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Biodiversity of deep-sea demersal megafauna in western and central Mediterranean basins

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SUMMARY: Abundance, biomass and diversity patterns of bathyal and abyssal Mediterranean megafauna (fishes and invertebrates) were analyzed in the western Balearic Sea, the western Ionian Sea and the eastern Ionian Sea. Sampling was conducted with a Otter-trawl Maireta System (OTMS) at depths ranging from 600 to 4000 m. A series of ecological indicators were computed: total abundance and biomass, Margalef species richness, Shannon-Wiener diversity and Pielou's index of evenness. A multidimensional scaling was applied, indicating that the megafauna communities were grouped by depth, while geographic area had a less defined influence. Margalef richness declined with depth in all three areas, but more steeply in the western Ionian Sea. Pielou's evenness behaved differently in the three zones, showing a V-shaped curve in the eastern Ionian while showing a decreasing pattern in the other two areas. At lower slope depths, massive presence of the fishes *Alepocephalus rostratus* in the western basin and *Bathypterois mediterraneus* in the central basin caused a sharp reduction in evenness.

Keywords: diversity, megafauna, deep sea, western Mediterranean, western Ionian, eastern Ionian.

RESUMEN. PATRONES DE BIODIVERSIDAD DE LA MEGAFUNA DEMERSAL DEL MAR PROFUNDO EN LAS CUENCAS OCCIDENTAL Y CENTRAL DEL MEDITERRÁNEO. – Se analizaron los patrones de abundancia, biomasa y diversidad de la megafauna (peces y invertebrados) batial y abisal del Mediterráneo. El muestreo se llevó a cabo con el Sistema de Arrastre Maireta a profundidades entre 600 y 4000 m, en el mar Balear occidental, el mar Jónico occidental y el mar Jónico oriental. Por cada pesca, se calculó una serie de indicadores ecológicos, después de estandarizar por el área de barrido: abundancia y biomasa totales, riqueza específica de Margalef, diversidad de Shannon-Wiener y el índice de equitatividad de Pielou. Se aplicó un *multidimensional scaling* (MDS) que indicó un agrupamiento de las comunidades de megafauna por profundidad, mientras que el área geográfica tiene una influencia menos definida. El índice de riqueza específica de Margalef disminuye con la profundidad en las tres áreas, pero de manera más pronunciada en el Mar Jónico occidental. La equitatividad de Pielou se comporta de manera diferente en las tres zonas, presentando una curva en forma de V en el Jónico oriental, y un patrón decreciente en las otras dos áreas. En el talud continental inferior, la presencia masiva de los peces *Alepocephalus rostratus* en la cuenca occidental y *Bathypterois mediterraneus* en la zona central causan una reducción drástica de la equitatividad.

Palabras clave: diversidad, megafauna, mar profundo, Mediterráneo occidental, Jónico occidental, Jónico oriental.

INTRODUCTION

Deep-sea ecosystems are known to be the largest repository of biodiversity of the biosphere (Sanders, 1968; Gage and Tyler, 1991), but remain mostly unknown because of extreme conditions in sampling techniques. New insights into deep-sea biodiversity are thus necessary in order to better understand the grade of

stability and vulnerability of these environments (Merrett and Haedrich, 1997), but should focus on large-scale analyses (Bianchi and Morri, 2000) dealing, for example, with a whole enclosed deep-sea environment.

The Mediterranean Sea is an optimal environment for studying the patterns of biodiversity for several reasons. First of all, it is an enclosed sea with limited connection with the outer Atlantic ocean. Its constant

deep water temperature of between 13 and 14°C and its high coastal input related to its closeness to land (Tyler, 2003; Sardà *et al.*, 2004a) make it a natural laboratory for studying the factors involved in determining community diversity. Fishing pressure typically reaches depths of 800–900 m in the western basin, while in the rest of the Mediterranean it barely reaches 600 m (Mytilineou *et al.*, 2005; Sardà *et al.*, 2009). In addition, a trawling ban is in effect in the whole basin below 1000 m depth—a unique situation at present for an enclosed sea (EC Regulation 1967/2006), allowing us to study quasi-pristine environments. Below these depths direct human impact is reduced to a minimum and is usually caused by litter discharge (Galil *et al.*, 1995), whose impact has not yet been clarified.

Most bathyal and abyssal soft bottoms—with the exception of chemosynthetic habitats such as hydrothermal vents and cold seeps—are driven by organic matter input from the upper strata (Smith *et al.*, 2008; Corliss *et al.*, 2009; Lampadariou *et al.*, 2009). The case of the Mediterranean is unique, because it is a semi-enclosed sea that has a gradient of decreasing availability of organic matter from west to east (Bethoux *et al.*, 1999; Danovaro *et al.*, 1999). The Levantine deep basin, known to be generally highly oligotrophic (Azov, 1991; Psarra *et al.*, 2000; Danovaro *et al.*, 2001), also shows a clear scarcity of all size classes of benthic fauna (Danovaro *et al.*, 1999; Basso *et al.*, 2004; Lampadariou *et al.*, 2009; Danovaro *et al.*, 2010).

In the western Mediterranean basin, a series of studies have been conducted regarding the deep-sea megafaunal assemblages down to 2800 m depth (Abelló *et al.*, 1988; Cartes and Sardà, 1993; Stefanescu *et al.*, 1993; Sardà *et al.*, 1994; Moranta *et al.*, 1998; Carrassón and Cartes, 2002; D’Onghia *et al.*, 2004b), but addressing only fishes and crustaceans. Few studies have dealt with non-crustacean invertebrates (Ramírez-Llodra *et al.*, 2008; Ramírez-Llodra *et al.*, 2010). Regarding the central basin, information about lower slope megafauna is scarce as studies conducted until now have focused on the upper and middle slope communities, and addressed only particular assemblages such as fishes (D’Onghia *et al.*, 1998; Mytilineou *et al.*, 2005) and crustaceans (Company *et al.*, 2004; Politou *et al.*, 2005). Concerning the whole Mediterranean Sea, studies conducted to date have shown the existence of a depth zonation of megafauna on the continental slope (Pérès, 1985; D’Onghia *et al.*, 1998; Moranta *et al.*, 1998; D’Onghia *et al.*, 2004b), with peaks of biomass and abundance around 1200 m depth and a subsequent fall in ecological indicators below 1500 m depth (for a review, see Sardà *et al.*, 2009). Another branch of studies, particularly carried out in the western Mediterranean, have dealt with the diet (Carrassón *et al.*, 1997; Carrassón and Matallanas, 1998, 2001, 2002) and biology (Stefanescu *et al.*, 1992; Massutí *et al.*, 1996; Morales-Nin *et al.*, 1996a, b) of the main fish species of the continental slope, as well as the biology of de-

capod crustaceans (Company and Sardà, 2000; Puig *et al.*, 2001; Company *et al.*, 2003).

