



## Historical macrobenthic community assemblages in the Avilés Canyon, N Iberian Shelf: Baseline biodiversity information for a marine protected area

Maite Louzao <sup>\*</sup>, Nuria Anadón, Julio Arrontes, Consuelo Álvarez-Claudio, Dulce María Fuente, Francisco Ocharan, Araceli Anadón, José Luis Acuña

Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, Catedrático Rodrigo Uría s/n, Oviedo 33071, Spain

### ARTICLE INFO

#### Article history:

Received 12 December 2008

Received in revised form 7 September 2009

Accepted 25 September 2009

Available online 9 October 2009

#### Keywords:

Historic biological data

Baseline biodiversity information

Macrobenthic assemblages

Marine protected areas

Bay of Biscay

### ABSTRACT

Deep-sea ecosystems are highly diverse, and European countries seek to protect these environments by identifying conservation targets. One of these is the Avilés Canyon, southern Bay of Biscay, NE Atlantic, Spain. We present the first analysis of historical benthic communities (1987–1988) of this canyon ecosystem, which is a valuable source of biodiversity baseline information. We found 810 taxa divided in five main macrobenthic assemblages, showing a highly diverse benthic community. Bathymetry was the major structuring agent of benthic community, separating shallow (assemblages I and II, 31 to 307 m depth) from deep stations (assemblages III, IV and V, 198 to 1400 m depth). Especially diverse was assemblage IV, located at the easternmost part of the continental slope (378–1100 m depth) where we found reef-forming corals *Lophelia pertusa* and *Madrepora oculata*. These and other communities (sea-pens [Order Pennatulacea, Phylum Cnidaria] and burrowing macrofauna) represent key habitats in NE Atlantic continental slopes, which are currently threatened. The present dataset has produced the most comprehensive assessment of diversity in this area to date, focusing on the taxonomic groups which may best reflect the health of the marine ecosystem and supporting previous studies which indicate that the continental slope of the southern Bay of Biscay hosts key benthic habitats.

© 2009 Elsevier B.V. All rights reserved.

### 1. Introduction

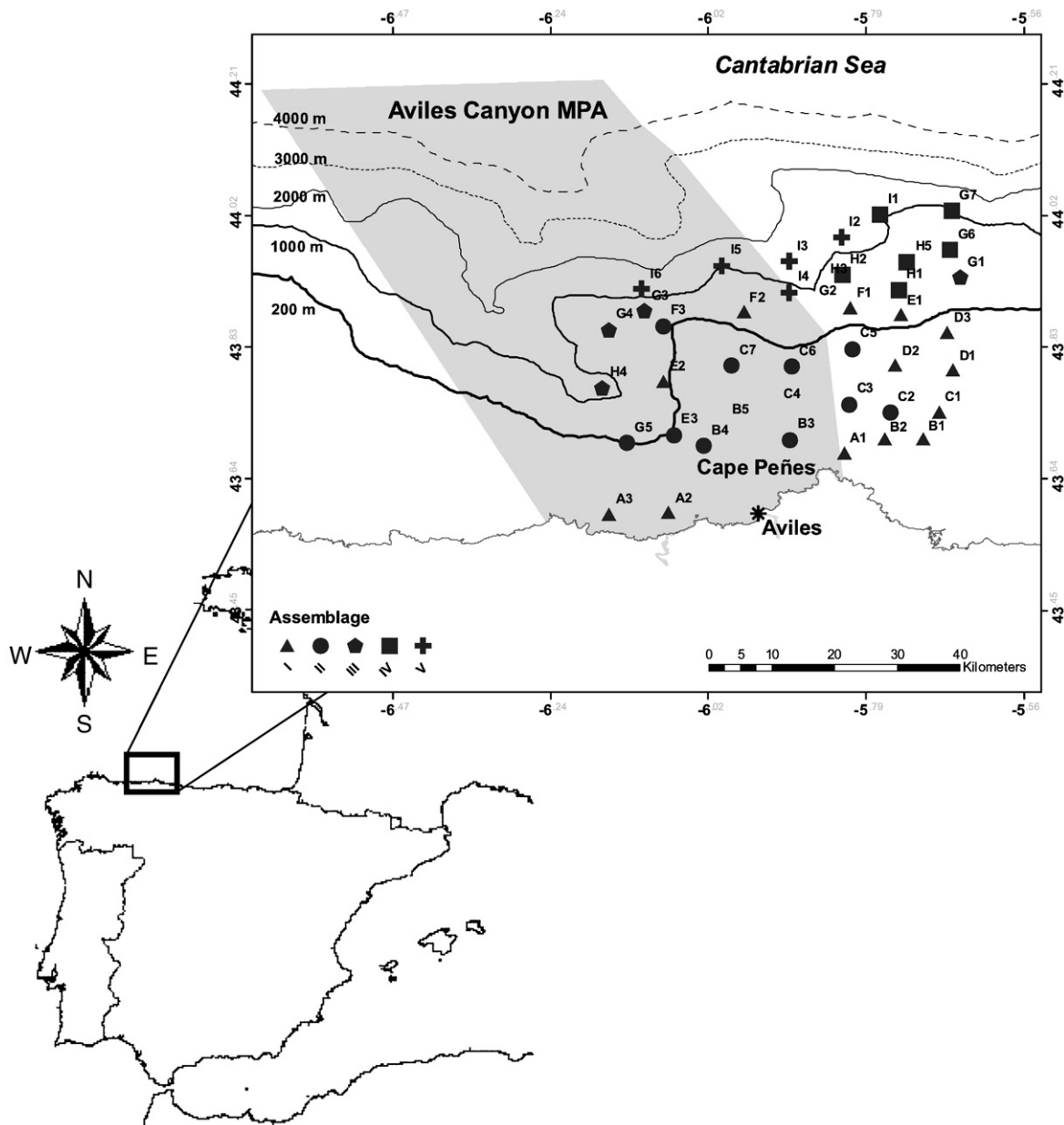
Biological communities in coastal areas are highly sensitive to a range of natural and anthropogenic impacts which operate at both regional (e.g., fisheries overexploitation, introduced species, aquaculture, coastal degradation and infrastructures) and global scales (e.g., sea level change, global warming). Management requires the integration of previous baseline information with contemporary ecological conditions to allow managers to develop effective tools capable of predicting changes and impacts on particular species and communities, as well as to preserve natural habitats (Carter, 1990). Spatially explicit management practices are increasingly taking the central stage of marine conservation strategies (Pikitch et al., 2004). For example, networks of marine protected areas (hereafter MPAs) are being used to manage fisheries, and to protect threatened species and marine habitats around the globe. Within the EU, Spain has been urged to protect 10% of its marine territory before year 2020, and 64 prospective MPAs have already been identified on the basis of the best available knowledge (WWF/ADENA, 2005) due to their exceptional geomorphological or biological characteristics (15 of high priority).

The Avilés Canyon (AC, southern Bay of Biscay in the North of Iberian Peninsula) is one of such high priority areas. It is one of the deepest canyons of the world, very large (32 km in length from the 1000 to the 200 m isobaths; 15 km in width at the 200 m isobath), and very close to the coast (Fig. 1). The AC is of conservation concern due to the presence of the giant squid *Architeuthis dux* (WWF/ADENA, 2005) and supports populations of small pelagic fishes of commercial value (e.g., sardine *Sardina pilchardus*; González-Quirós et al., 2003) and marine top predators (e.g., seabirds, cetaceans; Ruano et al., 2007). Interactions between hydrography and bottom topography at the AC lead to enhanced biomass and primary production, and to marked aggregation of organisms of different trophic levels (González-Quirós et al., 2003). Thus, conservation plans for the AC are based mostly on striking characteristics of water column or surface biota, but much less on our scarce knowledge on benthic communities (but see Ocharan et al., 1989; Vernet and Anadón, 1991; Anadón, 1993; Álvarez-Claudio, 1994; Anadón, 1994; Álvarez-Claudio, 1996; Cristobo et al., 2009). No preliminary descriptions are available on the species composition of the benthic assemblages, the environmental factors that affect their patterns of distribution and abundance, or anthropogenic activities influencing community structure such as fishing (Sánchez and Olaso, 2004).

Within this context, we present an analysis of benthic communities in the AC ecosystem using a uniquely available and spatially

<sup>\*</sup> Corresponding author. Present address: Helmholtz Centre for Environmental Research-UFZ, Permoserstraße 15, 04318 Leipzig, Germany.

