

Epibenthic communities of trawlable grounds of the Cantabrian Sea

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SUMMARY: Epibenthic communities of the Cantabrian shelf were sampled in October 2000 and October 2001 using a 3.5 m beam trawl. The surveys were undertaken following a pattern of stratified sampling in four transects perpendicular to the coastline and included three depth strata (30-100, 101-200, 201-400 m). The total number of species collected was 241, belonging to 9 taxa, of which the best represented were molluscs and crustaceans. Longitudinal differences in ecological indices were detected in relation to biogeographical and hydrographic patterns. Three main assemblage groups were identified using cluster analysis. The effect of environmental variables (depth, near-bottom temperature and salinity, sediment morphology, Atlantic influence) on assemblages was also identified by canonical ordination, showing a pattern of two gradients: depth/water temperature and sediment characteristics. Assemblages identified by both methods were spatially coherent. The hermit crab *Diogenes pugilator* typifies the poor fine sands of the inner shelf; fishes (*Arnoglossus laterna*, *Callynimum maculatus*, *Pomatochistus* sp.) and a hermit crab, *Anapagurus laevis*, characterise the assemblage of inner and middle shelf sediments with higher organic content, and the echinoderm *Ophiura affinis*, the fish *Lepidorhombus boschii* and Crangonidae Crustacea typify the deeper community of medium and fine sediments with intermediate levels of organic content.

Keywords: epibenthic communities, faunal assemblages, Cantabric Sea, beam trawl, canonical ordination.

RESUMEN: COMUNIDADES EPIBENTÓNICAS DE LAS PLAYAS DE ARRASTRE DEL MAR CANTÁBRICO. – Las comunidades epibentónicas del mar Cantábrico fueron muestreadas en octubre de 2000 y 2001 usando un bou de vara de 3.5 m. Las campañas se realizaron siguiendo un muestreo estratificado en 4 transectos perpendiculares a la costa, con 3 estratos batimétricos (30-100, 101-200, 201-400 m). Un total de 241 especies fueron identificadas, pertenecientes a 9 taxa, de los cuales los mejor representados fueron Moluscos y Crustáceos. Se detectaron diferencias longitudinales en los índices ecológicos, en relación a factores biogeográficos e hidrográficos. Mediante un dendrograma se identificaron 3 agrupaciones principales. El efecto de las variables ambientales (profundidad, temperatura y salinidad, morfología sedimentaria, influencia atlántica) sobre las agrupaciones fue identificado mediante análisis canónico, mostrando un patrón con 2 gradientes: profundidad/temperatura y características sedimentarias. Las agrupaciones identificadas por ambos métodos son espacialmente coherentes. El cangrejo ermitaño *Diogenes pugilator* caracteriza las arenas finas pobres de la plataforma interna; especies de peces (*Arnoglossus laterna*, *Callynimum maculatus*, *Pomatochistus* sp.) y otro ermitaño, *Anapagurus laevis*, caracterizan la agrupación de plataforma interna y media con sedimentos de alto contenido orgánico, mientras que el equinodermo *Ophiura affinis*, el pez *Lepidorhombus boschii* y crustáceos Crangonidae tipifican la comunidad de más profundidad con sedimentos finos y medios y niveles intermedios de materia orgánica.

Palabras clave: comunidades epibentónicas, agrupaciones faunísticas, bou de vara, ordenación canónica.

INTRODUCTION

The Cantabrian Sea area is located in the sub-tropical/boreal transition zone of the eastern Atlantic. Due to this location, its fauna is composed

of typical temperate water species from the south together with others of northern origin, and is therefore characterised by high biodiversity indices in comparison with adjacent areas (Olaso, 1990; Sánchez, 1993). In addition, the topographical com-

plexity and the wide range of substrates on its narrow continental shelf give rise to many different types of habitats. This environmental variability over the narrowest surface of the Cantabrian Sea shelf produces strong environmental gradients over a short distance. Previous papers have described how depth and bottom type are the main determining factors (Basford *et al.*, 1989; Olaso, 1990; Zendrera, 1990; Sánchez, 1993). At the same time, there is a longitudinal gradient because the Atlantic influence in the western area of the Cantabrian Sea is considered to diminish towards the eastern part of the Bay of Biscay.

The Cantabrian shelf is subject to strong fishing pressure affecting not only the target or commercial species, but also the structure of the ecosystem. Knowledge of the communities inhabiting this area is of great importance both for assessing possible changes in the structure of the ecosystem as a consequence of trawling and for putting into practice multispecific resource management systems requiring quantified data on all the species present in the ecosystem. New resource management tools require more detailed information on target species, and also on all the species present in the ecosystems inhabited by commercial species.

The Cantabrian shelf demersal communities have been sampled yearly since 1983 using bottom trawl surveys conducted by the Instituto Español de Oceanografía. These surveys use an otter trawl sampler (baca 44/60) with a cod end mesh of 20 mm and a horizontal opening of 18.9 m, thus giving information on demersal and benthic megafauna (Olaso, 1990; Sánchez, 1993; Sánchez *et al.*, 1995; García-Castrillo and Olaso, 1995; Sánchez and Serrano, 2003).

A new sampling experiment on epibenthic communities of the Cantabrian shelf was carried out in October 2000 and October 2001 with a beam trawl

sampler. This paper analyses the structure and composition of epibenthic communities living over the continental shelf of the Cantabrian Sea and the influence certain environmental variables have on them.

MATERIALS AND METHODS

The study area includes the Cantabrian shelf from Ribadeo (7.0°W) to Guetaria (2.2°W) between 30 and 400 m depth (Fig. 1). Four transects perpendicular to the coast (1=Ribadeo; 2=Gijón; 3= Santander; 4=Guetaria) and 3 depth strata (A=30-100 m; B=101-200; C=201-400) were determined. Each depth stratum from the 4 transects was sampled in October 2000 and October 2001, except strata 1A and 4C in 2000 due to rough seas. The total number of samples obtained was 22.

The sampler used was a beam trawl with a horizontal opening of 3.5 m, a vertical opening of 0.6 m, and a mesh size of 9 mm. The mean trawling speed was 2.5 knots, with a haul duration of 15 minutes from ground contact, monitored by a Scanmar net control system. The mean swept area was of 4099.9 m², with a standard deviation of 380.4 m².

Data were expressed in terms of number of individuals per 1000 m². For the multivariate analysis, data were log-transformed to minimise the effect of high values and satisfy data normality (Jongman *et al.*, 1987; Krebs, 1989). The decapod *Polybius henslowii* was removed from the matrices due to its semipelagic behaviour.

