J. Mar. Biol. Ass. U.K. (2000), **80**, 981–988
Printed in the United Kingdom

Demersal fish assemblages and habitat characteristics on the continental shelf and upper slope of the north-western Mediterranean

Montserrat Demestre*, Pilar Sánchez and Pere Abelló

Institut de Ciéncies del Mar (CSIC), P. Joan de Borbó, s/n, 08039 Barcelona, Spain. *E-mail: montse@icm.csic.es

Continental shelf and upper slope fish communities were studied along the Catalan coast based on 66 experimental bottom otter trawls. A total of 79 demersal fish species were studied by means of cluster analysis and multi-dimensional scaling (MDS) ordination for community structure. Analysis revealed the existence of five major location clusters. Similarity percentage analysis (SIMPER) was determined by comparing the dissimilarity between two groups of samples using the discriminating species. Geomorphological characteristics, bottom substratum and depth showed direct influences on species assemblages. High correlation between the biotic data samples and depth was observed. The fish species assemblages identified five main demersal fish associations which corresponded with the five location clusters and with five benthic sediments (mud of the upper slope, sand and gravel, mud of the shelf, muddy-sand and sand with rocky outcrops).

INTRODUCTION

The Mediterranean coasts support important demersal fisheries, with the Catalan coast being a typical example. It is approximately 550 km long with 28 ports, 18 of which have daily fishing activity (Martín, 1991; Lleonart, 1993). Surveys to study the demersal animal communities on the continental shelf and upper slope off the Catalan coast have been focused on faunistic studies of decapod crustaceans (Abelló et al., 1988; Cartes & Sardà, 1993), and studies related to fish communities have been conducted chiefly on bathyal and slope bottoms (Stefanescu et al., 1993, 1994). Studies performed on the continental shelf and upper slope in other areas of the Mediterranean are source material (e.g. D'Onghia et al., 1998; Moranta et al., 1998; Ungaro et al., 1998; Vassilopoulou et al., 1998).

The present study aims to analyse the structure and seasonality of the fish communities from the shelf and upper slope off the Catalan coast. The objective was to describe its faunistic composition and to establish the main faunistic assemblages of fish species based on interspecific associations according to bottom types and depth.

MATERIALS AND METHODS

Study area: topography and sediment structure

The Catalan coast (Figure 1) can be divided into three different topographic units (Demestre, 1986). The northern zone consists mainly of a rocky coast, with a predominance of sand and sandy-muddy bottoms. The distribution of superficial sediments on the continental shelf gradually changes from sand and gravel associated with rocky outcrops, carbonated sands with a gravel matrix, muddy carbonated sands, to the sandy-mud and finally the mud and clay of the outer part of the shelf and continental slope (Medialdea et al., 1986; Ercilla et al., 1995). The shelf is narrow, and can reach depths of 800 m on the slope at only 6 or 7 km from the coast, owing to the presence of submarine canyons. The southern zone has very different characteristics. Its shelf is very wide (at some points over 65 km), with a predominance of muddy-sand and mud bottoms inherent to the continental shelf. It is an area of influence for continental waters from the River Ebro. Six types of sediments have been defined in this area ranging from those with a minimum sand content, clay-muddy sediments, to those that have more than 50% sand, together with the sandy sediments with a high gravel content. Mud and clay with low percentages of sand are the predominant sediment, occupying a large part of the shelf. In the sediments from more coastal area, sand predominates over mud (Medialdea et al., 1986; Guillén & Palanques, 1997). In the central intermediate zone of the Catalan coast the shelf is not very wide, with some underwater canyons. The bottom is generally muddy-sand, as well as sand next to small formations of rocky barriers close to the coastal line. In this area the carbonated sedimentary facies are frequent. They are rich in calcareous algae, molluscs, echinoderms, and also sea grass meadows which contain an important fraction of epiphytic fauna (Guillén & Palanques, 1997).

Methodology

Sampling was performed quarterly during 1991 using otter bottom trawls along the Catalan coast (winter=17 hauls, spring=12, summer=14, autumn=23, Table 1). The areas exploited by three representative ports were chosen: Blanes in the north, Vilanova i la Geltrú in the central zone and Sant Carles de la Ràpita in the southern zone (Figure 1). A commercial fishing trawl with a distance between wings of approximately 30 m was used, with a stretched mesh size of 36 mm. A total of 66 experimental hauls were conducted out in a depth stratified sampling

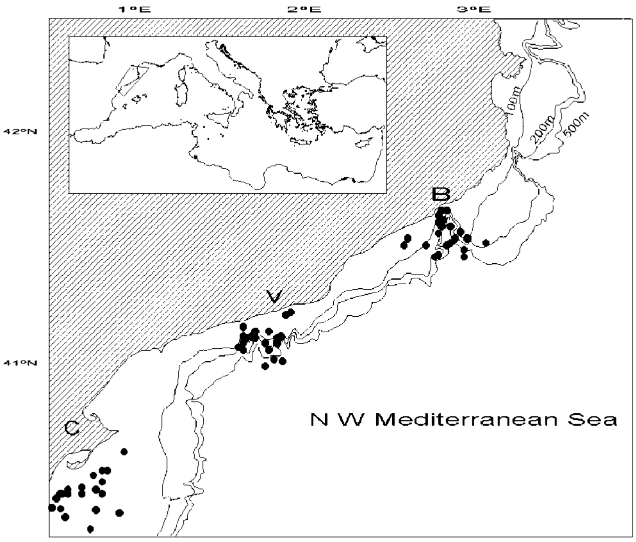

Figure 1. Map of the Catalan coast illustrating the position of the trawl samples and location of the three selected ports. B, Blanes; V, Vilanova; C, Sant Carles. 100 m, 200 m and 500 m isobaths are shown.

grid (in the northern area 21, 23 on the central and 22 in the southern; Table 1). Tows had a duration of 60–120 min depending on the bottom characteristics, and were standardized to 60 min [number individuals per hour hauling (ind h^{-1})], for subsequent numerical and comparative processing. The mean depth of the hauls ranged between 22 and 548 m (north=37–522 m, central=29–548 m, south=22–74 m; Table 1). All hauls were conducted during daylight hours.

