

# Variability of groundfish communities of the Cantabrian Sea during the 1990s

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Changes in the structure of fish communities of the Cantabrian Sea Shelf are analysed using information from bottom-trawl surveys carried out every autumn during the period 1990–1999. The trend of ecological indices (species richness and diversity) has been less stable in the shallowest strata during the decade. The effect of environmental variables on the fish communities is explained by inter-set correlation of canonical axis of canonical correspondence analysis (CCA) with the abiotic variables considered (depth, near-bottom temperature, near-bottom salinity, longitude, and geographic stratum) to determine the assemblages of fishes each year. Interannual variations in the structure of the communities are analysed using multitable methods. In contrast to adjacent areas, the narrowest surface of the Cantabrian Sea Shelf produces strong environmental gradients over a short distance. Depth is the most influential and stable factor determining the assemblages observed. The coastal, outer shelf, and shelf-break communities are the strongest sources of variation, both intra-annual and interannual. Using time-series of indices of the main hydrographic driving agents, Navidad current, and upwelling, we try to discover the causes of the instability of spatial structure of assemblages not explained by the abiotic variables considered in the analyses.

Keywords: canonical analysis, Cantabrian Sea, decadal changes, fish communities, multitable methods, Navidad current, upwelling.

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## Introduction

In terms of biogeography, the Cantabrian Sea area is the subtropical/boreal transition zone of the Eastern Atlantic. Typical temperate water species from the south cohabit along with others of northern origin and, consequently, high biodiversity indices exist in relation to adjacent areas (Olaso, 1990; Sánchez, 1993; OSPAR, 2000). In addition, the topographical complexity and the wide range of substrates on its narrow continental shelf give rise to many different types of habitat. This diversity is reflected in the biological richness of the region, which includes a wide range of species, many of which are of commercial interest. Fisheries, in which approximately 200 000 t of fish per year are landed, have an enormous effect on the structure and dynamics of the Cantabrian Sea ecosystem (Sánchez and Olaso, 2001, 2002).

Study of the temporal development of marine ecosystems through the analysis of historical time-series from surveys has usually centred on the study of

descriptive indices (richness, diversity, dominance, etc.) and on describing the structure of communities, through multivariate analyses, for one particular year. It has become evident in many studies that ecological indices show very poor descriptive effectiveness in this kind of work. Although a decline in richness and diversity with fishing effort has been described (Jennings and Reynolds, 2000), increases in diversity at low levels of fishing intensity (ICES, 2000) and even as a response to heavy exploitation (Bianchi *et al.*, 2000) have also been reported. Consequently, it is necessary to extend the information supplied by these indices by providing overall explanations on the changes in the environment.

The Atlantic influence in the western area of the Cantabrian Sea is considered to diminish towards the interior of the Bay of Biscay. More recently, two main seasonal hydrographic driving agents that establish the local oceanography of the Cantabrian Sea have been described: the winter Navidad current and the spring–summer upwelling. In winter, the Navidad appears as an eastward-flowing shelf-break

current that transports warm and saline waters along the continental shelf (Frouin *et al.*, 1990; Pingree and Le Cann, 1990). This current is a prolongation of Poleward Current coming from the Portuguese Shelf and partially aided by southwesterly winds. This flow is the main energy input in the Cantabrian Sea during wintertime (Gil and Sánchez, 2001). In spring–summer, westward winds force surface waters offshore by the Ekman effect, and these are replaced by subsurface cold waters, leading to seasonal upwelling and consequently high primary production events (Botas *et al.*, 1990). The intensity and frequency of both phenomena are highly variable, leading to very different non-mesoscale and non-permanent oceanographic scenarios along the Cantabrian Sea Shelf every year. Nevertheless, it is normally accepted that abundance and distribution patterns of groundfish reflect mainly depth and bottom characteristics. More recently, it has been shown that some demersal fish species in the study area also depend upon the physical dynamics and mesoscale water mass patterns (Sánchez and Gil, 2000; Sánchez *et al.*, 2001).

One problem facing the study of the impact of fisheries on ecosystems by means of the analysis of historical series from surveys is in discerning between the natural causes of variation and anthropogenic impacts (Rogers *et al.*, 1999; Bianchi *et al.*, 2000; Frid and Clark, 2000; Jennings and Reynolds, 2000; Rice, 2000). To this end, it is necessary to carefully determine the sources of spatial and temporal variation, and explain as far as possible the changes occurring each year with respect to the stable part of the series by means of environmental and biological information. In this article we analyse

the structure and composition of demersal fish communities living over the continental shelf of the Cantabrian Sea and the influence certain environmental variables have on them. Similarly, an attempt is made to explain the changes observed during the 1990–1999 decade in relation to the different environmental scenarios present in the area.

## Material and methods

The data of species abundance and distribution come from a series of bottom-trawl surveys carried out every autumn from 1990 to 1999 using standardized methodology (ICES, 1997). The survey area was stratified according to depth and geographical criteria and a stratified random sampling scheme was adopted (Figure 1A). In addition, extra hauls at less than 70 m and deeper than 500 m were accomplished during each survey. The first geographical sector (S1) of the historical series of surveys, situated to the south of Cape Finisterre, was not used in this study because of its different biogeographical characteristics. The number of hauls per stratum was proportional to the trawlable surface, and the sampling unit was made up of 30-min hauls at a speed of 3.0 knots using the baca 44/60 otter trawl gear (Sánchez, 1993; Sánchez *et al.*, 1995; ICES, 1997). The hydrographic characteristics were determined by Seabird CTD probe. Sampling stations were distributed throughout the area of study during the bottom-trawl survey, covering the continental shelf, slope, and adjacent oceanic areas (Figure 1B) according to mesoscale structure resolution criteria (Sánchez and Gil, 2000).