During the DESEAS trans-Mediterranean cruise conducted in 2001, benthic megafauna, including fishes and invertebrates of the western Balearic, western Ionian and eastern Ionian basins, was sampled (Sardà *et al.*, 2004b). A series of community structure and distribution studies were conducted and published on fishes and crustaceans (Company *et al.*, 2004; D’Onghia *et al.*, 2004b; Sion *et al.*, 2004), but the less abundant non-crustacean invertebrate species were not included in any of the subsequent analyses and detailed biodiversity studies of the whole megafauna community were not carried out. The objective of the present paper is to describe biodiversity patterns of whole benthic megafauna on Mediterranean continental slopes and deep basins, discussing the results in the light of recent advances in deep Mediterranean trophic characteristics.

MATERIALS AND METHODS

Megafaunal samples were collected during a trans-Mediterranean sampling cruise carried out in June 2001, in the framework of the DESEAS project (Sardà *et al.*, 2004b), aboard the R/V *García del Cid* (Fig. 1). A Otter-trawl Maireta system (OTMS) was used as sampling gear (Sardà *et al.*, 1998). A total of 26 trawls were conducted at depths ranging from 600 to 4000 m (Table 1): seven in the western Balearic basin, eight in the western Ionian Sea, nine in the eastern Ionian Sea, and two in the central abyssal plain. The OTMS is a benthic trawling net fitted with two divergent doors and a single warp cable. The total net length is 25 m, with a cod-end mesh size of 40 mm and an outer cover of 12 mm. Bridles of 67 m length were used. A SCANMAR system was used to estimate the mean net opening geometry during the trawl, showing a horizontal opening of 12.7 ± 1.4 m. As the SCANMAR system can only operate down to 1200 m depth, the same value was used for deeper trawls, considering that no technical changes were made to the sampler during the cruise. Vertical opening was estimated at 1.4 m, with substantially less variability due to the net building characteristics (Sardà *et al.*, 1998).

Every megafaunal individual was identified to species level, counted and wet-weighted (± 1 g). A faunal list was compiled, along with the total catch abundance of each species by sampling zone and the depth range of occurrence. The SCANMAR data were used to standardize abundance (number/km²) and biomass (kg/km²) data between trawls. Species richness, Shannon-Wiener H’, Margalef’s richness index and Pielou’s evenness index were calculated for each trawl (Shannon, 1948; Margalef, 1958; Pielou, 1966; Magurran, 2004). When replicate samples per depth were available, the mean Shannon index values were calculated. Similarity of community structure among samples from all geographic areas and depths was visualized

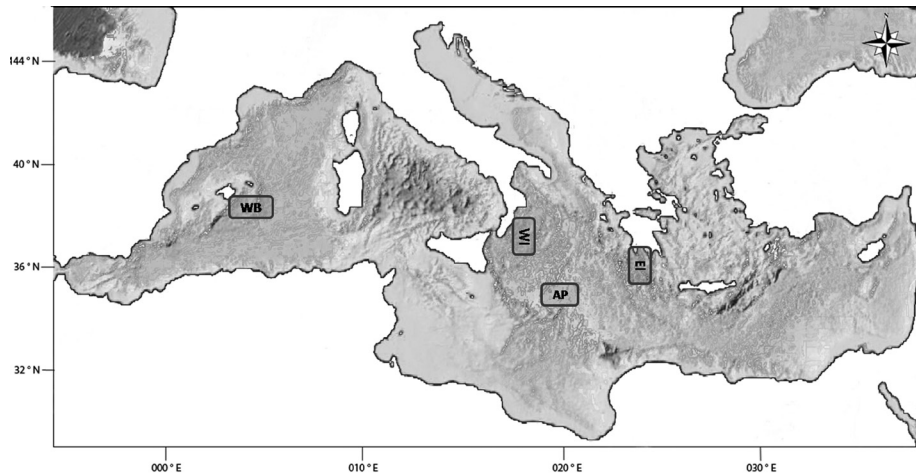


FIG. 1. – Map of Mediterranean Sea, including the sampled areas: western Balearic (WB), western Ionian (WI), eastern Ionian (EI) and the central abyssal plain (AP).

with a non-metric multidimensional scaling (MDS), after abundance data had been $\log(X+1)$ transformed. This analysis is an iterative procedure that minimizes the difference between ranked Bray-Curtis similarity values and 2-dimensional distance between each pair of samples. MDS analysis was reiterated 1000 times with a minimum stress value of 0.01, and was applied to all samples from all depths and geographic areas.

To assess what species mostly caused dissimilarities between trawls, the two-way similarity percentages (SIMPER) non-parametric statistical routine was conducted, using “depth” and “area” as crossed factors and the Bray-Curtis measure as similarity (Clarke and Warwick, 2001). All diversity analyses were conducted using the PRIMER-E 6 software package.

RESULTS

A total of 102 megafaunal species belonging to 5 phyla were collected and identified (Table 2). Of these, 15 species (14,7%) were non-crustacean invertebrates belonging to the phyla Mollusca (classes Cephalopoda and Gastropoda), Echinodermata, Brachiopoda and Chordata (represented by the pyrosomatid tunicate *Pyrosoma atlanticum*). The most speciose groups were Actinopterygii (45% of species), crustaceans (32.4% of species) and Chondrichthyes (7.8% of species).

