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Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian basin, western Mediterranean)

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ABSTRACT: A total of 13026 fishes belonging to 82 species and 43 families were collected in a continuous transect between depths of 200 and 1800 m south of the Balearic Islands (Algerian basin, western Mediterranean). The analysis of 32 bottom trawls showed the existence of 4 groups associated with the upper slope (groups 1 and 2, from 200 to 400 and 400 to 800 m, respectively), middle slope (group 3, from 800 to 1400 m) and lower slope (group 4, below a depth of 1400 m). The differences in the mean values of the ecological parameters species richness, abundance, biomass and mean fish weight were also indicative of distinctive characteristics between these fish assemblages. Species richness decreased significantly with depth. The highest values of diversity corresponded to the samples from group 2. Biomass did not show any specific trend throughout the whole bathymetric range. Mean fish weight show 2 different trends along the continental slope: a bigger-deeper phenomenon at the upper 1000 to 1200 m depth, and a smaller-deeper phenomenon below this depth. Our results are compared with those obtained in the north Atlantic basin and in the western Mediterranean (Balearic basin), and the main factors affecting these deep-sea fish assemblages are discussed.

KEY WORDS: Deep sea · Demersal ichthyofauna · Bathymetric distribution · Western Mediterranean

INTRODUCTION

The structure of faunal assemblages on the continental slope in different geographic areas is largely determined by spatial differences in environmental and oceanographic local conditions and in particular by depth, bottom type and characteristics of water masses (e.g. Haedrich & Krefft 1978, Haedrich et al. 1980, Carney et al. 1983, Haedrich & Merrett 1990, Hecker 1990, Bianchi 1992, Koslow 1993, Smale et al. 1993, Sardà et al. 1994).

Biological factors such as resource availability, predator-prey relationships and interspecific competition may also play a fundamental role in the local zonation pattern (e.g. Vinogradov & Tseitlin 1983, Sulak 1984, Anderson et al. 1985, Macpherson & Roel 1987, Merrett 1987, Mahaut et al. 1990, Gordon et al. 1995).

The distribution patterns and community structure of the fish community along the continental shelf and slope of the western Mediterranean are well known. However, most related studies are limited to data collected by fishing vessels and on oceanographic surveys at depths of less than 700 to 800 m (e.g. Maurin 1962, 1965, 1968, Matallanas 1979, Allué 1985, Gil de Sola 1994, Massutí et al. 1996b). Below these depths, the only available data are those provided by Stefanescu et al. (1992a, 1993, 1994) between 1000 and 2250 m in the Catalan Sea (Balearic basin), an area of the northwestern Mediterranean bounded by the Iberian peninsula coast to the north and west, and the Balearic Islands to the south.

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In this paper we describe the faunal composition, bathymetric distribution and zonation of the demersal fish fauna along a continuous transect between depths of 200 and 1800 m, south of the Balearic Islands (Algerian basin, western Mediterranean). This study is one of a series in order to compare the demersal fish assemblages of 2 areas (the northern and southern Balearic Islands, in the Balearic and Algerian basins, respectively, see Fig. 1) with different bottom topography and hydrographic conditions (e.g. Canals et al. 1982, EUROMODEL Group 1995). The main objective is to detect general trends in the distribution of the fish fauna in relation to environmental and biological variables.

MATERIAL AND METHODS

Study area. The Algerian basin, within the western Mediterranean, has maximum depths of around 2500 m and is connected with the Balearic basin by a series of sills that occur in the arc of the Balearic Islands: 800 m between Eivissa and the mainland, 600 m between Eivissa and Mallorca, and less than 100 m between Mallorca and Menorca (Fig. 1). This topography plays an important role in the general circulation and in the transport of the water masses between these areas.

Although the western Mediterranean is characterised by a degree of high environmental stability in both temperature and salinity below a depth of 200 m (Hopkins 1985), distinct oceanographic conditions with biological implications have been described in the area. The zone south of the Balearic Islands (our study area, Fig. 1) is influenced by the dynamics of the Algerian basin, which acts as a reservoir for water of Atlantic origin (Millot 1985). Moreover, in the Balearic basin (north of the Balearic Islands) the circulation of the water masses is similar to a large cyclonic gyre, controlled by 2 permanent front systems following slope bathymetric contours: cold Mediterranean Waters (MW) flow from the north along the continental shelf-break and warm Modified Atlantic Water (MAW) enter the Balearic basin from the south following the Balearic slope (Millot 1987, Font et al. 1988, Pinot et al. 1995). These frontal boundary regions are particularly relevant in the general oligotrophic context of the Mediterranean Sea, since they increase the biomass (Lhorenz et al. 1988) and further enrich already biologically active locations in the western Mediterranean.

Trawl data. All the material included in the present paper was collected south of Eivissa and the Formentera Islands during the QUIMERA-I cruise carried out on board the RV 'García del Cid' in October 1996 (Fig. 1). The sampling gear was an OTMS-27.5 benthic trawl (Spanish patent no. 9200614, Institut de Ciencies del Mar-CSIC), which consists of a semi-balloon otter trawl with square panels and wings and a 25 m headline. The gear is towed by a single warp attached to 2 wires on a crowfoot, which is in turn connected to two 450 kg iron otter boards (Sardà et al. 1998). Towing speed was 2.7 knots for all trawls. The arrival and departure of the net on the bottom in addition to the horizontal and vertical openings (14 m and 1.8 to 2 m, respectively) were measured using the SCANMAR system (cod end mesh size was 12 mm). The position at the start and the end of each trawl was recorded using GPS (Global Positioning System).

A total of 32 trawls were taken between depths of 200 and 1800 m, 2 for each of sixteen 100 m depth

