

Deep-water fish assemblages in the Mediterranean Sea*

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SUMMARY: Data collected during the DESEAS survey carried out in three areas of the Mediterranean Sea (Balearic Sea, western and eastern Ionian Sea) were used to describe the structure and spatial distribution of the fish assemblages at depths between 600 and 4000 m. A total of 55 species (8 chondrichthyes and 47 teleost fish) were sampled, 38 of them in the Balearic Sea, 30 in the western Ionian and 37 in the eastern Ionian. Multivariate analysis showed a clear pattern of zonation with depth and geographic area. Three main assemblages were identified across the vertical gradient investigated: on the upper slope around a depth of 600 m, on the middle slope between 800 and 1300 m, and on the lower slope below 1300 m. The geographic characterisation of the ichthyofauna structure was mainly observed on the upper and middle slope. The highest abundance and biomass values were found at depths of 1000-1200 m due to the presence of larger species with high energy requirements, such as *Alepocephalus rostratus*, *Mora moro* and *Galeus melastomus*. On the middle slope, significant differences in the abundance, biomass and mean fish weight were detected between the three areas. Significant differences for these parameters were also shown between the middle and lower slope assemblages. A significant decrease in species richness and diversity was shown with increasing depth, indicating an impoverishment of the megafauna with depth and a higher similarity between the Balearic Sea and the Ionian Sea with regard to the greatest depths. The dominant species on the deepest bottoms were *Bathypterois mediterraneus*, *Chalinura mediterranea* and *Coryphaenoides guentheri*. On the lower slope, the shark *Centroscyrmnus coelolepis* was also found to be relatively abundant off the Balearic Islands, *Etmopterus spinax* in the eastern Ionian Sea and the teleost fish *Cataetyx laticeps* throughout the three study areas. The deepest bottoms of the Mediterranean Sea shelter an ichthyofauna dominated by small-medium species living in a food scarce environment in which some large mobile fishes are widespread. The results are discussed in relation to previous studies mostly carried out in the Atlantic and western Mediterranean.

Key words: fishes, distribution, deep-sea, biodiversity, fish assemblages, Mediterranean Sea.

RESUMEN: ASOCIACIONES DE PECES PROFUNDOS EN EL MEDITERRÁNEO. – A partir de datos recolectados durante la campaña DESEAS, llevada a cabo en tres áreas del mar Mediterráneo (Mar Balear y Iónico occidental y oriental), se describe la estructura y la distribución espacial de las asociaciones de peces entre 600 y 4000 m de profundidad. Se obtuvieron un total de 55 especies (8 condricthios y 47 peces teleosteos), 38 de los cuales procedían del mar Balear, 30 del Iónico occidental y 37 del oriental. El análisis multivariante de los datos nos muestra un claro patrón en zonación tanto en profundidad como por área geográfica. Se identificaron tres asociaciones principales a través del gradiente batimétrico estudiado: en el talud superior a profundidades alrededor de los 600 m, en el talud medio entre 800 y 1300 m, y en el talud inferior por debajo de los 1300 m. La caracterización geográfica de la estructura de la ictiofauna se observó principalmente en el talud superior y medio. A profundidades comprendidas entre 1000 y 1200 m fue donde se encontraron los mayores valores de biomasa, debido a la presencia de especies más grandes y con mayores requerimientos energéticos como *Alepocephalus rostratus*, *Mora moro* y *Galeus melastomus*. En el talud medio se detectaron diferencias significativas en abundancia, biomasa y peso

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medio de los peces entre las tres áreas. También se encontraron en las asociaciones de peces diferencias significativas en estos parámetros en el talud superior e inferior. Con el aumento de profundidad se detecta una disminución de la riqueza específica y la diversidad, indicando un empobrecimiento de la megafauna con la profundidad. Sin embargo se observa alta similitud entre las áreas de estudio y en las máximas profundidades alcanzadas. Las especies dominantes en los fondos más profundos fueron: *Bathyporeia mediterranea*, *Chalinura mediterranea* y *Coryphaenoides guentheri*. En el talud inferior del mar Balear, el tiburón *Centroscymnus coelolepis* fue también relativamente abundante. *Etmopterus spinax* en el Iónico oriental y el teleosteo *Cataetx laticeps* en las tres áreas de estudio. Los fondos más profundos del Mediterráneo son refugio para una ictiofauna dominada por pequeñas y medianas especies que habitan en un ambiente escaso de alimento, en el cual solo algunos grandes peces móviles pueden extenderse. Los resultados se discuten en relación a estudios previos llevados a cabo mayoritariamente en el Atlántico y Mediterráneo occidental.

Palabras clave: peces, distribución, mar profundo, biodiversidad, asociaciones de peces, Mediterráneo.

INTRODUCTION

The various oceanographic expeditions carried out over the last two centuries, among which the *Challenger* was the most famous (Ryland, 2000), mostly increased knowledge on the taxonomy and biogeography of the fish species collected in the various geographic areas and at different depths. Studies outlining the ecology and zonation of deep-sea ichthyofauna only started in the 1960s and most of the progress in this direction has been achieved in both the western and eastern north Atlantic as a result of commercial and scientific trawling surveys, sampling with traps and long lines, and observations from submersibles and baited cameras (e.g. Isaacs and Schwartzlose, 1975; Haedrich and Rowe, 1977; Gordon, 1979; Hureau *et al.*, 1979; Haedrich *et al.*, 1980; Merrett and Marshall, 1981; Gordon and Duncan, 1985; Haedrich and Merrett, 1988; Hecker, 1990; Gage and Tyler, 1991; Merrett *et al.*, 1991; Gordon and Bergstad, 1992; Merrett and Haedrich, 1997).

These studies have provided many insights into the life adaptations and strategies, diversity and distribution of deep benthic and benthopelagic fish as well as vertical patterns and zonation of the fish assemblages. For both diversity and vertical zonation, investigated down to the abyssal plane, their patterns have been shown to vary from area to area in the north Atlantic (Snelgrove and Haedrich, 1985; Haedrich and Merrett, 1990; Hecker, 1990; Koslow, 1993). The sampling limitations and the different selectivity of each gear used can play an important role when the fish assemblages are compared between different areas. In other words, the assessment of biodiversity in the deep sea is highly influenced by the gear used. However, the pattern of diversity and vertical zonation are well known to be determined by both geomorphologic and oceanographic factors, such as depth, substrate type and hydrography, and biological conditions, such as resource availability, predator-prey relationships and intraspecific and interspecific competition

(Haedrich *et al.*, 1980; Merrett, 1987; Mahaut *et al.*, 1990; Bianchi, 1992; Koslow, 1993).