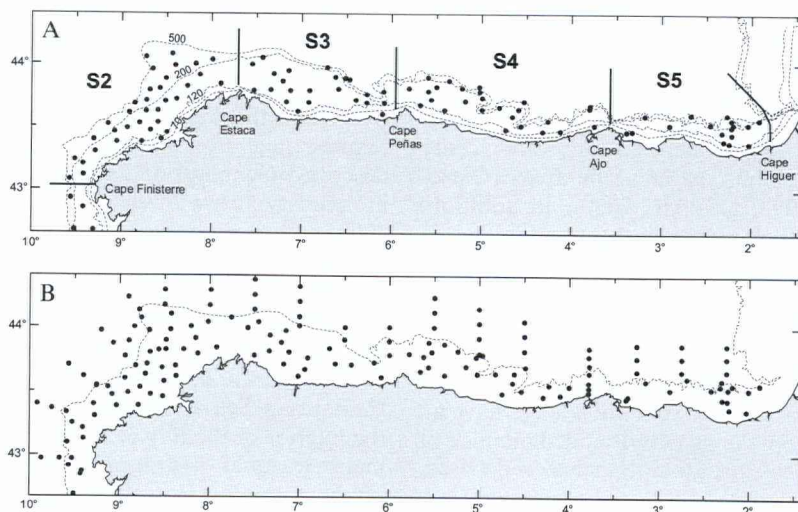


Figure 1. Study area: (A) Bottom-trawl survey stratification and hauls location during the 1998 survey; (B) hydrographic stations during the 1998 survey.

The total number of fish species caught over the trawlable area of the continental shelf, following the methodology previously described, was 152 (Sánchez *et al.*, 2002). For each year, the value of the mean richness indices (number of species by haul), biomass indices (weight in g by haul), and the mean Shannon-Wiener diversity index (Shannon and Weaver, 1963) were obtained.

For the multivariate analysis and based on previous studies (Sánchez, 1993, 1997), a group of only 46 species was selected (Table 1), rejecting pelagic species which were poorly represented in samples using the bottom trawl. In this way, rare or occasional species (i.e. those present in less than 5% of hauls) were eliminated with the aim of reducing the percentage of zeros in the matrices. In this group of 46 species, 6 were analysed by age classes (according to the age-length keys obtained in the surveys), due to age-related changes in their behaviour and habitat.

The explanation of temporal variability due to the effect of environmental variables on communities was carried out using canonical correspondence analysis (CCA) (Ter Braak, 1987, 1988; Ter Braak and Verdonschot, 1995). The statistical significance of the direct methods of ordination was obtained by the Monte Carlo test (Verdonschot and Ter Braak, 1994). From the CCA of each survey a biplot between species and environmental variables was obtained which represents the influence of these variables on the axes of the analysis, quantified in correlations with the factorial axes (Ter Braak, 1990).

The abiotic variables used in the analysis were depth, near-bottom temperature, near-bottom salinity, Western longitude (Atlantic influence), and geographical sector (Figure 1A). The inclusion of the geographical sectors as variable is due to its different geomorphologic characteristic (large shelf in S2 and S3, deeper canyons and rocky bottoms in S4 and very narrow shelf and muddy bottoms in S5). It is noted that depth changes involve subsequent changes in several environmental factors such as pressure, light, temperature, etc. The canonical analysis was only carried out for the period 1993–1999, since hydrographic measurements began on the bottom-trawl surveys in 1993.

For the multivariate analysis of interannual variability of the historical series, a multitable system was used, following the procedure described in Chessel and Gaertner (1997) and Gaertner *et al.* (1998). This system performs the analysis of K-tables with the logic of correspondence analysis (CA), and was carried out by means of the STATIS routine of the program ADE-4 (Thioulouse *et al.*, 1997). The use of these analyses is not widespread in articles on marine ecology, although in the few articles that exist its usefulness in analysing time or spatial series is proven (Gaertner *et al.*, 1998; Blanc, 2000; Ghertsos *et al.*, 2001). The biomass matrices of 51 species were transformed by  $\log(1+x)$  to minimize the dominant effect of exceptional catches.

In the STATIS multitable method, a CA was performed as the first step in calculating the matrix of scalar products between species for each survey, with the aim of standardizing the dimensions of

Table 1. List of 46 species of fishes (51, including age classes) considered in the multivariate analysis.

Code	Species	Code	Species
AMA	<i>Antonogadus macrophthalmus</i>	LCR	<i>Lampanyctus crocodilus</i>
ASP	<i>Argentina sphyraena</i>	LEQ	<i>Lepidion eues</i>
ALA	<i>Arnoglossus laterna</i>	MLA	<i>Malacocephalus laevis</i>
BPR	<i>Bathysolea profundicola</i>	MME0	<i>Merluccius merluccius</i> 0-group
BLU	<i>Buglossidium luteum</i>	MME1	<i>Merluccius merluccius</i> 1-group
CLY	<i>Callionymus lyra</i>	MME2	<i>Merluccius merluccius</i> 2-plus group
CMA	<i>Callionymus maculatus</i>	MVA	<i>Microchirus variegatus</i>
CAP	<i>Capros aper</i>	MPO	<i>Micromesistius poutassou</i>
CEP	<i>Cepola macrophthalma</i>	MSU	<i>Mullus surmuletus</i>
CCU	<i>Chelidonichthys cuculus</i>	NBO	<i>Notacanthus bonapartei</i>
CGU	<i>Chelidonichthys gurnardus</i>	PAC	<i>Pagellus acarne</i>
CLU	<i>Chelidonichthys lucerna</i>	PBO	<i>Pagellus bogaraveo</i>
COB	<i>Chelidonichthys obscura</i>	PER	<i>Pagellus erythrinus</i>
CMO	<i>Chimaera monstrosa</i>	PBL	<i>Phycis blennoides</i>
CCO	<i>Conger conger</i>	RCL	<i>Raja clavata</i>
DCA	<i>Deania calceus</i>	RMO	<i>Raja montagui</i>
ESP	<i>Etmopterus spinax</i>	SCA1	<i>Scyliorhinus canicula</i> 1-group
GAR	<i>Gadiculus argenteus</i>	SCA2	<i>Scyliorhinus canicula</i> 2-plus group
GME	<i>Galeus melastomus</i>	SLA	<i>Solea lascaris</i>
HDA	<i>Helicolenus dactylopterus</i>	SVU	<i>Solea vulgaris</i>
LBO0	<i>Lepidorhombus boschii</i> 0-group	TDR	<i>Trachinus draco</i>
LWH0	<i>Lepidorhombus whiffiagonis</i> 0-group	TSC	<i>Trachyrhynchus scabrus</i>
LBU0	<i>Lophius budegassa</i> 0-group	TLU	<i>Trisopterus luscus</i>
LBU1	<i>Lophius budegassa</i> 1-plus group	TMI	<i>Trisopterus minutus</i>
LP10	<i>Lophius piscatorius</i> 0-group	ZFA	<i>Zeus faber</i>
LP11	<i>Lophius piscatorius</i> 1-plus group		