E-mail address: [maite.louzao@ufz.de](mailto:maite.louzao@ufz.de) (M. Louzao).



**Fig. 1.** Map of the study area showing the sampling stations of the COCACE dataset (alphanumeric labels such as A1, A2, A3, etc), as well as Avilés harbour and isobaths between 200 and 4000 m. The shaded area represents the prospective Avilés Canyon marine protected area. Macrobenthic assemblages are also represented, except four stations (see Results for more details on the assemblages).

extensive, unpublished historical dataset obtained during the COCACE (Oceanographic Cruise of the Central Cantabria Sea) survey in 1987–1988, which comprises a substantial portion of the proposed MPA (Fig. 1; Ocharan et al. 1989). Historic survey datasets are invaluable, inherent depositories of knowledge, that provide baseline or reference conditions (e.g., low human impact) that help us understand community changes that can result from natural variability and/or anthropogenic sources. Building such a scenario would require information on historical and geographical trends and qualitative and quantitative ecological knowledge (de Heer et al., 2005).

Within this framework, our main objective was to provide historical, baseline data on benthic biodiversity for a prospective MPA in the AC. Specifically, we identified and characterized macrobenthic assemblages within this submarine canyon and adjacent areas. We also analyzed the past presence of biodiversity hotspots and key benthic habitats identified for Atlantic European waters.

## 2. Materials and methods

### 2.1. Macrofaunal sampling

Benthic sampling was conducted from April 1987 to February 1988 at 42 stations ranging from 31 to 1400 m depth in the southern Bay of Biscay, North of Iberian Peninsula (see Fig. 1). A shelf area of ca. 2.500 km<sup>2</sup> extending 41 km offshore, from 44.03° to 43.59° N and from 6.17° to 5.65° W, was covered.

Benthic communities were sampled using an anchor dredge and/or an epibenthic sledge (Hessler and Sanders model), depending on substrate characteristics and meteorological conditions. Specifically, both gears were used in 32 stations, whereas the anchor dredge and the epibenthic sledge were used only in 8 and 2 stations, respectively (see Table S1 for more details). A time limit was set to 5 min per tow, but this rendered quite variable results in terms of the amount of

material obtained. This problem was particularly marked in very deep stations where, due to the very large curvature of the cable, it was very difficult to ascertain whether the ship was actually towing the dredge, or simply stretching the cable. Thus, we usually towed more than 5 min and the tow was repeated if enough material was not obtained. Biological data for each station was pooled and converted to species presence/absence for statistical analysis since sampling effort varied among stations (i.e., 1 or 2 dredge samples per station), and a non-quantitative epibenthic sledge was also used.

Collected material was washed with seawater through a Holmer serial sieving box (the finest mesh size was 2 mm). The largest animals were collected manually and preserved in 70% alcohol or 4% formaldehyde in seawater, buffered with borax. Polychaetes, Cnidarians, Nemertean, and Sipunculians were anaesthetized with 7%  $\text{Cl}_2\text{Mg}$  in distilled water and fixed in formol. Echinoderms, Molluscs, Brachiopods, Bryozoans and Crustaceans were fixed in alcohol. Big stones or corals with abundant epifauna were transferred without fixation to the laboratory after examination on board the vessel. Associated fauna was sorted among broad taxonomic categories and identified using specialised literature for each taxonomic group (more than 1.500 references were used and identified by N Anadón, J Arrontes, C Álvarez-Claudio, DM Fuente, F Ocharan and A Anadón, within 5 years after sampling). Although our identification was particularly intense toward the identification of annelids, molluscs, cnidarians, echinoderms, and sipunculids compared with arthropods, studies on benthic assemblages in the Bay of Biscay have been focused on crustaceans (e.g. Marquegui and Sorbe, 1999; Sorbe, 1999; Cartes et al., 2007; but see Serrano et al., 2006a,b; Sánchez et al., 2008). Thus, this study complements our current knowledge on the sessile, infaunal, non-arthropod macrobenthos, a faunal fraction that is more likely to be affected by dredging or trawling activities and which may probably serve as better sentinel organism for the detection of impacts on the benthic ecosystem. The COCACE dataset has produced the most comprehensive phylogenetic list of the macrobenthic taxa in the Avilés Canyon and adjacent area to date, focused on the taxonomic groups with may best reflect the health of the marine ecosystem.

## 2.2. Environmental variables

A Geographical Information System (GIS) was used to explore spatial trends in biological and environmental data. We gathered information on 15 environmental variables and examined their relationship with the structure of benthic assemblages (Table S1). We considered the distance from the sampling stations to the nearest shoreline and the shelf-break (depth of 200 m) to account for inshore–offshore gradients, as well as the distance to Avilés, the main industrial harbour of the study area, to account for the effects of human activity in the sediments (Ocharan et al., 1989). Distances were calculated using the Nearest Features extension of ArcView 3.2 (Jenness, 2004). Additionally, we included water depth and slope (as percentage; using the 3D Analyst extension of ArcGIS 9.1), as well as geographic location (both latitude and longitude).

For sediment sampling, we used a Van Veen dredge (0.36 m<sup>2</sup>). Alternatively, we used an anchor-like dredge (0.08 m<sup>2</sup>) when bottom characteristics or meteorological conditions did not allow the use of the Van Veen (Ocharan et al., 1989). Granulometric analysis of sand (2 to 0.063 mm in diameter), silt (0.063 to 0.0039 mm) and clay (<0.0039 mm) were completed on 3/4 L samples following Buchanan and Kain (1971) and Guitián and Carballas (1976), as described in Ocharan et al. (1989). From weight percentages of each fraction, we derived the median grain size (Md) and the grain coefficient of selection (So) (Trask and Hammar, 1930). Additionally, two 100-mL samples were frozen at –17 °C for later analysis of both carbon and nitrogen organic content, following Guitián and Carballas (1976). All sediment analysis integrated a depth of 25–50 cm.