The catch of each sample was sorted, and all fish collected were identified to species level, counted and weighed. Analysis of data abundance was carried out by using the PRIMER (Plymouth Routines in Multivariate Ecological Research) package (Clarke & Warwick, 1994). Cluster analysis was applied to the species–hauls matrix using multidimensional scaling (MDS) techniques, and the double square root transformation. The percentage haul similarity was calculated by means of the Bray–Curtis index; a group average fusion strategy, with UPGMA (unweighted pair-group method using arithmetic averages) being applied to link similar samples into clusters. Similarities between samples were displayed on ordination plots following the application of

Table 1. *Summary of sampling data.*

Num	Date	Depth (m)	Area	Bottom	Num	Date	Depth (m)	Area	Bottom
1	06/03/91	154.8	V	M	34	10/07/91	21.6	C	S
2	07/03/91	189.0	B	M	35	18/09/91	57.6	V	R
3	27/03/91	41.4	C	X	36	05/09/91	423.0	B	M
4	06/03/91	175.5	V	M	37	02/10/91	24.3	C	S
5	07/03/91	333.0	B	M	38	18/09/91	212.4	V	M
6	27/03/91	45.9	C	X	39	05/09/91	180.0	B	M
7	06/03/91	59.4	V	X	40	02/10/91	42.3	C	X
8	07/03/91	436.5	B	M	41	18/09/91	180.0	V	M
9	27/03/91	27.0	C	S	42	05/09/91	110.7	B	T
10	06/03/91	48.6	V	R	43	02/10/91	47.7	C	X
11	07/03/91	128.7	B	X	44	18/09/91	36.9	V	R
12	27/03/91	25.2	C	S	45	05/09/91	100.8	B	X
13	06/03/91	63.9	V	R	46	02/10/91	21.6	C	S
14	07/03/91	127.8	B	X	47	18/09/91	31.5	V	S
15	27/03/91	45.9	C	X	48	02/10/91	36.0	C	S
16	06/03/91	30.6	V	R	49	20/10/91	57.6	B	R
17	27/03/91	47.7	C	X	50	20/10/91	247.5	B	M
18	29/05/91	193.5	B	M	51	20/10/91	351.0	B	M
19	29/05/91	270.9	B	M	52	20/10/91	109.8	B	X
20	29/05/91	522.0	B	M	53	20/10/91	36.9	B	R
21	29/05/91	104.4	B	T	54	20/10/91	42.3	B	R
22	29/05/91	95.4	B	T	55	13/11/91	196.2	V	M
23	29/05/91	98.1	B	T	56	27/11/91	27.0	C	S
24	05/06/91	48.6	V	X	57	13/11/91	548.1	V	M
25	05/06/91	54.0	V	X	58	27/11/91	30.6	C	S
26	05/06/91	65.7	V	R	59	13/11/91	465.3	V	M
27	05/06/91	65.7	V	R	60	27/11/91	27.9	C	S
28	05/06/91	57.6	V	R	61	13/11/91	32.4	V	S
29	05/06/91	57.6	V	R	62	27/11/91	22.5	C	S
30	10/07/91	73.8	C	X	63	13/11/91	38.0	V	S
31	10/07/91	72.0	C	X	64	27/11/91	22.5	C	S
32	10/07/91	45.9	C	X	65	13/11/91	28.8	V	S
33	10/07/91	21.6	C	S	66	27/11/91	23.4	C	S

Num, number of the haul; Area, selected ports—B, Blanes in the north; V, Lilanova i la Geltrú in the centre; C, Sant Carles de la Ràpita in the south; Bottom, bottom type—M, muddy bottoms on the upper slope; T, sandy and gravel bottoms; X, muddy mud-clay bottoms on the shelf; S, muddy-sand bottoms; R, muddy-carbonated sand bottoms associated with rocky outcrops.

MDS. To establish which were the main species that contributed to the average Bray–Curtis dissimilarity between two groups of samples, the SIMPER (similarity percentage analysis) routine was used (Clarke, 1993). The ten dominant species are presented in the results. Abundance and biomass were compared for the species of the groups obtained from cluster analysis and MDS.

In the case of species, the relationship between distribution and bottom types has been studied by means of MDS ordination. This relationship has been based on the type of sediment from each haul (Ercilla et al., 1995; Guillén & Palanques, 1997), and the characteristic habitats of each one of them (Pérès & Picard, 1964; Demestre, 1986). So each species has been assigned to a type of bottom based on the most frequent type in which it was present (see codes in Table 1).

RESULTS

Sample associations

A total of 124 fish species were captured in the present study, but only those appearing in over 3% of the samples were considered for further analysis (Table 2).

