J. Northw. Atl. Fish. Sci., Vol. 31: 413–430

Size Influence in Zonation Patterns in Fishes and Crustaceans from Deep-water Communities of the Western Mediterranean

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Abstract

Information was collected over two seasons on the depth distribution of the deep-water fishes and decapod crustaceans to the southwest of the Balearic Islands. The data were analysed to compare the intensity of faunal change with depth to individual size, measured as mean individual weight, both within and between fish and decapods. The results are discussed on the light of the biological characteristics of the populations studied. We conclude that there are complex distributions of mean weight by depth, determined mainly by trophic aspects and biological adaptations to the oligotrophic environment of the deep Mediterranean.

Key words: decapods, deep-sea, fishes, length, Mediterranean, megafaunal benthic communities, weight, zonation

Introduction

There have been an increasing number of studies on zonation in deep-sea megafaunal communities in recent years (Haedrich *et al.*, 1975; 1980; Smith and Hamilton, 1983; Hecker, 1990; among others). Because of their dominance at mid-latitudes most studies have been on fish (Haedrich and Krefft, 1978; Gordon and Duncan, 1985; Haedrich and Merrett, 1990; Koslow, 1993; Fujita *et al.,* 1995; Stefanescu *et al*., 1992; 1993; Moranta *et al*., 1998). Zonation has also been documented in other megabenthic taxa, such as crustaceans and other benthos (Rowe and Menzies, 1969; Abelló *et al.,* 1988; Fredj and Laubier, 1985; Cartes, 1993; Cartes and Sardà, 1993; Maynou and Cartes, 2000). Comparative zonation studies between different groups are, however, scarce (Gage and Tyler, 1991), although the taxon factor, together with bottom topography, has been one of the most widely argued reasons to explain discrepancies in zonation (the intensity of faunal change with depth) at a regional scale (Gage and Tyler, 1991). Differences in intensity of zonation amongst deep-sea fauna has been explained as a function of individual size (Gage and Tyler, 1991), with megafauna changing most rapidly and infaunal polychaetes the least. These differences amongst megafauna seem to be closely related to dispersal capability of species in their early development.

The deep-bathyal Mediterranean communities showed the co-dominance of two megabenthic taxa (fish and crustacean decapods) which permits a study of the influence of body size on depth zonation for these two diverse taxa. In the deep Northwest Mediterranean Sea, there is a boundary between 350 and 550 m, separating upper and middle slope decapod crustacean communities (Abelló *et al.,* 1988; Cartes *et al*., 1994). The boundary between the middle and lower slope was established at around 1200 m (Cartes and Sardà, 1992; Cartes, 1993). The zonation of fish communities is characterized by the presence of two boundaries, located at 800 and 1400 m depth between upper-middle and middle-lower slope, respectively (Stefanescu *et al*., 1993; Moranta *et al*., 1998). It has been suggested that this pattern of zonation is related to food availability, especially the influence of mesopelagic prey in the diet of bathyal species down to 1 200–1 300 m depth in the Catalan Sea (Cartes, 1998; and references cited therein). The different depth patterns shown by each taxon may be attributed to the different fractions of the food resource, or food spectrum, exploited by each taxon (Maynou and Cartes, 2000). Although the existence of boundaries or discrete faunistic groups related to sharp variations in environmental conditions are well known, zonation seems to depend both on local topographic features and of taxa studied, being more a regional than a general phenomenon and it seems problematic to extrapolate to wide geographical areas (Haedrich and Merrett, 1990).

Although the depth-size trends have been studied for decapod crustaceans (Sardà and Cartes, 1993) as well as for fishes (Macpherson and Duarte, 1991; Stefanescu *et al.*, 1992), there has been no comprehensive study of community size structure by depth. In the present study we tested faunal zonation for the different dominant taxa (fish and decapod crustaceans) composing deep-sea communities in the southern Balearic Islands (Algerian Basin).

Material and Methods

Sampling

The data examined in the present study were collected south of the Balearic Islands (Western Mediterranean), between 38°48'N and 38°05'N on two surveys, QUIMERA I (Q-I) in the autumn (October, 1996) and QUIMERA II (Q-II) in the spring (May 1998). The two surveys were carried out on board the RV "*Garcia del Cid*" (38 m length, 1500 HP), and the sampling gear used was an OTMS-27.5 (headline length 25 m) type bottom trawl, towed on a single warp (Sardà *et al.,* 1998).

A total of 46 hauls were taken between depths of 200 and 1 800 m (32 in the Q-I and 14 in the Q-II) (Fig. 1). Haul duration ranged from 30 to 60 min. Towing speed was 2.7 knots for all hauls. The arrival and departure of the net to and from 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. The cod-end mesh size was 12 mm. For each haul, the total amount of catch was weighed on board, all the individuals were counted, and all (or a subsample) were weighed and measured. The swept area of the trawl was calculated using the data from the SCANMAR system and was used to compute the standardised abundance (number and weight) of the catch per 10 000 m^2. The depth distribution of the hauls was stratified in 200 m intervals, with at least two hauls per stratum (up to 6 hauls in the 1 400–1 600 m range during Q-I) (Fig. 2). A Seabird 25 CTD probe was used to determine the environmental characteristics of the water column along a transect for each cruise.

Statistical analysis

The standardized abundances indices of the megafauna were plotted against depth and the mean weight by individual was also determined for decapods and fishes.

The bubble scatter plot was applied to the mean weight for the most frequent species to detect the observed abundance tendencies with depth.

The mean weight by species for fish and decapod crustaceans was calculated by haul and included in a species-sample matrix to apply cluster analysis, using the Bray-Curtis similarity index and the UPGMA clustering algorithm. Species that only occurred in 10 hauls or less were removed from the analysis. The mesopelagic fishes (*Argyropelecus hemigymnus, Stomias boa, Lampanyctus crocodilus, Chauliodus sloani*), although frequent, were not considered for the analysis because they were not adequatelyl sampled by the net. The main assemblages were also identified by multidimensional scaling (MDS). The similarity index used in the MDS ordination was Pearson's product moment correlation.