the tables for the calculation of a matrix of scalar products between the tables of the surveys. After the diagonalization of this matrix, 10 coefficients of the first eigenvector of each survey were used to weight the 10 matrices of scalar products between species and build a table of maximum inertia, called a compromise table. Surveys with common structures contribute to this table to a greater extent. The multivariate analysis through CA of the compromise table defines axes and coefficients which describe the stable part of the surveys. The projection of the analyses separated from the 10 matrices of surveys on the compromise analysis shows interannual variations and the trajectories of temporal variation of species with respect to the stable structure (Chessel and Gaertner, 1997; Gaertner *et al.*, 1998).

Lastly, and in order to make a comparison with the descriptors of variability observed in the decade, we used the indices of Navidad current and upwelling described in R. Sánchez R *et al.* (2003) as a measure of the influence of this main hydrographic

event each year. Upwelling strength has been estimated calculating the percentage of shelf planar (PA) area occupied by (negative) temperature anomalies (TA-) at 50 m depth with respect to the 1993–2000 mean. The relative Navidad strength has been evaluated with January salinities at 80 m, from a time-series of oceanographic recordings at a fixed station at the central shelf of the Cantabrian Sea (43°34.5'N–3°47.0'W).

## Results

The analysis of the evolution of mean values of species richness by haul (Figure 2A) showed a relatively stable pattern in the different strata. In general terms a decrease in richness was seen with depth. In the coastal stratum, two periods were observed: the first (1990–1994) was characterized by a fall in richness. After 1994, the richness index rose progressively from 17 species to about 25 (Figure 2A). The 121–200 and 201–500 strata (middle shelf and outer shelf) presented greater interannual stability.

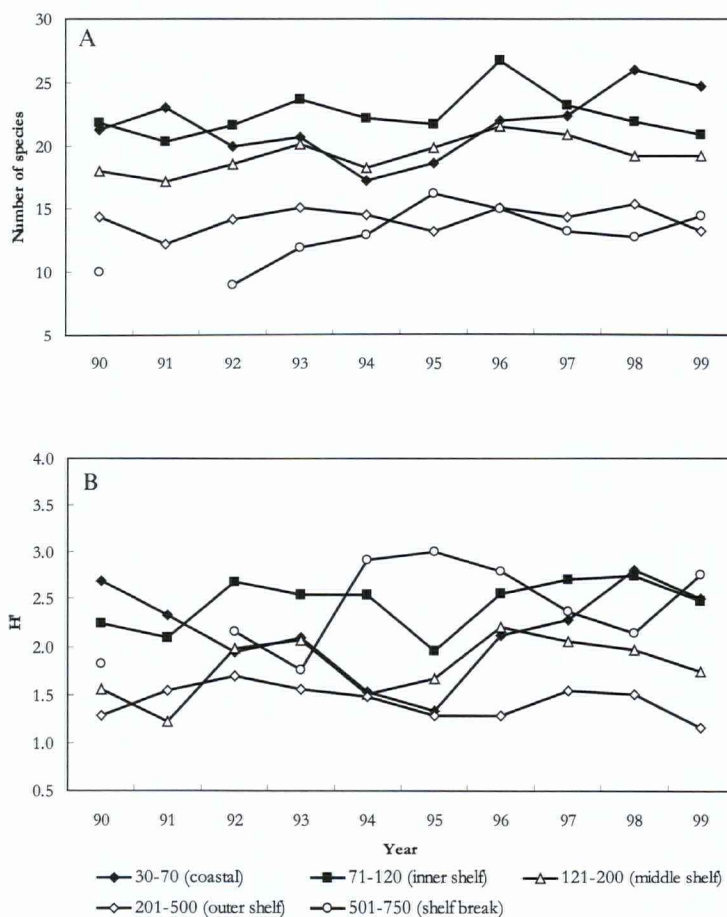


Figure 2. Mean values of indices by year for depth strata: (A) richness (number of species of fishes); (B) Shannon-Wiener diversity index of fish abundance in terms of number ( $H'$ ).

Regarding the diversity in number, as with richness, in the coastal stratum a decrease in values was observed from 1990 to 1995, followed by an increase to 1999. Although diversity was generally more variable than richness, the middle shelf and outer shelf strata were again the most stable, and show the lowest values in the time-series. The fall in diversity in the middle shelf strata in 1991 is noteworthy, although it is mainly due to a significant increase in blue whiting (*Micromesistius poutassou*) biomass. In general terms, the diversity increases towards the extreme strata (shallowest and deepest).