Cluster analysis of the samples (Figure 2) showed the occurrence of two main assemblages: (1) samples from the shelf edge and upper slope; and (2) those from more coastal areas (shallow waters and intermediate shelf). Within the shelf edge and upper slope group (1), two subgroups of samples were identified: (A) samples from the shelf edge with a mean ±SD depth of 109.5 ±12.7 m; and (B) samples from the upper slope, with a mean depth of 298.7 ±133.8 m. The coastal group (2) showed three main assemblages. The first division, (C) was formed by a group of samples from the northern area with a mean depth of 45.6 ±10.7 m; a second division contained two groups of samples (D and E) from the central and southern areas: group D with a mean depth of 49.2 ±13.0 m, and group E, the most coastal, with a mean depth of 35.8 ±15.5 m. The result of MDS analysis (Figure 3) confirmed the clear separation of the five groups of samples, with the separation of groups A and B from the others being especially evident. The analyses of relationship between depth and sample associations showed a high weighted Spearman correlation value, 0.747.

The results of the SIMPER (Table 3) showed the average dissimilarity between the five main location clusters. These groups appeared to be very well defined since the separation between them was very high. So the shallow water group (E) and the upper slope group (B) showed the highest average dissimilarity value, 92.79. The most similar were the shallow water group (E) and the intermediate shelf group (D) with an average dissimilarity value of 62.9. A different community structure strongly linked to seasonality appears to be the key factor differentiating the two shallow shelf assemblages, D and E. Hake, with its peak recruitment in spring (average abundance=815.42 ind h^{-1}; Table 3) in group D, vs gobiids and red mullet, with their peak recruitment in late summer and autumn in group E (*Lesuerigobius friesii*=116.69 ind h^{-1}; *Deltentosteus quadrimaculatus*=58.74 ind h^{-1} and *Mullus barbatus*=125.59 ind h^{-1}; Table 3), are the most

Table 2. *Total species caught off the Catalan coast. Code: Species identifying number used in the MDS ordination.*

Species	Code	Species	Code	Species	Code
Alosa fallax	1	*Gadiculus argenteus*	28	*Raja asterias*	55
Argentina sphyraena	2	*Gaidropsarus mediterraneus*	29	*Sardina pilchardus*	56
Arnoglossus laterna	3	*Glossanodon leioglossus*	30	*Scorpaena loppei*	57
Arnoglossus ruepelli	4	*Gobius niger*	31	*S. notata*	58
A. thori	5	*Helicolemus dactylopterus*	32	*Scyliorhinus canicula*	59
Aspitrigla cuculus	6	*Hymenocephalus italicus*	33	*Seriola dumerili*	60
A. obscura	7	*Lampanyctus crocodilus*	34	*Serranus cabrilla*	61
Blennius ocellaris	8	*Lepidopus caudatus*	35	*S. hepatus*	62
Boops boops	9	*Lepidorhombus boscii*	36	*Solea vulgaris*	63
Bothus podas	10	*Lepidotrigla cavillone*	37	*Sphyraena sphyraena*	64
Callionymus maculatus	11	*Lesueurigobius friesii*	38	*Spicara* spp.	65
C. reticulatus	12	*L. suerii*	39	*Stomias boa*	66
Capros aper	13	*Lophius boudegassa*	40	*Symphurus ligulatus*	67
Cepola rubescens	14	*L. piscatorius*	41	*S. nigrescens*	68
Chlorophthalmus agasizii	15	*Merluccius merluccius*	42	*Synchiropus phaeton*	69
Citharus linguatula	16	*Microchirus variegatus*	43	*Torpedo marmorata*	70
Coelorhinchus coelorhinchus	17	*Micromesisteus poutassou*	44	*Trachinus draco*	71
Conger conger	18	*Mullus barbatus*	45	*Trachurus* spp.	72
Crystallogobius linearis	19	*M. surmuletus*	46	*Trachyrhynchus trachyrhynchus*	73
Deltentosteus quadrimaculatus	20	*Notoscopelus elongatus*	47	*Trigla lucerna*	74
Diplodus annularis	21	*Ophidion barbatum*	48	*T. lyra*	75
D. sargus	22	*Pagellus acarne*	49	*Trigloporus lastoviza*	76
D. vulgaris	23	*P. bogaraveo*	50	*Trisopterus minutus*	77
Echelus myrus	24	*P. erythrinus*	51	*Uranoscopus scaber*	78
Engraulis encrasicolus	25	*Phycis blennoides*	52	*Zeus faber*	79
Etmopterus spinax	26	*P. phycis*	53		
Eutrigla gurnardus	27	*Pomatomus saltatrix*	54		

https://doi.org/10.1017/S0025315400003040 Published online by Cambridge University Press