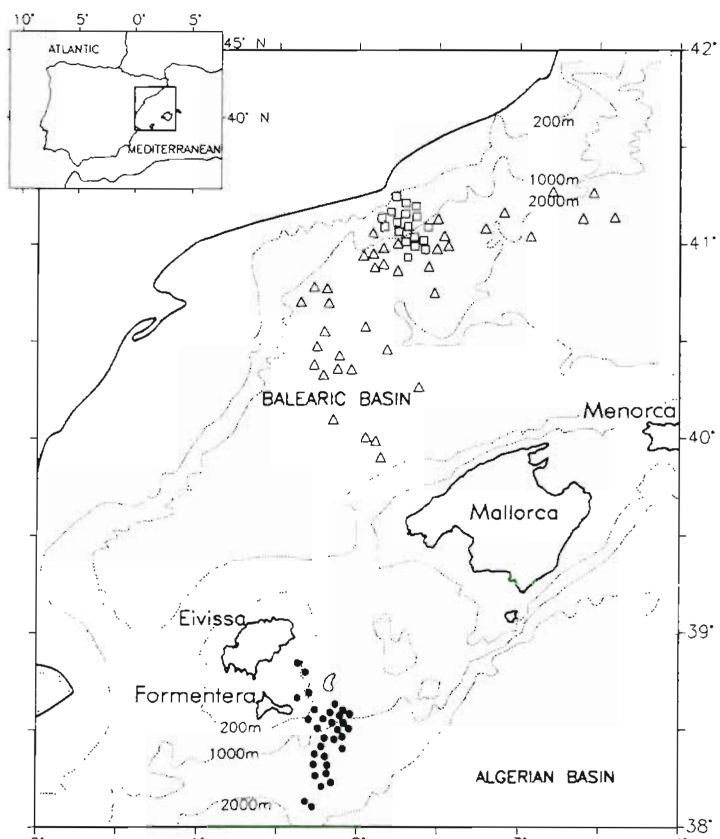

Fig. 1. General location of the study site in the western Mediterranean, showing the sampling stations on the continental slope of the Algerian basin and the hauls from the Balearic basin used for comparative purposes. The horizontal distance separating the Algerian basin sampling sites from the ones in the Balearic basin is around 100 nautical miles. (●) Samples obtained with an OTMS-27.5 (present study); (△) samples obtained with an OTSB-14 (from Stefanescu et al. 1993); (□) samples obtained with an OTMS-27.5 (from Stefanescu et al. 1994)

intervals. Trawl duration was normally from 30 to 60 min but was standardised to 1 h for subsequent numerical processing. The catch values (abundance and biomass) were standardised to 1000 m^2 in accordance with the methodology most commonly employed in studies of deep-sea fish assemblages (Stefanescu et al. 1994 and references cited therein). Those species regarded as markedly mesopelagic and bathypelagic in behaviour were disregarded in the quantitative calculations since they might have been captured at some distance from the bottom (see Table 1).

Data analysis. The quantitative species composition for each of eight 200 m intervals was analysed. In each interval the dominant species in terms of both abundance and biomass (expressed in percentages) were determined. To detect zonation patterns, cluster analysis was applied to the species abundance matrix. Species recorded only in a single sample were omitted from this analysis, since it was felt that the only effect of including such species would be to produce noise in the analysis. When the cluster analysis was carried out with the complete data set, excluding mesopelagic but not occasional species, a similar pattern arose. However, we found it difficult to identify some of the groups and therefore the species appearing in a single sample were not considered in the final cluster analysis. The Percentage of Similarity independent (PSi) was chosen as the similarity coefficient (Kohn & Riggs 1982) and Complete Linkage Clustering and Unweighted Pair-Group Mean Analysis (UPGMA) were utilised as the clustering algorithm (Sneath & Sokal 1973), since both are commonly used in deep-sea fish community studies. The application of other similarity coefficients for comparative purposes produced similar groupings.

The ecological parameters abundance, biomass, mean fish weight, species richness (S), mean species richness, Shannon-Wiener diversity index (Shannon & Weaver 1949) and evenness (Pielou 1969) were determined in each group resulting from the cluster analysis.

The geometric mean was preferred to the arithmetic mean in comparisons of abundance, biomass and mean fish weight between groups of cluster analysis, in order to minimise the negative effects caused by extreme values. Before using parametric tests (1-way analysis of variance), the assumptions of normality and homoscedasticity were tested by the Kolmogorov-Smirnov and Bartlett-Box tests, respectively. When these assumptions were not met, non-parametric tests (Kruskal-Wallis and Mann-Whitney) were used. Regression analyses were used to determine how species richness, abundance, biomass and mean fish weight changed with the water depth.

The Shannon-Wiener diversity index (H') was determined according to the information function:

$$H' = \Sigma pi \ln pi$$

where pi is the fraction of species i in the sample. Pairwise comparisons using the t-test (Hutchenson 1970) were used to detect significant difference in H' between groups.

The evenness index (J') was calculated according to:

$$J' = \frac{H'}{H_{max}}$$

where maximal diversity $H_{max} = \log S$, with S being the species richness.

The bathymetric distribution of demersal species captured on more than one occasion was calculated in a quantitative manner using the 'centre of gravity' (COG) (Daget 1976) and 'habitat width' (HW) (Pielou 1969) analyses. The COG model allows one to calculate and locate with precision the centre of species distributions by means of a descriptor (in this case depth). The HW model gives a measure of heterogeneity of the species distribution.

Both values were determined as follows:

$$\text{COG} = (x_1 + 2x_2 + 3x_3 + 4x_4 + \ldots + nx_n)/\Sigma x_i$$

where x_i represents the calculated mean abundance values of the species x present in the stratum i (before analysis the sampled depth was divided into 8 strata of 200 m).

$$\text{HW} = e^{H'}$$

where e is the natural log and H' the Shannon-Wiener function. The same models were applied by Stefanescu et al. (1992a) in a previous study of bathymetric distributions of deep-sea fishes.

To test the reliability of species richness estimates (S_t), cumulative species richness curves were constructed. These curves show an increase in species with increasing sampling intensity (cf. Blondel 1979). At a certain sample number (n) an asymptotic value is reached when the 2 values S_n and S_{n-1} are equal. The curve is obtained by calculating the mean value for each point S_x (x = 1, 2, ..., n) for all possible calculations of the n samples, taken as 1 in 1 (point S_1), 2 in 2 (point S_2), ..., n in n (point S_n).

RESULTS

A total of 13026 fishes belonging to 82 species and 43 families were collected, resulting in a biomass of 637.2 kg of fish from 32 trawls (Table 1)

The faunistic composition of abundance, biomass and frequency of occurrence, by species, for each 200 m depth interval is given in Table 2. In all aspects *Gadiculus argenteus* and *Helicolenus dactylopterus*

Table 1. Species caught off the southern Balearic Islands (western Mediterranean) between depths of 200 and 1800 m. A: abundance in number of individuals; B: biomass in kg; n: number of hauls in which these species were caught. (* indicates those species known to be markedly mesopelagic and bathypelagic in behaviour which were disregarded from the analysis)