Concerning the Mediterranean, although distribution and ecology of deep-sea ichthyofauna have been surveyed in the last thirty years both in the western basin (e.g. Carpine, 1970; Geistdoerfer and Rannou, 1972; Rannou, 1975, 1976; Allué *et al.*, 1984; Macpherson and Duarte, 1991; Stefanescu *et al.*, 1992a, 1992b; Massutí *et al.*, 1995; Carrassón and Matallanas, 2001) and in the eastern basin (e.g. Golani, 1986-87; Klauswitz, 1989; Albertelli *et al.*, 1992; Galil and Goren, 1994; Matarrese *et al.*, 1996; Goren and Galil, 1997; Kallianiotis *et al.*, 2000; Ungaro *et al.*, 2001), studies on fish assemblages and zonation patterns have been carried out in the last decade mostly at depths shallower than 800-1000 m (e.g. Biagi *et al.*, 1989; Stefanescu *et al.*, 1994; Massutí *et al.*, 1996; Ungaro *et al.*, 1998a, 1998b; D'Onghia *et al.*, 1998a; Kallianiotis *et al.*, 2000; Biagi *et al.*, 2002). Below these depths fish assemblages have only been identified in the western basin (Stefanescu *et al.*, 1993, 1994; Moranta *et al.*, 1998), while no studies of this type have been conducted in the eastern one.

The DESEAS project, funded by the EU, gave the opportunity to investigate the deep-sea fish fauna in three areas of the Mediterranean Sea for the first time, during the same period and with the same vessel and gear. Despite the several limitations of sampling bathyal and abyssal fish species (Merrett and Haedrich, 1997), this study represents the first attempt to identify deep-sea fish assemblages across a depth range of 600-4000 m and along a geographic gradient from the western to eastern Mediterranean.

MATERIALS AND METHODS

The deep-sea research cruise was carried out during June 2001 in three areas of the Mediterranean Sea (Fig. 1). The Balearic area extends from

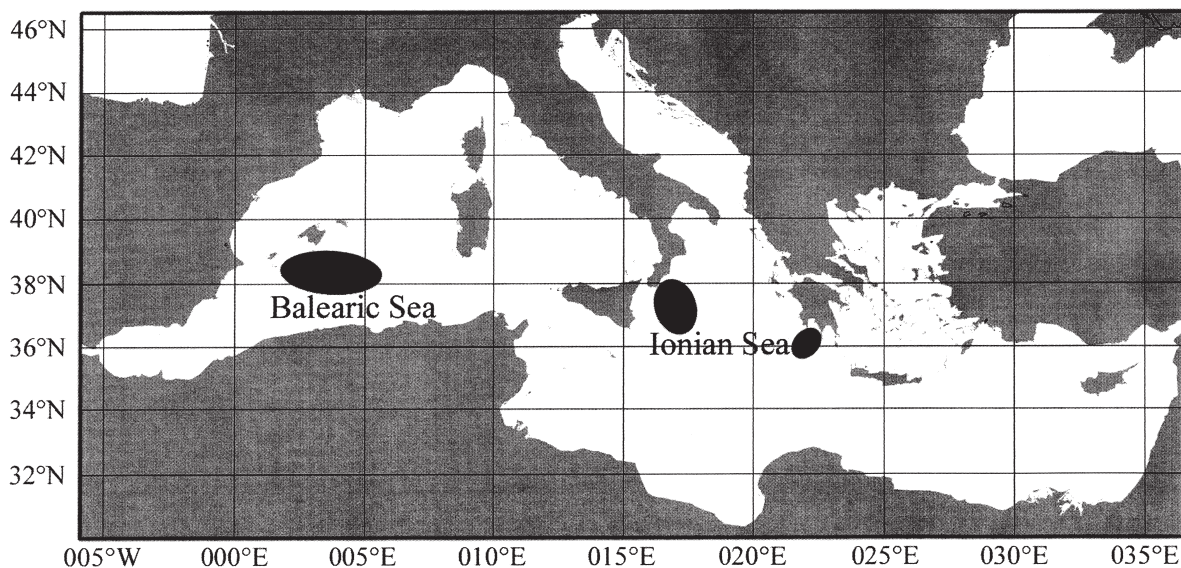


FIG. 1. – Map of the Mediterranean Sea with indication of the study areas during the DESEAS survey.

38°04'06"N 1°44'18"E to 40°48'18"N 5°34'36"E, the western Ionian area is comprised between 35°41'04"N 16°24'48"E and 38°18'30"N 17°47'00"E, the eastern Ionian area ranges from 36°19'31"N 21°54'23"E to 36°51'24"N 22°14'54"E.

The sampling was conducted with the otter trawl Maireta System (OTMS) using the R/V *García del Cid* (38 m long; 1500 HP). The OTMS (height 1.8-2 m; horizontal opening 14 m) was trawled by a single warp and operated with a pair of rectangular iron otter boards (1.20 x 2.0 m; 450 kg). A detailed description of the net can be found in Sardà *et al.* (1998). The initial and final tow time was measured by means of the SCANMAR sonar system. The ves-

sel speed and geographical position were measured using differential GPS. Profiles of turbidity, temperature and salinity were taken using a CTD probe from the surface to the bottom in each study area. Trawling was carried out during daylight hours. The number of hauls carried out in each area, with the indication of the depth, is reported in Table 1.

During the DESEAS survey, despite the long time employed in the exploration of trawlable bottoms, the sampling design was not completely satisfactory due to the different bathymetry and topography of the three areas. Many zones, mostly at depths greater than 1500 m, prevented trawling or caused the breaking of the net due to irregular bottoms. This explains the unbalanced number of hauls between the three areas, mostly below the abovementioned depth.

Specimens were identified on board following the nomenclature reported in Whitehead *et al.* (1984, 1986a, 1986b).

Haul duration ranged from 1 to 3 hours. The results obtained in number and weight were standardised to km² for subsequent numerical processing. Basic data were log-transformed to reduce the influence of the most abundant species. Classification and ordination were performed in order to identify demersal faunal assemblages. The former was carried out by means of cluster analysis using the Euclidean distance coefficient and the complete linkage and UPGMA methods (Ludwig and Reynolds, 1988), the latter through non-parametric multi-dimensional scaling (MDS) (Kruskall, 1964). Hauls were coded by geographic area (S, Balearic Sea; I, western Ionian Sea; G, eastern Ionian Sea).

TABLE 1. – Number of hauls by depth carried out in the three study areas during the DESEAS survey.