### Effect of environmental variables on the structure of communities over the 1993–1999 period

The previous canonical analyses, by means of DCCA, showed a unimodal response model of species against environmental variables; for this reason a CCA was chosen. The analysis for each year separately showed a constant structure of communities throughout the series, as can be seen in the examples of 1993 and 1998 in Figure 3. In each year, species groupings were determined, similar to the bathymetric groups described by Sánchez (1993) using principal component analysis (PCA), and were distributed on the biplot with a pronounced Guttman effect (Figure 3). The Guttman effect arises when the main two environmental factors are auto-correlated (Greenacre, 1984); in this case, depth and temperature. The most discriminatory were the coastal group and the deepest strata groups (outer shelf and shelf break), situated at the extremes of the environmental gradients analysed. On the other hand, in the middle segments of these gradients, the inner shelf and middle shelf groups displayed reduced dispersion, with a position closer to the centroid of the biplot. This centroid is occupied by ubiquitous species of a wide optimal environmental range.

As shown in Figure 4, the formation of the CCA axes according to the environmental variables is fairly constant throughout the decade. In all years the most discriminatory variable is depth, with an inter-set correlation higher than 0.90 with the first axis (Table 2), correlation that increases slightly throughout the decade. Axis 2 is correlated mainly with salinity and, to a lesser extent, with longitude. The variable longitude, i.e. the Atlantic factor, is much less discriminatory in the years 1994 and 1995, but is of greater importance in 1997 (Table 2). The westernmost sector (S2) is more discriminatory, and so more distinct, in the period 1996–1999 than in previous years, where sectors discriminate with similar weight. However, it is difficult to obtain clear conclusions of assemblages' spatial zonation from

the ordination of the different geographical sectors. The radial pattern is not constant, probably due to the interaction of salinity–temperature pattern of each sector with other abiotic variables, which were not taken into consideration.

Temperature contributes similarly to both axes, opposite to depth, salinity, and longitude. This depth–salinity–temperature–longitude relationship pattern obtained from CCA reflects the characteristic hydrological dynamics of the Cantabrian Sea and their influence on the main groundfish assemblages (Figure 3). The set of these four abiotic variables explains 21.4% of the variance of species data and 72.9% of the variance of species–environment relationship (mean values for the decade; Table 2).

### Stability of communities' structure over the 1990–1999 decade

A CA was performed among the 10 surveys and a very high value of intraperiod inertia (inertia is the multivariate measure of the amount of variation in a data set) was found (97.5%) against interperiod inertia (2.5%). The differences between surveys were considered significant ( $p < 0.05$ ) according to a permutation test. The multitable analysis shows a balanced contribution of surveys to the compromise analysis (Table 3). The best fits to the compromise table are found in 1990 and from 1994, 1996 being the survey which deviated the least ( $\cos^2 = 0.68$ ; Table 3). In contrast, the fit of the 1991 survey to the compromise is the lowest ( $\cos^2 = 0.28$ ) in addition to being the survey which contributes least to the analysis (weight = 0.28).

Figure 5 shows the structure of fish communities in the compromise analysis, i.e. the stable part of the 10 surveys used in the analysis. There is a great pattern of spatial reproducibility throughout the decade, since the representation of the compromise analysis (represented as an empty circle in Figure 5) faithfully reproduces the structure described by the canonical analysis from each year (Figure 3). A clear Guttman effect can also be observed, with two branches which separate the species into two well-differentiated groups of little more than 10 species, and a transition group very close to the origin, of less discriminatory species. This discrimination is a product of a first bathymetric factor, leading to the identification of axis 1 with depth. In this representation the 5 bathymetric groups already described can be distinguished, as in the canonical analysis.

The group of species situated in the negative quadrant of both axes corresponds to coastal species, where the most discriminatory ones are *Solea lascaris* and *Pagellus erythrinus*, along with a small group of species, all of them preferentially coastal (*Pagellus bogaraveo*, *Buglossidium luteum*, *Trachinus*