The mean general size (MGS) was calculated for each taxon. The mean weight for each species was plotted on a log-scale histogram and the median MGS was calculated for fishes and decapods. After establishing mean general size for each taxon, clustering was applied considering: 1) large fish, those exceeding mean general size (MGS), 2) small fish with mean size below MGS, 3) large decapods exceeding their

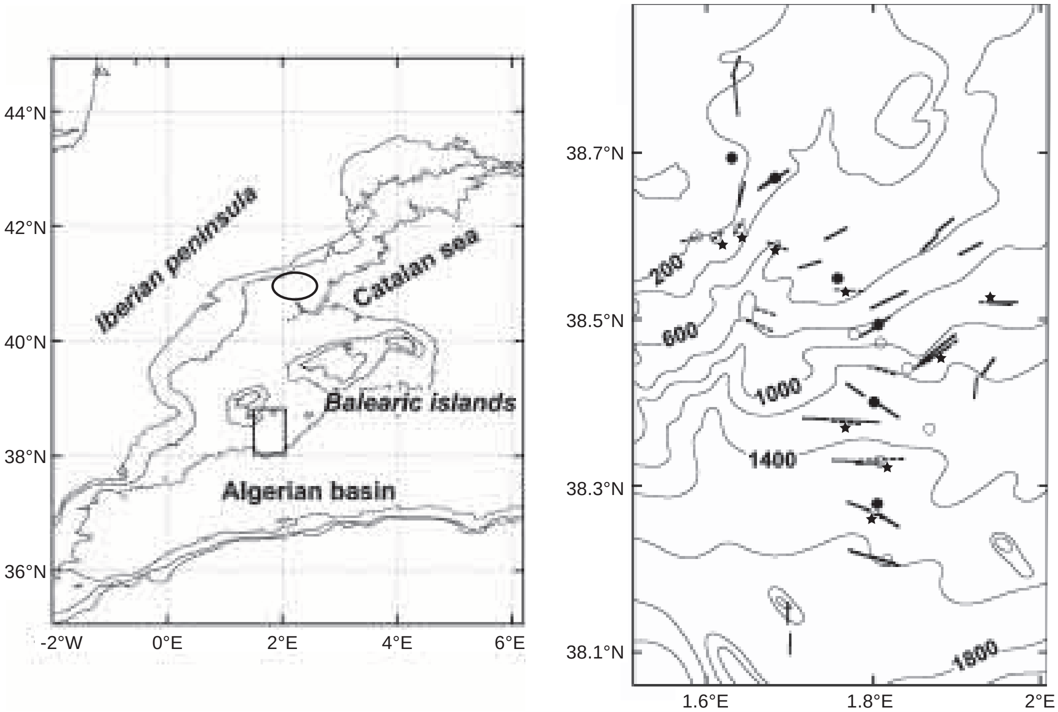

Fig. 1. Map of the study area with indication of the trawl positions and CTD casts on both cruises.

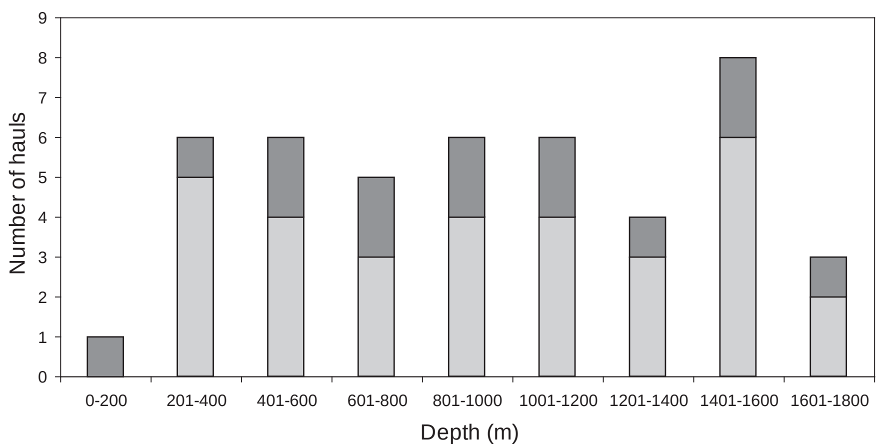

Fig. 2. Distribution of the number of hauls by depth range. Lighter bars QUIMERA-I cruise, darker QUIMERA-II cruise.

MGS, 4) small decapods with mean size below MGS. In this way the size factor can be further tested independently of taxa.

Results

Environmental features

The temperature and salinity stability of the deep-waters of the Mediterranean (Fredj and Laubier, 1985) was confirmed by the CTD casts. Temperature varied between 13.0 and 13.5°C and salinity between 38.3 and 38.5 psu, from 200 m to the bottom at all localities sampled. The depth profiles showed that the water masses were still structured in the Q-I cruise, with a surface temperature of 21°C and a strong gradient between 50 and 100 m depth corresponding to summer stratification. During the Q-II cruise, the surface temperature was 17.5°C and thermal stability was reached at around 200 m depth corresponding to early spring oceanographic conditions (Cartes *et al*., 2001).

Species composition and depth profiles

The mean weight and frequency of occurrence of fishes and decapod crustaceans are summarised in Tables 1 and 2. A total of 90 fish species and 48 decapod crustaceans were caught, the most frequent being the mesopelagic fish *Argyropelecus hemigymnus* followed by *Galeus melastomus* and for decapod crustaceans *Aristeus antennatus*. The mean weight ranged from 0.4 to 4 000 g for fishes and from 0.17 to 264.96 g for decapod crustaceans.

Similar tendencies were found in the depth profiles in both cruises for the total megafauna (fishes, decapods and cephalopods), fishes and decapod crustaceans, respectively (Fig. 3). The abundance decreased with increasing depth becoming more or less constant at 1 000 m with some oscillations. The fish abundance decreased sharply from the shelf break to 600 m depth, remaining more or less at the same levels and with a secondary peak at about 1 000 m due to the presence of *Alepocephalus rostratus*. Decapod crustaceans were numerically dominant between 400–800 m and also below 1 400 m depth (Fig. 3). The biomass was dominated by fishes due to their larger mean individual weight, and there was a decrease in

TABLE 1. Occurrence and mean individual weight (g) of fishes in the 46 trawl hauls in the West Mediterranean.

Family	Species	Occurrences	Mean wt (g)
Scyliorinidae	*Galeus melastomus*	33	307.84
	Scyliorhinus canicula	8	89.80
Squalidae	*Centrophorus uyato*	1	4 000.00
	Centroscymnus coelolepsis	13	992.77
	Dalatias licha	4	2 175.38
	Etmopterus spinax	24	223.58
	Squalus blainvillei	1	100.00
Rajidae	*Raja naevus*	2	371.00
	Raja asterias	2	559.50
	Raja polystigma	1	220.00
Alepocephalidae	*Alepocephalus rostratus*	26	289.66
Gonostomidae	*Cyclothone braueri*	7	0.88
	Cyclothone pygmaea	5	0.83
Sternoptychidae	*Argyropelecus hemigymnus*	34	0.88
	Maurolicus muelleri	3	1.17
Chauliodontidae	*Chauliodus sloani*	15	32.88
Stomiidae	*Stomias boa*	17	6.02
Argentinidae	*Argentina sphyiraena*	2	26.15
	Glossanodon leioglossus	4	21.33
Chlorophthalmidae	*Chlorophthalmus agassizii*	7	9.82
	Bathypterois mediterraneus	23	6.53
Myctophidae	*Benthosema glaciale*	11	1.06
	Lampanyctus crocodilus	34	11.76
	Myctophum punctatum	3	1.10
	Notoscopelus elongatus	3	1.22
	Electrona rissoi	1	3.00
	Lobianchia dofleini	1	2.00
	Symbolophorus veranyi	1	1.00
	Borostomias antarticus	1	5.00
	Cerasthoscopelus maderensis	2	2.00
Paralepididae	*Notolepis rissoi*	6	1.83
Nemichthyidae	*Nemichthys scolopaceus*	1	13.00
Nettastomatidae	*Nettastoma melanurum*	20	98.78
Congridae	*Conger conger*	4	1 518.25
Synaphobranchidae	*Dysomma brevirostre*	1	44.00

TABLE 1. (Continued). Occurrence and mean individual weight (g) of fishes in the 46 trawl hauls in the West Mediterranean.