Depth (m)	Balearic area	Western Ionian area	Eastern Ionian area
600		1	2
650	1		
800		1	2
802	1		
1000	1	1	
1100			1
1200	1	1	
1300			1
1500	1	2	
1700		1	1
2000		1	
2200			1
2500	1		
2600			1
2800	1		
3300		1	
4000		1	
Total hauls	7	10	9

TABLE 2. – Depth range (m) of the species collected in the Balearic Sea, in the Western and Eastern Ionian Sea during DESEAS survey, *, indicates the mesopelagic and bathypelagic species.

Species	Balearic Sea		Western Ionian Sea		Eastern Ionian Sea	
Chondrichthyes						
<i>Hexanchus griseus</i> (Bonnaterre, 1788)					1300	1300
<i>Galeus melastomus</i> Rafinesque, 1810	650	1500	600	1500	600	1300
<i>Oxynotus centrina</i> (Linnaeus,1758)			800	800		
<i>Centrophorus granulosus</i> (Schneider, 1810)					1100	1100
<i>Centroscymnus coelolepis</i> Bocage & Capello, 1864	1500	2800				
<i>Dalatias licha</i> (Bonnaterre, 1788)	802	1200	1200	1200	800	800
<i>Etmopterus spinax</i> (Linnaeus,1758)	802	1200	600	1500	600	2200
<i>Chimaera monstrosa</i> Linnaeus,1758	650	650			800	800
Teleosts						
<i>Alepocephalus rostratus</i> Risso, 1820	802	1500				
* <i>Cyclothone braueri</i> Jespersen & Taning, 1926	650	2800	1200	1200		
* <i>Argyropelecus hemigymnus</i> Cocco, 1829	650	2800	800	1500		
* <i>Chauliodus sloani</i> Schneider, 1801	650	2500	800	2000	600	2200
* <i>Stomias boa</i> (Risso, 1810)	802	802	4000	4000	600	1700
<i>Chlorophthalmus agassizii</i> Bonaparte, 1840					600	600
<i>Bathypterois mediterraneus</i> Bauchot, 1962	1000	2800	800	3300	800	2600
<i>Benthosema glaciale</i> (Reinhardt, 1837)					600	600
* <i>Ceratoscopelus maderensis</i> (Lowe, 1839)	650	2500			600	600
* <i>Diaphus metopoclampus</i> (Cocco, 1829)					600	800
* <i>Hygophum benoiti</i> (Cocco, 1838)			800	800		
* <i>Lampanyctus crocodilus</i> (Risso, 1810)	650	2500	600	3300	600	1300
* <i>Notolepis rissoi</i> Bonaparte, 1840	1000	1000				
* <i>Paralepis speciosa</i> Bellotti, 1878			600	600	800	800
<i>Nettastoma melanorum</i> Rafinesque, 1810	1000	1000	600	1500	600	1300
<i>Conger conger</i> Linnaeus, 1758					600	600
<i>Halosaurus ovenii</i> Johnson, 1863	2800	2800				
<i>Notacanthus bonapartei</i> Risso, 1840	1200	1200	600	1500	1100	1100
<i>Polyacanthonotus rissoanus</i> (Filippi & V��rany, 1859)					2200	2600
<i>Chalinura mediterranea</i> Giglioli, 1893	1500	2800	1500	4000	1300	2600
<i>Coryphaenoides guentheri</i> (Vaillant, 1888)	2500	2800	1500	1700	1700	2600
<i>Caelorhynchus caelorhynchus</i> (Risso, 1810)	650	650				
<i>Caelorhynchus mediterraneus</i> Iwamoto & Ungaro, 2002	1200	1500	1200	1500	1300	1300
<i>Hymenocephalus italicus</i> Giglioli, 1884	650	802	600	800	600	800
<i>Nezumia aequalis</i> (Gunther, 1878)	650	1500				
<i>Nezumia sclerorhynchus</i> (Valenciennes, 1838)			600	1500	600	1300
<i>Trachyrhynchus trachyrhynchus</i> (Risso, 1810)	802	1200	1000	1000		
<i>Merluccius merluccius</i> (Linnaeus, 1758)					600	600
<i>Micromesistius poutassou</i> (Risso, 1826)	650	650	600	600	600	600
<i>Phycis blennoides</i> (Brunnich, 1768)	650	1200	600	1000	600	800
<i>Lepidion lepidion</i> (Risso, 1810)	1000	1500	1200	1700	1300	1700
<i>Mora moro</i> (Risso, 1810)	802	1200	800	1200	800	1300
<i>Hoplostethus mediterraneus</i> Cuvier, 1829	650	802	600	800	600	800
<i>Epigonus constanciae</i> (Giglioli, 1880)					600	600
<i>Epigonus denticulatus</i> Dieuzeide, 1950	650	802				
<i>Epigonus telescopus</i> (Risso, 1810)			1000	1000		
<i>Pagellus bogaraveo</i> (Brunnich, 1768)	650	650	1000	1000		
<i>Lepidopus caudatus</i> (Euphrasen, 1788)	650	650				
<i>Cataetys laticeps</i> Koefoed, 1927	2500	2800	2000	3300	1700	2600
<i>Benthocometes robustus</i> (Goode & Bean, 1886)	1200	1200				
<i>Helicolenus dactylopterus</i> (Delaroche, 1809)	650	650			600	800
<i>Trachyscorpia cristulata echinata</i> (Koehler, 1896)	1500	1500				
<i>Peristedion cataphractum</i> (Linnaeus, 1758)					600	800
<i>Lepidorhombus boscii</i> (Risso, 1810)					600	600
<i>Lepidorhombus whiffiagonis</i> (Walbaum, 1792)					600	600
<i>Symphurus ligulatus</i> (Cocco, 1844)	650	650	600	600	600	800
<i>Symphurus nigrescens</i> Rafinesque, 1810	802	802	600	600		

Species recorded in a single haul and those with pelagic habits were excluded from the computations. Only *Lampanyctus crocodilus* was included in the analysis since the adult specimens of this species live close to the bottom (Stefanescu and Cartes, 1992). All these analyses were carried out using STATISTICA software (StatSoft, 1995).

Considering the different difficulties of this kind of research (among which the long time required for the exploration of unknown deep-sea bottoms suitable to be trawled, the long time required to make a single haul and the decreasing sampling efficacy with depth), the term “assemblage” refers to a cluster of fish species available to

the used gear in the investigated areas irrespective of whether they interact or not (Wootton, 1991), thus avoiding any confusion with other ecological meanings such as “community”.