Family	Species	A	B	n
Scyliorhinidae	*Galeus melastomus* Rafinesque, 1810	468	60.48	23
	Scyliorhinus canicula (Linnaeus, 1758)	231	10.40	7
Squalidae	*Centrophorus uyato* (Rafinesque, 1809)	1	4.00	1
	Centroscymnus coelolepis Bocage & Capello, 1864	29	16.50	9
	Dalatias licha (Bonnaterre, 1788)	5	9.01	4
	Etmopterus spinax (Linnaeus, 1758)	43	10.33	15
	Squalus blainvillei (Risso, 1826)	24	2.40	1
Rajidae	*Raja naevus* Müller & Henle, 1841	3	0.93	1
	Raja asterias Delaroche, 1809	2	0.90	1
	Raja polystigma Regan, 1923	1	0.22	1
Alepocephalidae	*Alepocephalus rostratus* Risso, 1820	723	200.21	18
Gonostomatidae	*Cyclothone braueri* Jespersen & Tåning, 1926*	25	0.02	7
	Cyclothone pygmaea Jespersen & Tåning, 1926*	14	0.01	5
Sternoptychidae	*Argyropelecus hemigymnus* Cocco, 1829*	44	0.04	23
	Maurolicus muelleri (Gmelin, 1788)*	2	0.00	2
Chauliodontidae	*Chauliodus sloani* Schneider, 1801*	13	0.49	10
Stomiidae	*Stomias boa* (Risso, 1810)*	17	0.12	9
Argentinidae	*Argentina sphyraena* Linnaeus, 1758*	255	1.14	2
	Glossanodon leioglossus (Valenciennes, 1848)*	142	11.41	3
Chlorophthalmidae	*Chlorophthalmus agassizii* Bonaparte, 1840	7	0.04	5
	Bathypterois mediterraneus Bauchot, 1962	410	2.81	15
Myctophidae	*Benthosema glaciale* (Reinhardt, 1837)*	19	0.02	7
	Lampanyctus crocodilus (Risso, 1810)*	308	2.75	24
	Myctophum punctatum Rafinesque, 1810*	5	0.00	2
	Notoscopelus elongatus (Costa, 1844)*	1	0.00	1
Paralepididae	*Notolepis rissoi* (Bonaparte, 1840)*	6	0.01	6
Nemichthyidae	*Nemichthys scolopaceus* Richardson, 1848*	1	0.01	1
Nettastomatidae	*Nettastoma melanurum* Rafinesque, 1810	30	2.95	13
Congridae	*Conger conger* (Linnaeus, 1758)	3	5.64	3
Synaphobranchidae	*Dysomma brevirostre* (Facciolà, 1887)	1	0.04	1
Notacanthidae	*Notacanthus bonapartei* Risso, 1840	14	0.51	9
	Polyacanthonotus rissoanus (Filippi & Vérany, 1859)	17	0.21	8
Macroramphosidae	*Macroramphosus scolopax* (Linnaeus, 1758)*	31	0.20	3
Macrouridae	*Chalinura mediterranea* Giglioli, 1893	142	1.06	10
	Caelorhynchus caelorhynchus (Risso, 1810)	239	3.92	5
	Caelorhynchus labiatus (Koehler, 1896)	122	2.34	14
	Coryphaenoides guentheri (Vaillant, 1888)	9	0.08	3
	Hymenocephalus italicus Giglioli, 1884	119	1.12	11
	Nezumia aequalis (Günther, 1878)	484	14.86	18
	Trachyrincus trachyrincus (Giorna, 1809)	15	3.24	3
Merluccidae	*Merluccius merluccius* (Linnaeus, 1758)	340	9.80	10
Gadidae	*Gadiculus argenteus* Guichenot, 1850	4761	16.36	9
	Micromesistius poutassou (Risso, 1926)	36	2.90	8
	Trisopterus minutus capelanus (Lacepède, 1800)	42	0.41	2
	Antonogadus megalokynodon (Kolombatovic,1894)	29	0.08	11
	Molva dipterygia macrophtalma (Pennant, 1874)	24	0.95	6
	Phycis blennoides (Brünnich, 1768)	1100	41.10	19
Moridae	*Laemonema* sp.	1	0.01	1
	Lepidion guentheri (Giglioli, 1880)	5	2.09	3
	Lepidion lepidion (Risso, 1810)	53	5.64	13
	Mora moro (Risso, 1810)	242	131.12	12
Regalecidae	*Regalecus glesne* Ascanius, 1772*	1	0.00	1
Zeidae	*Zeus faber* Linnaeus, 1758	1	0.15	1
Caproidae	*Capros aper* (Linnaeus, 1758)*	290	1.23	5
Apogonidae	*Epigonus denticulatus* Diuezeide, 1950	21	0.09	6
	Epigonus telescopus (Risso, 1810)	9	6.50	2
Carangidae	*Trachurus picturatus* (Bowdich, 1825)	2	0.39	1
	Trachurus trachurus (Linnaeus, 1758)	44	4.00	1
Mullidae	*Mullus surmuletus* Linnaeus, 1758	1	0.28	1
Sparidae	*Boops boops* (Linnaeus, 1758)*	8	0.95	3
Trachichthyidae	*Hoplostethus mediterraneus* Cuvier, 1829	64	2.61	9
Trichiuridae	*Lepidopus caudatus* (Euphrasen, 1788)	52	3.05	10
Gobiidae	*Lesueurigobius friesii* (Malm, 1874)	2	0.00	1
	Pomatoschistus minutus (Pallas, 1770)	1	0.00	1
Callionymidae	*Callionymus maculatus* Rafinesque-Schmaltz, 1810	7	0.01	2
	Synchiropus phaeton (Günther, 1861)	118	1.02	8
Bythitidae	*Cataetyx alleni* (Byrne, 1906)	6	0.05	5
	Cataetyx laticeps Koefoed, 1927	1	0.64	1
Centrolophidae	*Centrolophus niger* (Gmelin, 1788)*	1	3.00	1
Scorpaenidae	*Helicolenus dactylopterus* (Delaroche, 1809)	1252	19.07	9
	Scorpaena elongata Cadenat, 1943	3	0.91	3
Triglidae	*Aspitrigla cuculus* (Linnaeus, 1758)	1	0.07	1
	Lepidotrigla cavillone (Lacepède, 1801)	1	0.01	1
	Trigla lyra Linnaeus, 1758	20	0.29	6
Peristediidae	*Peristedion cataphractum* Linnaeus, 1758	186	5.36	5
Liparidae	*Paraliparis leptochirus* (Tortonese, 1960)*	8	0.01	7
Scophthalmidae	*Lepidorhombus boscii* (Risso, 1810)	38	2.19	7
Bothidae	*Arnoglossus laterna* (Walbaum, 1792)	29	0.14	2
	Arnoglossus rueppelli (Cocco, 1844)	23	0.12	2
Cynoglossidae	*Symphurus ligulatus* (Cocco, 1844)	90	0.21	9
	Symphurus nigrescens Rafinesque, 1810	86	0.38	10
Lophiidae	*Lophius budegassa* Spinola, 1807	2	0.42	2
		13026	637.2	

Table 2. Top ranking species at each 200 m depth interval. Abundance and biomass are expressed as a percentage of the total catch for each bathymetric range and frequency of occurrence (*f*) as the number of samples in which the species was caught in relation to the number of samples taken at each depth stratum. Only those species represented by more than 5% of the total catch are listed