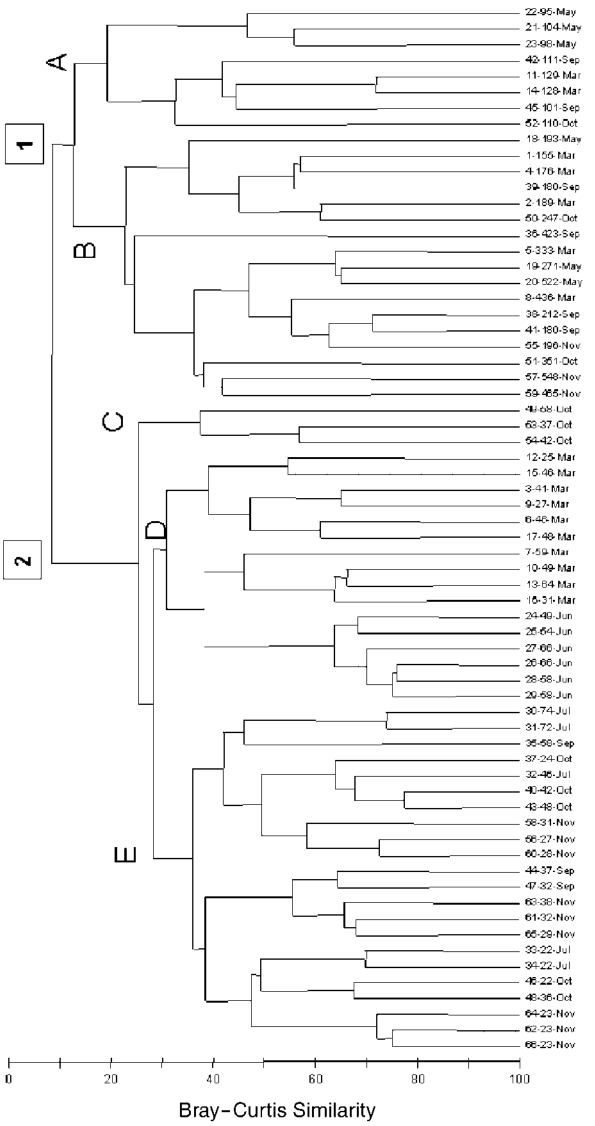

Figure 2. Dendrogram of trawl samples similarity based in Bray–Curtis distance and UPGMA, showing the major clusters: 1, shelf edge/upper slope (A and B clusters); 2, intermediate shelf/ shallow waters (C, D and E). Sample number, mean depth (m) and month are shown for each sample.

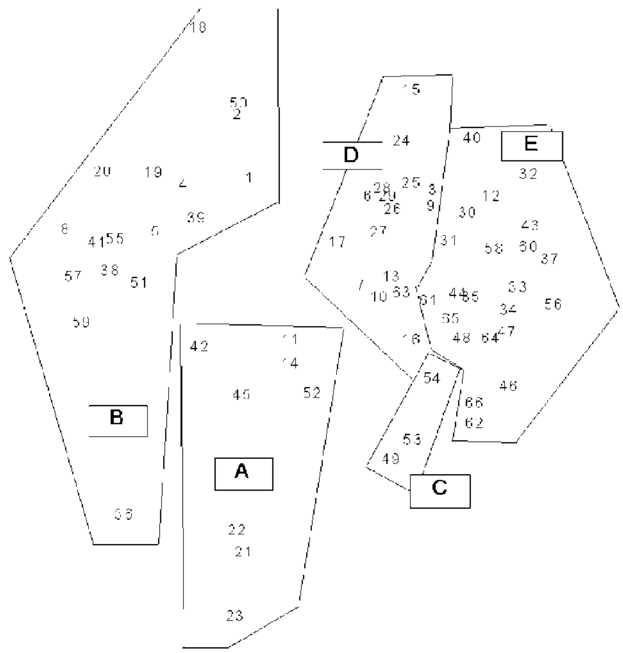

Figure 3. Multidimensional scaling diagram of trawl samples indicating the groupings obtained from the cluster analysis (Figure 2) (stress=0.18).

important controlling species of these assemblages. The species which appeared as excellent discriminators between groups are marked with an asterisk (*) in Table 3. Thus, *Micromesistius poutassou* and *Gadiculus argenteus* appear as characteristic species for group B; *Lophius piscatorius* and *Arnoglossus thori* for group A; *Trachinus draco* for group C; *Cepola rubescens* from group D and *Deltentosteus quadrimaculatus* from group E. Some species appeared in all the groups, although with very different abundances. This was the case for *Arnoglossus laterna* and *Merluccius merluccius*, since both had a wide bathymetric distribution range.

Species assemblages

The classification and ordination of the 79 species, as presented in the MDS diagram (Figure 4), showed five main associations. The five species associations identified by means of the classification analysis and ordination of the species had a good separation level (stress=0.25), and they also basically coincided with the five major location clusters.

The M group of species was associated with an average depth of 298.7 m. The most characteristic species in this group were *Micromesistius poutassou*, *Gadiculus argenteus*, *Lophius budegassa*, *Coelorhynchus coelorhynchus*, *Lepidopus caudatus* and *Phycis blennoides*. This group of species was strongly associated with the B cluster of samples. The association identified as T was caught at a mean depth of 102.2 m. The most representative species were *Lophius piscatorius*, *Arnoglossus thori*, *Arnoglossus rueppelli*, *Microchirus variegatus* and *Eutrigla gurnardus*. These species were gathered in part of A cluster of the samples. The association X represented the species distributed along the whole coast studied, being found at a greater or shallower depth depending on the configuration of the coast. Thus, in the northern area this community was found at a mean depth of 116.78 m, and was identified with part of the A cluster of the samples. On the remainder of the coast (wide shelf) this community appeared at a mean depth of 52.0 m. This group of species from the southern middle shelf was part of the D and E groups of samples. The most characteristic species of this community were *Cepola rubescens*, *Solea vulgaris*, *Lepidorhombus boscii*, *Conger conger*, *Merluccius merluccius* and *Trisopterus minutus capelanus*. Another identified assemblage (S) was that of species that lived on bottoms on the shallow shelf and were also found along the whole coast at a mean depth of 27.2 m. They were identified with part of groups D and E in the cluster of samples. The most characteristic species of this community were *Mullus barbatus*, *Deltentosteus quadrimaculatus*, *Pagellus acarne*, *Trigla lucerna*, *Lesueurigobius friesii*, *Citharus linguatula*, *Sardina pilchardus* and *Engraulis encrasicolus*. Finally, the association R

https://doi.org/10.1017/S0025315400003040 Published online by Cambridge University Press