The average abundance (N Km⁻²), biomass (g Km⁻²), mean fish weight (g/fish), species richness and Shannon-Wiener diversity index (H') were determined for the main groups resulting from the classification and ordination. The geometric mean was adopted in computation of abundance, biomass and mean fish weight to minimise the negative effect caused by extreme values (Stefanescu *et al.*, 1993). Differences between groups were evaluated using the non-parametric test of Kruskal-Wallis (Conover, 1980). Changes in the abundance, biomass, mean fish weight, species richness and diversity index with depth were evaluated both with regression analysis and Spearman non parametric correlation (Conover, 1980).

RESULTS

A total of 55 species (8 chondrichthyes and 47 teleost fish) were collected during the DESEAS survey and are listed in Table 2.

Excluding the mesopelagic and bathypelagic species (with the exception of *L. crocodilus*), 32, 24 and 31 species were captured off the southern Balearic Islands and in the western and eastern Ionian Sea respectively.

The resulting dendrogram of hauls indicates the presence of four main clusters related to the depth and geographic area (Fig. 2). The first cluster consisted of the two hauls from depths of 1000 and 1200 m in the Balearic Sea. The second cluster concerned the deepest stations covering the depth range between 1500 and 4000 m in all three areas. A third group was made up of the stations investigated between 800 and 1500 m in the Ionian Sea, both western and eastern. The fourth aggregation consisted of the shallower hauls carried out around 600 m together with the station conducted at 802 m in the Balearic Sea. In this last cluster a lower distance (higher similarity) was shown between the two hauls carried out at 600 m in Greek waters, due to the remarkable abundance of *Chlorophthalmus agassizii* and *Helicolenus dactylopterus*.

The two hauls at depths of 1000 and 1200 m in the Balearic Sea showed a higher similarity (lower distance) in relation to the exclusive presence of *Alepocephalus rostratus* and *Nezumia aequalis*. In the other three groups, the stations at approximately

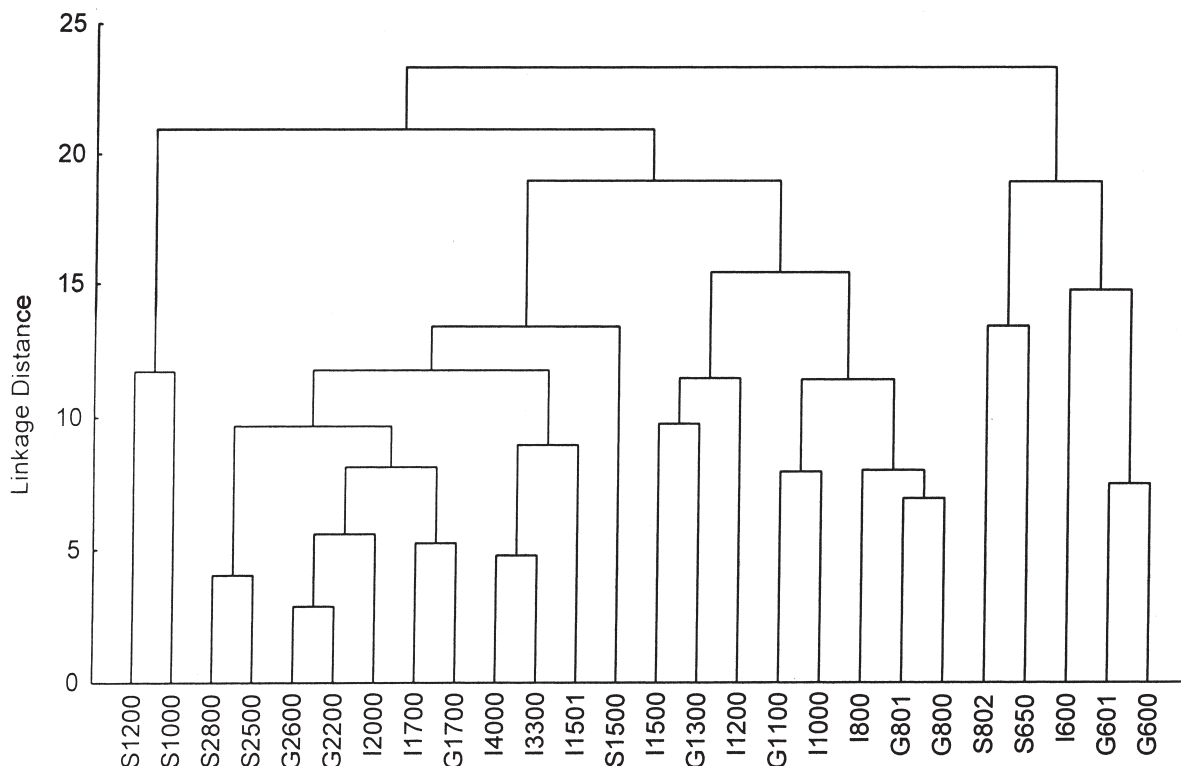


FIG. 2 – Dendrogram of 26 hauls carried out during the DESEAS cruise (S, Balearic Sea; I, western Ionian Sea; G, eastern Ionian Sea).

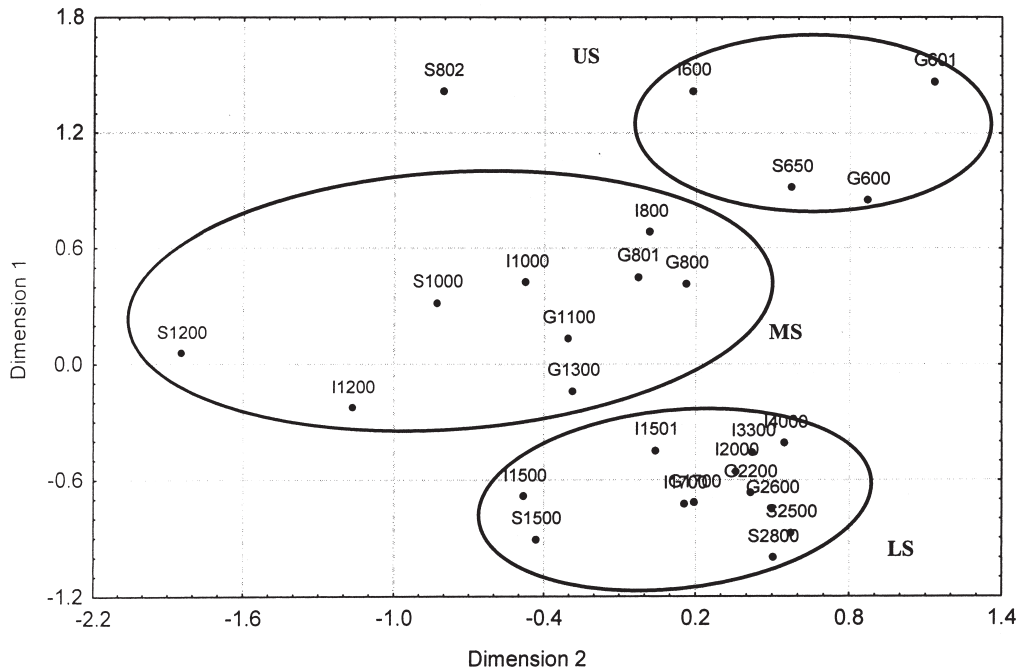


FIG. 3 – Non-parametric multi dimensional scaling (MDS) of the hauls carried out during the DESEAS cruise (S, Balearic Sea; I, western Ionian Sea; G, eastern Ionian Sea; US, upper slope; MS, middle slope; LS, lower slope).

the same depth showed the lowest distance values. Within the cluster of the deepest hauls, the two deepest hauls (3300 and 4000 m) were grouped together with one haul carried out at 1500 m in the same area. This latter sub-group is the result of a very low number of species at all three stations with the common occurrence of *Bathypterois mediterraneus* found in comparable densities.