To determine the influence of environmental variables on epibenthic communities, temperature and salinity data were taken using a CTD Seabird 25. Sedimentary characteristics were determined in each haul, using a box-corer only in the 2001 survey, except in 2C and 4B, which could not be sampled due

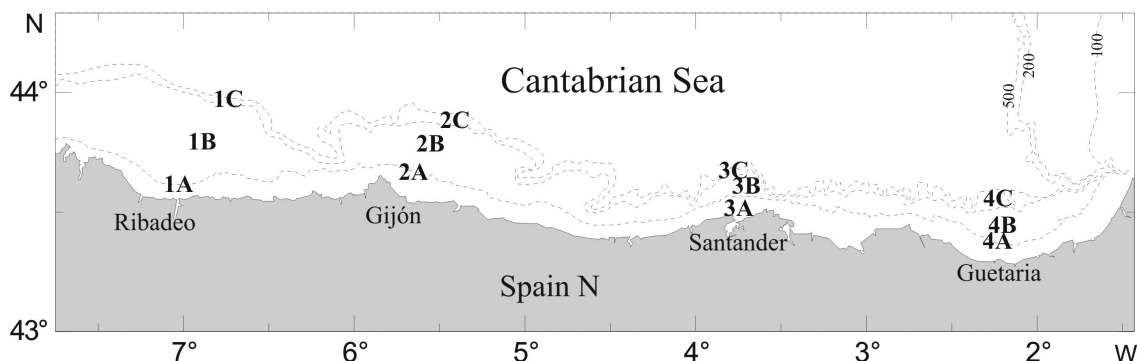


FIG. 1. – Study area and sampling stations by transect and depth strata

TABLE 1. – Characteristics of hauls performed in 2000-2001 and mean values of ecological indices ($\pm$ standard deviation) for depth strata and sector. Mean depth values between surveys (m) and sediment parameters; Q_{50} = mean particle diameter (mm); GCS= weight percentage of gravel and coarse sands ($>500 \mu\text{m}$); MFS= weight percentage of medium, fine and very fine sands ($63-500 \mu\text{m}$); Silt= weight percentage of silt ($<63 \mu\text{m}$); S_0 = sorting coefficient; %OM= weight percentage of organic matter; S= number of species by haul; N= number of individuals by 1000 m^2 ; H'= Shannon-Wiener diversity index

Stratum	Sector	Depth	Q_{50}	GCS	MFS	Silt	S_0	%OM	S	N	H'
A	1	100	0.144	1.4	81.4	17.2	1.47	1.85	$28.0 \pm *$	$75.4 \pm *$	$3.06 \pm *$
	2	96	0.165	3.3	87.7	7.7	1.27	5.00	28.5 ± 3.5	4723.6 ± 2466.2	0.59 ± 0.08
	3	41	0.200	3.1	96.2	0.1	1.29	2.20	23.5 ± 6.4	91.4 ± 53.6	2.26 ± 0.16
	4	98	0.233	28.0	39.1	20.3	4.44	5.60	62.5 ± 4.9	3257.5 ± 3890.5	1.99 ± 2.07
B	1	141	0.077	2.4	51.4	46.2	2.26	3.28	50.0 ± 2.8	178.5 ± 27.4	3.79 ± 0.05
	2	164	0.283	10.2	89.7	0.0	1.41	8.49	55.0 ± 5.7	382.6 ± 121.3	3.64 ± 1.25
	3	188	0.213	4.9	93.6	0.9	1.37	7.08	32.5 ± 9.2	81.6 ± 25.3	3.72 ± 0.59
	4	138	-	-	-	-	-	-	40.5 ± 0.7	319.1 ± 5.9	3.24 ± 0.85
C	1	300	0.177	2.2	82.4	15.4	1.37	2.80	42.5 ± 6.4	672.0 ± 442.1	2.27 ± 0.32
	2	291	-	-	-	-	-	-	39.5 ± 3.5	250.1 ± 135.3	3.91 ± 0.13
	3	262	0.274	10.6	86.4	2.0	1.49	7.01	32.5 ± 20.5	5953.9 ± 8389.4	1.99 ± 1.82
	4	354	0.095	6.0	65.7	26.4	1.66	2.20	$25.0 \pm *$	$150.5 \pm *$	$3.68 \pm *$

to rough seas. Median particle size (Q_{50}), sorting coefficient (S_0), the weight percentages of gravel and coarse sands ($>500 \mu\text{m}$), medium, fine and very fine sands ($63-500 \mu\text{m}$), and silt ($<63 \mu\text{m}$), and the weight percentage of organic matter were determined.

Similarity between samples was calculated using the Bray-Curtis index (Clarke and Warwick 1994; Field *et al.*, 1982) and the resultant dendrogram was obtained with the Group Average clustering algorithm using the PRIMER[®] package. The contribution of each species to the similarity of the cluster groups of samples was determined using the SIMPER (similarity percentages) routine.

The effect of environmental variables on communities was appreciated using canonical correspondence analysis, CCA (Jongman *et al.*, 1987; Ter Braak, 1987 and 1988; Ter Braak and Verdonschot, 1995). The abiotic variables used in the analysis were depth, near-bottom temperature, near-bottom salinity, temperature and salinity at 50 m (with the aim of identifying the effect of hydrographical anomalies), western longitude (Atlantic influence), and sediment characteristics. The representativeness of the ordination analysis is given in terms of eigenvalues of the axes and of variance explained by the biplots, and the statistical significance was calculated by the Monte Carlo test (Verdonschot and Ter Braak, 1994).

RESULTS

A total of 241 species belonging to 9 taxa were identified (see Appendix 1), of which the best repre-

sented were molluscs (59 species) and crustaceans (55). The remaining groups were fishes (44 species), Polychaeta (27), Cnidaria (22), Echinodermata (22), Porifera (9), Sipuncula (2) and Tunicata (1).

A great variability was found in the dominant species by station. In the shallowest stratum, the hermit crab *Anapagurus laevis* was the most abundant species at stations 1A and 2A, with a massive abundance in the latter; another hermit crab, *Diogenes pugilator*, was dominant at 3A, as is the gasteropod *Turritella communis* at 4A (massive abundance). The 101-200 stratum was dominated by fish species: *Arnoglossus laterna* at 1B, *Pomatochistus* sp. at 2B and *Gadiculus argenteus* at 3B and 4B. In the deepest stratum, the anthozoans *Epizoanthus papillosus* and *Cariophyllia smithii* dominated at stations 1C and 3C respectively, while the shrimp *Plesionika heterocarpus* was the most abundant species at stations 2C and 4C.