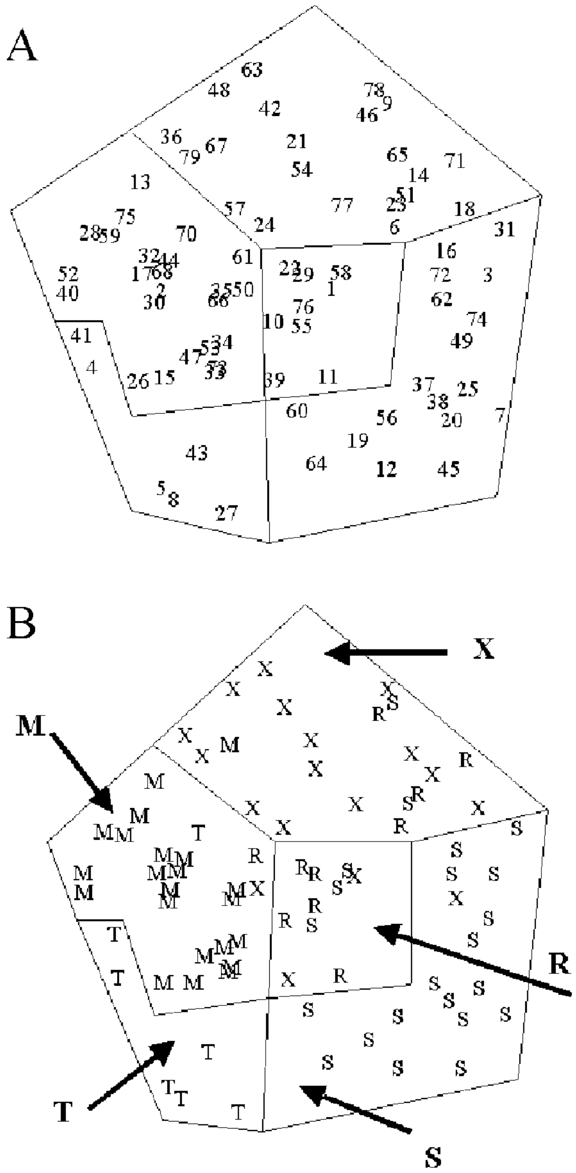

Figure 4. Multidimensional scaling diagram of the species: (A) species codes (see Table 2); (B) type of bottom for each species (codes in Table 1). The groups shown correspond to those obtained from the species dendrogram (not represented). Each species has been assigned to a type of bottom based on the most frequent type of bottom in which it was present (stress=0.27).

contained species characteristic of bottoms with a very direct influence from the sea-grass meadows, especially *Posidonia oceanica*. Typical species from these bottoms were *Trachinus draco*, *Mullus surmuletus*, *Pagellus erythrinus*, *Aspitrigla cuculus* and *Serranus cabrilla*. These habitats can be found at variable depths depending on the coastal area in which they are found. Part of D and E groups on samples represented these species associations, with a mean depth of 53.8 m, and also by group C with a mean depth of 45.6 m.

DISCUSSION

Depth is usually considered the main association factor between species, even in upwelling areas where the concentration of dissolved oxygen is one of the delimiting factors in the distribution of the species (Mas Riera et al., 1990; Bianchi, 1992). In the studied area of the Mediterranean, where the presence of anoxic areas does not occur, depth is the main factor affecting the associations of demersal fish. Additionally, the temperature of the water as a direct consequence of seasonality has a certain effect on the demersal fauna, and more specifically on its differential patterns of distribution during the life cycle of some species. This is reflected in the appearance of the juveniles or of reproductive adults of certain species on a particular bottom type and at a specific depth, such as in the hake, the red and stripped mullet or the different sparidae species (Aldebert et al., 1998; Demestre & Sánchez, 1998). There are different fractions of the same species, juveniles and adults, which are distributed in a different way. The seasonality of the studied area has been shown in various studies (Masó & Duarte, 1989; Sabatés, 1990) on the sequential nature in the appearance of planktonic organisms that constitute an important energy source.

The different types of bottom sediments, are also an important delimiting factor for the association of fish species in different communities. The clear differences between very defined habitats, such as those of mud bottoms on the slope and the sandy, much more coastal areas, support well-differentiated fish communities. In the Mediterranean, species such as *Mullus surmuletus*, *Pagellus erythrinus*, *Callyonimus maculatus*, *Diplodus vulgaris* and *D. sargus* clearly require coastal habitats of hard substratum (S and R), characteristic of slightly muddy carbonated sand bottoms generally related with rocky outcrops, with a carbonate component higher than 55%, sand (65%) and *Posidonia* (Demestre, 1986; Medialdea et al., 1986; Ercilla et al., 1995; Garcia-Rubies & Macpherson, 1995). In these habitats, temperature shows the characteristic seasonal variations (around 3°C) around mean temperature of 13.9°C (Font et al., 1988; EUROMODEL Group, 1995). In a parallel way, species such as *Micromesistius poutassou*, *Etmopterus spinax*, *Trachyrhynchus trachyrhynchus*, *Stomias boa*, *Lophius budegassa* and *Phycis blennoides* have been associated with muddy bottom habitats (M) typical of the upper slope and shelf edge (Maurin, 1962; Stefanescu et al., 1994; Moranta et al., 1998), with soft clay-muddy sediments with a low percentage of sand (<5%) (Guillén & Palanques, 1997). The environmental and hydrographic conditions on these bottoms are very stable throughout the year, with mean temperature of 13.1 ±0.2°C (EUROMODEL Group, 1995). It is noticeable that the species groupings were not clearly divided into one community type for each habitat. The great mobility of many of these species meant that there could be possible visitors from other habitats. A clear example of this behaviour are *Serranus cabrilla* and *Pagellus erythrinus*, species inhabiting mainly rocky shallow waters (R) which can be occasionally found at mud and muddy-sand bottoms (M and X) down to around 100 m depth.