The results of MDS (stress level = 0.133) are shown as a two-dimensional representation in Figure 3. The ordination of the 26 hauls was in general agreement with the clustering, showing the aggregation of the shallower and deeper hauls according to the positive and negative values of the first dimension respectively. In fact, the first dimension of the axes was highly correlated with depth ($r_{\text{spearman}} = -0.864$; $P < 0.01$) (Fig. 4). Moreover, the MDS representation shows more clearly that the hauls at 1500 m are grouped together with those carried out on the deepest bottoms.

A greater heterogeneity was evident in the ordination of the stations carried out between 800 and 1300 m. These stations reflect the geographic location due to the different abundance of the species in the three areas. The western Ionian stations are diagonally positioned between the Balearic and eastern Ionian ones according to the second dimension of the axes.

According to the results of the multivariate analysis, the values of the average abundance, bio-

mass, mean fish weight, mean species richness and diversity index were computed for the groups of hauls carried out at depths of 600-650 m (upper slope), 800-1300 m (middle slope) and below 1300 m (lower slope). The ecological parameters in the three areas were only calculated on the middle slope where a sufficient number of samples were collected at the same depths (Table 3).

Comparing the results between the three areas using the Kruskal-Wallis test, no significant differences were shown for species richness and diversity. Concerning the abundance, significant differences were detected between the western Ionian and eastern Ionian ($P = 0.02$) and between the Balearic Sea

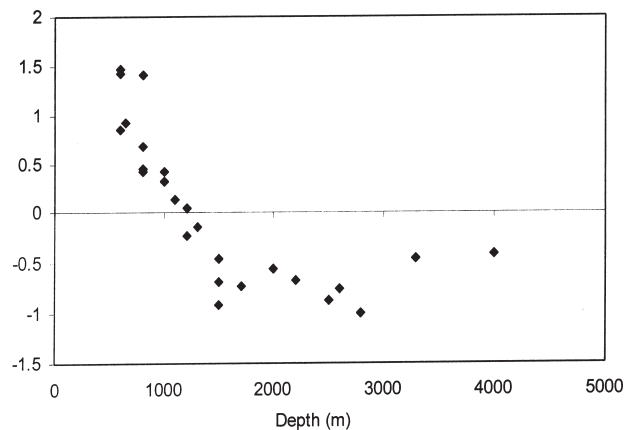


FIG. 4 – Plot of the first dimension resulting from the MDS vs depth.

TABLE 3. – Values of ecological parameters for each area in the middle slope (800-1300 m) and for all three areas in the upper (600-650 m) and in the lower slope (> 1300 m).

	600-650 m all three areas	Balearic Sea	800-1300 m W. Ionian Sea	E. Ionian Sea	> 1300 m all three areas
Mean abundance (N km ⁻²)	96	177	143	77	85
min-max	22-1330	33-4101	23-549	26-491	15-2494
Mean biomass (g km ⁻²)	2827	22893	8186	3477	2898
min-max	27-164822	868-813624	91-184245	142-125189	76-238526
Mean fish weight (g)	33	96	75	41	17
min-max	1-3300	1-3780	2-1619	1-17000	0.5-2046
Mean species richness	11 ± 2.08	9 ± 1.53	9 ± 1.53	7 ± 1.41	4 ± 2.63
Diversity (H')	2.43	1.83	2.27	2.00	1.56
Number of hauls	4	3	3	4	12

and eastern Ionian (P = 0.006), while the differences were not significant between the Balearic Sea and western Ionian Sea.

With regard to biomass, significant differences were shown between the Balearic Sea and western Ionian Sea (P = 0.05) and between the Balearic Sea and eastern Ionian (P = 0.0007), while no significant

differences were observed between the western and eastern Ionian.

The mean fish weight values showed significant differences between the three areas (P = 0.028 for Balearic-western Ionian; P = 0.0005 for western Ionian-eastern Ionian; P = 0.0001 for Balearic-eastern Ionian).

TABLE 4. – Percentage of abundance (N km⁻²) and biomass (kg km⁻²) of the dominant species in the upper slope (600-650 m) for all three areas, in the middle slope (800-1300 m) for each study area, and in the lower slope for all three areas divided into three sub-groups according to depth.