## 2.3. Data analysis

### 2.3.1. Biodiversity measures

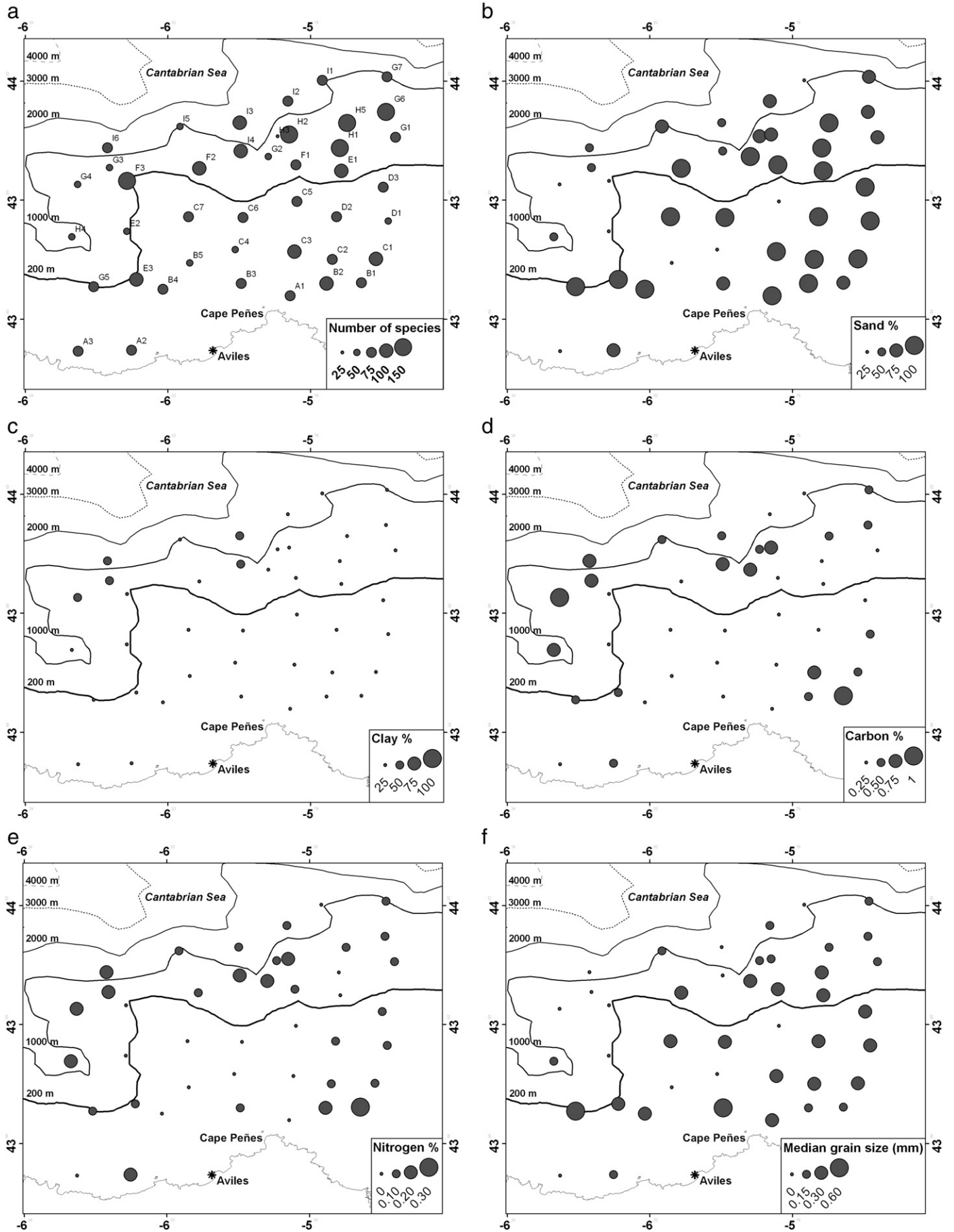
Species richness (number of taxa) was calculated for each station, as well as aggregation files to facilitate the analysis of benthic macrofauna using Average Taxonomic Distinctness (*AvTD*) and Variation in Taxonomic Distinctness (*VarTD*) (Warwick and Clarke, 1995; Clarke and Warwick, 2001). Average Taxonomic Distinctness is a measure of biodiversity based on taxonomic distance between species using presence/absence information, which is defined as the average taxonomic path length between any two randomly chosen species, traced through a phylogenetic classification of the full set of species involved (Clarke and Warwick, 1998). That is, the *AvTD* measures the diversity by taking into account the phylogenetic relatedness of the taxa of our benthic assemblage. An assemblage comprised of a group of closely related species is considered less diverse than one with the same species richness, but with more distantly related species (Clarke and Warwick, 2001). Therefore, *AvTD* can be thought of as measuring the taxonomic breadth of a sample. The variation in taxonomic distinctness (*VarTD*) complements the *AvTD* since it is the variance of these pair-wise path lengths and reflects the unevenness of the taxonomic tree (Clarke and Warwick, 2001). *AvTD* is independent, on average, on the degree of sampling effort involved in the data collection and can be used to compare studies with differing and uncontrolled degrees of sampling effort (Clarke and Warwick, 1999). We built our taxonomic classification tree following the species directory of the World Register of Marine Species (WoRMS, available at [www.marinespecies.org](http://www.marinespecies.org)).

### 2.3.2. Characterization of benthic assemblages

With the aim of setting the environmental context of the study area, we performed a principal component analysis (PCA) in order to explore the relationship between environmental variables by means of the Euclidean distance. To approximate (multivariate) normality, we excluded outliers in our data using the Draftsman Plot, applying the  $\log(x+1)$  transformation when needed (i.e., sand, clay, silt, both organic carbon and nitrogen, C/N, and Md) and normalised environmental variables prior to the PCA.

Faunal assemblages were compared among the 42 sampling stations using the Bray–Curtis coefficient of similarity (Bray and Curtis, 1957) prior to group average clustering of the data, and multidimensional scaling ordination (MDS). Following clustering, similarity profile permutation tests (SIMPROF) were used to look for statistically significant evidence of clusters in the data. In order to detect significant differences between assemblages identified by the clustering we applied the analysis of similarities (ANOSIMs) (Clarke and Warwick, 1994b). Once assemblages were identified, we estimated the average ‘within-assemblage’ similarity and the representative species for each assemblage based on the similarity percentages method (SIMPER). The BIO-ENV routine was used to identify the environmental variables which best explained the observed biological patterns (Clarke and Ainsworth, 1993). Highly collinear variables ( $r_s > 0.95$ ) were removed since no clear further explanation of the biotic data can be obtained by including variables carrying the same information (Clarke and Warwick, 1994a). Thus, distance to Avilés and latitude were excluded since they were highly correlated with distance to the coast.

Finally, we tested the null hypothesis that each macrofaunal assemblage has the same taxonomic distinctness structure than the total species pool. We applied a randomisation test to compare the observed value of *AvTD* and *VarTD* against an ‘expected’ value derived from the total species pool (Clarke and Warwick, 1998). If the procedure is repeated for different numbers of species, the expected values can be plotted as a probability funnel, against which the observed *AvTD* values from real samples may be plotted. Plotting a ‘significance level’ (formally a probability value) onto the funnel,



normally at the 5% level, addresses the question of whether a sample has a 'lower than expected' taxonomic spread (Clarke and Warwick, 1998). Multivariate analysis were performed using PRIMER statistical package (Clarke and Warwick, 1994a).

### 3. Results

#### 3.1. Benthic diversity

A total of 810 macrofaunal taxa belonging to eleven Phyla were identified (see Table S2 in the Appendix). The macrobenthos was characterized by a great dominance of polychaetes (the only class of Annelida) followed by molluscs, cnidarians, arthropods, and echinoderms (representing the 28.8%, 19.9%, 14.7%, 14.1%, and 12.6%, respectively). Our taxonomic resolution reached the species level in 608 cases, and only the genus, family, order, class or phylum level in 143, 57, 8, 1, and 1 of the cases, respectively.

Species richness ranged between 13 and 143 per station and reached local maxima at stations F3, H1 and H5, along the slope (Fig. 2a). A positive, statistically significant but moderate, correlation between  $S$  and  $AvTD$  ( $r_s = 0.38$ ,  $P < 0.05$ ) indicated some discrepancy between species diversity and phylogenetic distinctness. A significant, negative correlation between  $S$  and  $VarTD$  ( $r_s = -0.43$ ,  $P < 0.05$ ) suggested that a high species diversity was related to a more uniform distribution of species among the phylogenetic tree.

#### 3.2. Environmental context

The bathymetric data showed a strong depth gradient across the continental shelf-slope, particularly marked at the Avilés Canyon, and a narrow continental shelf (Fig. 1). A PCA on the environmental variables produced two principal components, PC1 and PC2, which accounted for 45.3 and 21.5% of the total variance respectively. Loading factors on PC1 (Fig. 3) indicated that the first axis was related to depth, with deep stations showing higher clay, silt and carbon content (variables with highly positive scores on PC1), and lower sand content and mean particle diameter (negative scores). PC2 summarized variance due to organic content, and its factor scores (Fig. 3) indicated that stations situated to the east or far from the coast had in general higher carbon and nitrogen contents, and higher C:N ratios (Fig. 2). In summary, medium and fine sandy bottoms with low organic content and C:N ratios alternating with rocky bottom characterized shelf waters above 400 m depth, while muddy sediments with high C and N contents and higher C:N ratios prevailed below the 400 m isobath (Fig. 2). An exception to this pattern were areas close to the Nalón River mouth and the eastern part of Cape Peñes, where shallow waters exhibited fine and rich sediments (Fig. 2).

#### 3.3. Characterization of benthic assemblages

Cluster analysis performed on the species presence/absence by station matrix indicated five main macrobenthic assemblages at the 22% similarity level (assemblages I to V, Fig. 4). This grouping was consistent with the position of the samples in the MDS plot (Fig. 5). ANOSIM dissimilarity analyses between groups were significant either pair-wise ( $P < 0.05$  for all pairs) or globally ( $R = 0.884$ ,  $P = 0.001$ ). Likewise, these assemblages was ranked along the sequence III < I < V < II < IV from lower to higher species diversity and III < V < I < II < IV from lower to higher taxonomic distinctness (see Table 1). Station groupings differed most markedly in their depth

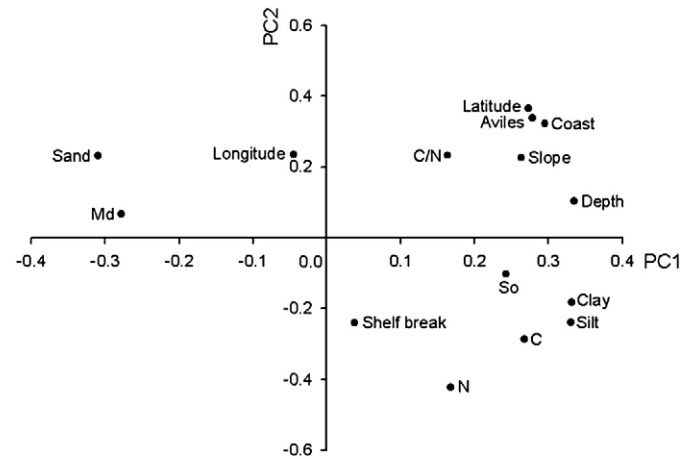


Fig. 3. PCA ordination plot of environmental variables. The first two principal components (PC1 and PC2) account for the 66.8% explained variance.

and sand percentage (BIO-ENV correlation with depth,  $r_s = 0.572$ ; with sand percentage,  $r_s = 0.486$ ; both variables,  $r_s = 0.611$ ).