Abundance	%	*f*	Biomass	%	*f*
200–400 m					
Gadiculus argenteus	60.85	100	*Helicolenus dactylopterus*	27.62	100
Helicolenus dactylopterus	17.18	100	*Gadiculus argenteus*	21.19	100
Phycis blennoides	5.46	100	*Phycis blennoides*	12.61	100
			Scyliorhinus canicula	11.32	100
			Peristedion cataphractum	7.87	100
			Merluccius merluccius	5.34	100
400–600 m					
Phycis blennoides	39.01	100	*Phycis blennoides*	32.06	100
Gadiculus argenteus	18.59	80	*Galeus melastomus*	26.04	100
Galeus melastomus	16.88	100	*Merluccius merluccius*	7.92	80
Caelorhynchus caelorhynchus	5.49	60	*Caelorhynchus caelorhynchus*	5.99	60
600–800 m					
Nezumia aequalis	23.02	100	*Galeus melastomus*	35.07	100
Symphurus ligulatus	17.46	100	*Phycis blennoides*	21.80	100
Phycis blennoides	16.93	100	*Nezumia aequalis*	10.67	100
Hymenocephalus italicus	12.96	100	*Hoplostethus mediterraneus*	8.52	100
Hoplostethus mediterraneus	8.20	100			
Galeus melastomus	7.94	100			
800–1000 m					
Nezumia aequalis	29.33	100	*Mora moro*	31.03	100
Phycis blennoides	16.49	100	*Galeus melastomus*	15.77	100
Mora moro	12.45	100	*Phycis blennoides*	12.26	100
Alepocephalus rostratus	11.04	50	*Alepocephalus rostratus*	8.10	50
Galeus melastomus	7.35	100	*Dalatias licha*	6.90	50
Hymenocephalus italicus	5.15	100			
1000–1200 m					
Alepocephalus rostratus	35.02	100	*Mora moro*	51.89	100
Nezumia aequalis	27.41	100	*Alepocephalus rostratus*	29.56	100
Mora moro	22.49	100	*Galeus melastomus*	8.27	100
Galeus melastomus	5.39	100			
1200–1400 m					
Alepocephalus rostratus	51.92	100	*Alepocephalus rostratus*	69.88	100
Nezumia aequalis	15.65	100	*Mora moro*	16.08	100
Caelorhynchus labiatus	9.74	100	*Galeus melastomus*	8.20	66.67
Mora moro	6.71	100			
Bathypterois mediterraneus	5.75	100			
Galeus melastomus	5.11	66.67			
1400–1600 m					
Bathypterois mediterraneus	40.13	100	*Alepocephalus rostratus*	82.67	100
Alepocephalus rostratus	29.33	100	*Lepidion lepidion*	6.25	100
Caelorhynchus labiatus	11.47	100	*Centroscymnus coelolepis*	6.15	75
Chalinura mediterranea	7.50	100			
Lepidion lepidion	5.40	100			
1600–1800 m					
Bathypterois mediterraneus	45.11	100	*Alepocephalus rostratus*	62.32	100
Chalinura mediterranea	23.56	100	*Centroscymnus coelolepis*	17.89	100
Alepocephalus rostratus	14.35	100			
Caelorhynchus labiatus	5.78	100			

were among the dominant species between depths of 200 and 400 m, as were *Phycis blennoides* and *Galeus melastomus* in the bathymetric range shallower than 1000 m. At intermediate depths, between 600 and 1400 m, *Nezumia aequalis* and *Mora moro* were among the dominant species, while *Alepocephalus rostratus* was a co-dominant between 1000 and 1800 m, and *Bathypterois mediterraneus* dominated in abundance at depths greater than 1400 m.

The bathymetric distributions, established using the COG and HW values, are shown in Fig. 2. From a total of 46 demersal species analysed, 34 were restricted to the depth interval surveyed. There were 4 different species groups: (a) species limited to the 200 to 800 m

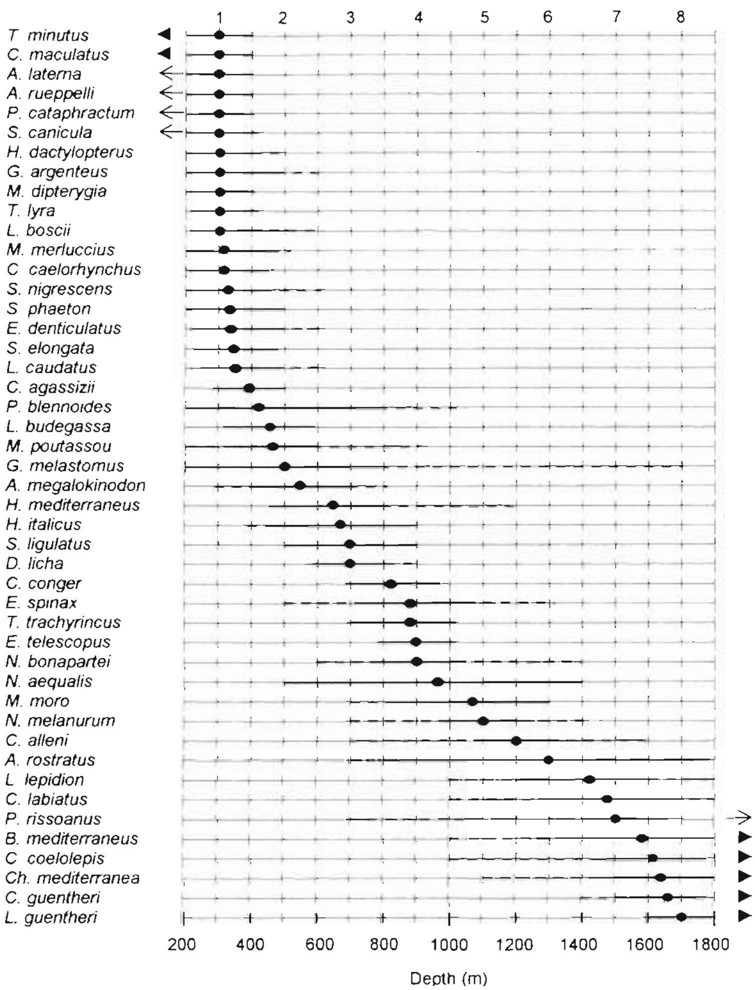

Fig. 2. Bathymetric distribution of demersal species sampled on more than 1 occasion. Black circles represent the centre of gravity (COG), black lines correspond to the habitat width (HW). Black arrowheads indicate a displacement in real terms of the COG beyond the depth range sampled according to other studies conducted in adjacent areas (Stefanescu et al. 1993, 1994, Massutí et al. 1996b). Thin arrows indicate a small displacement in real terms of the COG, but included in the depth range considered. Discontinuous lines indicate the bathimetric range over which given species were caught. Numbers 1 to 8 on the top axis correspond to the 8 sectors in which the sampled depth interval (200 to 1800) was divided. Full species names given in Table 1

depth interval (e.g. *Helicolenus dactylopterus*, *Gadiculus argenteus*, *Lepidorhombus boscii*, *Merluccius merluccius* and *Caelorhynchus caelorhynchus*), (b) species with a wide bathymetric distribution (*Phycis blennoides*, *Galeus melastomus*, *Nezumia aequalis* and *Alepocephalus rostratus*), (c) species present at intermediate depth between 800 to 1400 m (*Trachyrinchus trachyrinchus*, *Mora moro*, *Nettastoma melanurum* and *Cataetyx alleni*), and (d) species restricted to depths greater than 1400 m (*Lepidion lepidion*, *Caelorhynchus labiatus*, *Bathypterois mediterraneus* and *Centroscymnus coelolepis*).