Family	Species	Occurrences	Mean wt (g)
Notacanthidae	*Notacanthus bonapartei*	15	18.85
	Polyacanthonotus rissoanus	12	7.86
Macroramphosidae	*Macroramphosus scolopax*	4	9.75
Macrouridae	*Chalinura mediterranea*	15	8.34
	Caoelorhynchus caoelorhynchus	6	17.76
	Coelorhynchus labiatus	20	17.18
	Coryphaenoides guentheri	3	11.92
	Hymenocephalus italicus	16	9.93
	Nezumia aequalis	26	25.63
	Trachyrhynchus trachyrhynchus	5	207.07
Merluccidae	*Merluccius merluccius*	13	376.78
Gadidade	*Gadiculus argenteus*	9	4.99
	Micromesistius poutassou	10	153.20
	Trisopterus minutus capelanus	2	8.62
	Antonogadus megalokyinodon	12	3.81
	Molva dipterygia macrophthalma	5	41.76
	Phycis blennoides	26	138.92
Moridae	*Laemonema sp.*	1	10.00
	Lepidion guentheri	3	365.33
	Lepidion lepidion	19	115.20
	Mora moro	16	538.91
Regalecidae	*Regalecus glesne*	1	0.40
Zeidae	*Zeus faber*	2	184.50
Caproidae	*Capros aper*	7	5.82
Apogonidae	*Epigonus denticulatus*	8	80.73
	Epigonus telescopus	2	732.14
Carangidae	*Trachurus picturatus*	1	196.00
	Trachurus trachurus	3	80.95
Mullidae	*Mullus surmuletus*	2	175.75
Sparidae	*Boops boops*	3	108.77
Trichiuridae	*Lepidopus caudatus*	11	58.14
Gobiidae	*Lesueurigobius friesii*	1	1.00
	Pomatoschistus minutus	1	1.00
Callionymidae	*Callionymus maculatus*	3	1.11
	Synchiropus phaeton	9	12.25
Bythitidae	*Cataetyx alleni*	7	1014
	Cataetyx laticeps	1	641.00
Trachichthyidae	*Hoplostethus mediterraneus*	15	40.76
Centrolophidae	*Centrolophus niger*	1	3000.00
Scorpaenidae	*Helicolenus dactylopterus*	12	24.64
	Scorpaena elongata	4	250.13
Triglidae	*Aspitrigla cuculus*	2	61.86
	Lepidotrigla cavillone	1	14.00
	Trigla lyra	7	34.18
Peristeiidae	*Peristedion cataphractum*	7	32.39
Liparidae	*Paraliparis leptochirus*	8	1.25
Citharidae	*Citharus linguatula*	1	42.00
Scophthalmidae	*Lepidorhombus boscii*	9	75.41
	Lepidorhombus wiffiagonis	2	12.96
Bothidae	*Arnoglossus laterna*	2	4.71
	Arnoglossus rueppelli	2	4.86
Cynoglossidae	*Symphurus ligulatus*	14	2.47
	Syimphurus nigrescens	9	5.40
Lophiidae	*Lophius budegassa*	2	208.50
	Lophius piscatorius	1	1136.00

TABLE 2. Occurrence and mean individual weight (g) of decapod crustaceans in the 46 trawl hauls in the West Mediterranean.

Family	Species	Occurrences	Mean wt (g)
Aristeidae	*Aristaeomorpha foliacea*	3	13.77
	Aristeus antennatus	36	7.35
	Gennadas elegans	20	0.26
Peneaeidae	*Parapenaeus longirostris*	8	9.84
	Funchalia woodwardii	2	5.50
Solenoceridae	*Solenocera membranacea*	9	2.30
	Hymenopenaeus debilis	1	0.20
Sergestidae	*Sergestes arcticus*	19	0.33
	Sergestes henseni	6	0.92
	Sergia robusta	33	1.32
Stenopodidae	*Richardina fredericii*	5	0.17
Oplophoridae	*Acanthephyra eximia*	23	7.31
	Acanthephyra pelagica	24	5.10
Pasiphaeidae	*Pasiphaea multidentata*	19	5.97
	Pasiphaea sivado	5	1.42
Nematocarcinidae	*Nematocarcinus exilis*	16	0.76
Alpheidae	*Alpheus glaber*	5	0.42
Hippolitidae	*Ligur ensiferus*	1	3.02
Processidae	*Processa canaliculata*	7	1.77
	Processa nouveli	8	0.88
Pandalidae	*Chlorotocus crassicornis*	6	1.66
	Pandalina profunda	4	0.29
	Plesionika acanthonotus	24	1.88
	Plesionika antigai	5	1.21
	Plesionika edwardsi	5	4.91
	Plesionika gigliolii	8	2.23
	Plesionika heterocarpus	12	2.27
	Plesionika martia	13	6.11
	Plesionika narval	2	0.75
Crangonidae	*Philocheras echinulatus*	3	0.41
	Pontocaris lacazei	5	0.70
	Pontophilus norvegicus	12	0.65
Nephropidae	*Nephrops norvegicus*	7	22.99
Axiidae	*Calocaris macandreae*	9	0.41
Polychelidae	*Polycheles typhlops*	24	9.77
	Stereomastis sculpta	17	5.75
Diogenidae	*Dardanus arrosor*	1	20.00
Galatheidae	*Munida intermedia*	4	5.26
	Munida iris	7	5.49
	Munida tenuimana	27	2.76
Homolidae	*Paromola cuvieri*	12	264.96
Majidae	*Dorhynchus thomsoni*	3	0.47
	Macropodia longipes	7	0.68
Geryonidae	*Geryon longipes*	25	94.57
Portunidae	*Macropipus tuberculatus*	8	12.27
	Bathynectes maravigna	1	17.50
Goneplacidae	*Goneplax rhomboides*	4	1.23
Xanthidae	*Monodaeus couchi*	4	1.38