Marine epibenthic species are closely associated with specific substrata or community types (Kaiser et al., 1998; Thrush et al., 1995; Jennings & Kaiser, 1998). The results presented in this study clearly show that one of the key factors in the association of demersal and benthic fish species on the shelf and upper slope is the bottom type, which are clearly differentiated and identified by the composition of their different sediment facies. Obviously, this is all under the influence of depth, which is in turn a limiting factor of the presence of the different species and habitats in the studied area of the Mediterranean. We have detected that some species occur in a number of distinct assemblages across a gradient of habitats, e.g. from sand through gravel substrate whereas others only occur in very specific habitats. However, the perturbation of the structured bottom grounds by the fishery could modify the community structure and the pattern of some species, especially the scavengers due to a source of food supply (Demestre et al., 2000; Jennings et al., 1999; Ramsay et al., 1998). Those species that are able to live in different habitats and present a higher adaptability are expected to be more resilient to the effect of habitat disturbance. Such information will allow us to understand better the dynamics of the communities and populations of fish from the shelf and slope and their relationships with topographic and sediment structure of the habitats and physical environmental factors.

This study was funded by the Generalitat of Catalunya. We would like to thank the following colleagues for their participation on the project: Mr M. Marhuenda, Dr P. Martín, Ms B. Molí and Dr L. Recasens. We also thank Dr J. Guillen and Dr G. Ercilla for providing the information about sediment structure and the Oceanography Team of ICM-CSIC for information on physical parameters. We are grateful to the Fishermen Associations of Blanes, Vilanova and Sant Carles de la Ràpita ports and to the skippers of the trawl vessels used for the sampling.

REFERENCES

Abelló, P., Valladares, F.J. & Castellón, A., 1988. Analysis of the structure of decapod crustacean assemblages off the Catalan coast (north-west Mediterranean). *Marine Biology*, **98**, 39–49.

Aldebert, Y., Sánchez, P. & Demestre, M., 1998. Scales of temporal variability of groundfish landings in north-western Mediterranean. *Rapports et Procès-verbaux des Réunions. Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, **35**, 364–365.

Bianchi, G., 1992. Demersal assemblages of the continental shelf and upper slope of Angola. *Marine Ecology Progress Series*, **81**, 101–120.

Cartes, J.E. & Sardà, F., 1993. Zonation of deep-sea decapod fauna in the Catalan Sea (western Mediterranean). *Marine Ecology Progress Series*, **94**, 27–34.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.

Clarke, K.R. & Warwick, R.M., 1994. *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth: Natural Environment Research Council.

Demestre, M., 1986. Les diferents comunitats naturals de la Mediterrània. In *L'Oceanografia. II. Recursos pesquers de la mar catalana. Quaderns d'Ecologia Aplicada*, vol. 9 (ed. J. Lleonart), pp. 9–41. Barcelona: Diputación de Barcelona.

Demestre, M. & Sánchez, P., 1998.. Spatio-temporal distribution of the european hake *Merluccius merluccius* off Catalan coast (northwestern Mediterranean*). Rapports et Procès-verbaux des Réunions. Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, **35**, 420–421.

Demestre, M., Sánchez, P. & Kaiser, M.J., 2000. The behavioural response of benthic scavengers to otter-trawling disturbance in the Mediterranean. In *Effects of fishing on non-target species and habitats* (ed. M.J. Kaiser and S.J. de Groot), pp. 121–129. Oxford: Blackwell Science.

D'Onghia, G., Tursi, A., Moiorano, P., Matarrese, A. & Panza, M., 1998. Demersal fish assemblages fromm the bathyal grounds in the Ionian Sea (middle-eastern Mediterranean). *Italian Journal of Zoology*, **65**, 287–292.

Ercilla, G., Díaz, J.I., Alonso, B. & Farrán, M., 1995. Late Pleistocene–Holocene sedimentary evolution of the northern Catalonia continental shelf (northwestern Mediterranean Sea). *Continental Shelf Research*, **15**, 1435–1451.

EUROMODEL Group, 1995. Progress from 1989 to 1992 in understanding the circulation of the western Mediterranean Sea. *Oceanologica Acta*, **18**, 255–271.

Font, J., Salat, J. & Julià, A., 1988. Permanent features of the circulation in the Catalan Sea. *Oceanologica Acta*, **9**, 51–57.

Garcia-Rubies, A. & Macpherson, E., 1995. Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. *Marine Biology*, **124**, 35–42.

Guillén, J. & Palanques, A., 1997. A shoreface zonation in the Ebro Delta based on grain size distribution. *Journal of Coastal Research*, **13**, 867–878.