600-650 m		800-1300 m			
all three areas	%	Balearic Sea	%	W. Ionian Sea	%
Abundance					
<i>H. dactylopterus</i>	22.41	<i>A. rostratus</i>	47.88	<i>M. moro</i>	20.04
<i>C. agassizii</i>	17.62	<i>L. lepidion</i>	9.66	<i>N. sclerorhynchus</i>	19.07
<i>L. crocodilus</i>	10.20	<i>N. aequalis</i>	8.66	<i>G. melastomus</i>	17.86
<i>H. mediterraneus</i>	9.06	<i>G. melastomus</i>	8.05	<i>L. crocodilus</i>	7.88
<i>P. blennoides</i>	6.30	<i>M. moro</i>	6.87	<i>C. mediterraneus</i>	6.39
<i>N. sclerorhynchus</i>	5.00	<i>T. trachyrhynchus</i>	6.26	<i>N. melanorum</i>	5.22
Biomass					
<i>H. dactylopterus</i>	51.83	<i>A. rostratus</i>	46.56	<i>M. moro</i>	44.42
<i>P. blennoides</i>	9.46	<i>M. moro</i>	20.04	<i>G. melastomus</i>	20.17
<i>H. mediterraneus</i>	7.71	<i>G. melastomus</i>	15.95	<i>D. licha</i>	16.66
<i>G. melastomus</i>	7.70	<i>D. licha</i>	4.07	<i>T. trachyrhynchus</i>	4.55
<i>C. conger</i>	7.12	<i>T. trachyrhynchus</i>	2.96	<i>N. sclerorhynchus</i>	2.80
<i>C. agassizii</i>	5.22	<i>N. aequalis</i>	2.67	<i>H. mediterraneus</i>	2.42
1500-2000 m		2200-2800 m		3300-4000 m	
all three areas	%	all three areas	%	all three areas	%
Abundance					
<i>B. mediterraneus</i>	68.83	<i>B. mediterraneus</i>	33.40	<i>C. mediterranea</i>	84.62
<i>A. rostratus</i>	8.58	<i>C. mediterranea</i>	26.17	<i>B. mediterraneus</i>	7.69
<i>C. mediterraneus</i>	7.11	<i>C. guentheri</i>	15.99	<i>C. laticeps</i>	3.85
<i>L. lepidion</i>	4.81	<i>C. laticeps</i>	12.43	<i>L. crocodilus</i>	3.85
<i>C. mediterranea</i>	1.81	<i>C. coelolepis</i>	9.26		
<i>G. melastomus</i>	1.60				
Biomass					
<i>A. rostratus</i>	52.56	<i>C. coelolepis</i>	71.16	<i>C. mediterranea</i>	62.10
<i>B. mediterraneus</i>	9.83	<i>C. laticeps</i>	18.33	<i>C. laticeps</i>	33.39
<i>L. lepidion</i>	7.70	<i>C. mediterranea</i>	4.77	<i>B. mediterraneus</i>	3.17
<i>C. coelolepis</i>	7.35	<i>C. guentheri</i>	3.28	<i>L. crocodilus</i>	1.34
<i>G. melastomus</i>	4.93	<i>B. mediterraneus</i>	1.90		
<i>C. laticeps</i>	3.90				

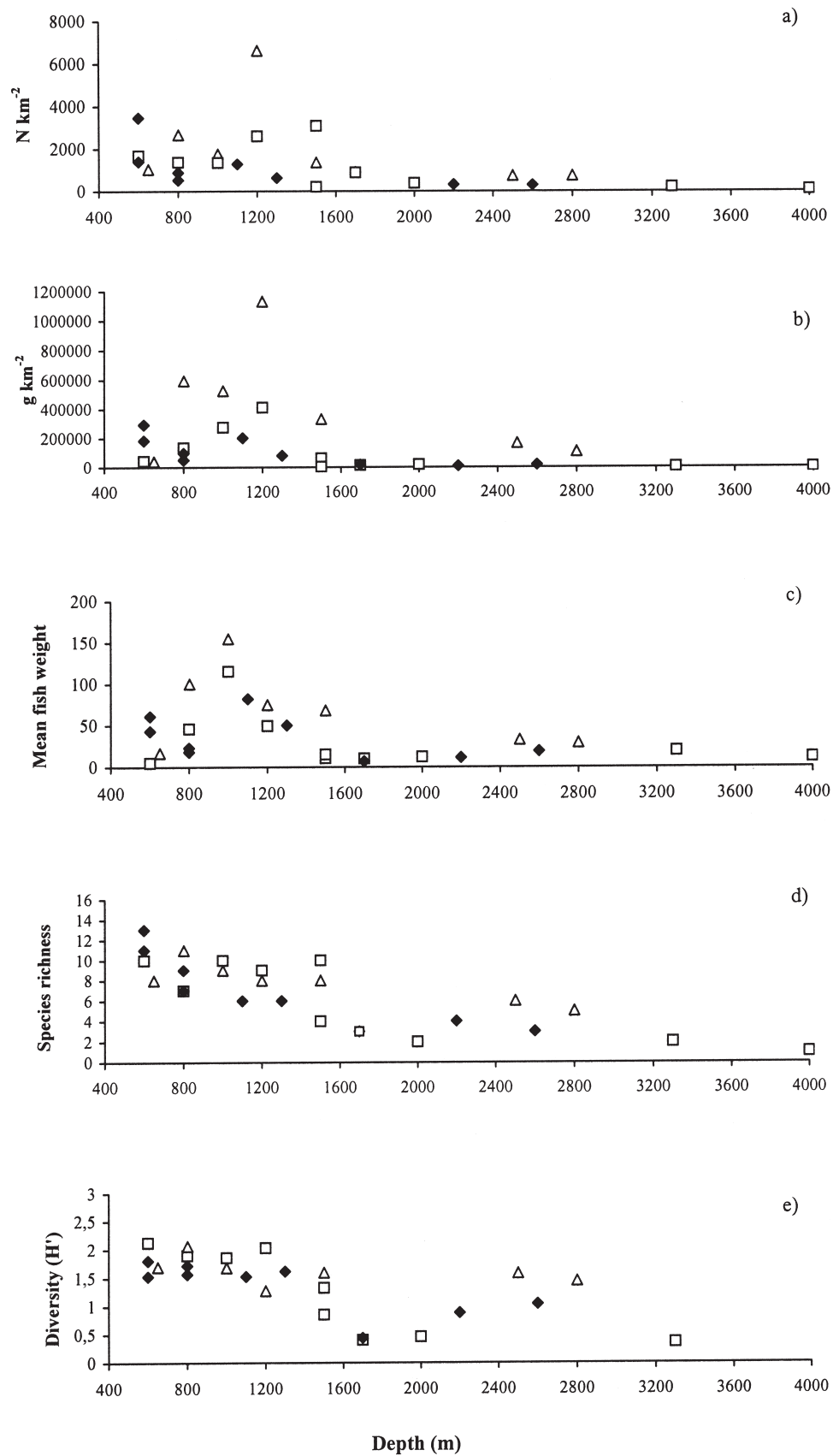


FIG. 5. – Relationship between abundance (a), biomass (b), mean fish weight (c), species richness (d), diversity (e) and depth during the DESEAS survey (Δ , Balearic Sea; $\square$, western Ionian Sea; $\blacklozenge$, eastern Ionian Sea).

Comparing the ecological parameters of the middle slope as a whole (800-1300 m) with those of the lower slope (> 1300 m), the Kruskal-Wallis test gave significant differences for the abundance ($P = 0.043$), biomass ($P = 0.0017$) and mean fish weight ($P = 0.0001$).

The changes of the ecological parameters across the whole depth range are presented in Figure 5. Significant variations were only detected for species richness (s.r. = $4991.3 \text{ depth}^{-0.9425}$; $r^2 = 0.66$, $P < 0.01$; $r_{\text{spearman}} = -0.795$; $P < 0.01$) and diversity ($H' = 2.0421 - 0.0005 \text{ depth}$, $r = -0.65$, $r^2 = 0.42$, $P < 0.01$; $r_{\text{spearman}} = -0.715$; $P < 0.01$). The increase in values at around 2600 m might be the consequence of insufficient samples.