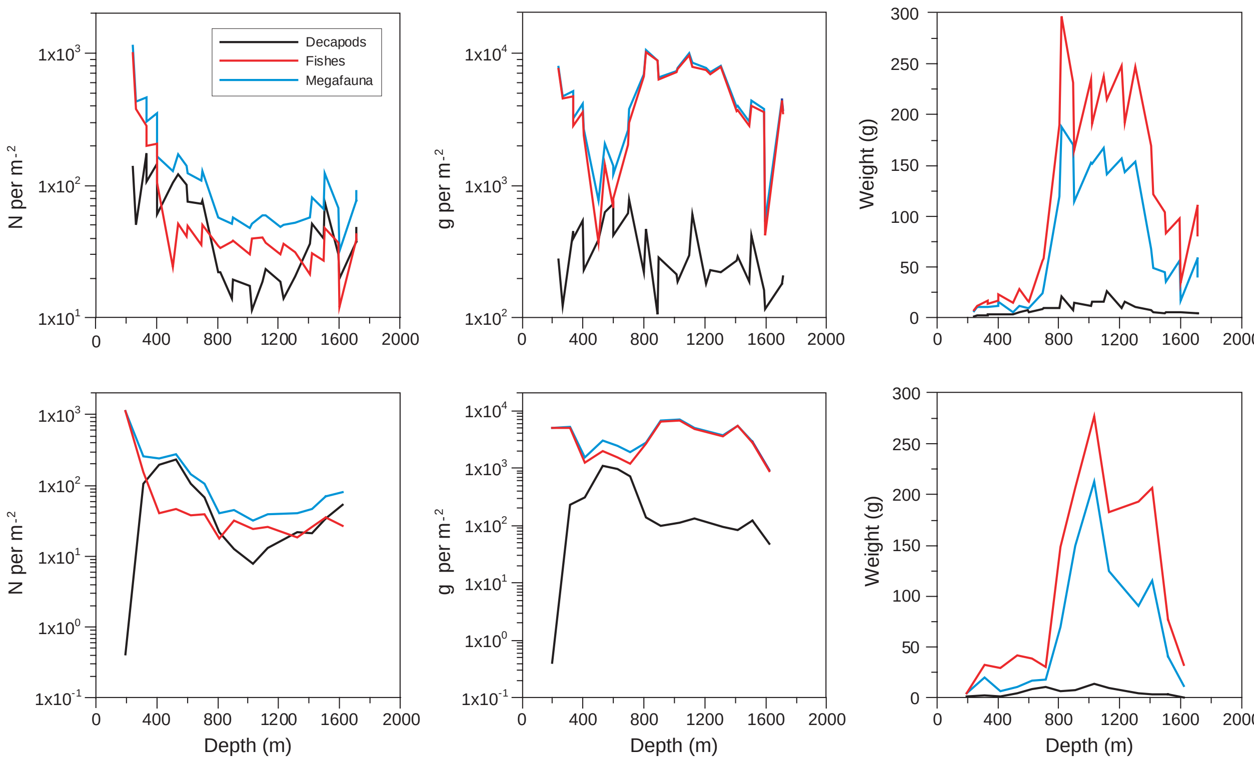

Fig. 3. Depth distribution of the number of individuals (No. per 10 000 m^2), biomass (g per 10 000 m^2) and individual weight (g) of fishes, decapod crustaceans and megafauna in Quimera-I (top) and Quimera-II (bottom) cruises.

biomass from the shelf break (200 m depth) with a minimum at 400–600 m depth. It increased again at 800 m, remained constant between 800–1 200 m and thereafter progressively decreased. The biomass of decapod crustaceans increased from 200 m peaking between 400–600 m and thereafter decreased. This peak is inverse to fish biomass that shows a minimum at this depth range. Fishes, although always having a higher mean individual weight, showed much higher individual weights between 800–1 400 m, with a peak at around 1 000 m depth which is related to the occurrence of the deep-dwelling *A. rostratus* (Fig. 3). The individual mean weight of decapod crustaceans was lower with a trend towards larger sizes at intermediate depths. The trend of the megafauna followed closely the spectrum of fishes. Some between cruise variations were found in biomass due to the lower values obtained in Q-II between 200 and 400 m depth.

The non-parametric Spearman correlation coefficient showed no significant relationships between the biomass distribution of fish and crustacean decapods over the whole bathymetric range in both cruises (Q-I n = 31, r = -0.2851, P = 0.09; Q-II n = 14, r = -0.4637, P = 0.09). Also, there was no correlation between mean weight and depth (r^2 = 0.0086, $F = 7.2962 > F_{0.05,722}$).

The size spectra for fishes and decapod crustaceans is shown in Fig. 4. Size-classes are according to log_2 (mean weight) and the height of each bar indicates the number of species present in the depth range considered that fall within the particular size-class. The size spectra of decapod crustaceans was consistently smaller than for fishes, while in both there is a discontinuity in the size distribution.

The bubble plot for the fishes and decapod crustaceans showed different mean individual weight tendencies with depth depending on the species. The fishes which corresponded to the dominant groups in the shallower depths (200–1 000 m) (Fig. 5) showed a trend to larger mean weight with depth, for instance *Galeus melastomus, Hymenocephalus italicus* and *Phycis blennoides*, exceptions are *Antonogadus megalokynodon* and *Hoplostethus mediterraneus* with a marked decrease in mean weight, due to the recruitment of small fish in deeper waters. In Fig. 6 the trends with depth for the fishes predominant at the deeper

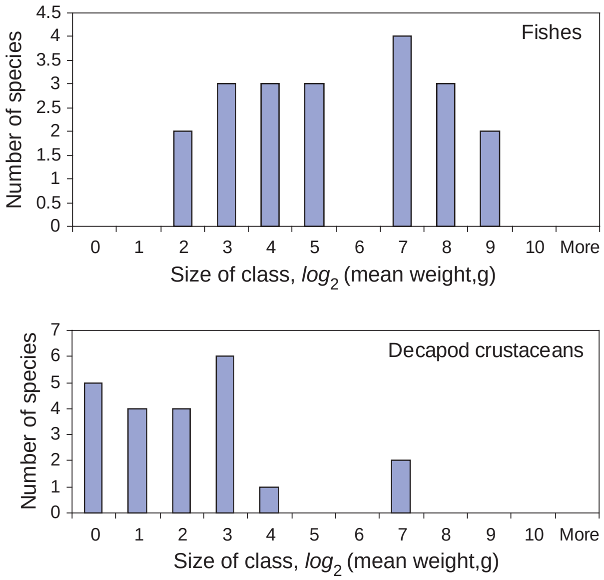

Fig. 4. Species size spectra for decapod crustaceans and fishes.

waters are included. The macrourids showed a clear depth zonation with *Nezumia aequalis* being the shallowest and *Chalinura mediterranea* the deepest dweller. The typical species of the deep Mediterranean fauna showed an increase in mean weigh with depth (*Lepidion lepidion*, *Alepocephalus rostratus, Caelorhynchus labiatus, Etmopterus spinax*).