##### 3.3.1. Assemblage I

These samples belonged to shallow, shelf and coastal stations (31 to 300 m depth, Fig. 1), with sandy and organically poor sediments (mean sand content  $82.0 \pm 13.2\%$ ,  $0.29 \pm 0.24\%$  C,  $0.09 \pm 0.09\%$  N, C:N =  $4.03 \pm 1.47$ , Table 1 and Fig. 5). This group included 314 taxa, with low species richness but intermediate taxonomic distinctness for individual samples ( $S = 64 \pm 18$ ,  $AvTD = 91.3 \pm 1.6$ , mean  $\pm$  SD, Table 1). This group was mainly composed of polychaete annelids (*Nephtys hombergii*) and bivalve molluscs (*Timoclea ovata*; SIMPER analysis, Table 2).

##### 3.3.2. Assemblage II

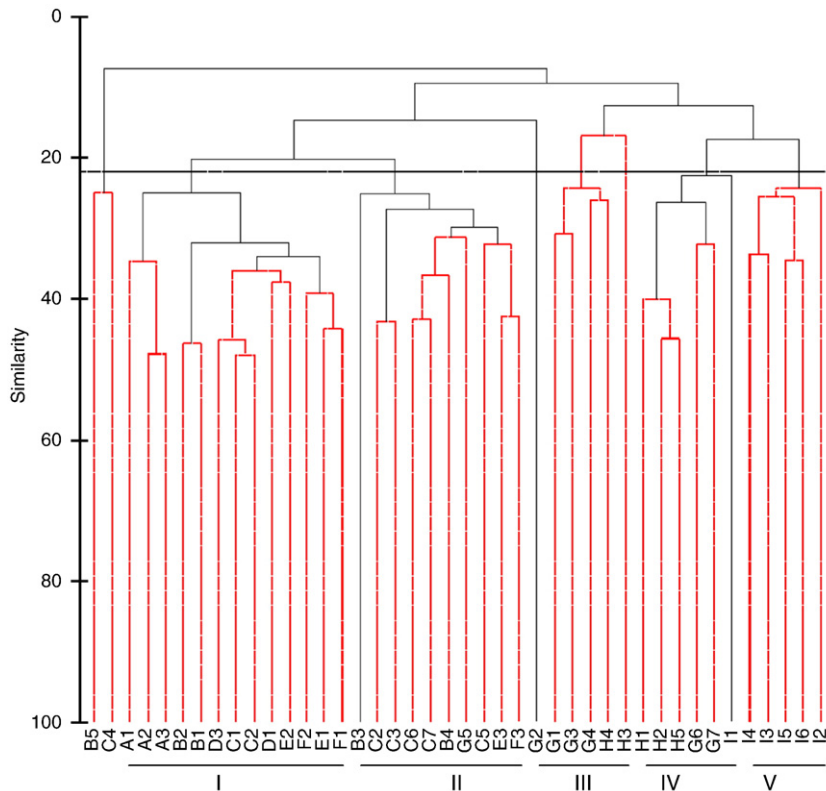
This group comprised samples collected at coastal and shelf stations (117 to 307 m depth, Fig. 1), with sandy and organically poor sediments ( $88.0 \pm 9.1\%$  sand content,  $0.25 \pm 0.18\%$  C and  $0.05 \pm 0.02\%$  N contents,  $4.89 \pm 0.97$  C:N, Table 1, Fig. 5). This group included 352 taxa, with high species richness and taxonomic distinctness within the samples ( $S = 75 \pm 23$ ,  $AvTD = 92.9 \pm 0.5$ , Table 1). It was represented by a diverse array of taxa belonging to the echinoderms (the starfish *Ophiocten affinis* and the sea urchin *Echinocyamus pusillus*), hydrozoan polyps (e.g. *Modeeria rotunda* and *Clytia hemisphaerica*), corals (*Cariophyllia smithii*), bivalve molluscs (e.g. *T. ovata*) or arthropods (e.g. *Pandalina brevirostris*) (Table 2).

##### 3.3.3. Assemblage III

These samples typically belonged to stations at the upper slopes of the Avilés Canyon, between 468 and 790 m depth (Fig. 1). These stations had the lowest sand and the highest organic content ( $43.2 \pm 21.6\%$  sand content,  $0.65 \pm 0.32\%$  C and  $0.13 \pm 0.07\%$  N content,  $5.01 \pm 1.37$  C:N, Table 1, Fig. 5). The group contained 119 taxa, had the lowest sample diversity ( $S = 41 \pm 16$ ,  $AvTD = 90.2 \pm 4.1$ , Table 1) and was characterized by polychaetes (*Lumbrineris latreilli* and *Nothria hispanica*, Table 2).

##### 3.3.4. Assemblage IV

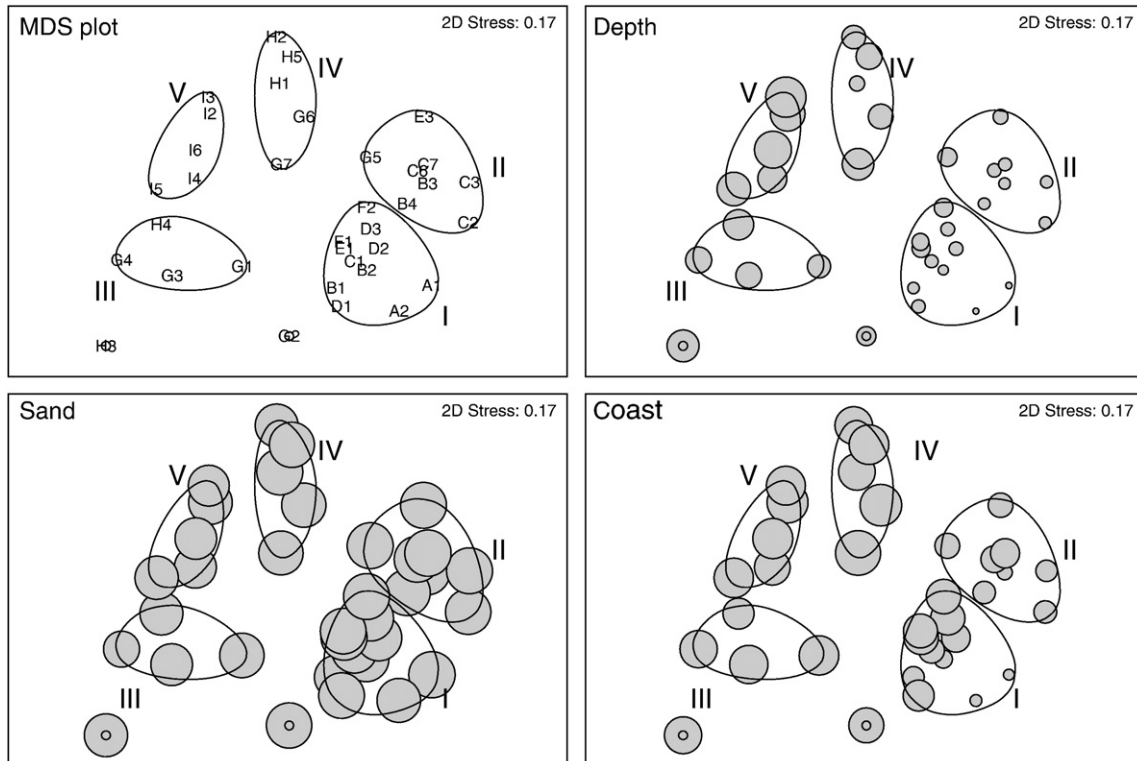
These samples were collected at deep stations (198 to 1100 m) located at the easternmost part of the shelf-break (Fig. 1), and were characterized by intermediate sand and organic contents ( $70.8 \pm 16.0\%$  sand content,  $0.35 \pm 0.17\%$  C and  $0.07 \pm 0.04\%$  N content,  $4.84 \pm$



**Fig. 4.** Macrobenthic faunal assemblages represented by means of a dendrogram (cluster analysis), resulting in five assemblages at the 22% similarity level. Shallow assemblages: I and II, deep assemblages: III, IV and V.