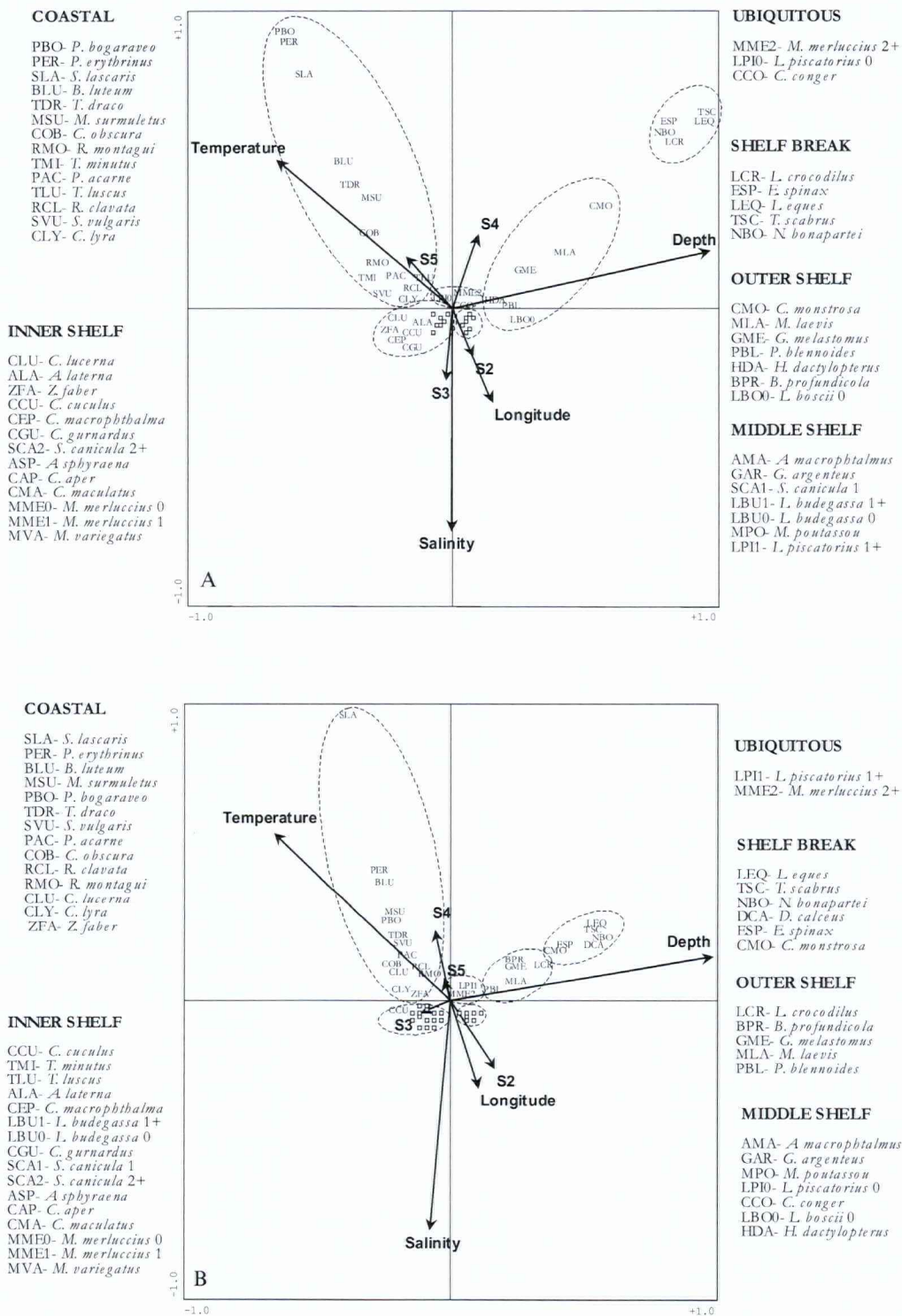


Figure 3. CCA biplot of species vs. environmental variables. (A) 1993 survey; (B) 1998 survey.

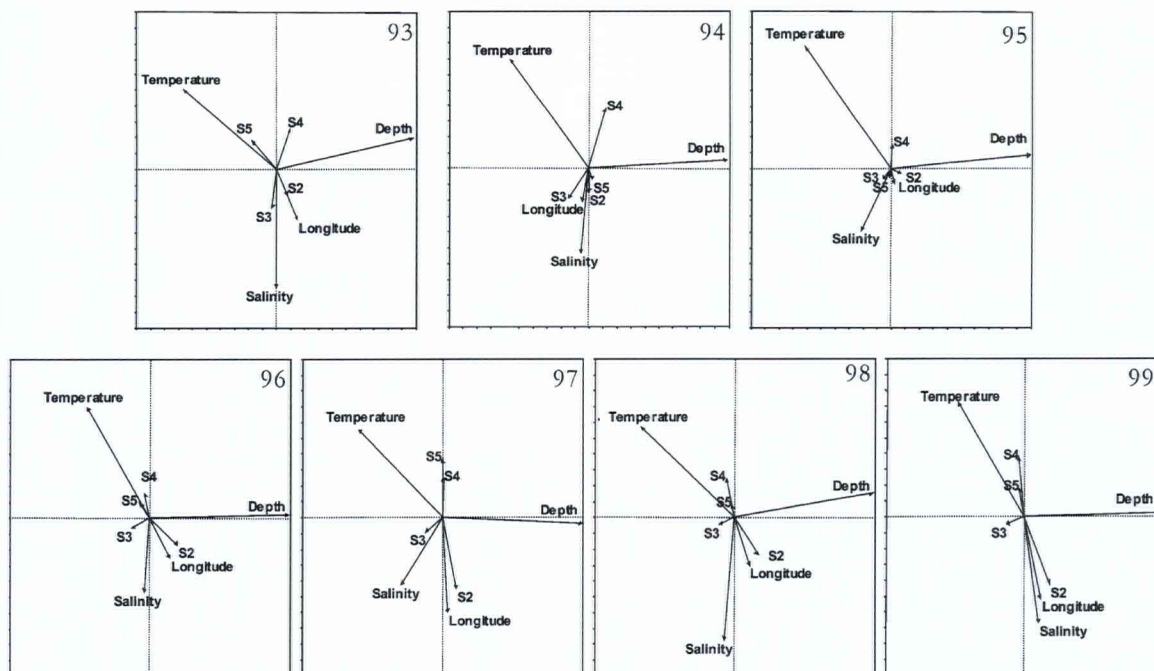


Figure 4. Correlation of environmental variables on the first two canonical axis of CCA for the surveys 1993–1999.

Table 2. Interset correlations by year between environmental variables and the first and second canonical axis. Eigenvalues and percentage of variance of species data and of species–environment relation explained by the CCA plane.