Multidimensional scaling analysis calculated a stress value of 0.1, which indicates an acceptable grade of ordination with little risk of misinterpretation (Clarke and Warwick, 2001). The plot suggests a

TABLE 1. – List of analyzed trawls with time and spatial characteristics.

Area	Haul	Date	Mean depth (m)	Start position		End position	
				Latitude N	Longitude E	Latitude N	Longitude E
Balearic Sea	W600	07.06.2001	650	38°36.51	001°53.29	38°39.27	001°55.12
	W800	08.06.2001	800	38°30.13	001°49.12	38°28.25	001°46.80
	W1000	08.06.2001	1000	38°28.47	001°53.20	38°26.44	001°50.41
	W1200	06.06.2001	1230	40°48.30	001°48.13	40°47.28	001°45.12
	W1500	08.06.2001	1500	38°17.15	001°48.10	38°18.16	001°44.30
	W2500	09.06.2001	2500	38°15.57	002°21.10	38°21.24	002°23.43
	W2800	10.06.2001	2800	38°04.10	005°27.40	38°05.24	005°34.60
Western Ionian Sea	C600	14.06.2001	600	38°18.50	016°37.28	38°17.37	016°33.51
	C800	14.06.2001	800	38°16.56	016°37.32	38°18.01	016°40.43
	C1000	15.06.2001	1000	38°15.11	016°34.44	38°15.25	016°40.13
	C1200	18.06.2001	1200	32°13.58	016°35.17	38°13.92	016°37.51
	C1500	15.06.2001	1500	38°10.16	016°38.34	38°12.17	016°44.17
	C1500	17.06.2001	1500	38°12.70	010°43.52	38°10.33	016°40.40
	C1700	18.06.2001	1700	38°06.13	016°42.10	38°08.17	016°48.80
	C2000	16.06.2001	2000	37°42.18	016°40.70	37°39.40	016°35.40
Eastern Ionian Sea	E600	22.06.2001	600	36°47.46	022°04.29	36°50.32	022°04.10
	E600	26.06.2001	600	36°47.43	022°04.28	36°51.40	022°03.55
	E800	22.06.2001	800	36°51.52	022°06.16	36°49.06	022°06.16
	E800	26.06.2001	800	36°51.39	022°06.12	36°48.80	022°06.17
	E1100	24.06.2001	1100	36°44.49	022°07.32	36°45.59	022°10.58
	E1300	22.06.2001	1300	36°42.52	022°10.25	36°39.16	022°10.55
	E1700	25.06.2001	1700	36°24.60	022°14.60	36°19.51	022°14.90
	E2200	23.06.2001	2200	36°32.17	022°01.46	36°32.32	022°09.83
	E2600	23.06.2001	2600	36°21.50	022°00.60	36°20.32	021°54.39
Central abyssal plain	A3300	02.07.2001	3300	36°08.21	016°32.90	36°10.24	016°24.80
	A4000	01.07.2001	4000	35°41.51	017°47.00	35°41.07	017°37.80

TABLE 2. – Species list of demersal megafauna sampled in the DESEAS cruise, along with their total collected abundance in each of the four samples areas, and their depth range of catch.