The mean values of the ecological indices related to depth and sediment parameters at each station (mean values between surveys) are shown in Table 1. Stratum B was the richest in all transects, except 4, where richness decreased with depth. As a general pattern, an increase in the number of species towards the east was observed in the shallowest stratum, and towards the west in the deepest.

The abundance (number of individuals by 1000 m^2) and diversity did not follow clear patterns, albeit for the obvious reason that great abundances correspond to low diversities. The three stations with highest abundances and lower diversity are those in which one species appeared massively. These were 2A (*A. laevis*, 90% of total abundance

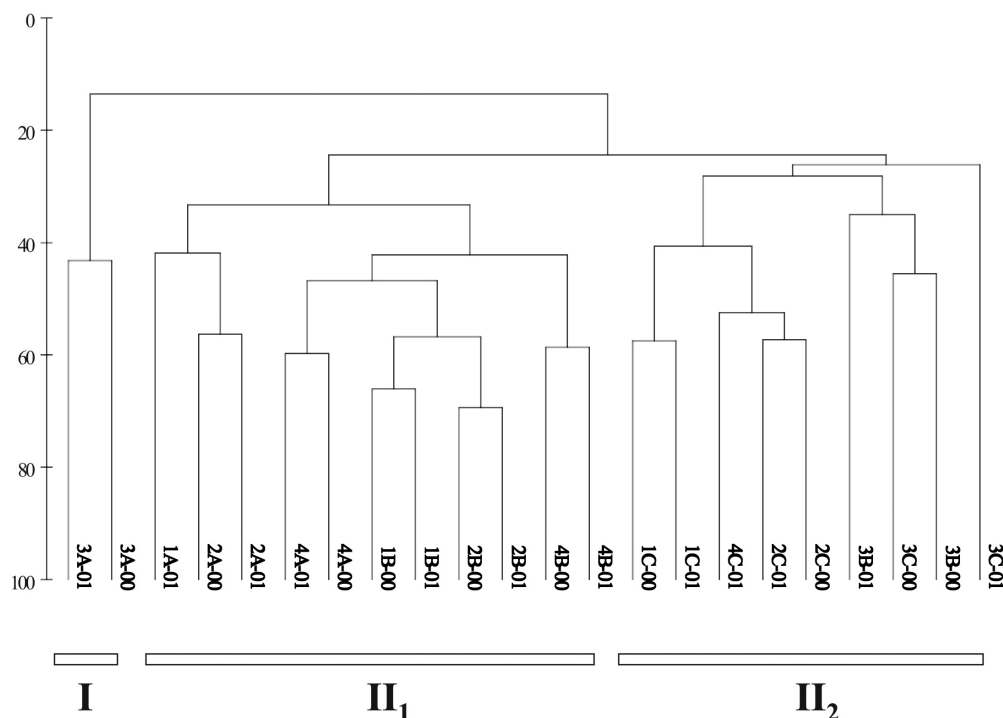


FIG. 2. – Dendrogram showing the clustering of hauls, using the Bray-Curtis similarity index

N), 4A (*T. communis*, 89% N) and 3C (*C. smithii*, 89% N). These stations showed high values of organic material and percentages of gravel and coarse sand. There were no clear connection patterns between the sedimentary variables and indices, although in some cases coincidences can be seen between high percentages of silt and richness, and high values of coarse sediments and low diversities. An interannual variability in abundance was also patent, as inferred by the high values of standard deviation, mainly at those stations which showed higher abundances. Variability was not so high in richness and diversity, with the exception of station 3C, where the huge abundance of *C. smithii* was only observed in the year 2000.

In the dendrogram of samples (Fig. 2) it can be seen how pairs of hauls from the same station are grouped in all cases, except for station 3C, in which the differentiation between samples has already been cited. This shows a maintenance of the faunistic assemblages throughout the study period, despite the differences in abundance cited in the previous point.

The clustering discriminates samples from station 3A (group I, Fig. 2), which is the shallowest. This station is typified by the two hermit crab species, *A. laevis* and *D. pugilator*, together with

TABLE 2. – SIMPER results: species typifying groups (5 more discriminant). Av.N: mean abundance in the group (ind. 1000 m⁻²); Sim(%): percentage of similarity explained; C.Sim(%): cumulative percentage of similarity(%)

	Av.N	Sim (%)	C. Sim (%)
Group I - Average similarity: 43.20			
<i>Diogenes pugilator</i>	55.0	30.22	30.22
<i>Anapagurus laevis</i>	9.8	18.90	49.13
<i>Arnoglossus laterna</i>	5.0	16.96	66.09
<i>Pomatochistus</i> sp	0.9	8.48	74.56
<i>Buglossidium luteum</i>	0.9	8.48	83.04
Group II ₁ - Average similarity : 41.82			
<i>Arnoglossus laterna</i>	29.9	10.77	10.77
<i>Callyonimus maculatus</i>	25.7	10.24	21.01
<i>Pomatochistus</i> sp.	36.0	6.30	27.31
<i>Anapagurus laevis</i>	798.2	4.76	32.07
<i>Gaidropsarus macrophthalmus</i>	4.1	3.70	35.76
Group II ₂ - Average similarity : 33.63			
<i>Ophiura affinis</i>	78.4	8.69	8.69
<i>Lepidorhombus boscii</i>	6.8	8.07	16.76
<i>Philocheras echinulatus</i>	9.9	6.20	22.96
<i>Pontophilus spinosus</i>	10.1	5.23	28.19
<i>Munida sarsi</i>	11.7	4.93	33.12

several fish species (Table 2). Table 3 shows the species whose differences in abundance between groups lead to this dichotomy. The crustacean *D. pugilator* was exclusive to station 3A, and the remaining species were less abundant at this station than at the other ones (Table 3).