		1993	1994	1995	1996	1997	1998	1999
Axis 1	Depth	0.902	0.925	0.944	0.964	0.966	0.952	0.971
	Temperature	−0.619	−0.526	−0.585	−0.437	−0.578	−0.642	−0.475
	Salinity	−0.004	−0.054	−0.203	−0.038	−0.281	−0.073	0.100
	Longitude	0.140	−0.049	0.022	0.138	0.038	0.102	0.117
	Sector 2	0.072	0.000	0.063	0.195	0.098	0.160	0.179
	Sector 3	−0.027	−0.135	−0.059	−0.123	−0.116	−0.103	0.126
	Sector 4	0.092	0.111	0.004	−0.037	0.007	−0.059	−0.042
	Sector 5	−0.163	0.021	−0.014	−0.067	−0.003	−0.019	−0.035
Axis 2	Depth	0.145	0.031	0.065	0.016	−0.028	0.120	0.018
	Temperature	0.374	0.429	0.597	0.504	0.386	0.460	0.546
	Salinity	−0.561	−0.330	−0.302	−0.338	−0.292	−0.628	−0.505
	Longitude	−0.239	−0.127	−0.072	−0.183	−0.417	−0.245	−0.391
	Sector 2	−0.124	−0.089	−0.029	−0.120	−0.310	−0.191	−0.319
	Sector 3	−0.184	−0.117	−0.051	−0.047	−0.064	−0.037	−0.037
	Sector 4	0.187	0.235	0.114	0.112	0.168	0.193	0.281
	Sector 5	0.132	−0.041	−0.043	0.068	0.253	0.060	0.130
Eigenvalues Axis 1		0.309	0.350	0.436	0.442	0.408	0.434	0.484
Eigenvalues Axis 2		0.180	0.103	0.188	0.180	0.122	0.211	0.190
% Var species data		19.3	17.7	23.7	24.3	20.0	22.4	22.1
% Var spp.–environment relation		67.1	70.5	72.3	76.6	74.0	74.4	75.1

*draco*, *Mullus surmuletus*). Near the centroid are the species of transition in the bathymetric gradient, characteristic of the continental shelf, with very poor discrimination. Two groups can be distinguished, one of inner shelf species which show more affinity for the shallowest waters (*S. canicula*, *M. merluccius* classes 0 and 1, *L. whiffiagonis* class 0, *L. budegassa* class 1 plus, *L. piscatorius* class 0) and

another of middle shelf species (*Micromesistius poutassou*, *L. budegassa* class 0, *Conger conger*, *L. boscii* class 0, *Helicolenus dactylopterus*, *Gadiculus argenteus*). The top predators of the demersal and benthic domains, respectively, *M. merluccius* (class 2 plus) and *L. piscatorius* (class 1 plus) do not belong to any group, and are situated closer to the centroid, indicating their wide optimal environmental range,

Table 3. Number of stations for survey, contribution of each survey in the compromise (weight), and fit of each survey to the compromise ( $\cos^2$ ).

Survey	Stations	Weight	$\cos^2$
1990	103	0.33	0.48
1991	88	0.28	0.28
1992	97	0.30	0.44
1993	92	0.29	0.44
1994	100	0.33	0.58
1995	101	0.32	0.58
1996	100	0.33	0.68
1997	104	0.32	0.46
1998	101	0.33	0.53
1999	105	0.31	0.45

which increases their number of available preys (Sánchez, 1993).

The other branch, situated in the positive x-axis quadrant, contains the deepwater species. This group can be split into two according to a bathymetric criterion. The cluster of outer shelf species groups together *Chimaera monstrosa*, *Bathysolea profundicola*, *Galeus melastomus*, *Phycis blennoides*, and *Malacocephalus laevis*. The other group corresponds to the shelf-break community and is made up of species such as *Notacanthus bonapartei*, *Trachyrhynchus scabrus*, *Lepidion eques*, *Deania calceus*, *Etmopterus spinax*, and *Lampanyctus crocodilus*.

Figure 5 also shows the interannual variations (represented as empty squares) from the stable structure. The largest interannual deviations are found in the coastal and shelf-break communities. The continental shelf (inner and middle shelf) communities are those that have the lowest range of variation.

In particular, the ubiquitous species *M. merluccius* (class 2 plus) and *L. piscatorius* (class 1 plus) present the lowest values of interannual variability.

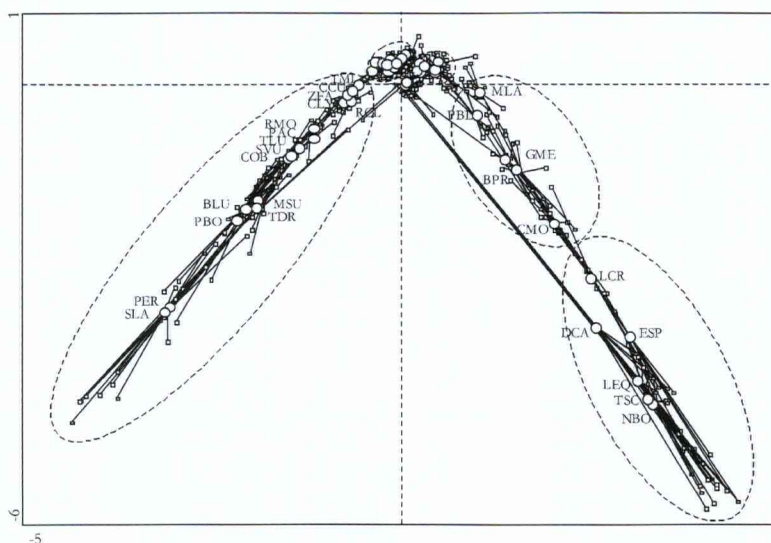
Finally, Figure 6 shows the relationship of the descriptive parameters of multivariate, canonical, and multitable analyses, and the external indices used to describe the main hydrographic driving agents. In the period with biological-physical data (1993–1999), three different hydrographic scenarios were observed: (A) strong *Navidad* current and weak upwelling index (years 1993, 1998, and 1999); (B) moderate *Navidad* current and high upwelling index (years 1994 and 1997), and (C) weak *Navidad* current and high upwelling index (years 1995 and 1996). The dynamics that originate these three types of scenarios in the area and their occurrence are described in Gil and Sánchez (2001). It can be seen that the years with the maximum percentage of variance explained by the abiotic variables considered in the CCA analysis correspond with scenario type C (24%). Low percentages of variance explained correspond with scenario type B (18–20%). Also, years with maximum values of upwelling indices (1994 to 1997) coincide with those of least discrimination in salinity and longitude (except 1997). A relationship also seems to exist between the variance explained by the environmental variables in the canonical analysis and the fit of each year to the stable part in the multitable analysis, since the years that contribute most to the stable part (Table 3) are those which are best explained by the set of environmental variables used.

