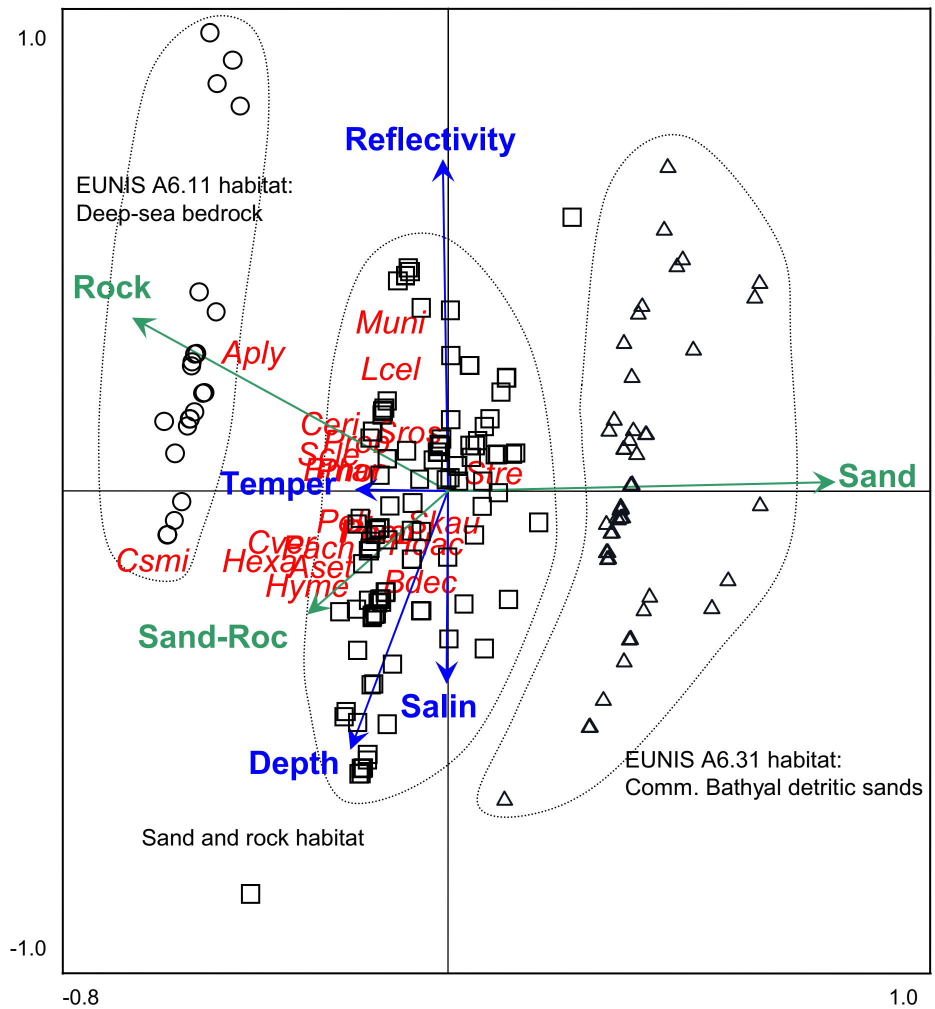

Fig. 11. Le Danois bank RDA ordination triplot of axis 1 and 2 with environmental variable contributions (arrows), photographic samples (symbols) and species (italics). Photographic sample groups identify the different habitats.

features, local changes in sediment coverage, although those towed samples are useful to aid identification of the difficult species seen in photos. The effect of microtopography and other small-scale features on species distribution has been widely described (Barros et al., 2004; Felley et al., 2008; Uiblein et al., 2003).