The percentages of abundance and biomass of the dominant species across the depth range are reported in Table 4. In this table, the percentage values in the three areas were only calculated in the middle slope for the abovementioned reasons; the lower slope assemblage was further divided into more coherent sub-groups according to depth.

In the upper slope group (600-650 m), though *H. dactylopterus* was found almost exclusively in Greek waters, it was the dominant species both in biomass and abundance. *C. agassizii*, *H. mediterraneus* and *Phycis blennoides* were among the most abundant species both in number and weight. The former was exclusively found in the eastern Ionian Sea.

Concerning the middle slope (800-1300 m), in the Balearic Sea the dominant species both in number and weight was *A. rostratus*. *Lepidion lepidion*, *N. aequalis* and *Galeus melastomus* provided noteworthy contributions to the abundance and *Mora moro* and *G. melastomus* to the biomass. In the western Ionian Sea the most abundant species was *M. moro* followed by *Nezumia sclerorhynchus* and *G. melastomus*. The greatest biomass contributions were made by *M. moro*, *G. melastomus* and *Dalatias licha*. In the eastern Ionian Sea the most abundant species were *G. melastomus*, *M. moro* and *L. crocodilus* in density and *Hexanchus griseus*, *M. moro* and *G. melastomus* in biomass.

On the lower slope, at 1500-2000 m, *B. mediterraneus* was the dominant species in number. It was mostly found in the Ionian Sea (54% on the western side, 11% on the eastern and 4% in the Balearic Sea). Although *A. rostratus* was exclusively captured off the southern Balearic Islands down to 1500 m, it provided the greatest biomass contribution in this depth stratum.

At depths of 2200-2800 m, *B. mediterraneus* was the most abundant species followed by *Chalinura mediterranea*, *Coryphaenoides guentheri* and *Cataetys laticeps*. The dominant species in biomass was *Centroscymnus coelolepis* followed by *C. laticeps*.

On the abyssal plane (3300-4000 m) the dominant species was *C. mediterranea* both in number and weight.

DISCUSSION

In spite of the sampling limitations encountered throughout the three investigated areas, this study reveals the existence of deep water fish assemblages in which depth and geographic location play the main role in megafaunal group differentiation.

Basically, the faunal zonation by depth can be identified in an upper slope (around 600 m), middle slope (800-1300 m) and lower slope (> 1300 m) assemblage as shown in the north Atlantic (Haedrich *et al.*, 1980; Haedrich and Merrett, 1988; Hecker, 1990) and in the western Mediterranean (Stefanescu *et al.*, 1993; Moranta *et al.*, 1998). In agreement with these studies, the peak of abundance and biomass was found around 1200 m and the main faunal change along the depth gradient was shown at around 1500 m. According to Hecker (1990) and Stefanescu *et al.* (1993), this bathymetric zone can be considered to be within a "transitional" zone where an important species turnover occurs. The former author found this transitional zone varying from a depth interval ranging from 100 m (1200-1300 m) to 400 m (1200-1600 m) in four geographic locations in the north Atlantic, reflecting differences in local topography and geology. The latter identified a transitional zone in the lower slope around 1400 m due to the substitution of some dominant and subdominant species. Cartes and Sardà (1992) and Cartes (1993), studying the deep-sea decapod crustaceans, reported a faunal discontinuity at around 1200 m in the Catalan Sea.

The small differences in the boundaries between the middle and lower slope shown in the various studies (op. cit.) might be due to the different number of samples and to the geographic characterisation of the trawl stations (Haedrich and Merrett, 1990; Koslow, 1993). This latter aspect was particularly evident in the upper and middle slope, where the main differences in the faunistic abundance between the Balearic and Ionian areas were detect-

ed. Although the small number of hauls and the gear selectivity could affect the finding of the different species whose abundance appears to decrease with depth, the abundant presence of *C. agassizii* and *H. dactylopterus* exclusively on the upper slope of the eastern Ionian Sea might be due to the absence of fishing activity in this area below 400-500 m in depth (D'Onghia *et al.*, 2003). Though on the deepest bottoms the occurrence of some species and their abundance (e.g. *A. rostratus* only found off the Balearic Islands down to 1500 m) influenced the linkage between the hauls, the assemblage detected on the lower slope indicates a higher homogeneity between the three areas and thus a higher similarity in the ecological conditions between the Balearic Sea and the Ionian Sea at the greatest depths.

Considering the stability of the environmental parameters in the deep water of the Mediterranean Sea, the ichthyofauna zonation has been attributed to the trophic resources available above and below a depth of 1200 m linked to the distribution of mesopelagic organisms and the particular hydrological conditions of this basin (Carrassón and Matallanas, 1990; Stefanescu *et al.*, 1992b, 1993; Morales-Nin *et al.*, 1996; Moranta *et al.*, 1998; Maynou and Cartes, 2000; Carrassón and Matallanas, 2001). The larger species with high energy requirements, such as *A. rostratus*, *Trachyrhynchus trachyrhynchus*, *M. moro* and *G. melastomus* are replaced at greater depths by smaller species which utilise a broad spectrum of benthopelagic prey, such as *B. mediterraneus*, *C. mediterranea* and *C. guentheri*. However, on the lower slope the presence of large fishes, such as *C. coelolepis* off the Balearic Islands, *Etmopterus spinax* in the eastern Ionian Sea and *C. laticeps* in all three study areas, is also important in the structure of the deep-sea Mediterranean ichthyofauna.

Although it is generally accepted that the megafauna changes between the middle and the lower slope may be due to the sharp reduction in the mesopelagic fauna, its excretory products and detritus sedimenting down from shallower layers, most of the studies on these bioenergetic aspects have been conducted in the Atlantic (e.g. Gordon, 1979; Vinogradov and Tseitlin, 1983; Merrett, 1987; Gage and Tyler, 1991; Mauchline and Gordon, 1991), while very little is known about them in the Mediterranean (Stefanescu *et al.*, 1993) and particularly in the eastern basin.