PHYLUM	Family	Species	Western Balearic N km ⁻²	Depth (m)	Western Ionian N km ⁻²	Depth (m)	Eastern Ionian N km ⁻²	Depth (m)	Central abyssal plain N km ⁻²	Depth (m)
MOLLUSCA										
	Octopodidae	<i>Bathypolipus sponsalis</i>	34.9	1230						
		<i>Illex coindetii</i>					11.0	600		
	Enoplateuthidae	<i>Abralia veranyi</i>					11.6	1700		
	Histioteuthidae	<i>Histioteuthis bonnelli</i>	11.6	1230						
		<i>Histioteuthis reversa</i>	13.2	600	81.7	600-1200				
	Ommastrephidae	<i>Todarodes sagittatus</i>	42.2	600-800						
	Sepiolidae	<i>Heteroteuthis dispar</i>			49.9	1200	24.1	600-800		
		<i>Neorossia caroli</i>			9.6	1500	46.4	600		
	Aporrhaididae	<i>Aporrhais serresiana</i>			55.9	800	757.0	600-800		
	Naticidae	<i>Natica</i> sp.			18.6	800				
	Cymbuliidae	<i>Cymbulia peronii</i>			105.5	600				
BRACHIOPODA										
	Terebratulidae	<i>Gryphus vitreus</i>					131.5	600-800		
ARTHROPODA										
	Phronimoidea	<i>Phronima sedentaria</i>			18.6	800				
	Aristeidae	<i>Aristaeomorpha foliacea</i>	26.3	600	13.2	600	10926.8	600-1100		
		<i>Aristeus antennatus</i>	3473.7	600-2800	1456.5	600-2000	1381.0	600-1700	11.1	3300
	Benthescymnidae	<i>Gennadas elegans</i>	82.6	800-2800	446.6	800-1500	62.0	800-2200		
	Crangonidae	<i>Pontocaris lacazei</i>	13.2	600						
		<i>Pontophilus norvegicus</i>	23.2	1230	758.5	800-1700				
	Galatheididae	<i>Munida tenuimana</i>	223.7	600-1500	57.3	1500				
	Geryonidae	<i>Chaceon mediterraneus</i>	136.1	2500-2800			19.1	1700-2200	22.2	3300
		<i>Geryon longipes</i>	792.4	600-1500			15.4	1300		
	Goneplacidae	<i>Goneplax rhomboides</i>			13.2	600				
	Hippolytidae	<i>Ligur ensiferus</i>			11.4	1000				
	Homolidae	<i>Paromola cuvieri</i>	48.6	800-1230	43.2	600-1000				
	Nematocarcinidae	<i>Nematocarcinus exilis</i>	699.9	1500-2800	496.8	1500-1700	2657.7	1700-2600	488.9	3300-4000
	Nephropidae	<i>Nephrops norvegicus</i>					62.2	600		
	Oplophoridae	<i>Acantephyra eximia</i>	1276.9	800-2800	613.8	1000-2000	1287.5	1300-2600	333.3	3300-4000
		<i>Acantephyra pelagica</i>	90.9	100-2800	132.1	1000-2000			22.2	3300-4000
	Paguridae	<i>Pagurus alatus</i>	14.5	800			39.4	800		
	Palaemonidae	<i>Periclimenes granulatus</i>			18.6	800				
	Pandalidae	<i>Plesionika martia</i>	462.4	600-800	395.5	600	658.2	600-800		
		<i>Plesionika acanthonotus</i>	554.2	600-1000	82.8	600-1000	369.0	600-800		
		<i>Plesionika edwardsii</i>					13.4	600		
		<i>Plesionika gigliolii</i>	26.3	600			90.3	600		
	Pasiphaeidae	<i>Pasiphaea multidentata</i>	72.7	800-2500	71.9	600-1500				
		<i>Pasiphaea sivado</i>			31.8	600-800	13.1	800		
	Peneidae	<i>Parapeneaus longirostris</i>					44.0	600		
	Polychelidae	<i>Polycheles typhlops</i>	65.3	800-1000	1060.9	600-2000	605.9	600-2200		
		<i>Stereomastis sculpta</i>	319.5	2500-2800						
	Portunidae	<i>Bathynectes maravigna</i>	14.5	800	76.2	1000-1500	30.8	1300		
	Processidae	<i>Processa canaliculata</i>	13.2	600	26.4	600-1500				
	Sergestidae	<i>Sergestes arcticus</i>	13.2	600	53.1	600-1500	13.4	600		
		<i>Sergestes corniculum</i>			87.7	600-1200	39.6	600-1100	22.2	3300-4000
		<i>Sergia robusta</i>	242.7	600-2800	1851.0	600-2000	184.0	800-2600	33.3	3300-4000
	Xanthidae	<i>Monodaeus couchi</i>	72.6	800			13.4	600		
ECHINODERMATA										
	Astropectinidae	<i>Astropecten irregularis</i>	23.2	1230						
	Echinidae	<i>Echinus</i> sp.					12.9	800		
CHORDATA										
	Pyrosomatidae	<i>Pyrosoma atlanticum</i>					15.4	1300		
	Scyliorhinidae	<i>Galeus melastomus</i>	1003.1	600-1500	1085.6	600-1500	917.5	600-1300		
	Chimaeridae	<i>Chimaera monstrosa</i>	13.2	600			26.0	800		
	Hexanchidae	<i>Hexanchus griseus</i>					15.4	1300		
	Centrophoridae	<i>Centrophorus granulosus</i>					13.3	1100		
	Dalatiidae	<i>Dalatias licha</i>	26.1	800-1230	99.9	1200	26.0	800		
	Etmopteridae	<i>Etmopterus spinax</i>	150.9	800-1230	194.2	600-1500	219.8	600-2200		
	Oxinotidae	<i>Oxinotus centrina</i>			18.6	800				
	Somniosidae	<i>Centroscymnus coelolepis</i>	237.8	1500-2800						
	Halosauridae	<i>Halosaurus ovenii</i>	7.7	2800						
	Notacanthidae	<i>Notacanthus bonaparte</i>	11.6	1230	425.9	600-1500	26.5	1100		
		<i>Polyacanthonotus rissoanus</i>					20.7	2200-2600		
	Congridae	<i>Conger conger</i>					13.4	600		
	Nettastomatidae	<i>Nettastoma melanurum</i>	32.5	1000	376.5	600-1500	307.5	600-1300		
	Chlorophthalmidae	<i>Chlorophthalmus agassizi</i>					1369.7	600		
	Ipnopidae	<i>Bathypterois mediterraneus</i>	641.0	1000-2800	3910.6	800-2000	1500.9	800-2600	22.2	3300
	Paralepididae	<i>Arctozenus risso</i>	10.8	1000						
		<i>Paralepis speciosa</i>			13.2	600	12.9	800		

TABLE 2 (cont.). – Species list of demersal megafauna sampled in the DESEAS cruise, along with their total collected abundance in each of the four samples areas, and their depth range of catch.