#### INNER SHELF

LNWH0-*L. whiffiagonis* 0  
SCA1-*S. canicula* 1  
SCA2-*S. canicula* 2+  
MMH0-*M. merluccius* 0  
MMH1-*M. merluccius* 1  
MVA-*M. variegatus*  
ALA-*A. laterna*  
CHP-*C. macrophthalmus*  
CMA-*C. maculatus*  
ASP-*A. sphyraena*  
TLU-*T. luscus*  
CAP-*C. aper*  
CGU-*C. gurnardus*  
LPI0-*L. piscatorius* 0  
LBU1-*L. budegassa* 1+

#### COASTAL

TMI-*T. minutus*  
CCU-*C. cuculus*  
ZFA-*Z. faber*  
CLY-*C. lyra*  
RCL-*R. clavata*  
RMO-*R. montagu*  
PAC-*P. acarne*  
SVU-*S. vulgaris*  
CLU-*C. lucerna*  
COB-*C. obscura*  
MSU-*M. surmuletus*  
TDR-*T. draco*  
BLU-*B. luteum*  
PBO-*P. bogaraveo*  
PER-*P. erythrinus*  
SLA-*S. lascaris*



#### UBIQUITOUS

MMH2-*M. merluccius* 2+  
LPI1-*L. piscatorius* 1+

#### MIDDLES SHELF

GAR-*G. argenteus*  
LBO0-*L. bosci* 0  
CCO-*C. conger*  
MPO-*M. pontassou*  
AMA-*A. macrophthalmus*  
HDA-*H. dactylopterus*  
LBU0-*L. budegassa* 0

#### OUTER SHELF

MLA-*M. laevis*  
PBL-*P. blennoides*  
GME-*G. melastomus*  
BPR-*B. profundicola*  
CMO-*C. monstrosa*

#### SHELF BREAK

LCR-*L. crocodilus*  
ESP-*E. spinax*  
DCA-*D. calceus*  
LEQ-*L. eques*  
TSC-*T. scabrus*  
NBO-*N. bonapartei*

Figure 5. Stable structure of species projected on the first factorial plane of compromise in the decade of 1990s and variations inter-surveys of the species around the stable structure. Position in the compromise (O); position in each survey (□).

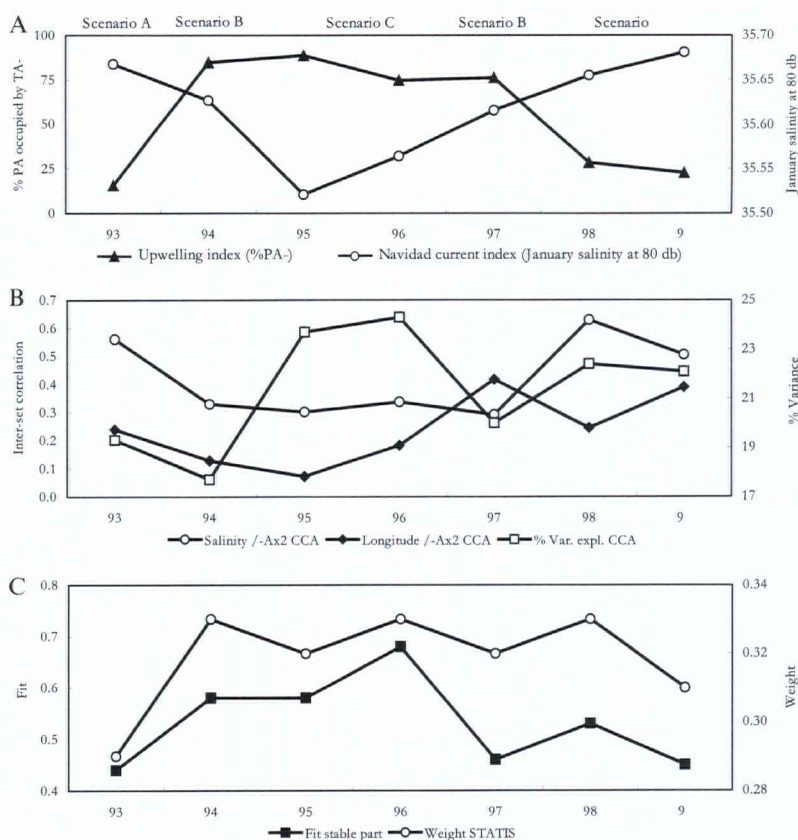


Figure 6. Values during the 1993–1999 period of (A) main hydrographic driving agents indices and scenarios, (B) correlation between environmental variables and canonical axis of CCA, and variance of species data explained by this first CCA plane, (C) fit of each survey with the stable part (compromise) and weight of this surveys in the multitable analysis.

## Discussion

The sources of variation existing in the results may differ in spatial variability, which has been revealed to be mainly bathymetric, and temporal variability, which is partly related to the evolution of the main hydrographic driving agents described in the area.