The dendrogram of similarities for the trawls is shown in Fig. 3. The first cluster separates those samples taken at a depth of 200 to 800 m from the rest. Within this group an additional subdivision can be discerned, and a second cluster separates the hauls shallower than 400 m (group 1) and those from 400 to 800 m (group 2). The rest of the samples are arranged into 2 groups delimited by the 1400 m isobath: from 800 to 1400 m (group 3) and samples below a depth of 1400 m (group 4). The number of hauls in each group resulting from cluster analysis was adequate to describe the different assemblages, as shown by the cumulative species richness curves (Fig. 4).

The values of some ecological parameters in the different groups and the results of the statistical analysis are given in Table 3. The relationships between some of these parameters and depth, calculated by regression analyses, are shown in Fig. 5.

Both species richness and mean species richness, were higher in groups 1 (200 to 400 m) and 2 (400 to 800 m), than in groups 3 (800 to 1400 m) and 4 (1400 to 1800 m). Nevertheless, although species richness decreased significantly with depth (Fig. 5a), no significant differences were found between groups 3 and 4. The highest values of diversity corresponded to the samples from group 2 (Table 3). Group 1 showed the lowest evenness and the highest abundance values, as a consequence of the predominance of *Gadiculus argenteus*, which appeared in vast numbers in all samples between a depth of 200 to 400 m and represented 60.9% of the specimens caught. Despite high species richness (Fig. 5a), this resulted in an abnormally low value on the Shannon-Wiener index for group 1 (Table 3).

Abundance was correlated with depth but this trend was accentuated in the first 500 m depth interval (Fig. 5b). Biomass did not show any specific trend in the first 1100 m depth interval but decreased significantly from 1100 to 1800 m. Moreover, careful analysis revealed the existence of a minimum and a maximum located around 500 and 1100 to 1200 m, respectively (Fig. 5c). Mean fish weight showed 2 different trends within the studied range. A steady increase was observed from 200 to 1100 m, while a converse trend was noted from 1100 m down to the maximum depth sampled (Fig. 5d).

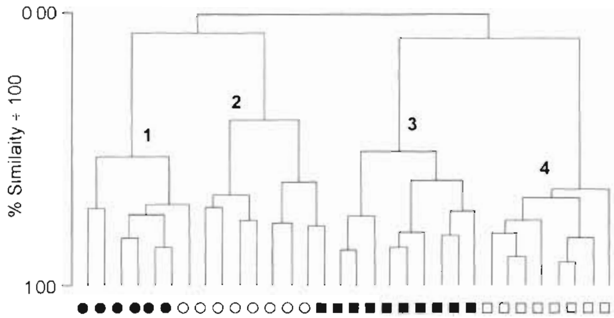

Fig. 3. Dendrogam of trawls during the QUIMERA I cruise showing 4 major clusters. (●) Stations at 200 to 400 m; (○) stations at 400 to 800 m; (■) stations at 800 to 1400 m; (□) stations at 1400 to 1800 m

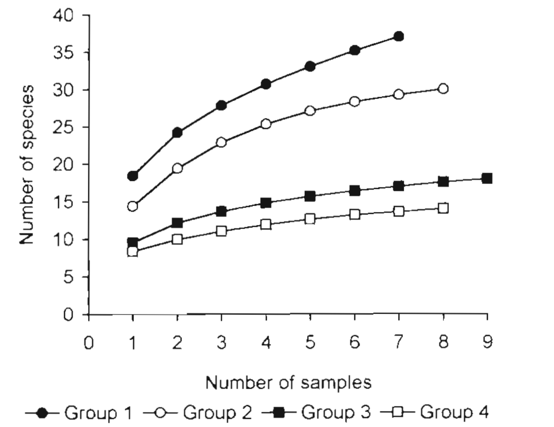

Fig. 4. Cumulative species richness curves in the 4 groups identified by cluster analysis (group 1: 200 to 400 m; group 2: 400 to 800 m; group 3: 800 to 1400 m; and group 4: 1400 to 1800 m)

DISCUSSION

The continental slope south of the Balearic Islands is characterised by 4 distinct fish assemblages. The zonation pattern obtained in our study can be associated with different bathymetric strata. Following the arbitrary separation proposed by Haedrich & Merrett (1988) in North Atlantic waters, the 4 groups obtained in the cluster analysis (Fig. 3) can be associated with the upper slope (groups 1 and 2, between 200 and 800 m), middle slope (group 3, from 800 to 1400 m) and lower slope (below a depth of 1400 m). These results agree with previous data available from the Catalan Sea (Balearic basin, Fig. 1). In this area, north of the Balearic Islands, different fish assemblages at depths of 350 to 650 and 1150 to 1300 m have been described by Stefanescu et al. (1994), and a boundary between the middle and lower slope was located around the 1400 m isobath (Stefanescu et al. 1993). The depth gradient, with its associated environmental and biological changes, is the main factor responsible for faunal change in demersal fish communities (e.g. Haedrich et al. 1975, Bianchi 1992, Stefanescu et al. 1993, Fujita et al. 1995, Gordon et al. 1995).

According to Hecker (1990), the changes in faunistic composition between different megafaunal assemblages are due to the substitution of the dominant and subdominant species, throughout the depth gradient, by a continuous faunistic turnover. This can be observed in our results (Table 2). For example, *Phycis blennoides* was caught at depths from 242 to 1022 m, but was a dominant species from 400 to 600 m and sub-

Table 3. Ecological parameters for each group resulting from cluster analysis (see Fig. 3) and summary of statistical tests. Means are ranked sequentially, with the higher values on the left. Values underlined with the same line do not show significant differences. (*p < 0.05, **p < 0.01)

Group:	1 (200–400 m)	2 (400–800 m)	3 (800–1200 m)	4 (1200–1800 m)	Statistical test	Groups
Abundance (fish/10^3 m^2)	23.5 (11.8–46.0)	2.7 (2.3–3.1)	3.3 (2.9–3.8)	3.1 (2.0–4.4)	Kruskal-Wallis ($H_{9,8,8,7}$ = 18.5*)	G1>G3>G4>G2
Biomass (g/10^3 m^2)	346.2 (231.8–517.0)	164.7 (59.3–453.9)	764.1 (684.4–861.6)	297.9 (147.4–606.9)	Kruskal-Wallis ($H_{9,8,8,7}$ = 12.9*)	G3>G1>G4>G2
Mean fish weight (g)	14.9 (10.5–21.2)	61.8 (24.3–155.0)	229.4 (205.4–258.8)	101.5 (69.1–147.4)	Kruskal-Wallis ($H_{9,8,8,7}$ = 21.6**)	G3>G4>G2>G1
Species richness (*S*)	37	30	18	14		
Mean species richness	17.4±0.9	14.4±0.5	9.6±0.53	8.38±0.38	One-way ($F_{(1),3,28}$ = 58.62**)	G1>G2>G3>G4
Diversity (*H'*)	1.78	2.36	1.76	1.64	Student's *t* *	G2>G1>G3>G4
Evenness (*J'*)	0.38	0.49	0.42	0.43		
Mean depth (± SD)	339.3±66.1	656.7±115.5	1087±145.5	1553.9±119.2		
Number of samples	7	9	8	8		