PHYLUM Family	Species	Western Balearic		Western Ionian		Eastern Ionian		Central abyssal plain	
		N km ⁻²	Depth (m)	N km ⁻²	Depth (m)	N km ⁻²	Depth (m)	N km ⁻²	Depth (m)
Trachichthyidae	<i>Hoplostethus mediterraneus</i>	345.8	600-800	349.9	600-800	638.1	600-800		
Gadidae	<i>Micromesistius poutassou</i>	13.2	600	13.2	600	35.4	600		
	<i>Phycis blennoides</i>	531.9	600-1230	145.1	600-1000	121.4	600-800		
Macrouridae	<i>Coelorinchus mediterraneus</i>	530.5	600-1500	599.7	1200-1500	30.8	1300		
	<i>Coryphaenoides guentheri</i>	295.0	2500-2800	85.1	1500-1700	54.6	1700-2600		
	<i>Coryphaenoides mediterraneus</i>	569.5	1500-2800	28.7	1500	94.9	1300-2600	244.5	3300-4000
	<i>Hymenocephalus italicus</i>	307.2	600-800	270.0	600-800	96.6	600-800		
	<i>Nezumia aequalis</i>	174.3	1230						
	<i>Nezumia sclerorhynchus</i>	1146.2	600-1500	1229.8	600-1500	443.7	600-1300		
	<i>Trachyrincus scabrus</i>	697.1	800-1230	125.5	1000				
Merlucciidae	<i>Merluccius merluccius</i>					13.4	600		
Moridae	<i>Lepidion lepidion</i>	1160.0	1000-1500	376.5	1200-1700	115.8	1300-1700		
	<i>Mora moro</i>	765.0	800-1230	1095.7	800-1200	738.2	800-1300		
Myctophidae	<i>Benthoosema glaciale</i>					11.0	600		
	<i>Ceratoscopelus maderensis</i>	174.9	600-2500			13.4	600		
	<i>Diaphus metopoclampus</i>					251.1	600-800		
	<i>Hygophum benoiti</i>			18.6	800				
	Unidentified myctophid							11.1	4000
	<i>Lampanyctus crocodilus</i>	242.7	600-2500	873.9	600-1500	995.5	600-1300	11.1	3300
Ophidiidae	<i>Benthoicometes robustus</i>	11.6	1230						
Bythitidae	<i>Cataetx laticeps</i>	98.9	2500-2800	65.9	2000	175.6	1700-2600	11.1	3300
Alepocephalidae	<i>Alepocephalus rostratus</i>	5922.2	800-1500						
Epigonidae	<i>Epigonus constanciae</i>					11.0	600		
	<i>Epigonus denticulatus</i>	69.9	600-800						
	<i>Epigonus telescopus</i>			22.8	1000				
Trichiuridae	<i>Lepidopus caudatus</i>	13.2	600						
Sparidae	<i>Pagellus bogaraveo</i>	26.3	600	11.4	1000				
Cynoglossidae	<i>Symphurus ligulatus</i>	13.2	600	52.7	600	23.9	600-800		
	<i>Symphurus nigrescens</i>	14.5	800	290.0	600				
Scophthalmidae	<i>Lepidorhombus boscii</i>					92.7	600		
	<i>Lepidorhombus whiffiagonis</i>					13.4	600		
Scorpaenidae	<i>Helicolenus dactylopterus</i>	13.2	600			1741.8	600-800		
	<i>Trachyscorpia cristulata</i>	28.1	1500						
Triglidae	<i>Peristedion cataphractum</i>					171.6	600-800		
Gonostomatidae	<i>Cyclothone braueri</i>	20.8	600-2800	49.9	1200				
Sternoptychidae	<i>Argyropelecus hemigymnus</i>	273.9	600-2800	128.0	800-1500				
Stomiidae	<i>Chauliodus sloani</i>	56.8	600-2500	52.3	800-2000	85.5	600-2200		
	<i>Stomias boa</i>	14.5	800			138.1	600-1700	33.3	4000

bathymetric pattern of species distribution from 600 to 4000 m depth, as shown in Figure 2.

Across the whole dataset, Margalef's richness index (Fig. 3) shows a significant decrease with depth ($R^2 = 0.746$, $p < 0.001$, $n = 26$). Non-linear regression found a negative exponential relation:

$$SR = 4.483 e^{-0.0005D},$$

where SR is Margalef's richness index and D is depth (m).

Negative linear correlations between species richness and depth were found for each of the three zones considered separately (Fig. 4). The slopes of the regression lines were higher for the two Ionian sea zones than for the Balearic basin, indicating a steeper decrease in species diversity with depth in the central basin than in the western zone. Margalef index ranged from a maximum of 3.66 at 600 m depth in the eastern Ionian to a minimum of 0.92 at 2600 m depth in the same zone.

Values of Pielou's evenness index are plotted against depth for the three sampling zones in Figure 4. In the western Balearic basin, values of Pielou's index for the deepest depths were higher than the shallowest ones, with an outlier at 1230 m, although no significant

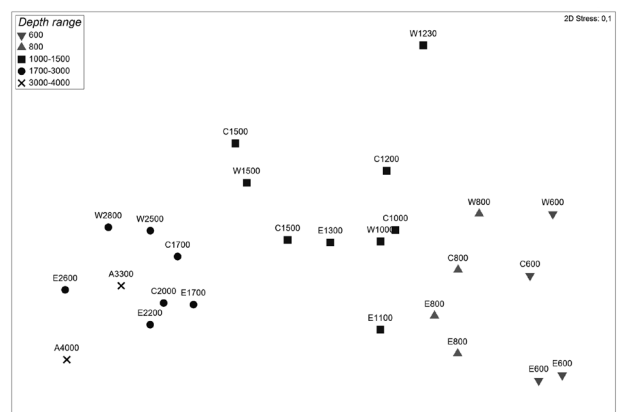


FIG. 2. – Multidimensional scaling plot of the whole abundance dataset. Points are pooled into depth-range groups, for 600-650 m (downward-pointing triangles), 800 m (upward-pointing triangles), 1000-1500 m (squares), 1700-3000 m (circles), and abyssal plain depths at 3300 and 4000 m (crosses). The code letter represents the sampling zone: western Balearic (W), western Ionian (C), eastern Ionian (E) and central abyssal plain (A).

trend was observed. A similar pattern was present in the western Ionian, with a decrease in the index at 1500 and 1700 m depth. In the eastern Ionian Sea, the even-

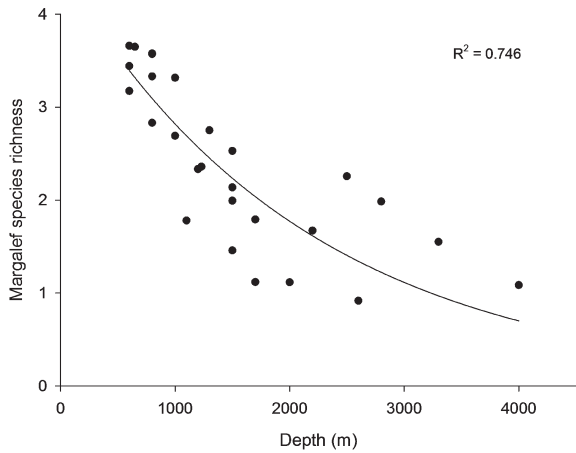


FIG. 3. – Margalef species richness index for the whole studied area (western and central Mediterranean basins).

ness index showed an inverted V-shaped tendency.

Shannon’s diversity index for the three zones is plotted against depth in Figure 4. In the western Balearic basin, the Shannon index is highest (2.64) at 800 m depth and then shows a significant fall, with the lowest value (1.67) at 1230 m. From 1500 m the diversity increases to relatively constant values of between 2.23 and 2.30 down to the deepest depths. In the western Ionian basin, the Shannon index shows its highest values between 600 and 1200 m (2.62-2.72), falling sharply afterwards. Its lowest value (1.36) stands at 1700 m depth, and below this point it does not increase above 1.8. The eastern Ionian basin shows a pattern with two peaks, one at 800 m (2.31) and one at 1300 m (2.60). Below 1300 m the index steadily decreases down to 1.07 at 2800 m depth, which is the lowest value found in our dataset.