This complex mean weight pattern depending on the species was also found in decapod crustaceans (Fig. 7 and 8). The crustaceans more abundant in water shallower than 800 m show an increasing trend in mean weight (Fig. 7). Large shrimps (*Aristeus antennatus* and *Acanthephyra eximia*) showed a decreasing trend of mean weigh with depth while mesopelagic decapods showed an increasing trend (*Acanthephyra pelagica*, *Gennadas elegans*, *Sergia robusta, Pasiphaea multidentata*). Typical deep-sea species (appearing below 1 000 m: *Stereomastis sculpta* and *Nematocarcinus exilis*) (Fig. 8) show an increase in mean weigh, while benthic eurybathic decapods (*Geryon longipes*, *Polycheles typhlops* and *Munida tenuimana*) show complex patterns (U-shaped, parabola). *M. tenuimana* has a patchy distribution, thus the weigh pattern withy great biomass at the two extremes of the depth range, might be due to fortuitous catches in the trawl hauls.

Community characteristics and results of the multifactorial analyses

The species present in more than 10 hauls (Tables 1 and 2) were analysed for size-depth trends. The dendrogram of similarities for the hauls is shown in Fig. 9a. Four main groups were evident representing a depth gradient with samples taken between: i) 195–415 m depth, ii) 502–816 m depth, iii) 813–1 416 m depth, and iv) 1 407–1 713 m depth. The results of the multidimensional scaling (MDS) analysis are shown in Fig. 9b. There are no clearly differentiated groups although it appears that the deeper hauls (<1 000 m depth) are grouped at the right side of the graph.

The dendrogram of similarities for the species is shown in Fig. 10. The first cluster separates fishes and decapod crustaceans from the upper slope with a relative big size, the rest of species are grouped clearly as a medium slope group and a deeper dwelling group. The fishes are grouped in three main groups: i) shallower (*Merluccius merluccius*, *Helicolenus dactylopterus* and *Antonogadus megalokynodon*), ii) intermediate species (*Notacanthus bonapartei, Symphurus ligulatus, Hymenocephalus italicus, Hoplostethus mediterraneus, Phycis blennoides, Nezumia aequalis, Nettastoma melanurum, Mora moro, Galeus melastomus, Etmopterus spinax*) and iii) deeper water species (*Polyacanthonotus rissoanus, Chalinura mediterranea, Caelorhynchus labiatus, Bathypterois mediterraneus, Lepidion lepidion, Alepocephalus rostratus*). There is also a further grouping inside each main group, with the species with similar mean size placed more closely than the smaller ones.

When the fish and decapod crustaceans below the MGS (small crustaceans: < = 2.7 g/ind, small fishes < = 50 g/ind) and over the MGS (large crustaceans >2.7 g/ind, large fishes >50 g/ind) are analysed the deep gradient is also evident. The small fish show four main groupings, corresponding to upper (195–415 and 502–898 m depth), middle (908–1 407 m depth) and lower slope (>1 307 m depth) (Fig.11a). Large fish showed three main groups, due to the fact that the upper boundary is not well established, corresponding to 195–710 m, 802–1 416 m and >1 307 m depth (Fig.11b). Large decapod crustaceans are present only below 300 m depth but showed a similar pattern to large fishes, with a first boundary at

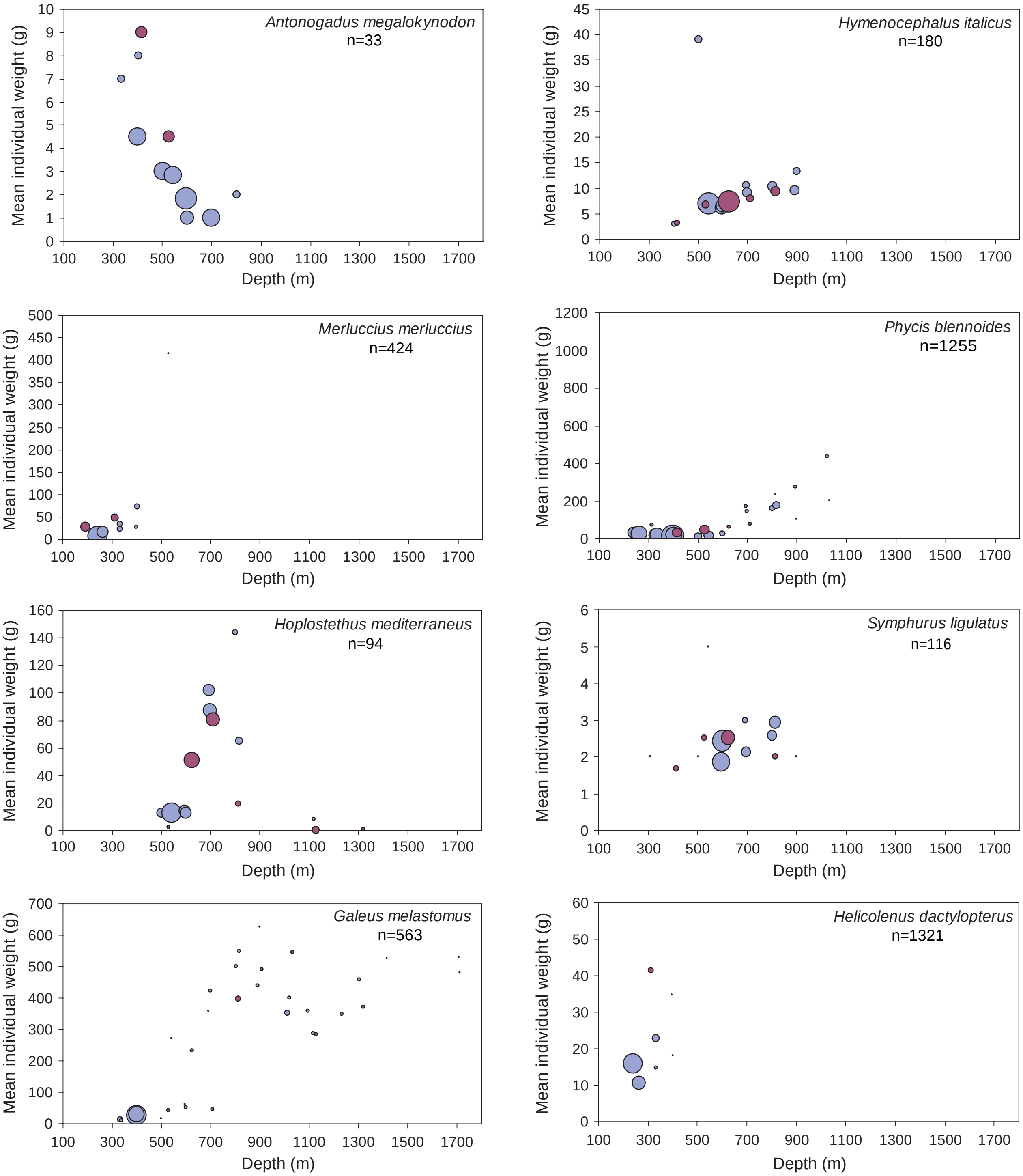

Fig. 5. Bubble plot showing the depth distribution of the mean individual weight of the fish species predominant at lower depths. *n* = number of analyzed individuals. The size of the bubble is proportional to the number of individuals present. Blue corresponds to Quimera-I and red to Quimera-II cruises, respectively.