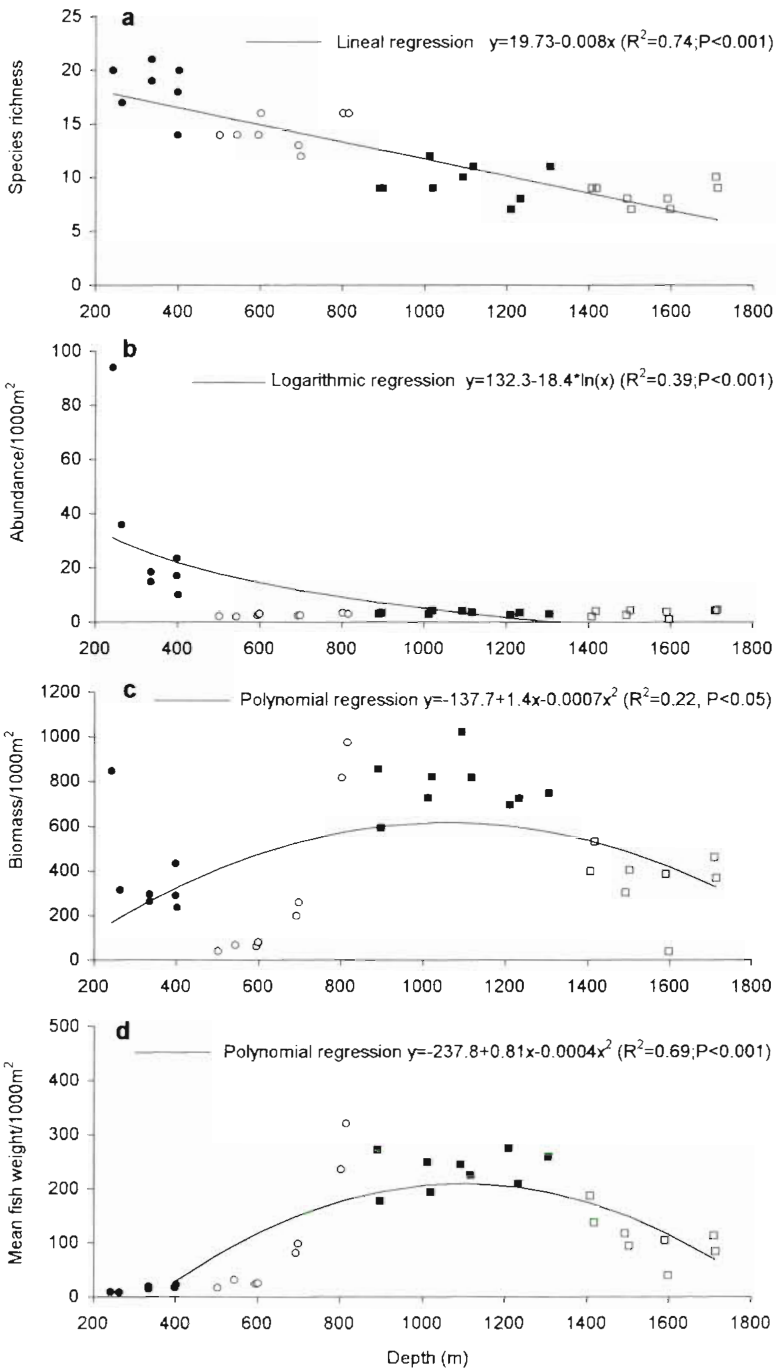

Fig. 5. Relationship between (a) species richness, (b) abundance, (c) biomass and (d) mean fish weight and depth, calculated by regression analyses. The symbols correspond with the different groups identified by cluster analysis. (●) Group 1, stations at 200 to 400 m; (○) group 2, stations at 400 to 800 m; (■) group 3, stations at 800 to 1400 m; (□) group 4, stations at 1400 to 1800 m

dominant in the other depth groups in which the species was present. In the same way, *Alepocephalus rostratus* appeared between 700 m and the maximum depth surveyed, but was dominant from 1000 to 1600 m and subdominant at depths of 800 to 1000 and 1600 to 1800 m. *Bathypterois mediterraneus* was caught in all the hauls below a depth of 1013 m but was only abundant at 1400 to 1800.

On the other hand, other species such as *Peristedion cataphractum, Scyliorhinus canicula, Trisopterus minutus capelanus, Arnoglossus rueppelli, A. laterna, Callionymus maculatus, Molva dipterygia macrophtalma* and *Trigla lyra* showed a narrow bathymetric distribution within the depth range surveyed and appeared only between 200 and 400 m (Fig. 2). These species accounted for the 2 different assemblages obtained on the upper slope: groups 1 and 2 at 200 to 400 and 400 to 800 m, respectively (Fig. 3).

The differences in the mean values of the ecological parameters analysed (Table 3, Fig. 5) are also indicative of distinctive differences which characterise the various fish assemblages found in this study. Species richness decreased progressively throughout the whole depth range surveyed (Figs. 4 & 5a) and suggested a real faunistic impoverishment with depth. This trend has been reported from the upper slope down to about 2000 m in Atlantic (e.g. Haedrich et al. 1980, Gordon & Duncan 1985) and Pacific waters (Pearcy et al. 1982). A similar pattern was described by Stefanescu et al. (1993) in western Mediterranean waters deeper than 1000 m.

The number of demersal fish species recorded in the western Mediterranean in a series of comparable studies has been 57, 27, and 16 for the upper, middle and lower slope, respectively (Stefanescu et al. 1992a, Massutí et al. 1996b, and the present study). A comparison of these numbers with those recorded by Haedrich & Merrett (1988) in 4 regions around the north Atlantic Basin with a similar number of samples and bottom trawls (Bahamas, middle Atlantic Bight, Rockall Trough and Porcupine Seabight), reveals different trends along the entire range of the slope. Thus, in our study, the number of demersal species recorded on the upper slope represents an increase of 33.3 and 15.8% with respect to Rockall Trough and Porcupine Seabight (no data are available for the Bahamas and the middle Atlantic Bight). These differences may be explained by the effect of a narrow continental shelf in our surveyed area and the subsequent increase in the capture of species such as *Peristedion cataphractum*, *Scyliorhinus canicula*, *Trisopterus minutus capelanus*, *Callionymus maculatus*, *Molva dipterygia macrophtalma*, *Raja naevus*, *R. asterias*, *Zeus faber*, *Trachurus picturatus*, *T. trachurus*, *Mullus surmuletus*, *Aspitrigla cuculus*, *Lepidotrigla cavillone*, *Trigla lyra*, *Arnoglossus rueppelli* and *A. laterna*, which generally display a wide bathymetric distribution range throughout the continental shelf and the upper slope (Massutí et al. 1996b). Moreover, these differences may be influenced in part by the general latitudinal trend towards decrease in species richness with increasing latitude (Macpherson & Duarte 1994, and references cited therein).