Jenning, S., Greenstreet, S.P.R. & Reynolds, J.D., 1999. Structural changes in an exploited fish community: a consequence of different fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, **68**, 617–627.

Jenning, S. & Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology*, **34**, 201–352.

Kaiser, M.J., Armstrong, P.J., Dare, P.J. & Flatt, R.P., 1998. Benthic communities associated with a heavily fished scallop ground in the English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **78**, 1045–1059.

Lleonart, J., ed., 1993. Northwestern Mediterranean fisheries. *Scientia Marina*, **57**, 271.

Martín, P., 1991. La pesca en Cataluña y Valencia (NO Mediterráneo): análisis de las series históricas de captura y esfuerzo. *Informes Técnicos de Scientia Marina*, **162**, 43.

Masó, M. & Duarte, C., 1989. The spatial and temporal structure of hydrographic and phytoplankton biomass heterogeneity along the Catalan coast. *Journal of Marine Research*, **47**, 813–827.

Mas Riera, J., Lombarte, A., Gordoa, A. & Macpherson, E., 1990. Influence of the Benguela upwelling on the structure of the demersal fish populations off Namibia. *Marine Biology*, **104**, 175–182.

Maurin, C., 1962. Étude des fonds chalutables de la Méditerranée occidentale (Écologie et Pêche). Résultats des campagnes des navieres océanographiques 'President-Théodore-Tissier' 1957 à 1960 et 'Thalassa' 1960 à 1961. *Revues des Travaux de l'Institut des Pêches Maritimes. Paris*, **26**, 163–218.

Medialdea, J. et al., 1986. *Mapa geológico de la plataforma continental española y zonas adjacentes, 1:200000. Memoria y Hojas N° 41 y 42, Tortosa-Tarragona*. Madrid: Servicio de Publicaciones del Ministerio de Industria y Energia, Madrid.

Moranta, J., Stefanescu, C., Massutí, E., Morales-Nin, B. & Lloris, D., 1998. Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian Basin, western Mediterranean). *Marine Ecology Progress Series*, **171**, 247–259.

Pérès, J.M. & Picard, J., 1964. Nouveau manuel de bionomie benthique de la Mer Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume*, **31**, 1–137.

Ramsay, K., Kaiser, M.J. & Hughes, R.N., 1998. Responses of benthic scavengers to fishing disturbance by towed gears in different habitats. *Journal of Experimental Marine Biology and Ecology*, **224**, 73–89.

Sabatés, A., 1990. Distribution pattern of larval fish populations in the northwestern Mediterranean. *Marine Ecology Progress Series*, **59**, 75–82.
Stefanescu, C., Lloris, D. & Rucabado, J., 1993. Deep sea fish assemblages in the Catalan Sea (western Mediterranean) below a depth of 1000 m. *Deep-Sea Research*, **40**, 695–707.
Stefanescu, C., Morales-Nin, B. & Massutí, E., 1994. Fish assemblages on the slope in the Catalan Sea (western Mediterranean): influence of a submarine canyon. *Journal of the Marine Biological Association of the United Kingdom*, **74**, 499–512.
Thrush, S.F., Hewitt, J.E., Cumming, V.J. & Dayton, P.K., 1995. The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? *Marine Ecology Progress Series*, **129**, 141–150.
Ungaro, N., Marano, G., Marsan, R. & Osmani, K., 1998. Demersal fish assemblage biodiversity, as an index of fishery resources explotation. *Italian Journal of Zoology*, **65**, 511–516.
Vassilopoulou, V., Papaconstantinou, C. & Bekas, P., 1998. Demersal fish community patterns in two areas of the Aegean Sea Greece. *Italian Journal of Zoology*, **65**, 293–298.

Submitted 13 March 2000. Accepted 11 May 2000.

Appendix 1. *Between-group discrimination species. Species contribution to the average abundance (Av. ab.) dissimilarity between samples grouped as determined by SIMPER analyses; R: (Av. te/ sd).*

A. Shelf edge A vs upper slope B.
Average dissimilarity=85.29

Species	Av. ab. A	Av. ab. B	R
Micromesistius poutassou	0	179.22	*2.23
Gadiculus argenteus	0	87.78	*1.85
Arnoglossus thori	12.89	0	1.46
Phycis blennoides	0	21.88	*1.68
Lepidopus caudatus	0	137.88	1.17
Merluccius merluccius	10.38	128.02	*1.52
Helicolenus dactylopterus	0	79.84	1.49
Lepidorhombus boscii	0.13	12.04	1.45
Lophius piscatorius	4.53	1.69	1.4
Capros aper	1.25	20.42	1.4

B. Northern intermediate shelf C vs shelf edge A.
Average dissimilarity=77.52

Species	Av. ab. C	Av. ab. A	R
Arnoglossus laterna	56.56	0	*1.69
Trachinus draco	9.04	0	*5.44
Lophius piscatorius	0	4.53	*3.74
Citharus linguatula	8.62	0	*2.22
Mullus surmuletus	6.53	0	*3.38
Arnoglossus thori	5.31	12.89	1.34
Aspitrigla cuculus	16.01	0.25	1.13
Merluccius merluccius	19.86	10.38	1.2
Deltentosteus quadrimaculatus	7.64	0.63	1.33
Serranus hepatus	9.02	2	1.41