TABLE 3. – SIMPER results: Species responsible for the intergroup dissimilarity in the two main dichotomies. Av.N: mean abundance in the group (ind. 1000 m⁻²); δ_i (%): percentage of dissimilarity explained; C. δ_i (%): cumulative δ_i (%)

Groups I and II - Average dissimilarity (δ) = 86,49				
	Av.N I	Av.N II	δ_i (%)	C. δ_i (%)
<i>Diogenes pugilator</i>	55.0	0.0	5.30	5.30
<i>Callyonimus maculatus</i>	0.0	14.9	2.77	8.07
<i>Anapagurus laevis</i>	9.8	439.8	2.46	10.54
<i>Arnoglossus laterna</i>	5.0	16.7	2.10	12.63
<i>Pagurus prideaux</i>	0.1	15.9	2.06	14.69

Groups II ₁ and II ₂ - Average dissimilarity (δ) = 75,62				
	Av.N I	Av.N II	δ_i (%)	C. δ_i (%)
<i>Arnoglossus laterna</i>	29.9	0.5	3.38	3.38
<i>Anapagurus laevis</i>	798.2	1.6	2.61	5.98
<i>Callyonimus maculatus</i>	25.7	1.7	2.57	8.55
<i>Turritella communis</i>	555.2	0.0	2.53	11.09
<i>Ophiura affinis</i>	2.6	78.4	2.34	13.43

The following dichotomy separates the rest of the samples (group II) into two large sub-groups, II₁ and II₂. Sub-group II₁ is made up of strata A and B of sectors 1, 2 and 4, and is characterised by sandy bottom fishes from the shelf, together with the crustacean *A. laevis*, which was the most abundant species of the assemblage (Table 2). Group II₂ includes all samples from stratum C, and station 3B,

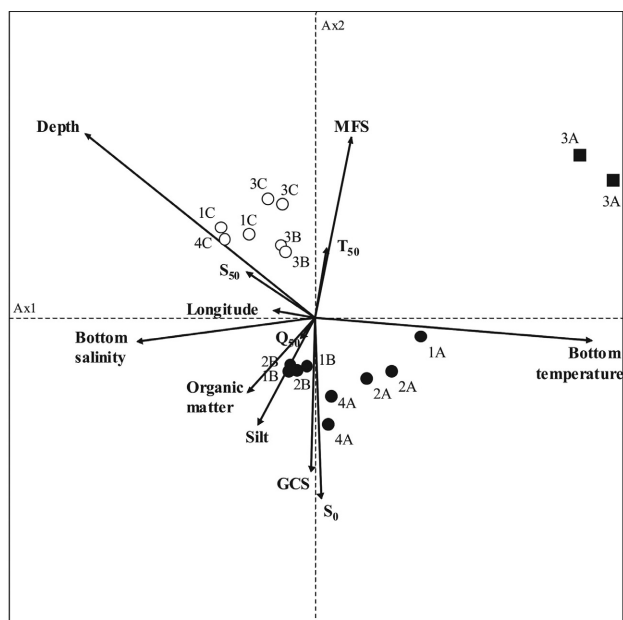


FIG. 3. – CCA biplot of environmental variables versus hauls (cluster groups: solid square I; solid circle II₁; empty circle II₂). Eigenvalues: Ax1: 0.503, Ax2: 0.424; % variance explained=26.9; significance of Montecarlo test=0.005; Temperature and Salinity= near-bottom T and S; T₅₀= temperature at 50 m depth; S₅₀= salinity at 50 m depth; Q₅₀= median particle diameter; S₀= sorting coefficient; GCS= weight percentage of gravel and coarse sands (>500 μ m); MFS= weight percentage of medium, fine and very fine sands (63-500 μ m); Silt= percentage weight of silt (<63 μ m)

which was the deepest in stratum B. This sub-group is typified by the echinoderm *Ophiura affinis*, the fish *Lepidorhombus boscii*, and the crustaceans *Philocheras echinulatus*, *Pontophilus spinosus* and *Munida sarsi* (Table 2), although the most abundant species in the sub-group was the anthozoan *C. smithii* (1203.5 ind. 1000 m⁻² in sub-group II₂), which contributed a lesser percentage to the intra-group similarity, since it is a species with little presence in all the hauls, except in one, in which its presence was massive.

Table 3 shows the species responsible for the separation between sub-groups II₁ and II₂, all of which were more abundant in sub-group II₁, except *O. affinis*.

Regarding dominance in the communities described, the most abundant species in group I are *D. pugilator*, *A. laevis*, *A. laterna* and *Pagurus bernhardus*; in sub-group II₁ *A. laevis*, *T. communis*, *Pomatoschistus* sp., *A. laterna*, *C. maculatus* and *Pagurus prideaux*; and in sub-group II₂ *C. smithii*, *E. papillosus*, *O. affinis*, *Galathea dispersa*, *M. sarsi*, *P. heterocarpus* and *G. argenteus*.

The direct gradient ordination analysis shows the same discrimination of the three communities as that

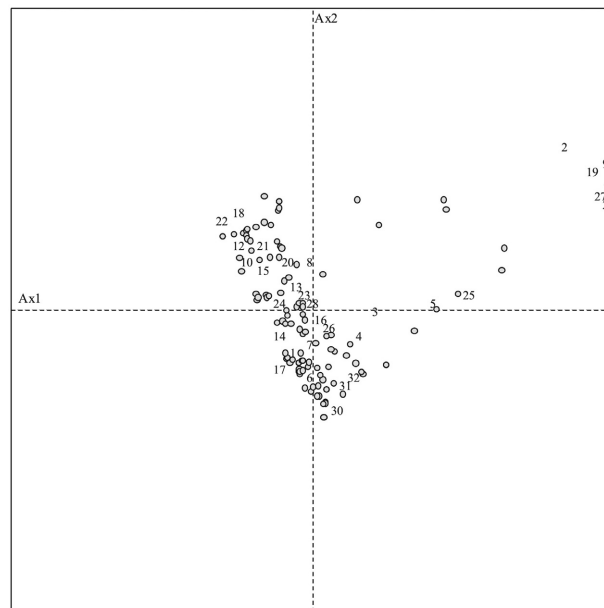


FIG. 4. – CCA plot of species. Points of species cited in the text have been substituted by the following numbers. 1: *A. glaber*; 2: *A. kirchenpaueri*; 3: *A. laevis*; 4: *A. laterna*; 5: *B. luteum*; 6: *C. crassicornis*; 7: *C. maculatus*; 8: *C. smithii*; 9: *D. pugilator*; 10: *E. papillosus*; 11: *E. pusillus*; 12: *G. argenteus*; 13: *G. dispersa*; 14: *G. macrophthalmus*; 15: *L. boscii*; 16: *L. depurator*; 17: *M. merluccius*; 18: *M. sarsi*; 19: *M. surmuletus*; 20: *O. affinis*; 21: *P. echinulatus*; 22: *P. heterocarpus*; 23: *P. prideaux*; 24: *P. spinosus*; 25: *P. bernhardus*; 26: *Pomatoschistus* sp.; 27: *S. lascaris*; 28: *S. membranacea*; 29: *S. officinalis*; 30: *S. scutata*; 31: *T. communis*; 32: *T. ovata*

described above (Figs. 3 and 4). The first discriminatory factor (axis 1) is produced by the opposition of two related variables, bottom water temperature and depth (Fig. 3). This autocorrelation is the reason for the shape of the parabola, called the Guttman effect (Greenacre, 1984), which can be seen in the samples (Fig. 3), though most clearly in the species plot (Fig. 4). The variable near-bottom salinity also contributes with great weight to axis I, in the same direction as depth and opposite to temperature (Fig. 3).