In contrast, the number of demersal species recorded in the middle and lower slope represents a decrease of 32.5 and 59.7% with respect to the values reported in the north Atlantic by Haedrich & Merrett (1988). This fits well with the general assumption that the demersal fish fauna in the Mediterranean deep-sea is poorer than in the north Atlantic basin (Haedrich & Merrett 1988, Stefanescu et al. 1992a). In this way, the Gibraltar sill, 280 m deep, has been regarded as the main physical barrier for the potential colonization of the Mediterranean from the rich deep-sea Atlantic fauna (Bouchet & Taviani 1992). Therefore, those fish species with a distribution range starting below a depth of 300 m cannot colonize the Mediterranean unless they have pelagic larvae. Moreover, the hydrological nature of the Mediterranean bottom water (high temperature and high salinity) can act as another important barrier to the successful establishment of species with such a larval dispersal capacity (Bouchet & Taviani 1992). This relative isolation may explain the evolution of endemic species such as *Bathypterois mediterraneus* and *Lepidion lepidion*, 2 main constituents of the deep-sea Mediterranean fish fauna (Stefanescu et al. 1993, Morales-Nin et al. 1996). In addition, it is interesting to note that the differences in number of demersal species between the northern Atlantic and western Mediterranean are greater with increasing depth. The greatest impoverishment occurring on the lower slope may be related to the sharp reduction in available trophic resources below 1000 to 1200 m, that is, below the depth range of greatest potential vertical and horizontal impingement of the epipelagic and mesopelagic fauna on the slope (Mauchline & Gordon 1991, Stefanescu et al. 1993).

Fish abundance decreased significantly only on the upper slope, and remained constant below 500 m (Fig. 5b). An exponential decrease of abundance with depth has been reported by several authors in other areas (Grassle et al. 1975, Cohen & Pawson 1977, Merrett & Marshall 1981, Merrett & Domanski 1985, Gordon 1986, Merrett et al. 1991). The stable tendency in the values between depths of 500 and 1800 m coincides with the previous results obtained in the Catalan Sea below 1000 m (Stefanescu et al. 1993) and are in accordance with those obtained in other oligotrophic areas of the Atlantic Ocean (Sulak 1984).

The maximum biomass values were obtained at around a depth of 1100 to 1200 m (Table 3, Fig 5c). This peak of biomass on the middle slope has been reported both in the Atlantic (Marshall & Merrett 1977, Gordon & Duncan 1985, Gordon 1986) and in the western Mediterranean (Stefanescu et al. 1993). As abundance remained uniform below 800 m (Fig. 5b), high values of biomass on the middle slope must be due to an increase in fish size rather than an overall increase in number. Consequently, a bigger-deeper trend appeared on the upper and middle slopes. Middle and large-sized species (e.g. *Mora moro*, *Alepocephalus rostratus*, *Galeus melastomus*, *Phycis blennoides* and *Nezumia aequalis*) reach their highest abundance between 800 and 1200 m and replace smaller species that dominate at lesser depths (e.g. *Gadiculus argenteus*, *Symphurus ligulatus* and *Hymenocephalus italicus*), which accounts for the observed pattern. Moreover, at the species level a bigger-deeper phenomenon is also a characteristic feature of some dominant species of the upper and middle slope assemblages such as *Symphurus ligulatus*, *G. argenteus*, *N. aequalis* and *P. blennoides* (cf. Massutí et al. 1995, 1996a).

The decrease in biomass below 1100 m, coupled with the uniformity in abundance values, results in a smaller-deeper trend from this depth (Fig. 5d). Large-sized species become scarcer and are replaced by smaller ones such as *Bathypterois mediterraneus*, *Lepidion lepidion*, *Caelorhynchus labiatus* and *Chalinura mediterranea*. At the species level a larger-deeper trend also disappears at most depths (e.g *B. mediterraneus*; Morales-Nin et al. 1996) or is even replaced by a smaller-deeper trend (e.g. *L. lepidion* and *C. labiatus*; Stefanescu et al. 1992b).

When a comparison of our results with those obtained by Stefanescu et al. (1993) in the Balearic basin is made, similar trends in fish assemblages are evident. Nevertheless, some differences in the relative abundance and biomass of several species become apparent between the 2 areas (Fig. 6). In this way, the percentages obtained for the large-sized fish *Alepocephalus rostratus*, the most abundant species in the surveyed area, are higher than those reported in the Balearic basin, where this is a subdominant species. On the other hand, the small-sized species *Lepidion lepidion*, which is dominant and subdominant on the middle and lower slopes, respectively, off the Balearic basin, shows low values of relative abundance and bio-