800 m and a secondary one at approximately 1 300 m (Fig. 11d). Small decapod crustaceans showed an arrangement by depth a first boundary at 600 m and a second one at 1 300 m (Fig.11c).

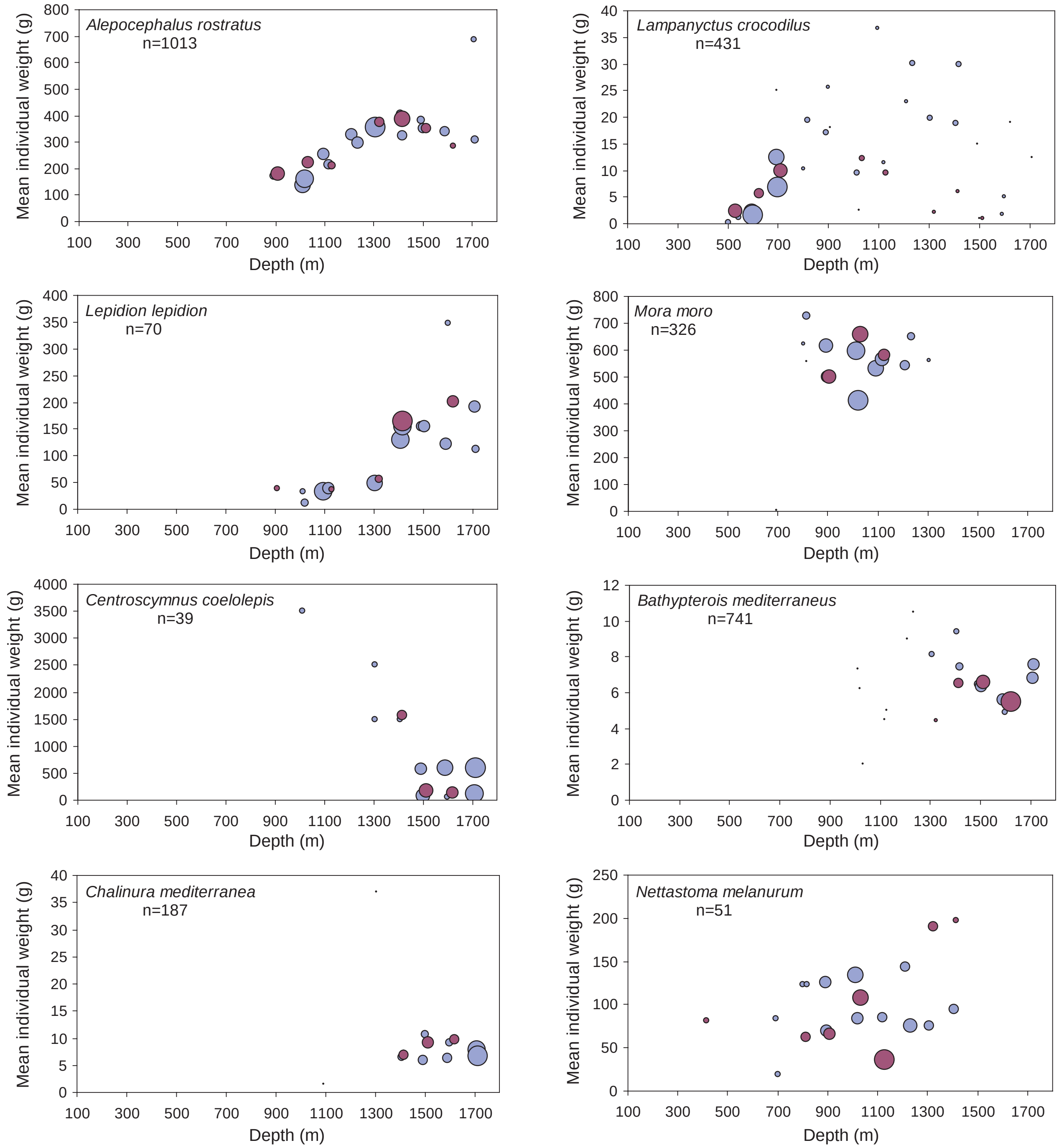

Fig. 6. Bubble plot showing the depth distribution of the mean individual weight of the fish species predominant at higher depths. *n* = number of analyzed individuals. The size of the bubble is proportional to the number of individuals present. Blue corresponds to Quimera-I and red to Quimera-II cruises, respectively.

Discussion

The western Mediterranean slope communities show complex patterns with depth, which differ from the nearby Atlantic Ocean, where fish always dominate and where echinoderms constitute the major invertebrate group (Cartes and Sardà, 1992). In the western Mediterranean decapod crustaceans are the