1.19 C:N, Table 1, Fig. 5). Although the group contained a moderate total of 332 taxa, individual samples had the highest diversity ( $S = 98 \pm 34$ ,  $AvTD = 94.1 \pm 1.0$ , Table 1). The assemblage was characterized by a

phylogenetically and functionally diverse group of polychaetes (genus *Harmothoe*), bivalves (*Limopsis aurita*), scyphozoan and hydrozoan polyps (genus *Stephanoscyphus* and *Eudendrium ramosum*), sipunculids



**Fig. 5.** Macrobenthic faunal assemblages represented by means of MDS plots (at 22% similarity level) and superimposed with depth, sand percentage and distance to the coast ( $n = 35$ ).

**Table 1**  
Biodiversity indices and environmental characteristics (mean  $\pm$  s.d.) of 5 assemblages identified by cluster analysis.

|                  | Assemblages                 |                             |                             |                             |                               |  | Total                       |
|------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-------------------------------|--|-----------------------------|
|                  | I                           | II                          | III                         | IV                          | V                             |  |                             |
| Stations (n)     | 13                          | 10                          | 4                           | 6                           | 5                             |  | 42                          |
| Species richness | 64.69 $\pm$ 18.03           | 75.00 $\pm$ 23.78           | 41.50 $\pm$ 15.93           | 98.83 $\pm$ 34.41           | 72.40 $\pm$ 22.70             |  | 67.34 $\pm$ 28.61           |
| AvTD             | 91.33 $\pm$ 1.61            | 92.92 $\pm$ 0.55            | 90.92 $\pm$ 4.11            | 94.07 $\pm$ 0.96            | 91.09 $\pm$ 2.00              |  | 92.12 $\pm$ 2.05            |
| VarTD            | 280.55 $\pm$ 43.15          | 243.51 $\pm$ 13.24          | 259.65 $\pm$ 86.18          | 189.03 $\pm$ 29.16          | 254.27 $\pm$ 43.63            |  | 249.55 $\pm$ 50.53          |
| Depth (m)        | 151.92 $\pm$ 88.07          | 166.4 $\pm$ 60.25           | 603.75 $\pm$ 134.79         | 624.33 $\pm$ 313.01         | 1060.20 $\pm$ 253.18          |  | 394.12 $\pm$ 359.69         |
| Slope (%)        | 358,659.24 $\pm$ 568,702.03 | 154,353.21 $\pm$ 110,214.26 | 435,481.35 $\pm$ 248,029.43 | 942,174.62 $\pm$ 327,530.77 | 1,671,945.37 $\pm$ 455,136.78 |  | 614,906.87 $\pm$ 675,606.11 |
| Coast (km)       | 15.34 $\pm$ 9.37            | 14.33 $\pm$ 6.37            | 28.82 $\pm$ 5.72            | 35.54 $\pm$ 5.54            | 32.65 $\pm$ 3.29              |  | 21.74 $\pm$ 11.08           |
| Shelf-break (km) | 8.78 $\pm$ 6.63             | 5.55 $\pm$ 5.16             | 5.58 $\pm$ 1.98             | 10.75 $\pm$ 4.59            | 9.36 $\pm$ 3.06               |  | 7.88 $\pm$ 5.13             |
| Avilés (km)      | 25.58 $\pm$ 8.60            | 21.05 $\pm$ 6.39            | 35.09 $\pm$ 7.13            | 45.51 $\pm$ 5.67            | 39.81 $\pm$ 3.52              |  | 30.08 $\pm$ 11.20           |
| Stations (n)     | 11                          | 8                           | 4                           | 5                           | 5                             |  | 35                          |
| Sand (%)         | 81.98 $\pm$ 13.24           | 88.04 $\pm$ 9.13            | 43.29 $\pm$ 21.66           | 70.87 $\pm$ 16.02           | 45.87 $\pm$ 9.79              |  | 71.33 $\pm$ 21.31           |
| Silt (%)         | 9.30 $\pm$ 9.08             | 4.65 $\pm$ 3.88             | 29.22 $\pm$ 11.35           | 14.00 $\pm$ 8.05            | 27.51 $\pm$ 7.62              |  | 14.26 $\pm$ 11.77           |
| Clay (%)         | 8.72 $\pm$ 4.71             | 7.30 $\pm$ 5.27             | 27.49 $\pm$ 10.32           | 15.13 $\pm$ 8.47            | 26.61 $\pm$ 3.62              |  | 14.41 $\pm$ 9.93            |
| C (%)            | 0.29 $\pm$ 0.24             | 0.25 $\pm$ 0.18             | 0.65 $\pm$ 0.32             | 0.35 $\pm$ 0.17             | 0.49 $\pm$ 0.15               |  | 0.38 $\pm$ 0.24             |
| N (%)            | 0.09 $\pm$ 0.09             | 0.05 $\pm$ 0.02             | 0.13 $\pm$ 0.07             | 0.07 $\pm$ 0.04             | 0.09 $\pm$ 0.03               |  | 0.08 $\pm$ 0.06             |
| C/N              | 4.03 $\pm$ 1.47             | 4.89 $\pm$ 0.97             | 5.01 $\pm$ 1.37             | 4.84 $\pm$ 1.19             | 5.42 $\pm$ 0.29               |  | 4.75 $\pm$ 1.21             |
| Md (mm)          | 0.15 $\pm$ 0.05             | 0.32 $\pm$ 0.18             | 0.04 $\pm$ 0.04             | 0.11 $\pm$ 0.06             | 0.05 $\pm$ 0.04               |  | 0.15 $\pm$ 0.14             |
| So               | 1.87 $\pm$ 0.84             | 2.41 $\pm$ 1.79             | 3.96 $\pm$ 1.89             | 3.11 $\pm$ 1.54             | 6.11 $\pm$ 2.29               |  | 3.08 $\pm$ 2.04             |

AvTD: average taxonomic distinctness, VarTD: variation in taxonomic distinctness, Md: median grain size, So: grain coefficient of selection.

(*Aspidosiphon muelleri*), isopods (family *Arcturidae*) and sea cucumbers (*Echinocucumis hispida*).

### 3.3.5. Assemblage V

These samples belonged to the deepest stations (720 to 1400 m, Fig. 1) and were characterized by low sand and high organic content (45.8  $\pm$  9.7% sand content, 0.49  $\pm$  0.15% C and 0.09  $\pm$  0.03% N content, 5.42  $\pm$  0.29 C:N, Table 1, Fig. 5). They contained 233 taxa, had a moderate sample diversity ( $S = 72 \pm 22$ , AvTD = 91.0  $\pm$  2.0, Table 1) and were characterized by arthropods (orders Cumacea and Isopoda and subclass Copepoda) and polychaetes (family Maldanidae and *Melinna cristata*, Table 2).

Fig. 6 shows the 95% confidence levels for bootstrapped values of AvTD and VarTD using the full species list as source for the bootstrap sampling and with a sample size varying from 20 to nearly 400 species. Most of the samples fell within the limits of the confidence funnel, although some of the samples of assemblages I and V failed below the confidence funnel for AvTD (Fig. 6a), what indicated that these samples had a lower phylogenetic diversity than expected from the full species list. Similarly, samples from assemblages I and V failed above the confidence funnel for VarTD (Fig. 6b), what indicated that phylogenetic distances among these samples were less homogeneously distributed than expected.

## 4. Discussion

Despite the limitations of historic biological records for assessing the current ecological and conservation status of the deep-sea habitats, they provide valuable baseline information of biodiversity patterns in order to set the ecological basis for further research in benthic habitats. In fact, the COCACE dataset has produced the most comprehensive assessment of biodiversity patterns in the Avilés Canyon and adjacent area to date focusing on the taxonomic groups with may best reflect the health of the marine ecosystem.