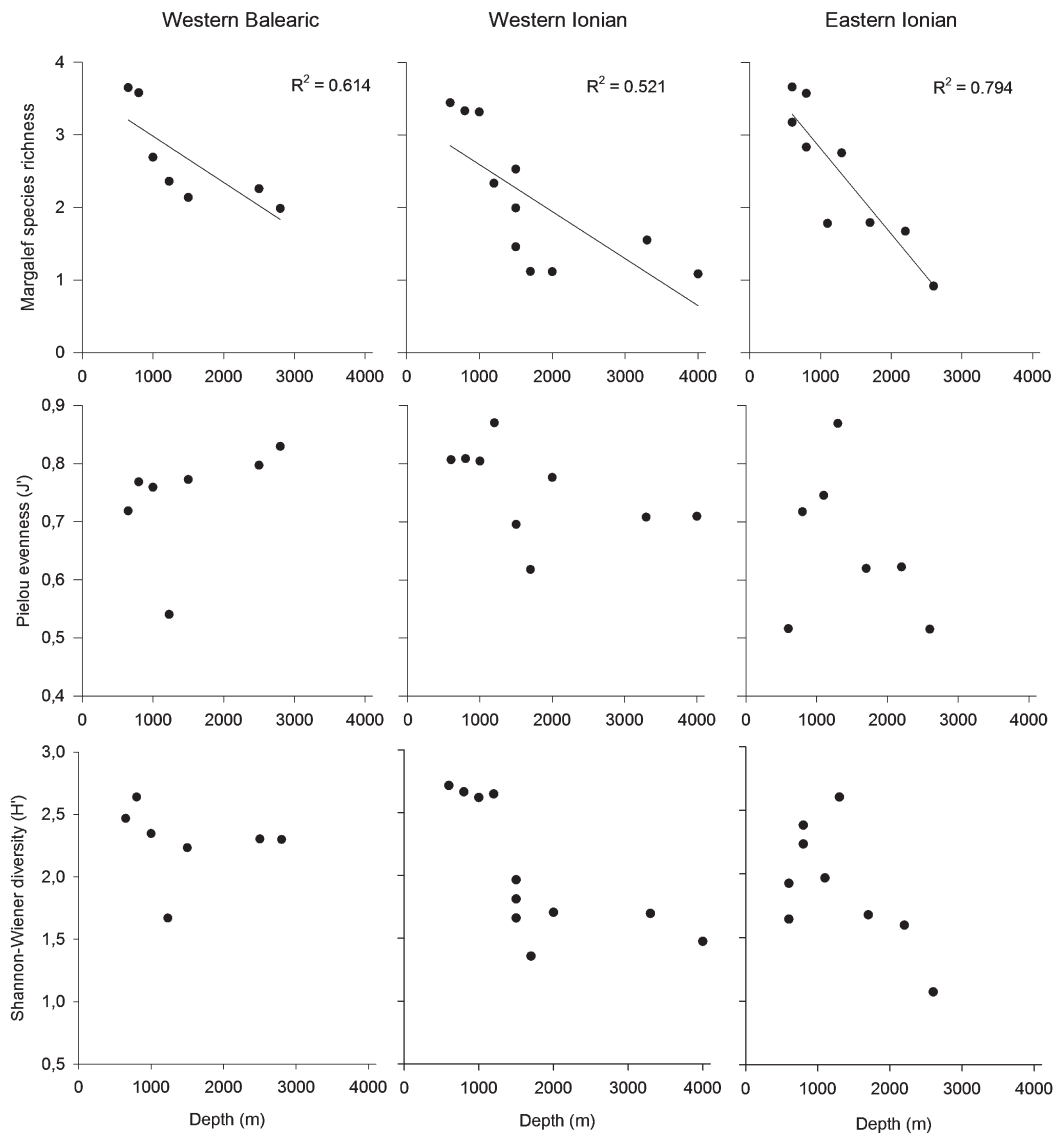


FIG. 4. – Margalef species richness, Pielou evenness and Shannon-Wiener diversity indices for the western Balearic Sea, the western Ionian sea (including the two central abyssal plain samples), and the eastern Ionian Sea. Linear regression lines are shown only when significant ($p < 0.05$).