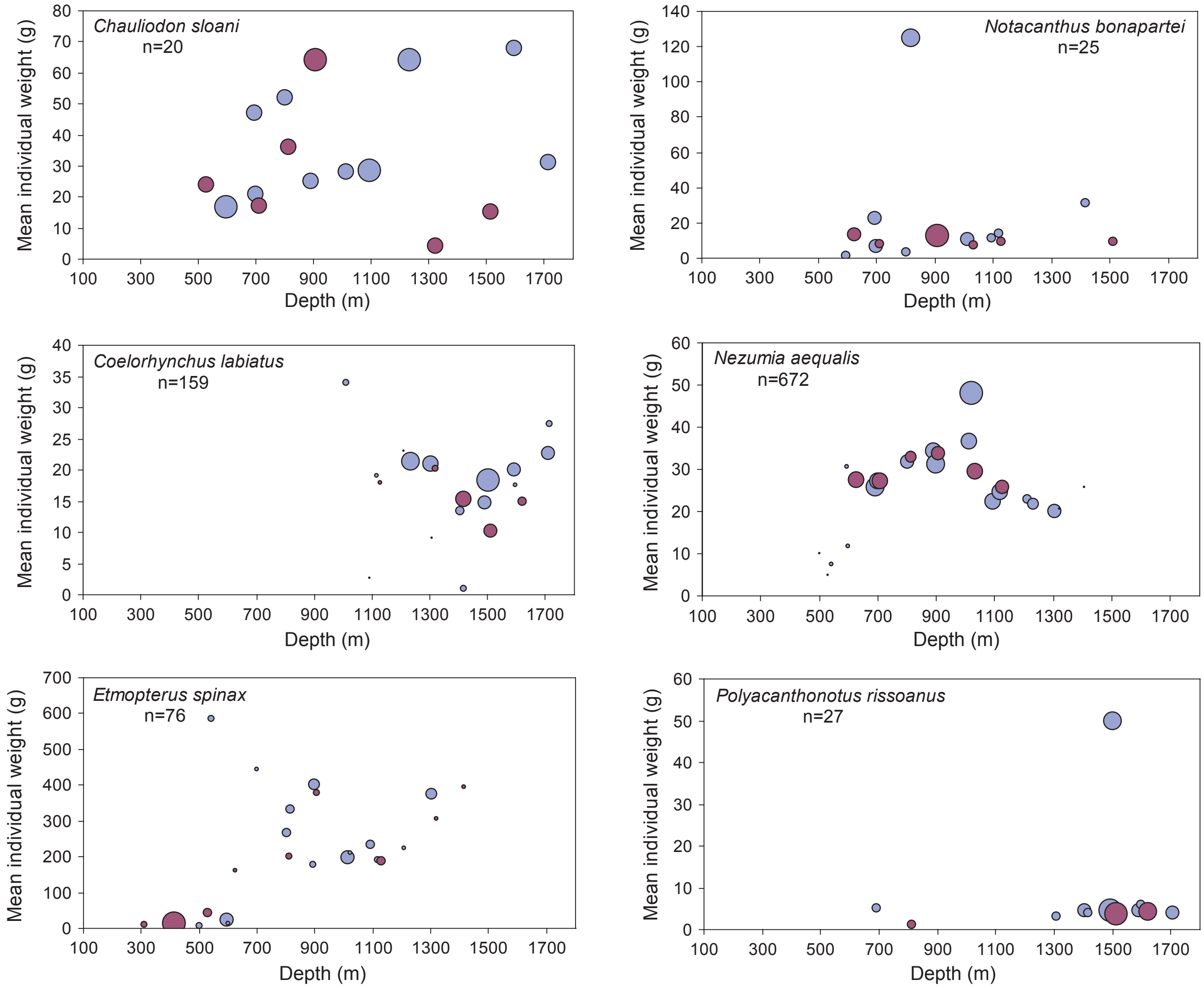

Fig. 6. (Continued). Bubble plot showing the depth distribution of the mean individual weight of the fish species predominant at higher depths. *n* = number of analyzed individuals. The size of the bubble is proportional to the number of individuals present. Blue corresponds to Quimera-I and red to Quimera-II cruises, respectively.

dominant invertebrates, and are abundant and even dominant in terms of number at mid-slope depths (400–800 m) when total megafaunal biomass is low. The relative importance of crustacean decapods in the oligotrophic Mediterranean waters has been hypothesized as a result of their highest competitive trophic strategy (Cartes and Sardà, 1992; Maynou and Cartes, 2000). Although the megafaunal abundance decreases from the shelf break downwards, the biomass which initially decreases, it increases to similar values at 800 m depth. This is due to the higher mean individual weight of fishes between 800–1 400 m depth. There is a clear zonation in species, which result in the described trends. The dominance of species and their relative size show differences depending of the depth range considered. For instance, below 800 m the larger sizes are found from the species that are characterized by a bigger-deeper trend such as *Phycis blennoides* (Massutí *et al.*, 1996), *Trachyrhynchus trachyrhynchus* (Massutí *et al.*, 1995), *Lepidion lepidion* and *Mora moro* (Rotlland *et al.*, 2002). Moreover, *Alepocephalus rostratus*, a dominant fish in the deep communities which exhibits a clear bathymetric segregation of sizes (Morales-Nin *et al.,* 1996), has a high mean individual weight which determines most of the biomass trends at this depth. The biomass of decapod crustaceans decreased with depth while their abundance increased below 1 000 m, due

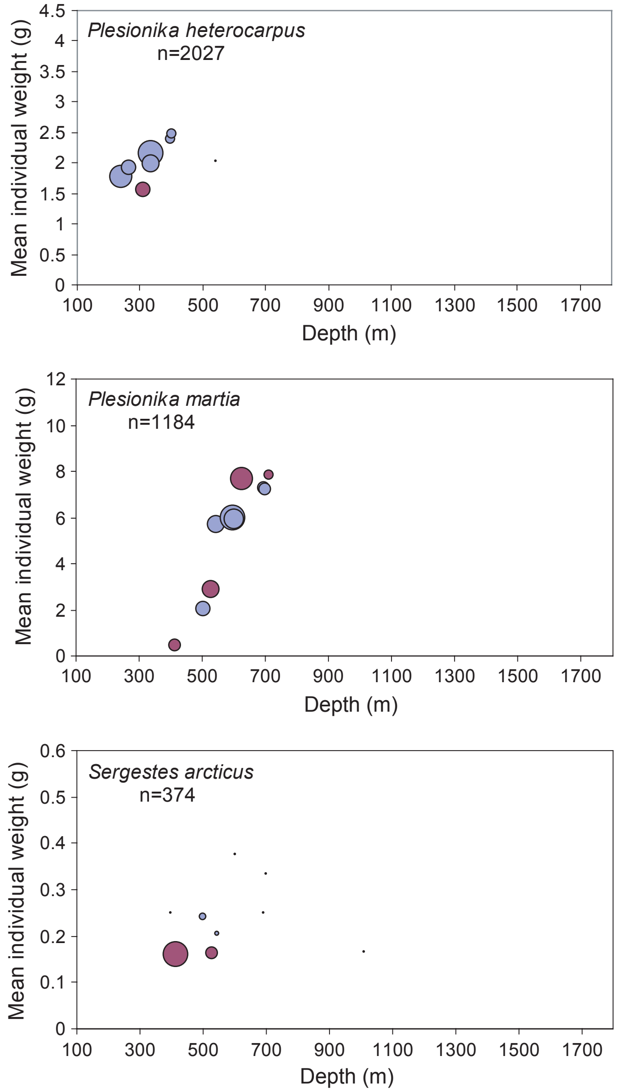

Fig. 7. Bubble plot showing the depth distribution of the mean individual weight of the decapod crustaceans predominant at lower depths. *n* = number of analyzed individuals. The size of the bubble is proportional to the number of individuals present. Blue corresponds to Quimera-I and red to Quimera-II cruises, respectively.

to the small size of abundant species (*Gennadas elegans, Sergia robusta, Acanthephyra eximia*).