### 4.1. Macrobenthic community

We identified 810 taxa, 608 of them to the species level, which indicates a highly historic diverse benthic community and supports the perception of the Cantabrian Sea as more diverse than adjacent areas (Olaso, 1990; Sánchez, 1993). Also, Sánchez et al. (2008) in a more recent epibenthic-demersal survey (2003–2004) found 221

species (including 71 species of fishes, 65 crustaceans, 35 molluscs, 29 echinoderms, 10 cnidarians and 5 sponges) in the nearby Le Danois Bank, an important marginal shelf located in the Cantabrian Sea, using both beam- and beam-trawls. Local diversity might have been affected by regional scale processes, since local communities are integral components of larger biogeographic regions (Witman et al., 2004). In this regard, the Cantabrian Sea is located within the subtropical/boreal transition zone of the Eastern Atlantic, where both south temperate and cold boreal species co-occur, what may explain this high local diversity (Sánchez and Olaso, 2004; Hemery et al., 2008).

Diversity indices indicated that benthic communities were not distributed randomly, and multivariate analyses found that local factors such as depth, sediment characteristics and topographical effects also contributed to the high local diversity and distinct community structure. In particular, the result of the BIO-ENV analysis suggested that depth was a major structuring agent of the benthic community, and CLUSTER analysis clearly separated shallow (assemblages I and II, 31 to 307 m depth) from deep stations (assemblages III, IV and V, 198 to 1400 m depth), on the basis of characteristic species for each assemblage. Bathymetric differentiation of benthic communities is a global pattern (Gage and Tyler, 1991; Flach and de Bruin, 1999) which has been repeatedly confirmed in the Cantabrian Sea (e.g. Sorbe, 1999; Serrano et al., 2006a; Serrano et al., 2006b). Sediment characteristics were also an important factor influencing macrobenthic community structure. In general, grain size decreased from the coast to the continental slope, except in areas close to the Nalón River mouth and the eastern part of Cape Peñes (Ocharan et al., 1989).

An alongshore trend was superimposed on the bathymetric pattern, which divided shallow shelf stations among assemblage I to the East, assemblage II to the West, and deep slope stations among groups IV  $\rightarrow$  V  $\rightarrow$  III, from East to West. This variation may have been associated with a range of topographical effects. Cape Peñes is at the fringe of an active summer coastal upwelling (Botas et al., 1990) and the Avilés Canyon seems to play a role in enhancing the upwelling of cold, nutrient-rich water West of Cape Peñes and close to the coast, which leads to pulses of primary production based on large sized phytoplankton cells (Botas et al., 1990). These large particles may sink rapidly and fuel the benthic community, affecting its structure (Sorbe, 1999; Cartes et al., 2004). Another typical hydrographic feature in this area is the Iberian Poleward Current, runs along the slope and which may exert an influence on the across-shore distribution of plankton

**Table 2**  
Contribution of representative species to each assemblage based on PRIMER analysis (cut-off at 20%).

| Species                            | Phylum        | Class             | Sim (%)                   | C.Sim (%) |
|------------------------------------|---------------|-------------------|---------------------------|-----------|
| <b>Assemblage I</b>                |               |                   |                           |           |
|                                    |               |                   | Average similarity: 31.48 |           |
| <i>Nephtys hombergii</i>           | Annelida      | Polychaeta        | 5.1                       | 5.1       |
| <i>Timoclea ovata</i> <sup>a</sup> | Mollusca      | Bivalvia          | 5.1                       | 10.2      |
| <i>Liocarcinus depurator</i>       | Arthropoda    | Malacostraca      | 3.49                      | 13.68     |
| <i>Anchialina agilis</i>           | Arthropoda    | Malacostraca      | 3.38                      | 17.06     |
| <i>Lophogaster typicus</i>         | Arthropoda    | Malacostraca      | 3.02                      | 20.08     |
| <b>Assemblage II</b>               |               |                   |                           |           |
|                                    |               |                   | Average similarity: 29.51 |           |
| <i>Ophiocten affinis</i>           | Echinodermata | Stelleroidea      | 3.83                      | 3.83      |
| <i>Modeeria rotunda</i>            | Cnidaria      | Hydroidomedusa    | 3.61                      | 7.44      |
| <i>Pandalina brevisstris</i>       | Arthropoda    | Malacostraca      | 3.61                      | 11.05     |
| <i>Timoclea ovata</i> <sup>a</sup> | Mollusca      | Bivalvia          | 3.22                      | 14.27     |
| <i>Clytia hemisphaerica</i>        | Cnidaria      | Hydroidomedusa    | 2.86                      | 17.14     |
| <i>Echinocyamus pusillus</i>       | Echinodermata | Echinoidea        | 2.84                      | 19.98     |
| <i>Caryophyllia smithii</i>        | Cnidaria      | Hexacorallia      | 2.8                       | 22.78     |
| <b>Assemblage III</b>              |               |                   |                           |           |
|                                    |               |                   | Average similarity: 25.81 |           |
| <i>Lumbrineris latreilli</i>       | Annelida      | Polychaeta        | 9.7                       | 9.7       |
| <i>Nothria hispanica</i>           | Annelida      | Polychaeta        | 9.7                       | 19.4      |
| <i>Paradiopatra quadricuspis</i>   | Annelida      | Polychaeta        | 5.73                      | 25.13     |
| <b>Assemblage IV</b>               |               |                   |                           |           |
|                                    |               |                   | Average similarity: 28.64 |           |
| <i>Harmothoe</i>                   | Annelida      | Polychaeta        | 3.69                      | 3.69      |
| <i>Limopsis aurita</i>             | Mollusca      | Bivalvia          | 3.69                      | 7.39      |
| <i>Stephanoscyphus</i>             | Cnidaria      | Scyphozoa         | 3.69                      | 11.08     |
| <i>Aspidosiphon muelleri</i>       | Sipuncula     | Phascolosomatidea | 2.49                      | 13.58     |
| <i>Arcturidae</i>                  | Arthropoda    | Malacostraca      | 2.25                      | 15.82     |
| <i>Echinocucumis hispida</i>       | Echinodermata | Holothuroidea     | 2.25                      | 18.07     |
| <i>Eudendrium ramosum</i>          | Cnidaria      | Hydroidomedusa    | 2.25                      | 20.32     |
| <b>Assemblage V</b>                |               |                   |                           |           |
|                                    |               |                   | Average similarity: 26.86 |           |
| <i>Cumacea</i>                     | Arthropoda    | Malacostraca      | 5.31                      | 5.31      |
| <i>Maldanidae</i>                  | Annelida      | Polychaeta        | 5.31                      | 10.62     |
| <i>Melinna cristata</i>            | Annelida      | Polychaeta        | 5.31                      | 15.92     |
| <i>Copepoda</i>                    | Arthropoda    | Maxillopoda       | 3.39                      | 19.31     |
| <i>Isopoda</i>                     | Arthropoda    | Malacostraca      | 3.39                      | 22.7      |

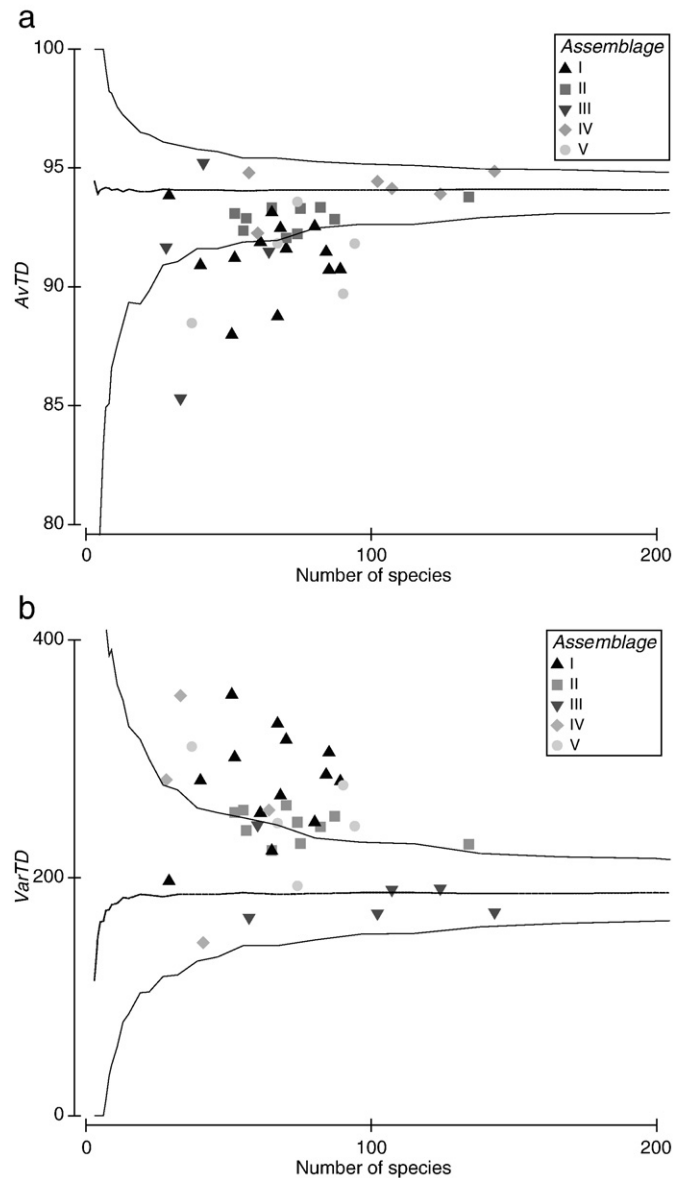
Sim (%): percentage of similarity explained; C.Sim (%): cumulative percentage of similarity.