The second discrimination factor is related to the sediment characteristics and opposes homogeneous medium and fine sands (lower values of sorting coefficient) that are poor in organic matter to a mixture of silt and coarse elements that is more heterogeneous (a higher sorting coefficient) and richer in organic matter. Variables such as longitude, median particle size (Q_{50}), temperature and salinity at 50 m show a low weight in both axes (Fig. 3).

Station 3A (group I) is separated from the rest due to its higher temperature, lower depth, and fine sand sediment that is poor in organic matter. This community is characterised by *D. pugilator*, accompanied by the fishes *Mullus surmuletus* and *Solea lascaris*, the cephalopod *Sepia officinalis*, the echinoderm *Echinocyanus pusillus* and the hydrozoan *Aglaophenia kirchenpaueri* (Fig. 4).

The samples from group II₁ are located in the negative segment of axis 2, showing their affinity for depths, temperatures and salinities intermediate to the other two groups, and a substrate made up of sediments with a very poor selection (higher S_0) as a consequence of a mixture of silt and coarse elements, and greater organic contents than those of group I. This group gives the lowest discrimination of species, demonstrated by the greater density of points on the plot in Figure 4, particularly over the stations from stratum B (Fig. 3). Species which contribute to the similarity of groups I and II₁ (*A. laevis*, *A. laterna* and *Pomatochistus* sp.; Table 2), together with species which typify one of the groups but which are also abundant in the other, such as *Buglossidium luteum*, show greater discrimination with respect to samples 3A, and are situated at the stations of group II₁ corresponding to stratum A. The species which characterise group II₁ that are more closely related to stratum B include *Gaidropsarus macrophthalmus* and *Callyonimus maculatus* (typifying group II₁, Table 2), *Merluccius merluccius* and *Alpheus glaber*. The species more closely related to station 4A, characterised by a higher sorting coefficient

and a higher percentage of silt, are the gastropod *T. communis*, the bivalve *Timoclea ovata* and the polychaete *Sternaspis scutata*.

With greater depths, the lowest temperatures and highest salinities of the environmental range in the study area, subgroup II₂ appears, made up of stratum C and station 3B. This group has a sediment of medium and fine sands, with a sorting coefficient and an organic content that are intermediate to those of the other two groups (Fig. 3). The discrimination of species in this group is higher than that in group II₁ (Fig. 4). We can highlight the species that typify the group according to similarity (Table 2): the echinoderm *O. affinis*, the fish *L. boschii*, the Crangonids *P. echinulatus* and *P. spinosus*, and the anomuran *M. sarsi*.

DISCUSSION

The results show an absence of significant correlations between environmental variables and the ecological indices, with no linear bathymetric or geographical patterns. The progressive increase in mean species richness with depth described by Olaso (1990) and García-Castrillo and Olaso (1995) for the megabenthic communities in the area was not found in the case of epibenthic communities. On the other hand, a great variability was observed in the species dominances by station. These results coincide with models of patch distribution of communities in which the combination of limitations imposed on species by environmental factors has the effect of partitioning the environment, causing patchiness rather than linear gradients (Pérès, 1982). In the Cantabrian Sea area this effect is highly pronounced since, due to its narrow shelf, strong environmental gradients—and therefore great environmental heterogeneity—are generated, creating a patchy distribution.

The only linear pattern observed was an increase in species richness towards the east in the shallowest stratum, and in the opposite direction in the deepest. The eastward increase in the number of species in the shallowest stratum coincides with previous observations on meridionalisation of the Cantabrian coast, according to which surface warming of waters towards the east favours the presence of meridional species against an exclusively Atlantic fauna in the westernmost part of the coast (Fischer-Piette, 1938; Ibáñez, 1987, 1988, 1989, 1990). This

explanation is not so clear for the deepest stratum. One possible reason for the westward increase of species richness may be the fact that, due to its coastal morphology, the western area of the outer Cantabrian shelf (Ribadeo) is an area of retention of hydrographic anomalies (eddies). These eddies have been related to processes of water column production and enrichment of the shelf sedimentary regime (López-Jamar *et al.*, 1992) and—specifically in the Ribadeo area—to hake recruitment (Sánchez and Gil, 2000). Whatever the case, the study of the shelf break communities would involve a more detailed hydrographic and sedimentary study due to its environmental, mainly hydrographic, complexity.

The above-mentioned absence of correlations between the ecological indices and the sedimentary characteristics shows a more diffuse relationship of epibenthic organisms than that described for endobenthic communities, in which lower richness and diversity were observed in coarse or fine sediments, and greater richness in the medium ones (Craig and Jones, 1966; Gray, 1974; Nicolaidou and Papadopoulos, 1989). Zühlke (2000) concluded that sediment composition did not seem to affect epibenthic diversity, and Duineveld *et al.* (1991) also mentioned that the obscure relationship between epibenthic organisms and sediment type does not allow for a classification based on bottom characteristics. Brown *et al.* (2001) cited that particle size distributions alone may not always be the best guide to predicting community types, and that other factors, such as seabed morphology and sediment heterogeneity, appeared to have a greater influence. However, other studies suggest that the sediment type is a main factor structuring the epibenthic community (Basford *et al.*, 1989; Rees *et al.*, 1999) and that the epifaunal assemblages may reflect the infaunal communities (Eleftheriou and Basford, 1989). According to Hartnoll (1983), the epifauna is more abundant in gravel sands, but this relationship is not clear in the present study, in which denser sampling would be required to obtain reliable correlations.

In this study, the particle size and organic content pattern was not related to bathymetry and the presence of rías (sea drowned valleys), as it is on the Galician Atlantic shelf (López-Jamar *et al.*, 1992). However, a much more detailed sedimentary determination would be needed to typify the sediment pattern in the area.

Despite there also being a certain interannual variability, the temporal stability of assemblages

could be established through multivariate techniques. Depth is the main decisive factor determining the assemblages observed, as a consequence, of the narrow surface of the Cantabrian Sea shelf (Olaso, 1990; Sánchez, 1993; Sánchez and Serrano, 2003). The second factor, the near-bottom temperature, is derived from depth, since depth changes involve subsequent changes in several environmental factors such as pressure, light and temperature. The second gradient is produced by the sedimentary characteristics which, while they do not seem to be determining with respect to the univariate indices, do show a certain discriminatory weight when direct gradient multivariate techniques are used. In this second axis, the heterogeneity of the sediment has been shown to be a factor of discrimination (Brown *et al.*, 2001). Therefore, depth and sediment characteristics may be considered as priority factors in structuring communities, and therefore determining in the presence of species. These conclusions coincide with those obtained in numerous studies (Poore and Mobley, 1980; Basford *et al.*, 1989; Olaso, 1990; Zendrera, 1990; Dahle *et al.*, 1998). Another conclusion is that the communities of the coastal stratum and shelf break are more discriminatory than the shelf communities, showing greater environmental variability in the coastal and shelf break strata, as found in other papers (Abelló *et al.*, 1988; Sánchez, 1993; Sánchez and Serrano, 2003). The formation of the axes from environmental variables perfectly reflects the hydrological characteristics of the Cantabrian Sea, with temperature and salinity opposed, and with a fall in temperature and a rise in salinity with W longitude and depth.