Another strength of the photogrammetric sledge is its 'stealthiness' (no engines or propellers) and the fact that it does not require the strong and constant illumination needed by video. The strobe flash is instantaneous and hardly detectable at a distance. These two factors greatly impede the estimation of the density of highly mobile species when performing visual strip transects using ROVs. There is evidence that natural and reaction behaviours of fish influence ROV visual transect counts. Trenkel et al. (2004) demonstrated that the degree of reaction to the approaching ROV varied between deepwater fish species. Whereas some benthic fish never reacted, such as spiny scorpion fish (*Trachiscorpia cristulata echinata*), nearly all cat sharks reacted after being detected. The video strip transect carried out at two light levels revealed a significant effect for other fish species (opposite effects for morid cods and cutthroat eel). The authors concluded that the study failed to allow quantification of the bias that these reactions might introduce. Nevertheless, the two transects analysed in this study show the scarce presence of mobile species, particularly fishes. In spite of this, if we compare the values obtained in the area of Le Danois Bank using an otter trawl survey (Sánchez et al., 2008), whose swept area by haul (57,461 m^2) is 36.7 greater than the visual transect of this study, this fishing gear gives rise to a clear underestimate of some fish in relation to the visual transect. The density estimates of blue mouth (*Helicolenus dactylopterus*) from the otter trawl is just a twentieth (0.34 specimens/ha) of the visual transect estimates (6.38 specimens/ha, Table 2). For the cutthroat eel (*Synaphobranchus kaupi*), the bottom trawl abundance index is 4.33 times lower than that from the still image visual transect. This means that although the visual transect with photographs is more efficient (less gear catchability bias) it probably demands a greater surface with images than that covered in this study in order to achieve the minimum size of the sample for the less abundant species to be correctly quantified. For example, assuming that the density of the forkbeard (*Phycis blennoides*) in the Le Danois area from a bottom trawl survey (Sánchez et al., 2008) is 4.77 specimens/ha, it is necessary to take 2450 valid pictures in order to get just one positive contact with a fish. This would imply a considerable increase in the time needed to analyse correctly the high number of images necessary to quantify the less abundant species.

To solve this problem with the minimum sampling area it is also important to increase as much as possible the distance