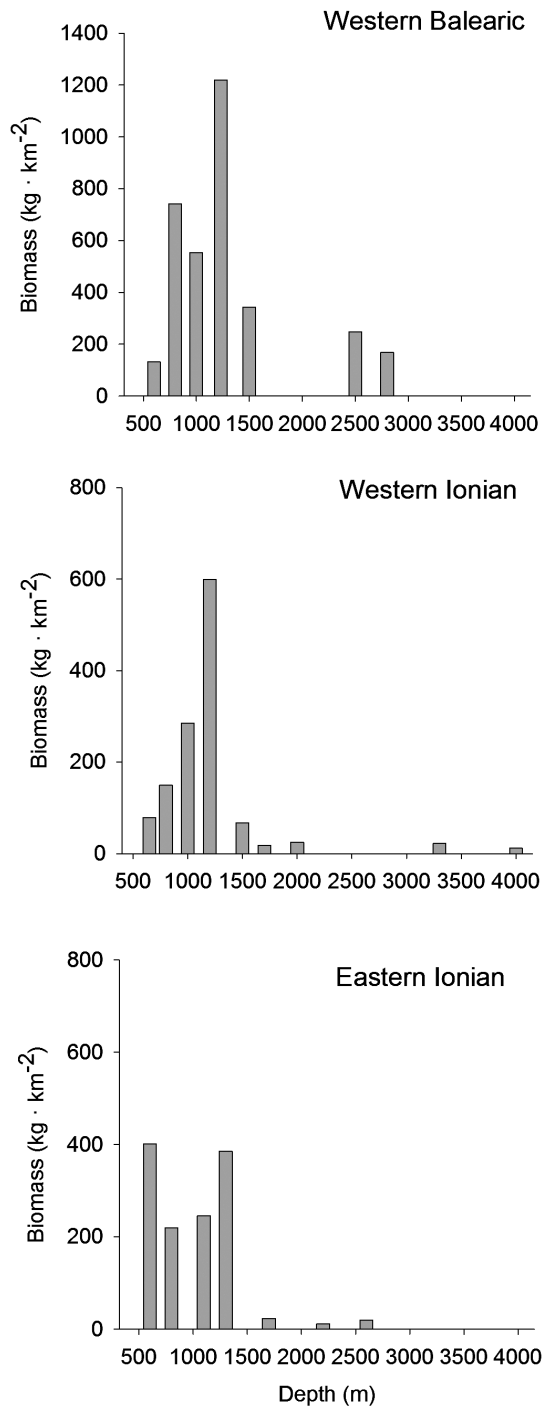


FIG. 5. – Standardized values of total catch biomass for the western Balearic Sea, the western Ionian sea (including the two central abyssal plain samples), and the eastern Ionian Sea.

Total catch biomass in the three zones was higher at the shallower depths (600–1230 m) than at the deeper depths (Fig. 5). In the Balearic basin the biomass at 800–1000 m depth was dominated by the fishes *Alepocephalus rostratus*, *Mora moro* and the shark *Galeus melastomus*; at 1200 m a peak was present, mainly caused by *A. rostratus*, and at depths of 2500–2800

TABLE 3. – Dissimilarities between the three geographic zones as calculated by the SIMPER statistical routine.

Species	Dissimilarity / S.D.	Contrib. %
Western Balearic – western Ionian (average dissimilarity: 51.17)		
<i>Alepocephalus rostratus</i>	1.42	6.24
<i>Polycheles typhlops</i>	1.65	4.31
<i>Geryon longipes</i>	1.53	4.13
<i>Coryphaenoides mediterraneus</i>	0.89	3.75
Western Balearic – eastern Ionian (average dissimilarity: 48.12)		
<i>Alepocephalus rostratus</i>	0.92	4.73
<i>Polycheles typhlops</i>	1.29	4.13
<i>Centroscymnus coelolepis</i>	0.94	3.85
<i>Aristeus antennatus</i>	1.43	3.58
Western Ionian – eastern Ionian (average dissimilarity: 41.70)		
<i>Acantephyra pelagica</i>	1.11	4.64
<i>Coryphaenoides mediterraneus</i>	0.95	4.26
<i>Polycheles typhlops</i>	0.93	3.98
<i>Lepidion lepidion</i>	0.83	3.95

m the shark *Centroscymnus coelolepis* dominated the biomass. The western Ionian sea showed a single peak of biomass at 1200 m due to a high retrieval of the fish *M. moro* and the sharks *G. melastomus* and *Dalatias licha*. Two peaks were present at 600 and 1300 m in the eastern Ionian, the shallower one caused mainly by the fish *Helicolenus dactylopterus* and the crustacean *Aristaeomorpha foliacea*, while the deeper one was produced by a concentration of *M. moro*. At the two abyssal stations, biomass was comparable with that at shallower depths (1700 and 2000 m) in the same western Ionian zone.

According to SIMPER analysis, dissimilarity in community composition between the western Balearic basin, the western Ionian and the eastern Ionian across all depth ranges is mainly caused by the fishes *A. rostratus* and *Coryphaenoides mediterraneus*, the shark *C. coelolepis* and the decapods *Aristeus antennatus*, *Polycheles typhlops* and *Geryon longipes* (Table 3).

DISCUSSION

The paucity of robust biodiversity analyses in deep sea ecosystems is mainly caused by sampling difficulties that often result in low replicate numbers. The DESEAS sampling project provided a wide spectrum of novel data about deep-sea megafauna, making it possible to conduct new biodiversity analyses of the bathyal and abyssal megafauna communities as a whole along a longitudinal and bathymetric gradient (Sardà *et al.*, 2004b).

Few non-crustacean invertebrates were retrieved, with molluscan cephalopods and gastropods making up the most part. The number of species in this group was considerably lower than that of deep-sea faunistic studies conducted in the northeastern Atlantic (Billett *et al.*, 2001), where the dominance of non-crustacean invertebrates is well documented (Gage and Tyler, 1991). Integrating data with other types of gear that stay more in contact with the substrate (e.g. an Agassiz dredge) may help to clarify this point.

Results from the multidimensional scaling routine showed a clear segregation by depth of benthic megafauna in the Mediterranean. The trawls at 600-800 m grouped together, confirming the *middle slope* subdivision (Pérès, 1985). Differences in this depth range between the western Balearic basin and the two study sites of the central basin were more marked than at the other depths. The depth range 1000-1700 m showed the highest dispersion between trawls, as was previously reported for fishes (Stefanescu *et al.*, 1993; D'Onghia *et al.*, 2004b) and crustacean assemblages (Maynou and Cartes, 2000; Company *et al.*, 2004) in the Mediterranean. The present study included non-crustacean invertebrates in the analyses and this did not change the overall community structure pattern, suggesting that the megafaunal invertebrates follow the same pattern of depth zonation as the other taxa. The deepest assemblages at 1700-3000 m, along with the two trawls conducted at 3300 and 4000 m in the central Ionian abyssal plain, grouped together, indicating a reduction in depth influence below 1500 m. There was no clear pattern in the MDS plot that could be interpreted as an influence of longitude, except at middle slope depths where samples showed a slight grouping by geographic area. This suggests that depth is a stronger driver than geographic area for community composition, as was previously pointed out for the eastern Mediterranean basin megafauna (Kallianiotis *et al.*, 2000) and meiofauna (Lampadariou *et al.*, 2009). Influence of depth alone as a physical factor in determining assemblage composition is currently a matter of discussion, and some authors propose that megafaunal zonation is mainly controlled by food availability (Jones *et al.*, 2003; Tyler, 2003; Soltwedel *et al.*, 2009). Coupling biodiversity studies with trophic analyses of key species in each basin may shed light on this result. As reported by Politou *et al.* (2004), temperature showed a slight increase in a west-east axis (12.8-13.9 in the western basin, 13.3-14.2 in the central Mediterranean), while salinity showed no differences between zones. It is generally known that the hydrology of the deep Mediterranean is relatively stable and dissolved oxygen is also believed not to be limiting, with values constantly above 4 mlO₂/l (Miller *et al.*, 1970). Therefore, relating faunistic assemblages with available environmental data is currently difficult and further detailed abiotic studies are necessary.