Concerning the faunistic affinities of the groups described, the coastal stratum constitutes a very favourable habitat for the presence of pagurid crabs (Le Danois, 1948), with an outstanding abundance of *Pagurus prideaux* and to a lesser extent *Pagurus bernhardus* (Selbie, 1921; Basford *et al.*, 1989; Olaso, 1990) to which, in this paper, we can add smaller species, such as *Anapagurus laevis* and *Diogenes pugilator*, as dominant pagurid species on the inner and middle Cantabrian shelf.

The coastal community of fine poor sands (group I) is characterised by these two last species of pagurids, together with fish species. *Diogenes pugilator* is a crustacean of fine sand and shallow depth (Falciai and Minervini, 1995; Sánchez-Mata *et al.*, 1993), while *A. laevis*, more abundant in group II₂, is a species of wide bathymetric distribution (Ingle,

1993) with a preference for depths of up to 100 m (Falciai and Minervini, 1995; Jennings *et al.*, 1999) and sandy bottoms with a broad size range and sorting coefficient (Lagardère, 1973; García-Gómez, 1994). Regarding fishes, *Arnoglossus laterna* is a species with a wide bathymetric range of 50-200 m (Sánchez, 1993) and a preference for sediments containing mud (Freire *et al.*, 1993), and this explains its importance in the two shallower clusters for bathymetric reasons, and in the shelf group with coarse/silt mixed sediments for sedimentary reasons. On the other hand, *Buglossidium luteum* is a species restricted to sandy bottoms of the inner shelf, at 50-100 m (Sánchez, 1993), which gives it a greater weight in the shallowest station group. This station group has highly mobile sands which explain its low indices and the differentiation from the rest of the stations. According to the stability-time hypothesis (Sanders, 1968), habitats exposed to highly hydrodynamic variable conditions have less stable sediments and thus a less diverse community, avoiding the development of long-lived species (Hiscock, 1983).

The shelf stratum with mixed coarse/silt sediments is characterised by fishes, such as *A. laterna*, and the spotted dragonet *Callyonimus maculatus*. This latter species is described as common in sediments with the presence of mud at between 125 and 250 m (Sánchez, 1993). The ordination analysis included shelf species from fine sandy bottoms with the presence of mud, such as *Chlorotocus crassicornis* or *Alpheus glaber* (Lagardère, 1970 and 1973; Smaldon, 1979; Holthuis, 1980; Sorbe, 1987; Olaso, 1990), species with an affinity for the presence of silt with a reasonable proportion of gravel, such as *Turritella communis* (Yonge, 1946), silt affined species, such as *Sternaspis scutata* (Glémarec, 1969; Amoureux, 1971), and eurybathic species in this study depth range, such as *Solenocera membranacea* and *Liocarcinus depurator* (Lagardère, 1973; Sorbe, 1987; Abelló *et al.*, 1988; Olaso, 1990). These eurybathic species are located practically at the centroid of the analysis, also showing a low discrimination by the sedimentary gradient. *Pontophilus spinosus* is located between the shelf group and that of the shelf edge, showing its affinity for the outer shelf and lower optimum depth than another related species, *Philocheras echinulatus* (Abelló *et al.*, 1988; Olaso, 1990).

The shelf break group, more closely related to medium, fine and very fine sands analogous to the sands at the shelf break of the nord-Gascogne slope

described by Le Danois (1948) and Glémarec (1969), is characterised by the echinoderm *Ophiura affinis*, common in muddy fine and gravelly sands (Holme, 1953; Moyse and Tyler, 1990), and the fish *Lepidorhombus boscii*, which is a species with a preference for depths between 250 and 400 m (Sánchez, 1993). *Munida sarsi* is one of the most abundant species on the shelf, with a greater density at 275 m (Olaso, 1990). The crangonid *P. echinulatus* is considered characteristic of the shelf edge (Olaso, 1990).

These faunistic patterns of spatial distribution are comparable to those obtained by Martínez and Adarraga (2001) for the Basque Cantabrian shelf, by Lauroz (1993) for the French Atlantic shelf, and by Abelló *et al.* (1988) for decapod crustacean assemblages of the northwest Mediterranean, with the obvious biogeographical differences, of shelf width and sediment distribution.

Obtaining taxonomic lists and clarifying the spatial and interspecific relationships of the epibenthic organisms will be of great help in understanding ecosystems of areas submitted to fishing disturbance processes, such as the Cantabrian Sea. This information will serve as a reference for monitoring the environmental changes resulting from trawl fishery. In addition, the quantified information on small epibenthic organisms represents an advance in the knowledge of the behaviour of the trophic selection of commercial species, by comparison with stomach contents (Serrano *et al.*, 2003a, b).

Future works will attempt to further the study of these epibenthic communities and complete it with the endobenthic communities, with the aim of obtaining full information on Cantabrian shelf ecosystems.

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APPENDIX I. – Complete list of species and mean abundance (n° ind. · 1000 m⁻²) by stratum