In the context of the oligotrophic Mediterranean conditions, abundance, biomass and mean fish

weight values came out significantly greater in the Balearic Sea than in the western and eastern Ionian. In addition, the abundant occurrence of *A. rostratus* (between 800 and 1500 m) and *C. coelolepis* (on the lower slope) was only recorded in the Balearic Sea. These differences between the study areas could be linked to the fact that the western basin shows a higher productivity than the eastern one (Danovaro *et al.*, 1999; Maynou and Cartes, 2000; Melley *et al.*, 2000). In fact, megafaunal biomass in the deep sea largely depends on the surface productivity regime (Haedrich and Rowe, 1977; Gordon 1979; Merrett, 1987). *A. rostratus* feeds mainly on gelatinous macroplankton (Carrassón and Matallanas, 1990) and it has never been recorded in the eastern Mediterranean. In the Atlantic, Anderson *et al.* (1985) and Merrett (1987) reported that the Alepocephalidae family is abundant in oligotrophic and less seasonal areas and is usually replaced by other families, such as Macrouridae and Moridae, in more eutrophic areas. This contrasts with our findings, since Macrouridae and Moridae were captured throughout the basin compared to *A. rostratus* only on the western side, which is assumed to be less oligotrophic than the eastern side. In addition, Moranta *et al.* (1998) reported that *A. rostratus* is more abundant south of the Balearic Islands (Balearic Sea in this study) than to the north of these islands, where the species *L. lepidion* and *B. mediterraneus* are more abundant. These differences seem to be due to the differences in the trophic web (Massutí *et al.*, 2004). South of the Balearic Islands, where the food of planktonic origin is more important, the dominant species is *A. rostratus*, which feeds mainly on macroplankton (Carrassón and Matallanas, 1990), while north of the Balearic Islands, where there are submarine canyons and the benthic and benthopelagic organisms play an important role in the food web (Cartes *et al.*, 1994), the most abundant species are *L. lepidion* and *B. mediterraneus*, which prey on benthic decapods (Carrassón *et al.*, 1997) and benthopelagic crustaceans (Carrassón and Matallanas, 2001) respectively. These different conditions in the trophic web, due to the surface productivity and the presence of canyons, could explain the absence of *A. rostratus* in the Ionian Sea, where submarine canyons on the slope are widespread (D'Onghia *et al.*, 1998b). Reflecting these remarks, *A. rostratus* and *B. mediterraneus* showed striking dominance in the Balearic Sea and Ionian Sea respectively.

The reason for the absence of *C. coelolepis* in the samples taken in the Ionian Sea during this study remains unclear. In fact, the presence of *C. coelolepis* is known in the eastern Mediterranean. It has been recorded together with *H. griseus*, *G. melastomus*, *E. spinax* and *Centrophorus* spp. between 1500 and 2500 m in the Cretan Sea, and between 2300 and 3850 m in the Rhodes Basin (Jones in Priede and Bagley, 2000; Jones *et al.*, 2003). However, the presence of shark species recorded during this and previous studies in both the western and eastern Mediterranean Sea indicates that the trophic system depending on the pelagic input and involving large mobile fishes occurs throughout the basin, although with possible qualitative-quantitative differences between the western and eastern side.

Compared with the Atlantic, the depths of the Mediterranean show an impoverishment of megafauna as well as lower abundance and biomass in the structure of the ichthyofauna. These differences have long been considered to be due to historical factors, energetic constraints and physical conditions (Tortonese, 1960; Fredj and Maurin, 1987; Bouchet and Taviani, 1992; Quignard and Tomasini, 2000).

The abrupt reduction of abundance, biomass and mean fish weight at depths greater than 1200 m and the significant decrease in species richness and diversity across the whole depth range indicate the existence of a deep-sea ichthyofauna dominated by small species living in a food-scarce environment in which some large mobile fishes are widespread. According to studies in the Atlantic ocean (e.g. Dayton and Hessler, 1972; Isaacs and Schwartzlose, 1975; Haedrich and Rowe, 1977; Mahaut *et al.*, 1990; Merrett and Haedrich, 1997), the smaller fish species, such as tripodfish and grenadiers, are adapted to a food-limited regime, feeding on epibenthic and benthopelagic organisms, while the larger species, such as sharks, depend on food arriving from the pelagic domain, such as dead animals descending from above, mid-water organisms that approach the bottom and juveniles of bathyal and abyssal species that return to deep water during their ontogenetic migration. In the deep sea the bottom can be considered as a wide barren area where distribution of food is patchy. The large and more motile animals are generalist feeders which utilise a broad spectrum of prey (Hureau *et al.*, 1979; Haedrich *et al.*, 1980). Haedrich and Rowe (1977) reported that the need

to search a wide area for a few randomly occurring food items and the lower metabolic demand per unit weight in large animals should select for large efficient seekers in the deep-sea megafauna. Albertelli *et al.* (1992), casting traps at 4500 m in the eastern Mediterranean, did not find small scavenger crustaceans and echinoderms but only relatively large swimming prawns and mysids, and specimens of *Chalinura mediterranea*. In the opinion of these authors, the high activity and the long range foraging needed in an unpredictable food environment would exclude or drastically limit the smaller groups of crustaceans. Jones *et al.* (2003) recorded only the caridean shrimp *Acantheephyra eximia* and the macrourid *C. mediterranea* below 4000 m, indicating that the presence of these two species at depths at which the other species were absent might be due to a combination of their small size and mobility as well as their opportunistic and euryphagic feeding strategy (Cartes and Maynou, 1998; Carrassón and Matallanas, 2002).

Many studies on feeding habits in deep-sea fish species have indicated the presence of both active predators such as *C. coelolepis* and *E. spinax* feeding on a wide range of benthic and free swimming organisms, and species such as *B. mediterraneus* with reduced mobility and a microphagous filtering diet (e.g. Hureau *et al.*, 1979; Haedrich *et al.*, 1980; Mauchline and Gordon, 1984a, 1984b; Carrassón and Matallanas, 1990; Mahaut *et al.*, 1990; Carrassón *et al.*, 1992; Merrett and Haedrich, 1997; Carrassón and Matallanas, 2001). In addition, a degree of overlapping between these two extreme trophic strategies seems to be found in other species belonging to the Macrouridae, Moridae and Bythitidae families, which feed on food occurring within the benthic boundary and at the bottom interface (Isaacs and Schwartzlose, 1975; Geistdoerfer, 1978; Macpherson, 1979; Mauchline and Gordon, 1984a, 1984b; Carrassón and Matallanas, 1990; Mahaut *et al.*, 1990; Carrassón and Matallanas, 2002). According to these studies, the present results would indicate that: 1) the differences in the ichthyofauna structure between the Balearic Sea and the Ionian Sea are more marked on the upper and middle slope than on the lower slope; and 2) in the Mediterranean lower slope assemblage, which is very little diversified, several life styles coexist: the smaller and medium sized species feeding mainly on benthopelagic plankton or strictly benthic organisms are widespread throughout the basin as typical species of food-limited assemblages; the large car-

nivorous species, roaming a vast area searching for randomly occurring large food items, seem to be differently distributed between the Balearic and Ionian Sea. These findings indicate that our knowledge on the distribution of deep-sea organisms and its causes is still fragmented.

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