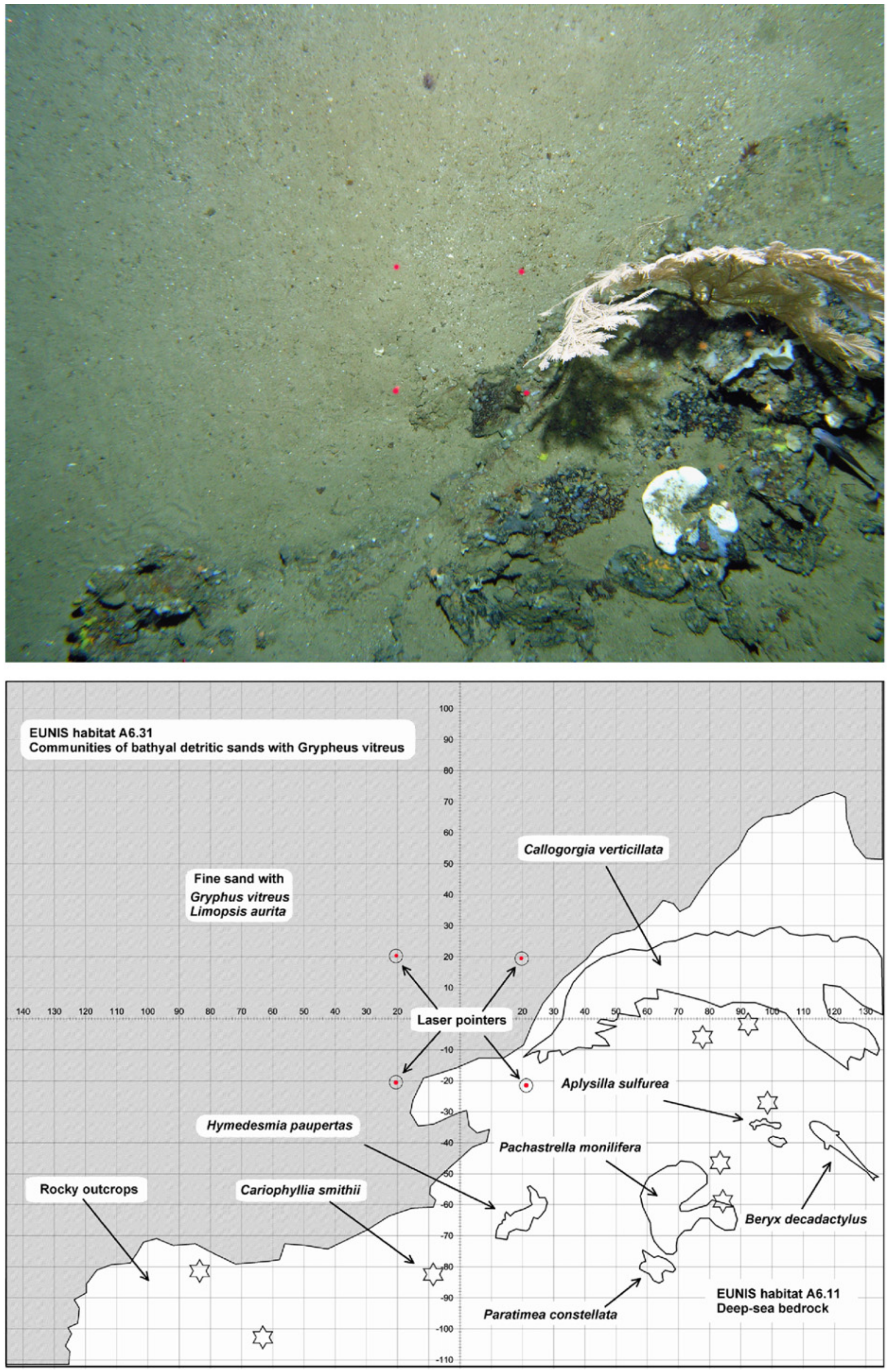

Fig. 12. Biotope characteristic and species identification on the Le Danois Bank (551 m depth). Image surface 6.11 m^2 and substrate coverage: 55.4% medium sand and 44.6% rocky outcrops. Two EUNIS habitats and eight species were identified. *Beryx* length was 28.6 cm and *Callogorgia* gorgonian width was 115.8 cm.

between the sled and the seafloor and simultaneously to improve image resolution to avoid reliability identification problems. However, this depends mainly on water clarity in the study area, if the photographs are to be really valid. In this way, the stealth capacity of the system is also increased, minimizing the evasive reaction of swimming species. In this respect, Trenkel et al. (2004) show by visual strip transect that most deepwater demersal fish live in the two metres of the water column closest to the bottom. Therefore, the operative distance of the sled (2–6 m over the bottom) seems to be more appropriate than the 80 cm above the seafloor at which a ROV usually works. The range of vertical opening of the trawl gears used in standard surveys to estimate the abundance indices of commercial species is normally between 2 and 4 m.

The optical properties of water and water quality, which are variable in space and time, limit the penetration of light into the water column. This visibility restriction results in low maximum imaging heights, thus limiting the area covered by the visual transects. The maximum viewing distance that allows clear identification and views of species in our study areas was approximately 4–6 m, resulting in a coverage of no more than 12–16 m^2 (depending on the camera focal length and image format size). Therefore, there is an evident coverage limitation for transects using still images. There are two possible options. One is to reduce the photo time interval (close to the strobe recycling time), and the other is to increase the transect length or make several transects in each area.

Water current strength is a very important environmental variable in explaining species variability. For example, the cutthroat eel is a scavenger that detects its preys by olfaction (Uiblein et al., 2002) and might therefore be more or less abundant depending on current conditions. For suspensivorous sessile species, such as corals, gorgonians and sponges, this environmental factor is the absolute determinant of their abundance distribution (e.g. Rice et al., 1990). The use of a Doppler-effect current meter (ADCP) on the hull of the vessel or placed on the sled during transects would bring about a large increase in information for explaining the distribution and density of many species.

The slope of the seabed is also important for habitat characterization and, consequently, for species distribution. This can be estimated from information coming from the multibeam echosounder (Wilson et al., 2007), but the resolution at great depths ($\pm$ 10 m) is not sufficiently fine as to be able to link it to each photograph (5 m), as occurs with reflectivity. Also, to improve precision in the exact location of the photographs over the ground, a Trackpoint Ultra Short Base Line (USBL) tracking system is useful to detect movement of the sled relative to the support ship. Future technological developments which combine automatic altitude control, high penetration lighting in the water (HMI or HID) and high resolution sonar should help to overcome these sampler difficulties. Using the detailed methodology of image rectification from photogrammetry seafloor mosaics, considerable increase and detail in the surface covered can be obtained. This technique is particularly useful for interpreting the values of reflectivity supplied by the multibeam backscatter with greater accuracy.

4.2. Habitat selection of species

In both areas, species richness was higher on hard grounds where epibenthos predominated, unlike sandy habitats where endobenthic species predominated (not visible in the photographs). On the Le Danois Bank, the highest number of species has been found on the mixed sand and rock substrates, in contrast with sandy or rocky grounds. Increase of heterogeneity favours the presence of species, and augments the trophic complexity of the area (Diehl, 1992). Therefore, on mixed bottoms soft-ground species cohabit together with hard ground species, as well as species that derive a benefit from boundary environments.

Detailed substrate and community spatial distribution based on image analyses were conducted on the hard grounds of the Le Danois Bank summit. The results showed a pattern which can be attributed to local current effects on sea-floor escarpment. The EUNIS habitat A6.31 (communities of bathyal detritic sands with *Gryphus vitreus*) was the most extended in the soft sediment of the Le Danois Bank, but the increase of the water current speed in some areas of the Le Danois summit limits the presence of sedimentary coverage and facilitates the presence of rocky outcrops. Here, live structure-forming invertebrates occurred, such as the community characterized by the gorgonians *Callogorgia verticillata*, which also includes large-sized *Geodidae* and *Hexactinellidae* sponges (*Asconema setubalense*, *Geodia megastrella*) together with the cnidarians *Caryophyllia smithii* and *Acanella arbuscula*. A clear increase of megafaunal concentration and species richness is recognized for biocoenoses where gorgonians live and sponges are rather abundant (Bradshaw et al., 2003), and probably the high presence in the study area of fish spawners in relation to the same depths of the Cantabrian Sea (Sánchez et al., 2008) is originated by their biogenic habitat.