The bathymetric differences show a progressive decrease in mean fish species richness with depth, as described in the Cantabrian Sea by Sánchez (1993) and in adjacent areas by Fariña *et al.* (1997a). This pattern is reasonably stable in the decade. The decline in the number of species with depth is probably brought about by the higher productivity of the coastal waters, in contrast to the inverse phenomena appearing in invertebrates (Olaso, 1990; Fariña *et al.*, 1997b), which prefer deeper water and muddy substrates because of their predominantly detritivorous feeding habits. Interannual variations of diversity can be explained only in part by the action of the main hydrographic events which govern the area, because this index is strongly affected by the values of dominance of migratory gregarious species

with a wide range of distribution area (i.e. blue whiting, horse mackerel, and silvery pout (*Gadiculus argenteus*)). The period of years with strong upwelling indices corresponds to the lowest diversity of the coastal community. This may be caused by the direct effect of the increase in primary production in the coastal area, and consequently on the levels of biomass of some planktophagous fish (with high reproductive rates and fast growth) and particularly schools of juveniles of horse mackerel. The spatial structure shows how variability is mainly detected in the coastal, outer shelf and shelf break strata, that is, at the extremes of the environmental gradients, while the central continental shelf strata are more stable. This difference in stability is visible in all the analyses performed: in the ecological indices (especially for the coastal stratum), in the canonical analyses by survey, in the representation of the stable part of the decade and in the trajectories followed by species around this stable structure. The central strata of the continental shelf are those that have suffered greater pressure from the trawl fleet for decades, and consequently a greater degree of simplification of communities must be expected

(Sánchez, 1993). At the same time, the geomorphology of the ground is more homogeneous, minimizing the ecotonal effect.

Overlying the temporal variability, there is a reproducible spatial structure throughout the decade, in which some unvarying bathymetric groups can be found. It can therefore be said that fish communities remained relatively stable throughout the period studied, with a high degree of reproducibility of the bathymetric spatial pattern. This defined bathymetric structure has been described in previous studies carried out in the area (Sánchez, 1993, 1997; Fariña *et al.*, 1997a) and in other nearby areas (Zendrera, 1990; Lauroz, 1993; Gaertner *et al.*, 1998; Souissi *et al.*, 2001). The smaller depth discrimination on the demersal fish assemblages obtained by Fariña *et al.* (1997a) in the area near Galicia is due to the lack of sampling on the coastal and shelf-break strata during the study period (1980–1991). Our results identify the most extreme strata of the Cantabrian sea shelf (coastal and shelf break) as the main source of variability in the decade. In the Gulf of Lions area, Gaertner *et al.* (1998) derived similar results through a multitable analysis, finding the greatest trajectories of species for each year in the extreme strata (coastal region and continental slope) with respect to the representation of the stable part of the period 1983–1992. A possible explanation for this larger variability in the Cantabrian Sea (usually considered as a nursery area) is a greater influence over the coastal communities of recruitment to the bottom of abundant species in the area, which are driven by yearly hydrographic scenarios (Sánchez and Gil, 2000; Sánchez *et al.*, 2001; Gil and Sánchez, 2001). The subsequent ontogenetic migratory behaviour towards deeper zones, described for some species (Fariña and Abaunza, 1991; Sánchez, 1993), increases this variability. On the other hand, the shelf-break communities may be influenced by the environmental variability on the eastward slope current, which has a strong impact in the distribution and dispersion of the early stages of fish in the area (Reid, 2001). Also, the vertical motion of the water, produced by the associated eddies, enhanced the production processes of subsurface layers (Piontkovsky *et al.*, 1995) over the shelf break. This fact determines the reproductive behaviour of many demersal species that migrate to these shelf-break areas with larger productivity and transport mechanisms facilitating larval survivorship (i.e. hake, red sea-bream).

On the other hand, the Navidad current seems to determine haline-longitudinal variability. Years with strong current indices (1993, 1998, and 1999) of hydrographic scenario type A create haline gradients which are translated into greater discrimination of the salinity factor in the CCA analysis, and because of its entrance from the west, of the longitudinal

factor. A moderate Navidad current is required to prevent larvae and pre-recruits of demersal fish being transported off the progressively narrow shelf of the Cantabrian Sea. Scenario type B is an optimal situation that occurs after the adequate development of an upwelling front over the shelf area and surrounded by its associated mesoscale structures. This energetic scenario is responsible for high hake recruitment in the period considered (Sánchez and Gil, 2000; Sánchez *et al.*, 2001; Sánchez *et al.*, 2002), and probably also has similar consequences for many other demersal species. The mesoscale dynamics have a strong impact on biological variability and patchiness (Mann and Lazier, 1991) and are probably the cause of the low variance value explained in our CCA analysis for the years 1994 and 1997.

Finally, our results show that the hydrographic scenario type C is the one that is better explained by the set of environmental variables used in the CCA analysis, and makes up the most stable structure of groundfish assemblages throughout the decade. This scenario (i.e. 1995 and 1996) is characterized by the considerable width of the cold coastal fringe and by the anticyclonic eddies located further away from the shelf area (Sánchez and Gil, 2000; Gil and Sánchez, 2001). The lack of mesoscale activity over the shelf probably produces a more homogeneous situation over the bottom, with less disturbance of the stable structure of the communities, increasing the discriminant value of depth, near-bottom temperature, near bottom salinity, and the other abiotic variables considered.

The aim of the present article is not to draw conclusions relating to the evolution of ecological structures ascribed to the fishing pressure, which has been applied to the area, but to establish this evolution and explain it through the environmental information available. In this sense, the combined analysis of individual surveys with a multitable analysis, which separates the stable part from the interannual variations, seems useful for the interpretation of historical series. Later, with more information on the changes in fishing fleet strategies, distribution of effort in the area, identification of vulnerable species (Rogers *et al.*, 1999; Jennings and Reynolds, 2000), and with experiments on fishing exclusion areas (Hoffmann and Dolmer, 2000; Sumaila *et al.*, 2000), the effect of fishing on groundfish communities in the Cantabrian Sea may be determined.

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