	A	B	C		A	B	C
Porifera				<i>Phyllodoce groenlandica</i>			2.93
<i>Axinella egregia</i>	1.95			<i>Serpula vermicularis</i>	1.63	0.49	
<i>Axinella</i> sp.	7.07			<i>Sternaspis scutata</i>	8.90	30.25	
<i>Mycale lingua</i>	0.49			<i>Sthenelais limicola</i>		0.24	
<i>Myxilla rosacea</i>	0.24			<i>Sthenolepis yhleni</i>	1.71	6.83	
<i>Phakellia ventilabrum</i>	1.46	0.24	1.10	<i>Syllis parapari</i>			0.98
<i>Spongia officinalis</i>		0.24		<i>Terebellides stroemi</i>	0.24	1.95	
<i>Spongionella pulchella</i>			1.22				
<i>Suberites</i> sp.		0.24		Sipuncula			
<i>Sycon ciliatum</i>			1.95	<i>Golfingia vulgaris</i>	0.24		
				<i>Phascolion strombii</i>	3.37		
Cnidaria				Crustacea			
<i>Abietinaria abietina</i>			7.81	<i>Alpheus glaber</i>	11.30	5.81	2.27
<i>Actinauge richardi</i>		2.34	2.07	<i>Anapagurus bicorniger</i>	11.95		
<i>Actinia cari</i>		0.24		<i>Anapagurus hyndmani</i>	64.65		1.22
<i>Adamsia carcinopados</i>	8.61	7.29	19.10	<i>Anapagurus laevis</i>	894.80	1.54	5.51
<i>Aglaophenia kirchenpaueri</i>	2.93			<i>Anapagurus pusillus</i>	0.98	0.24	
<i>Aglaophenia pluma</i>			1.71	<i>Atelecyclus rotundatus</i>	6.10		0.98
<i>Aglaophenia tubulifera</i>	14.15			<i>Bathynectes maravigna</i>			2.44
<i>Alcyonium digitatum</i>	1.05	0.49		<i>Chlorotocus crassicornis</i>	2.20	2.98	0.49
<i>Amphisbetia operculata</i>	0.24			<i>Cirolana cranchii</i>	0.24		
<i>Calliactis parasitica</i>	10.54	0.41	0.73	<i>Corystes cassivelaunus</i>	0.02		
<i>Caryophyllia smithii</i>	10.25	4.46	3603.56	<i>Cymodoce truncata</i>			1.95
<i>Diphasia alata</i>	0.24			<i>Dichelopandalus bonnieri</i>			11.54
<i>Epizoanthus papillosus</i>	490.19	0.24	293.90	<i>Diogenes pugilator</i>	33.91		76.12
<i>Funiculina quadrangularis</i>		3.78	2.20	<i>Ebalia cranchii</i>	7.86	2.07	
<i>Hydractinia echinata</i>			1.46	<i>Epimeria parasitica</i>			13.91
<i>Lytocarpia myriophyllum</i>	24.03	2.07	0.41	<i>Eurydice affinis</i>			0.24
<i>Nemertesia ramosa</i>		0.37		<i>Eurynome aspera</i>	0.49		
<i>Pennatula rubra</i>	1.83	11.22	0.24	<i>Galathea dispersa</i>	4.51	2.51	58.43
<i>Plumularia setacea</i>	28.30			<i>Galathea intermedia</i>	0.05		
<i>Polyplumularia flabellata</i>		0.24		<i>Goneplax rhomboides</i>	5.73	1.61	0.90
<i>Pteroeides griseus</i>	0.24			<i>Heterocrypta maltzani</i>	0.73		
<i>Sertularella polyzonias</i>	5.29	0.49		<i>Inachus dorsettensis</i>	0.02		
Polychaeta				<i>Inachus leptochirus</i>	1.34	0.24	0.98
<i>Acholoe squamata</i>	0.02			<i>Liocarcinus depurator</i>	8.03	2.22	18.74
<i>Amphicteis gunneri</i>		0.24		<i>Liocarcinus holsatus</i>	0.05		
<i>Aphrodita aculeata</i>	0.49			<i>Liocarcinus marmoreus</i>	24.64		
<i>Arabella iricolor</i>		0.24		<i>Liocarcinus pusillus</i>	2.37	0.49	1.95
<i>Chloeia venusta</i>			0.24	<i>Lophogaster typicus</i>	21.08	0.56	
<i>Clymene</i> sp.		0.49		<i>Macropipus tuberculatus</i>		0.24	7.76
<i>Eteone barbata</i>		0.24		<i>Macropodia rostrata</i>	0.05		
<i>Euclymene</i> sp.		0.24		<i>Macropodia tenuirostris</i>	0.24	1.32	1.10
<i>Glycera rouxii</i>	1.22	0.32		<i>Maja squinado</i>	1.46		
<i>Hyalinoecia tubicola</i>	102.15	5.20	0.61	<i>Monodaeus couchii</i>	0.24		
<i>Hydroides norvegica</i>	0.61			<i>Munida intermedia</i>	5.37	3.17	6.73
<i>Laetmonice filicornis</i>			0.49	<i>Munida iris</i>		41.96	18.54
<i>Lanice conchylega</i>	0.05			<i>Munida sarsi</i>		1.46	20.79
<i>Nephtys cirrosa</i>		0.24		<i>Nephtys norvegicus</i>	0.24		2.44
<i>Nephtys hombergi</i>		0.37		<i>Pagurus alatus</i>	0.24	0.98	4.39
<i>Nephtys incisa</i>	0.24	3.90		<i>Pagurus bernhardus</i>	3.05		9.27
<i>Nereis fucata</i>	0.24		0.37	<i>Pagurus chevreuxi</i>	12.93		
<i>Notomastus profundus</i>		0.98		<i>Pagurus excavatus</i>	7.03	0.90	1.10
<i>Orbinia cuvieri</i>	0.24			<i>Pagurus prideaux</i>	32.62	7.29	13.66
<i>Petaloproctus</i> sp.		0.49		<i>Pagurus pubescentulus</i>			0.24