Canonical ordination has shown the higher weight of geological features over depth, salinity or temperature. This is an expected result since changes in depth–temperature–salinity gradients are very low at the micro-scale (see standard deviation in Table 1), whereas faunal differences caused by the presence/absence of rock are very important. Differences were found between both areas. On the Cantabrian shelf, mixed sand and rock substrates seem to conform to a distinct habitat, and to a group of typical species (highest abundances of the sponge *Phakellia ventilabrum*). On the contrary, Le Danois Bank mixed sand and rock substrates respond like a transitional environment between rock and sand, but species that dwell here are more abundant in rock habitats.

Patterns are similar in both areas with cnidarians and sponges characterising rocky habitats and mixed rock and sand substrates. Nevertheless, on the Cantabrian shelf some species prefer rock outcrops and others mixed facies, whereas on the Le Danois Bank these species are always more abundant on rock than on mixed sand-rock. These inter-area differential responses of species may be a consequence of the different position in the environmental gradients for the species dwelling in them: the Cantabrian Sea is located in the middle of a depth gradient, whereas Le Danois Bank is located at an extreme (lower, for shelf species, higher, for slope species). This may mean that Le Danois species are more specialised, and show a clearer preference for rock or sand, whereas on the Cantabrian shelf several generalistic species prefer mixed facies.

Inter-species differences in habitat selection are rather informative from an autoecological point of view. Differences in the abundance on the Cantabrian shelf of two of the more abundant species, the sponge *Phakellia ventilabrum* and the coral *Dendrophyllia cornigera*, can be explained using photographic analysis. *Phakellia ventilabrum* showed a higher tolerance to the presence of sediment, in contrast to the yellow coral, *D. cornigera*, which prefers rock without nearby sand. This difference may have a trophic component, since the sponge is a suspension-feeder which gets a benefit from resuspension of deposited sediments and organic matter, whereas the yellow coral is a plankton-feeder, with polyps sensitive to high sedimentation values. *Phakellia ventilabrum* prefers a mixed rock–sand habitat where deposition processes predominate, and hence sedimentation, together with hard substrates where it settles. In contrast, *Dendrophyllia cornigera* needs a habitat where transport processes predominate, where currents provide food to the polyps.

The Le Danois Bank is an area where primary production is enhanced due to a topographic retention effect, and it is affected by strong currents (Sánchez et al., 2008), therefore, there is a clear dominance of filter-feeders (sponges) and plankton-feeders (corals, gorgonians). For these dominant sessile species food is not the limiting factor, since hard substrata where they can settle becomes the limiting factor, therefore, these species increase their abundance in relation to the surface occupied by hard substrata.

This study can therefore have an important role in determining the characteristics of the habitat at a higher scale, particularly for vulnerable ecosystems and MPAs. The use of this non-extractive methodology, which does not cause damage or alterations to benthic communities, is particularly necessary when establishing a programme of MPA monitoring using a visual transect, in order to groundtruth the image records by either incorporating information into in situ survey data, and studying the effectiveness of closed areas on the recovery of structure-forming invertebrates from disturbance, particularly bottom trawling and gillnets. Anthropogenic pressure is also identified by means of this methodology, but this issue has not been analysed in this first approach. However, some remnants of trawl codends were observed on the rocky grounds of the Cantabrian outer shelf visual transect. Also, the remains of lost gillnets and longlines on the rocky outcrops of the Le Danois Bank are worth mentioning, since they reveal a high fishery impact from both gears.

Acknowledgements

The authors are very grateful to Stefán Áki Ragnarsson for helpful comments that have substantially improved the manuscript, the geologists Araceli Muñoz (SGPM), who collaborated in providing the multibeam echosounder data analysis needed to describe transects, and to Javier Cristobo and Pilar Ríos who identified sponge species. Also, to the crew of the RV *Vizconde de Eza* for the invaluable work that made possible the use of the photogrammetric sled during the TREBOL survey. This survey was supported by the SGPM (Fisheries Secretariat of the Agriculture and Fisheries Ministry) in order to study impact on the seafloor habitats caused by trawl gears using the rock-hopper as a groundrope. In addition, we would like to thank two anonymous referees who helped to improve the paper considerably.

This study was partially funded by the Spanish Science and Technology Ministry and was included in the ECOMARG Project (REN2002-00916/MAR).

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