A difference in equation fits for Margalef species richness was found between the whole dataset and the three zones considered separately. These differences could be caused by a relatively low number of samples. Further analyses with a larger dataset may bring to light patterns different from linear relations. Although Margalef index is more dependent than other diversity measures on sampling effort (Magurran, 2004), which in our case was higher at shallower stations, a negative linear correlation was found in all three basins, confirming the expected general reduction in megafaunal richness with depth (Gage and Tyler, 1991). The three zones exhibited a comparable species richness up

to 1500 m depth, but after this limit only the western Mediterranean maintained a Margalef index of above 2.0, while in the Ionian basins (both western and eastern) values decreased rapidly. The Mediterranean sea is known to show a west-east gradient of decreasing productivity (Danovaro *et al.*, 1999; Tselepidis *et al.*, 2004). It is therefore possible that higher surface productivity and coastal input of the western Balearic basin supply the necessary energy to sustain a diverse community down to deeper depths. Furthermore, the western Mediterranean is exposed to cyclic downslope dense shelf-water cascading events, which provide massive inputs of organic matter to bathyal and abyssal depths (Canals *et al.*, 2006; Company *et al.*, 2008). In the more oligotrophic Ionian Sea, organic matter reaching the lower slope and the deep basin is reduced, so there is a decrease in diversity early in the depth range.

Pielou's index of evenness expresses the degree of dissimilarity of the observed sample with a hypothetical situation of all equally abundant species. In the western Balearic Pielou's index showed a dramatic reduction at 1230 m depth, caused by the peak of abundance of the fish *Alepocephalus rostratus*. This dominance has been already pointed out in several studies (Stefanescu *et al.*, 1993; Morales-Nin *et al.*, 1996b; Sardà *et al.*, 2009), and may be caused by specific trophic conditions (Carrassón and Matallanas, 1998) and by the occurrence of shelf-water cascading events that bring enriched water at these depths (Canals *et al.*, 2006). A similar effect is present in the western Ionian at lower slope depths, and is caused by the spiderfish *Bathypterois mediterraneus*. The biology of this species is more adapted to the scarce trophic resources (Carrassón and Matallanas, 2001; D'Onghia *et al.*, 2004a), although the exact reasons for this dominance of *B. mediterraneus* are, at present, not described.

In the two samples collected from abyssal depths, few species were collected: 11 at 3300 m and 8 at 4000 m. In both cases, the catch composition was dominated by the macrourid *Coryphaenoides mediterraneus* and by the deep water shrimps *Acanthephyra eximia* and *Nematocarcinus exilis*. These occurrences have already been described as the deepest records for these species (Company *et al.*, 2004; D'Onghia *et al.*, 2004b). Species evenness at these two depths was low compared to the rest of the western Ionian basin. Food scarcity has been shown to limit the presence of large-sized species, favouring settlement of small-sized species that can *crop* more efficiently on a broader range of preys (*sensu* Dayton and Hessler, 1972). *C. mediterraneus* and *N. exilis* had lower mean sizes than other species of macrourid fishes and decapod crustaceans that inhabit the deep Mediterranean bottoms, suggesting that these species may be the only ones that can efficiently inhabit these low-energy environments.

Regarding biomass, in the western Balearic basin the pattern obtained is in accordance with that of previous studies conducted in this basin (Moranta *et al.*, 1998; Massutí *et al.*, 2004). In the western Ionian sea,

biomass values remain low down to the abyssal plain at 4000 m depth. Biomass flow in the eastern Ionian sea essentially follows the same pattern, with a biomass fall starting from 1700 m, showing that, even with different diversity patterns, the three basins exhibit a consistent biomass decrease starting from lower slope depths.

According to SIMPER analysis, dissimilarity in community composition between the Balearic basin and the Ionian Sea (both western and eastern zones) is mainly caused by a few species of Actinopterygii and decapod crustaceans. *A. rostratus* has its distribution limited to the western Mediterranean basin (Morales-Nin *et al.*, 1996b; D'Onghia *et al.*, 2004b) but the reasons for this spatial segregation are yet to be identified. The brachyuran crab *Geryon longipes* were found in the western Ionian and in the eastern Ionian in relatively low abundances. The trophic strategy of this species is less adapted to the scarcity of energy resources in the eastern basin (Kitsos *et al.*, 2005), where another crab of the family Geryonidae, *Chaceon mediterraneus*, is beginning to be present. *C. mediterraneus* was also found in the western Balearic basin at depths of 2500 and 2800 m. No occurrences of these two species at the same time were recorded, in agreement with another study which addressed the eastern basin megafauna (Jones *et al.*, 2003).

The changes in megafaunal biodiversity across a geographical axis in the Mediterranean Sea have been partly addressed in this work, which has evaluated patterns of species substitution and biomass decline with depth and longitude. At depths of 1200-1500 m an interruption in the expected pattern of biodiversity across depth ranges takes place, with two distinct actinopterygian species—*A. rostratus* in the western basin and *B. mediterraneus* in the Ionian sea—dominating the abundance and biomass. This is an important matter for further exploration, with the hope of possibly extending the study to the whole longitudinal axis of the Mediterranean basin including the easternmost areas, where deep-sea megafauna sampling is at present very scarce. In addition, focused analyses to relate biodiversity to food availability and ecosystem functioning will provide essential information to better understand the observed community structure and diversity patterns in deep Mediterranean megafauna.

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