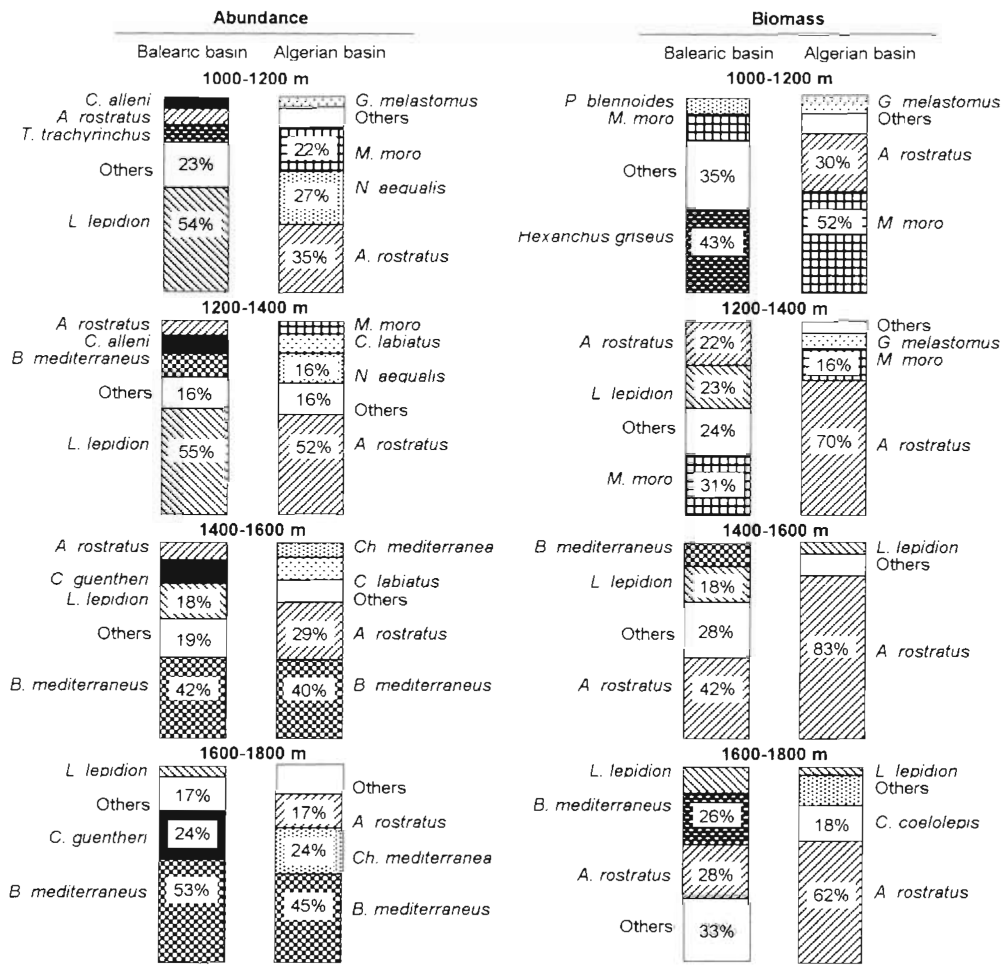

Fig. 6. Relative abundance and biomass by depth strata of the dominant and subdominant species in 2 areas of the western Mediterranean, north (Balearic basin) and south (Algerian basin) of the Balearic Islands (see Fig. 1). The results obtained in this study have been adapted to the depth intervals selected by Stefanescu et al. (1993). Samples were obtained with 2 different semi-balloon otter trawls towed from a single warp: an OTMS-27.5 with an effective horizontal opening of 14 m (Sardà et al. 1994) in the Algerian basin and an OTSB-14 with an effective horizontal opening of 6.7 m (Sulak 1984) in the Balearic basin. For both gears vertical opening ranged from 1.5 to 2 m (Merrett & Marshall 1981, Sulak 1984, Sardà et al. 1994). Full species names given in Table 1

mass off the southern Balearic Islands. The few specimens of the rare large species *Hechanchus griseus* (Bonnaterre, 1788) represents the 43% of the biomass in the Balearic basin and were trawled from submarine canyons, where food trophic availability is presumably greater (Stefanescu et al. 1993).

In the Algerian basin, the subdominant species in terms of abundance are the middle and large-sized fish *Nezumia aequalis*, *Mora moro* and *Galeus melastomus*. By contrast, in the Balearic basin, the subdominant species are the small-sized species *Cataetyx alleni* and *Coryphaenoides guentheri*, and the large-sized fish *Trachyrincus trachyrinchus*, which was caught in very low numbers in the study area (Table 1). On the other hand, *Bathypterois mediterraneus* has similar relative abundances in both areas, but its proportion within the fish assemblages, in terms of biomass, seems to be higher in the Balearic basin than in the Algerian basin.

The differences observed between the 2 areas might be explained in relation to the distinct effectiveness of the 2 bottom trawls used, because the relative sampling capacities of different gears used in deep demersal fish studies vary between species (Merrett et al. 1991, Gordon & Bergstad 1992). In this way, the high catches of larger species on the middle and lower slopes off the southern Balearic islands are most probably due in part to the use of the more efficient OTMS-27.5 gear with a horizontal opening twice that of the OTSB-14. To assess this effect, the abundance values of the main species caught with an OTMS-27.5 in the Balearic basin between 1100 and 1300 m (Stefanescu et al. 1994) were

Table 4. Abundance (fishes per 1000 m^2) of the main species caught in 2 areas of the western Mediterranean, the Balearic basin (Stefanescu et al. 1994) and the Algerian basin (present study), between depths of 1000 and 1300 m obtained with the same gear, an OTMS-27.5 trawl

	Abundance Algerian basin (n = 11)	Balearic basin (n = 7)	*t*-test
Alepocephalus rostratus	1.48 ± 0.09	2.14 ± 0.30	$t_{11.58}$ = 2.13; p > 0.05
Nezumia aequalis	0.82 ± 0.14	0.07 ± 0.01	$t_{6.11}$ = −5.13; p < 0.01
Mora moro	0.59 ± 0.15	0.25 ± 0.06	t_{16} = −2.41; p < 0.05
Galeus melastomus	0.19 ± 0.04	0.02 ± 0.01	$t_{6.45}$ = −4.34; p < 0.01
Phycis blennoides	0.02 ± 0.02	0.00	
Cataetyx alleni	0.01 ± 0.01	0.06 ± 0.01	t_{16} = 3.20; p < 0.01
Trachyrinchus trachyrinchus	0.00	0.19 ± 0.07	
Caelorhynchus labiatus	0.15 ± 0.09	0.13 ± 0.02	$t_{6.69}$ = −0.27; p > 0.05
Lepidion lepidion	0.07 ± 0.03	0.88 ± 0.08	$t_{13.25}$ = 9.74; p < 0.01
Bathypterois mediterraneus	0.11 ± 0.03	0.85 ± 0.16	$t_{10.69}$ = 4.6; p < 0.01

compared with the samples taken at the same depth interval with the same gear in our study area. Some significant differences, with the same trend described in Fig. 6, are observed (Table 4). *Nezumia aequalis*, *Mora moro*, *Galeus melastomus* and *Phycis blennoides* were more abundant in the Algerian basin, and *Cataetyx alleni*, *Trachyrincus trachyrinchus*, *Lepidion lepidion* and *Bathypterois mediterraneus* were more abundant in the Balearic basin. Nevertheless, in the case of *Alepocephalus rostratus* no significant differences between the 2 areas were found once the same sampling gear was used. Thus, the differences observed in the relative composition shown in Fig. 6 could be due not only to the different efficiency of the sampling gear but to other factors as well. In the Balearic basin samples were taken all year round, whereas in the Algerian basin samples were taken only in autumn. Thus, seasonal events such as spawning aggregation and annual cycles of abundance cannot be excluded as determinants of the differences found.

In summary, the deep-sea fish assemblages on the continental slope in the Algerian basin showed a general trend in biomass and abundance similar to those found in the Balearic basin, but some differences were evident for several species between the 2 areas. These differences are probably caused by an insignificant exchange of bathyal fish fauna between the 2 areas due to the existence of topographical and associated hydrographic barriers. Submarine canyons on the slope in the Balearic basin (Monaco et al. 1990) exert an important influence not only on the environment but also on the megafaunal populations (Reyss 1971, De Bovée et al. 1990). Finally, the fish assemblages found in both areas appear to have evolved in a relatively independent manner in relation to different ecological parameters.

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