<sup>a</sup> Species present in assemblages I and II.

during the spring, when the most important production events take place in the upper water column (e.g. Fernández et al., 1991). It is unclear, however, how this might influence the spatial distribution of export production to the benthos in an alongshore direction.

#### 4.2. Implications for conservation

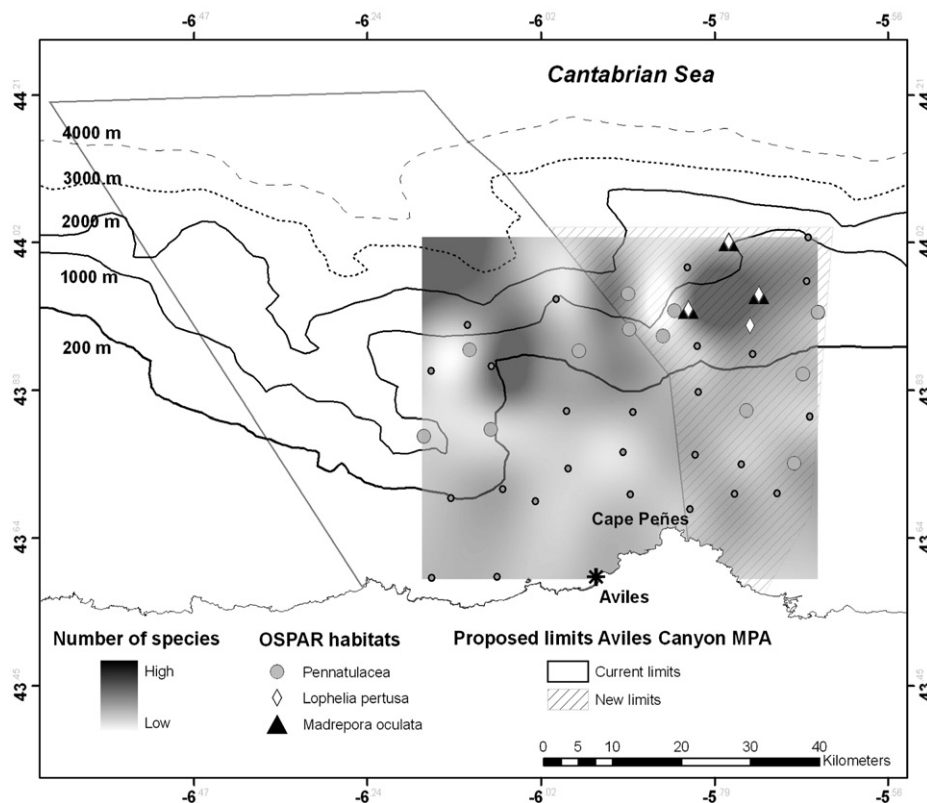
From a biological diversity point of view, deep-sea habitats are considered exceptional ecosystems (Sánchez et al., 2008). In this sense, a salient feature in our results is the high benthic diversity of assemblage IV, which includes stations located in the easternmost part of the continental slope, between 378 and 1100 m depth. This high diversity may be a result of more complex habitat structure, since we found reef-forming corals *Lophelia pertusa* and *Madrepora oculata* in 3 and 4 stations out of the 6 stations in the IV assemblage (Fig. 7), first recorded by Alvarez-Claudio (1994) in the study area. These species have been found in the northern slope of the nearby Le Danois Bank, as well as in the whole Bay of Biscay, and are usually associated to hard or slightly sandy substrates at depths between 150 and 2000 m (Sánchez et al., 2008). Deep coral *L. pertusa* reefs have been included in the Initial OSPAR (Convention for the Protection of the Marine Environment of the North-East Atlantic) List of Threatened



**Fig. 6.** (a) Average taxonomic distinctness (AvTD) and (b) variation in taxonomic distinctness (VarTD) of the macrofaunal community. Note the significant negative relationship between AvTD and VarTD (Spearman rank correlation =  $-0.93$ ,  $P < 0.001$ ).

and/or Declining Species and Habitats for the NE Atlantic, where they are reported as habitats at risk in all OSPAR regions, including the Bay of Biscay (<http://www.ospar.org/>).

Moreover, the COCACE survey also identified another important OSPAR habitat: sea-pen (Order Pennatulacea, Cnidaria) and burrowing megafaunal communities. Eleven of the 42 stations contained pennatulaceans, most of these stations were located at the continental slope (Fig. 7). Pennatulaceans have also been reported at similar depths at the northern slopes of the Le Danois Bank by Sanchez et al. (2008), in association with deep coral reefs. They are reported as endangered in regions II (the Greater North Sea) and III (the Celtic Seas), but not in Spain, although OSPAR recognizes that no distributional information exists for Spain, and map their southernmost limit at the British Isles (<http://www.ospar.org/>). It would be an interesting exercise to compare the coral and pennatulacean distributional data gathered during COCACE 20 years ago with data from future surveys, to establish whether these habitats are also declining and if so, determine the rate and spatial pattern of their



**Fig. 7.** OSPAR habitats identified in the COCACE dataset: deep coral *Lophelia pertusa* reefs (Álvarez-Claudio, 1994), sea-pen (order Pennatulacea) and, burrowing megafauna's communities. Another deep coral species, *Madrepora oculata*, was also plotted. Rich species hotspots are represented by dark grey areas. The grey area represents the current limits of the prospective Avilés Canyon MPA, and the striped area represents the new proposed limits for the prospective Avilés Canyon in order to encompass keystone habitats, identified under the OSPAR Convention.

decline alone with possible reasons for it. In any case, data from various sources, including COCACE, indicate that the continental slope of the Cantabrian Sea hosts rich benthic communities that include madreporic and pennatulacean habitats (Sánchez et al., 2008), and which should be the target of conservation efforts. Interestingly, none of the 810 COCACE benthic taxa have been included in the European Habitats Directive, the cornerstone of Europe's nature conservation policy ([http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index\\_en.htm](http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm)).

With all its limitations, the COCACE dataset identified two areas of high benthic diversity in the Central Cantabrian coast (Fig. 7). One of these biodiversity hotspots might have contained key habitats such as deep coral and pennatulacean at the continental slope in front of Cape Peñes (between 161 and 1400 m depth) 20 years ago, an area that is out of the limits of the prospective Avilés Canyon MPA, and should be included. Thanks to historical datasets, we have delineated biodiversity hotspots that deserve further research and need to be re-examined. Whether these habitats and their associated high biodiversity are reconfirmed, we recommend that the proposed Avilés Canyon MPA includes the Cape Peñes area within its limits. In summary, the historical COCACE survey, despite some limitations, involved a great sampling and taxonomic effort which is exemplified by its relatively large spatial coverage and remarkable number of taxa identified. Thus, it provides us with rare and valuable baseline information of biodiversity patterns for this important area with which we can contrast contemporary benthic community structure and use to focus future benthic research and conservation efforts.

#### Acknowledgements

We wish to thank to all participants on the COCACE project for their help and support. Also, we would like to thank to WWF/ADENA for

supplying information on the prospective network of MPAs in Spain, and Pablo Otero from the Spanish Institute of Oceanography of A Coruña and Principado de Asturias for bathymetric data. The COCACE project was funded by Hidroeléctrica del Cantábrico S.A and the COSTAS project is funded by the Spanish Ministry of Education and Science (ref. MEC-06-CTM2006-05588). This article is dedicated to the memory of Emilio Anadón, who coordinated the COCACE project and played a key role in the initial development of the Biological Oceanography in the University of Oviedo. ML was partially funded by a Marie Curie Individual Fellowship (PIEF-GA-2008-220063).