C. Central and southern intermediate shelf D vs shelf edge A.
Average dissimilarity=86.3

Species	Av. Ab. D	Av. Ab. A	R
Arnoglossus laterna	87.95	0	*4.57
Merluccius merluccius	815.42	10.38	1.31
Gobius niger	34.35	0	*1.75
Engraulis encrasicolus	118.55	0	1.17
Trachurus spp.	25.19	0	*2.05
Arnoglossus thori	0	12.89	*1.62
Citharus linguatula	27.77	0	1.24
Lepidorhombus boscii	83.7	0.13	0.78
Spicara maena	46.86	0.38	1.14
Lophius piscatorius	0.12	4.53	*2.83

D. Northern intermediate shelf C vs upper slope B.
Average dissimilarity=84.81

Species	Av. ab. C	Av. ab. B	R
Micromesistius poutassou	0	179.22	*2.15
Gadiculus argenteus	0	87.78	*1.73
Arnoglossus laterna	56.56	1.77	1.43
Trachinus draco	9.04	0	*3.47
Phycis blennoides	0	21.88	*1.63
Helicolenus dactylopterus	0.12	79.84	1.39
Merluccius merluccius	19.86	128.02	*1.64
Lepidopus caudatus	2.22	137.88	1.15
Mullus surmuletus	6.53	0.81	2
Citharus linguatula	8.62	3.29	*1.63

E. Central and southern intermediate shelf D vs upper slope B.
Average dissimilarity=85.83

Species	Av. ab. D	Av. ab. B	R
Arnoglossus laterna	87.95	1.77	*2.49
Merluccius merluccius	815.42	128.02	1.26
Micromesistius poutassou	0.19	179.22	*1.99
Gobius niger	34.35	0.03	*1.65
Gadiculus argenteus	0	87.78	*1.68
Cepola rubescens	17.02	1.04	*2.25
Engraulis encrasicolus	118.55	0	1.12
Lepidorhombus boscii	83.7	12.04	1.22
Trachurus spp.	25.19	0.03	*1.86
Phycis blennoides	0	21.88	*1.61

F. Central and southern intermediate shelf D vs northern intermediate shelf C. Average dissimilarity=69.94

Species	Av. ab. D	Av. ab. C	R
Merluccius merluccius	815.42	19.86	1.25
Gobius niger	34.35	0.52	*1.74
Engraulis encrasicolus	118.55	0	1.14
Arnoglossus laterna	87.95	56.56	*1.5
Cepola rubescens	17.02	0.28	*2.03
Lepidorhombus boscii	83.7	0.15	0.82
Spicara maena	46.86	0.16	1.15
Trachurus spp.	25.19	1.28	*1.6
Citharus linguatula	27.77	8.62	1.49
Aspitrigla cuculus	0.06	16.01	1.06

(Continued)

Appendix 1. *(Continued)*.

G. Shallow waters E vs Upper slope B.
Average dissimilarity=92.79

Species	Av. ab. E	Av. ab. B	R
Sardina pilchardus	1550.22	0	1.26
Engraulis encrasicolus	546.96	0	*1.57
Arnoglossus laterna	114.77	1.77	*2.77
Mullus barbatus	125.59	0.03	1.36
Micromesistius poutassou	0.3	179.22	*1.92
Lesueurigobius friesii	116.69	0	1.41
Deltentosteus quadrimaculatus	58.74	0	*1.95
Citharus linguatula	53.57	3.29	*1.85
Gadiculus argenteus	0	87.78	*1.63
Merluccius merluccius	29.31	128.02	*1.57

H. Shallow waters E vs northern intermediate shelf C.
Average dissimilarity=71.46

Species	Av. ab. E	Av. ab. C	R
Sardina pilchardus	1550.22	0	1.29
Engraulis encrasicolus	546.96	0	*1.63
Lesueurigobius friesii	116.69	0	1.48
Mullus barbatus	125.59	8.38	*1.53
Arnoglossus laterna	114.77	56.56	*1.6
Gobius niger	23.94	0.52	1.43
Deltentosteus quadrimaculatus	58.74	7.64	1.27
Pagellus acarne	67.3	0.62	1
Merluccius merluccius	29.31	19.86	1.35
Trachinus draco	3.95	9.04	*2.04

I. Shallow waters E vs shelf edge A.
Average dissimilarity=90.37

Species	Av. ab. E	Av. ab. A	R
Sardina pilchardus	1550.22	0	1.32
Engraulis encrasicolus	546.96	0	*1.66
Arnoglossus laterna	114.77	0	*6.1
Mullus barbatus	125.59	0.13	1.45
Lesueurigobius friesii	116.69	0	1.46
Citharus linguatula	53.57	0	*2.71
Deltentosteus quadrimaculatus	58.74	0.63	*1.83
Gobius niger	23.94	0	1.42
Arnoglossus thori	0	12.89	*1.55
Lophius piscatorius	0	4.53	*3.11

J. Shallow waters E vs central and southern intermediate shelf D.
Average dissimilarity=62.9

Species	Av. ab. E	Av. ab. D	R
Sardina pilchardus	1550.22	15.52	1.24
Merluccius merluccius	29.31	815.42	1.33
Engraulis encrasicolus	546.96	118.55	1.41
Lesueurigobius friesii	116.69	39.31	1.43
Mullus barbatus	125.59	2.24	1.46
Deltentosteus quadrimaculatus	58.74	0.54	*1.92
Cepola rubescens	6.46	17.02	*1.75
Pagellus acarne	67.3	6.64	1.27
Spicara maena	7.05	46.86	1.09
Lepidorhombus boscii	0.22	83.7	0.73

https://doi.org/10.1017/S0025315400003040 Published online by Cambridge University Press