	A	B	C		A	B	C
<i>Pandalina brevirostris</i>			31.47	Echinodermata			
<i>Philocheras echinulatus</i>	1.05	3.24	12.44	<i>Anseropoda placenta</i>	0.24	0.24	0.98
<i>Plesionika heterocarpus</i>		0.37	16.35	<i>Astropecten auranticus</i>			0.98
<i>Polybius henslowi</i>	113.78	1.66	0.73	<i>Astropecten irregularis</i>	1.85	4.00	7.64
<i>Pontophilus spinosus</i>	6.20	4.20	14.93	<i>Brissopsis lyrifera</i>	0.24	2.44	
<i>Processa canaliculata</i>	18.20	0.85	10.39	<i>Echinaster sepositus</i>	0.02		
<i>Processa nouveli</i>			6.83	<i>Echinocardium cordatum</i>	0.24		
<i>Rissoides desmaresti</i>			0.24	<i>Echinocyamus pusillus</i>			1.71
<i>Scalpellum scalpellum</i>	1.95	4.46		<i>Echinus acutus</i>	1.78	0.24	1.95
<i>Scyllarus arctus</i>	0.98	0.49	0.81	<i>Holothuria forskali</i>	0.24		
<i>Solenocera membranacea</i>	3.66	1.54	4.15	<i>Leptometra celtica</i>		5.61	
<i>Xantho pilipes</i>			1.22	<i>Leptosynapta inhaerens</i>		0.24	
Mollusca				<i>Luidia ciliaris</i>	0.24		1.22
<i>Acteon tornatilis</i>	0.05			<i>Luidia sarsi</i>	0.02		
<i>Alloteuthis media</i>	6.46	1.95	0.24	<i>Marthasterias glacialis</i>	0.24	0.24	
<i>Antalis entalis</i>	23.66		0.24	<i>Ophiothrix fragilis</i>	0.24	0.49	0.37
<i>Aperiovula adriatica</i>	0.24			<i>Ophiura affinis</i>	21.40	8.61	97.58
<i>Aporrhais pespelicani</i>	0.56	0.73	0.24	<i>Ophiura ophiura</i>	9.81	1.83	2.27
<i>Aporrhais serresianus</i>	0.49	0.98	0.24	<i>Psammechinus miliaris</i>	0.24		
<i>Arminia trigina</i>		0.24		<i>Stichastrella rosea</i>		0.24	
<i>Astarte sulcata</i>			1.46	<i>Stichopus regalis</i>	0.49	0.37	0.24
<i>Bathypolipus sponsalis</i>			0.24	<i>Trachythione elongata</i>	1.22		
<i>Bela ornata</i>	0.24			<i>Trachythione tergestina</i>	3.17	3.05	
<i>Bela sp.</i>		0.24		Tunicata			
<i>Calliostoma granulatum</i>	6.78	1.05	0.98	<i>Corella paralelograma</i>	0.73	0.24	
<i>Charonia lampax</i>	0.37			Fishes			
<i>Chlamyx varia</i>	1.22			<i>Argentina sphyraena</i>	0.81	1.71	0.24
<i>Colus gracilis</i>		0.98	0.37	<i>Arnoglossus imperialis</i>	6.83	0.24	0.24
<i>Colus jeffreysianus</i>		1.71		<i>Arnoglossus laterna</i>	19.74	25.30	3.59
<i>Comarmondia gracilis</i>	1.54	0.24		<i>Aspitrigla cuculus</i>	2.81		
<i>Coralliophila squamosa</i>	6.22	0.49	4.34	<i>Bathysolea profundicola</i>			1.22
<i>Corbula gibba</i>			0.49	<i>Blennius ocellaris</i>		0.24	
<i>Crassopleura maravignae</i>	0.24			<i>Buglossidium luteum</i>	5.86	0.24	0.98
<i>Cuspidaria cuspidata</i>	0.73	2.07		<i>Callionymus lyra</i>	0.44		0.49
<i>Dosinia exoleta</i>	0.73	1.54	0.24	<i>Callionymus maculatus</i>	27.76	22.10	2.85
<i>Eledone cirrhosa</i>	0.73			<i>Capros aper</i>	2.27	3.73	
<i>Epitonium clathrus</i>	0.24			<i>Cepola rubescens</i>	0.85	0.41	
<i>Epitonium turtonis</i>	0.24			<i>Chelidonichthys gurnardus</i>	2.24	1.27	
<i>Fusinus rostratus</i>	0.24			<i>Chimaera monstrosa</i>			0.37
<i>Galeodea rugosa</i>	0.73	0.24	0.24	<i>Conger conger</i>	0.24	0.24	0.49
<i>Glycimeris glycimeris</i>	10.37			<i>Crystalllogobius linearis</i>	0.05		
<i>Hiatella arctica</i>	0.02			<i>Deltentosteus quadrimaculatus</i>		0.24	
<i>Hinia reticulata</i>	9.20			<i>Gadiculus argenteus</i>		54.23	7.68
<i>Lunatia catena</i>		0.24	0.49	<i>Gaidropsarus macrophthalmus</i>	1.54	6.46	5.07
<i>Lunatia fusca</i>	0.24	1.46	0.24	<i>Galeus melastomus</i>			0.73
<i>Lunatia pulchella</i>	0.73			<i>Labrus bimaculatus</i>		0.24	
<i>Mytilus edulis</i>		1.15		<i>Lepidorhombus boscii</i>	0.73	0.83	8.61
<i>Neptunea contraria</i>	0.93			<i>Lepidorhombus whiffiagonis</i>	0.66	2.51	0.37
<i>Nucula sulcata</i>	18.25	9.71	0.24	<i>Lesueurigobius friesii</i>	3.90	33.91	0.49
<i>Ocenebra erinaceus</i>	1.22			<i>Leucoraja naevus</i>	0.24	0.37	
<i>Octopus salutii</i>		0.24	0.41	<i>Lophius budegassa</i>	0.24	0.49	
<i>Octopus vulgaris</i>	0.24		0.24	<i>Lophius piscatorius</i>	0.24	0.24	
<i>Pseudamussium septenradiatum</i>		0.24	12.69	<i>Maurollicus muelleri</i>			0.24
<i>Pseudosimnia carnea</i>		0.24		<i>Merluccius merluccius</i>	0.66	0.98	
<i>Pteria hirundo</i>	1.22	0.24		<i>Microchirus variegatus</i>	1.85	4.37	0.61
<i>Pygnodontha cochlear</i>	2.68		0.24	<i>Micromesistius poutassou</i>	2.44	0.37	0.98
<i>Rondeletiola minor</i>		0.24	0.49	<i>Molva dipterygia</i>			0.24
<i>Rossia macrosoma</i>		0.49	0.61	<i>Mullus surmuletus</i>	0.24		0.24
<i>Scaphander lignarius</i>		3.22	5.49	<i>Pagellus bogaraveo</i>	0.24		
<i>Sepia elegans</i>	0.85	0.61		<i>Phycis blennoides</i>		0.24	0.24
<i>Sepia officinalis</i>			0.73	<i>Pomatoschistus sp.</i>	22.71	39.40	3.90
<i>Sepia orbignyana</i>	1.34	0.24		<i>Scyliorhinus canicula</i>	0.49	0.66	0.49
<i>Sepietta oweniana</i>		0.24	1.83	<i>Serranus cabrilla</i>	0.37		
<i>Sepiolo atlantica</i>	1.95			<i>Solea lascaris</i>			0.98
<i>Sepiolo sp.</i>		0.24	0.66	<i>Solea vulgaris</i>	0.24		
<i>Spisula subtruncata</i>			0.24	<i>Trachinus draco</i>	4.32		
<i>Tellina donacina</i>	1.95			<i>Trigla lucerna</i>	0.24		0.24
<i>Timoclea ovata</i>	25.54		0.24	<i>Trisopterus luscus</i>	0.24		
<i>Turritella communis</i>	873.65	6.03		<i>Trisopterus minutus</i>	0.24		
<i>Venus casina</i>	0.24			<i>Zeus faber</i>	0.24	0.24	
<i>Venus striatula</i>	1.22		0.49				
<i>Venus verrucosa</i>	7.07						