#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.jmarsys.2009.09.006](https://doi.org/10.1016/j.jmarsys.2009.09.006).

#### References

- Álvarez-Claudio, C., 1994. Deep-water Scleractinia (Cnidaria: Anthozoa) from southern Biscay Bay. *Cah. Biol. Mar.* 35, 461–469.
- Álvarez-Claudio, C., 1996. Some records of the superfamily Plumularioidea L. Agassiz, 1862 (Cnidaria, Hydrozoa) from the Bay of Biscay. *Mis. Zool.* 18, 9–20.
- Anadón, A., 1993. Misidáceos (Crustacea: Mysidacea) de la plataforma y talud continentales de la costa central asturiana. *Bol. Asoc. Esp. Ent.* 17, 191–204.
- Anadón, N., 1994. Braquiópodos actuales de la plataforma y talud continental de la costa central de Asturias (Norte de España). *Bol. R. Soc. Esp. Hist. Nat.* 91, 65–77.
- Botas, J.A., Fernández, E., Bode, A., Anadón, R., 1990. A persistent upwelling off the Central Cantabrian Coast (Bay of Biscay). *Est. Coast. Shelf Sci.* 30, 185–190.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* 27, 325–349.
- Buchanan, J.B., Kain, J.M., 1971. Measurement of the physical and chemical environment. In: Holme, N.A., McIntyre, A.D. (Eds.), *Methods for the Study of Marine Benthos*. Blackwell Scientific Publications, Oxford, pp. 30–51.
- Carter, R.W., 1990. *Coastal Environments: An Introduction to the Physical, Ecological, and Cultural Systems of Coastlines*. Academic Press, London.

- Cartes, J.E., Maynou, F., Moranta, J., Massutí, E., Lloris, D., Morales-Nin, B., 2004. Patterns of bathymetric distribution among deep-sea fauna at local spatial scale: comparison of mainland vs. insular areas. *Prog. Oceanogr.* 60, 29–45.
- Cartes, J.E., Huguet, C., Parra, S., Sanchez, F., 2007. Trophic relationships in deep-water decapods of Le Danois bank (Cantabrian Sea, NE Atlantic): trends related with depth and seasonal changes in food quality and availability. *Deep-Sea Res. Part I* 54, 1091–1110.
- Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. *Mar. Ecol. Prog. Ser.* 92, 205–219.
- Clarke, K.R., Warwick, R.M., 1994a. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Natural Environment Research Council, Plymouth Marine Biological Laboratory, Plymouth, UK.
- Clarke, K.R., Warwick, R.M., 1994b. Similarity-based testing for community pattern: the two-way layout with no replication. *Mar. Biol.* 118, 167–176.
- Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. *J. Appl. Ecol.* 35, 523–531.
- Clarke, K.R., Warwick, R.M., 1999. The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. *Mar. Ecol. Prog. Ser.* 184, 21–29.
- Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar. Ecol. Prog. Ser.* 216, 265–278.
- Cristobo, J., Ríos, P., Sánchez, F., Anadón, N., 2009. Redescription of the rare species *Podospongia loveni* (Porifera) from the Cantabrian Sea. *Cont. Shelf Res.* 29, 1157–1164.
- de Heer, M., Kapos, V., ten Brink, B.J.E., 2005. Biodiversity trends in Europe: development and testing of a species trend indicator for evaluating progress towards the 2010 target. *Philos. Trans. R. Soc. Lond. B* 360, 297–308.
- Fernández, E., Bode, A., Botas, A., Anadón, R., 1991. Microplankton assemblages associated with saline fronts during a spring bloom in the central Cantabrian Sea: differences in trophic structure between water bodies. *J. Plankton Res.* 13, 1239–1256.
- Flach, E., de Bruin, W., 1999. Diversity patterns in macrobenthos across a continental slope in the NE Atlantic. *J. Sea Res.* 42, 303–323.
- Gage, J.D., Tyler, P.A., 1991. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, Cambridge.
- González-Quirós, R., Cabal, J., Álvarez-Marques, F., Isla, A., 2003. Ichthyoplankton distribution and plankton production related to the shelf break front at the Avilés Canyon. *ICES J. Mar. Sci.* 60, 198–210.
- Guitián, F., Carballas, T., 1976. Técnicas de análisis de suelos. Pico Sacro, Santiago de Compostela.
- Hemery, G., D'Amico, F., Castellón, A., Dupont, B., D'Elbee, J., Lalanne, Y., Mouches, C., 2008. Detecting the impact of oceanic-climatic changes on marine ecosystems using a multivariate index: the case of the Bay of Biscay (North Atlantic–European Ocean). *Global Change Biol.* 14, 27–38.
- Jenness, J., 2004. Nearest features (nearfeat. avx) extension for ArcView 3. x, v.3.8a. Available online at: [http://www.jennessent.com/arcview/nearest\\_features.htm](http://www.jennessent.com/arcview/nearest_features.htm).
- Marquiegui, M.A., Sorbe, J.C., 1999. Influence of near-bottom environmental conditions on the structure of bathyal macrobenthic crustacean assemblages from the Capbreton canyon (Bay of Biscay, NE Atlantic). *Acta Oecol.* 20, 353–362.
- Ocharan, F.J., Álvarez-Claudio, C., Anadón, N., Arrontes, J., Quirce, J.A., Anadón, A., Fuente, D.M., 1989. Estudio sedimentológico de la plataforma y talud continentales de la zona central de Asturias (N de España). *Thalassas* 7, 21–28.
- Olaso, I., 1990. Distribución y abundancia del megabentos invertebrado en fondos de la plataforma Cantábrica: Publ. Espec. Inst. Esp. Oceanogr., vol. 5.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., 2004. Ecosystem-based fishery management. *Science* 305, 346–347.
- Ruano, A., Silva, P., Solano, S., Naves, J., 2007. Cetáceos del litoral asturiano. Áreas de interés para la conservación. Principado de Asturias, Oviedo.
- Sánchez, F., 1993. Las comunidades de peces de la plataforma del Cantábrico: Publ. Espec. Inst. Esp. Oceanogr., vol. 13.
- Sánchez, F., Olaso, I., 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem. *Ecol. Model.* 172, 151–174.
- Sánchez, A., Serrano, A., Parra, S., Ballesteros, M., Cartes, J.E., 2008. Habitat characteristics as determinant of the structure and spatial distribution of epibenthic and demersal communities of Le Danois Bank (Cantabrian Sea, N. Spain). *J. Mar. Sys.* 72, 64–86.
- Serrano, A., Sánchez, F., García-Castrillo, G., 2006a. Epibenthic communities of trawlable grounds of the Cantabrian Sea. *Sci. Mar.* 70, 149–159.
- Serrano, A., Sánchez, F., Preciado, I., Parra, S., Frutos, I., 2006b. Spatial and temporal changes in benthic communities of the Galician continental shelf after the Prestige oil spill. *Mar. Pollut. Bull.* 53, 315–331.
- Sorbe, J.C., 1999. Deep-sea macrofaunal assemblages within the Benthic Boundary Layer of the Cap-Ferret Canyon (Bay of Biscay, NE Atlantic). *Deep-Sea Res. Part II* 46, 2309–2329.
- Vernet, G., Anadón, N., 1991. Continental shelf and littoral Nemeriteans from the North and North-West Spanish Atlantic coast. *Cah. Biol. Mar.* 32, 45–56.
- Warwick, R.M., Clarke, K.R., 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar. Ecol. Prog. Ser.* 129, 301–305.
- Witman, J.D., Etter, R.J., Smith, F., 2004. The relationship between regional and local species diversity in marine benthic communities: a global perspective. *Proc. Natl. Acad. Sci. USA* 101, 15,664–15,669.
- WWF/ADENA, 2005. Conservando nuestros paraísos marinos. *Propuesta de Red Representativa de Áreas Marinas Protegidas en España*. Available at [http://assets.wwwf.es/panda.org/downloads/conservando\\_nuestros\\_paraísos\\_marinos\\_\\_\\_peninsula\\_iberica\\_y\\_baleares1.pdf](http://assets.wwwf.es/panda.org/downloads/conservando_nuestros_paraísos_marinos___peninsula_iberica_y_baleares1.pdf).