The depth distribution of each sex might also be important in the resulting trends, for instance *Galeus melastomus* and *Etmopterus spinax*, found in the upper slope and the middle slope, respectively, show a similar mean size trend due to the sexual dimorphism with females reaching bigger sizes and being at the deepest range of the species distribution (Carrasón *et al*., 1992).

The upper slope (200–800 m), with two zones (200–400 m and 400–800 m), the medium slope (800-1 400 m), and lower slope (>1 400 m) zones were identified by the mean size of fishes and decapod crustaceans. The boundaries between assemblages for megafauna vary among locations (Haedrich and Merret, 1990), however we can compare our results meaningfully with analysis carried out from the same samples (Moranta *et al*., 1998; Maynou and Cartes, 2000). Our results show the same zones in terms of the mean weight of the fish and decapod crustaceans, as those obtained when the fish abundance was used to determine the demersal fish assemblages (Moranta *et al*., 1998). However, the zonation of the decapod crustacean communities was different, with faunal discontinuities not coincident across taxa (Maynou and Cartes, 2000). This is due to the dominance by weight of fishes that determine the results of the analysis when the mean weight trends are considered to determine the assemblages.

The commonly accepted factors that are responsible for the boundaries found in the size distribution, within a given habitat, are food availability coupled with how species exploit existing food resources and patterns of energy distribution with their overall life strategies (Rowe, 1971; Carey, 1981). However, fish and decapod biomass seem poorly related along the total depth gradient studied. Both taxa did not seem to have a significant trophic dependence between them (Cartes *et al.,* 2001). The zonation might be directly or indirectly related to changes in food webs, particularly in the deep Mediterranean where thermal and saline stability occur below 200 m. The major part of deep-water megafaunal predators has a highly diverse diets and a variety of trophic guilds can be identified within each taxa (Cartes, 1998). It is also well documented that deep-water species prey on different compartments (plankton-benthos) as a function of depth (Cartes, 1993). Trophic aspects have been considered as a determinant in the size structure of decapod crustaceans in a neighbouring area (Sardà and Cartes, 1993).

Previous detailed studies on both decapod crustaceans and fishes in the Catalan Sea area demonstrated, both at autoecological (see Macpherson, 1979) and assemblages levels (Cartes, 1998), the existence of resource partitioning in the exploitation of prey by bathyal species, though with an increasing dietary overlap with increasing depth among decapods (Cartes, 1998). The fish species with a positive relationship between mean weight and depth are the ones

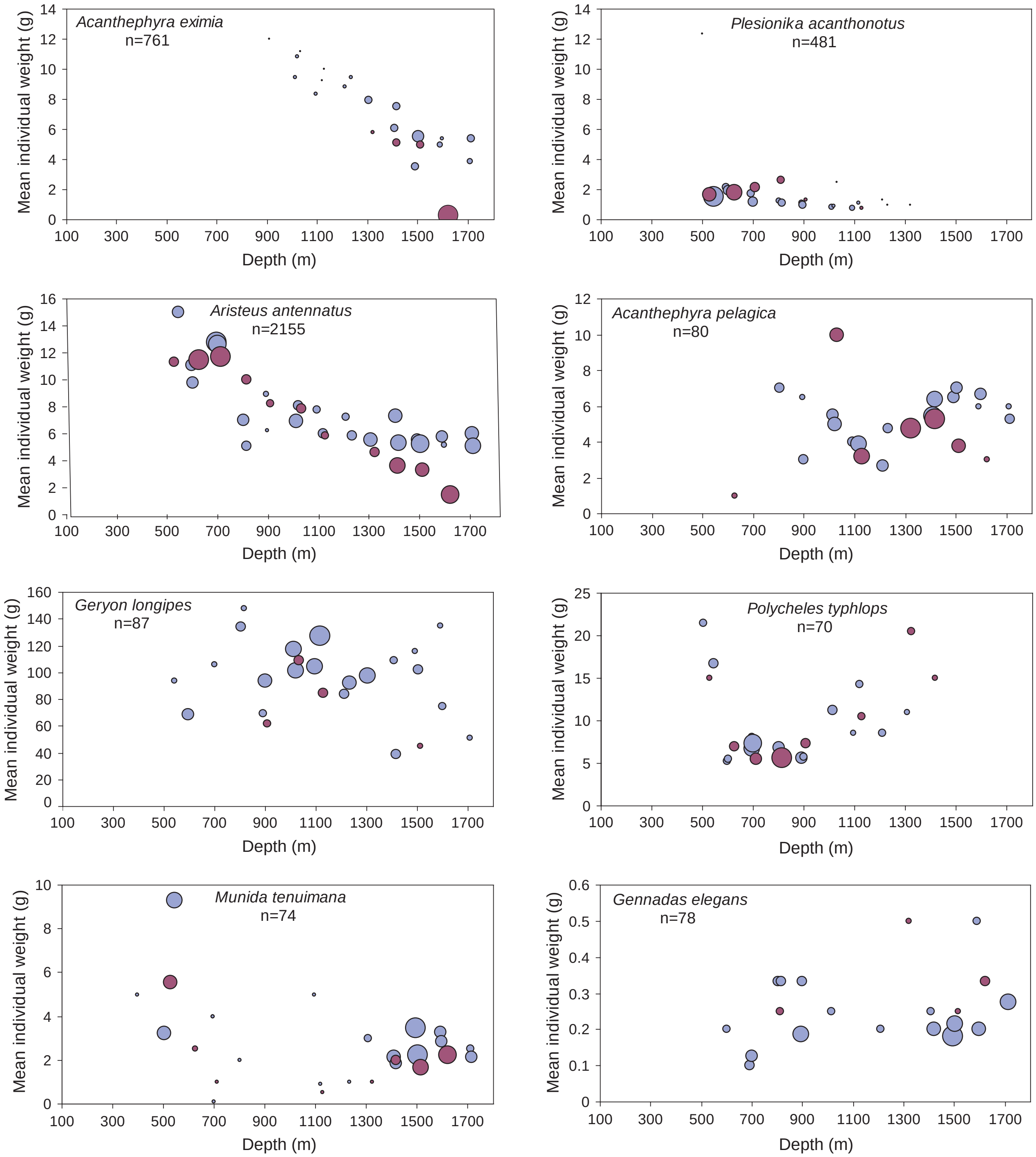

Fig. 8. Bubble plot showing the depth distribution of the mean individual weight of the decapod crustaceans predominant at higher depths. n = number of analyzed individuals. The size of the bubble is proportional to the number of individuals present. Blue corresponds to Quimera-I and red to Quimera-II cruises, respectively.

feeding on the water column (*Merluccius merluccius, Galeus melastomus*, *Hymenocephalus italicus*), while the ones that utilise mainly benthic prey do not show any clear relationship between size and depth, except for *Phycis blennoides* and *Lepidion lepidion*. On the upper slope the dominant fish prey on zooplankton

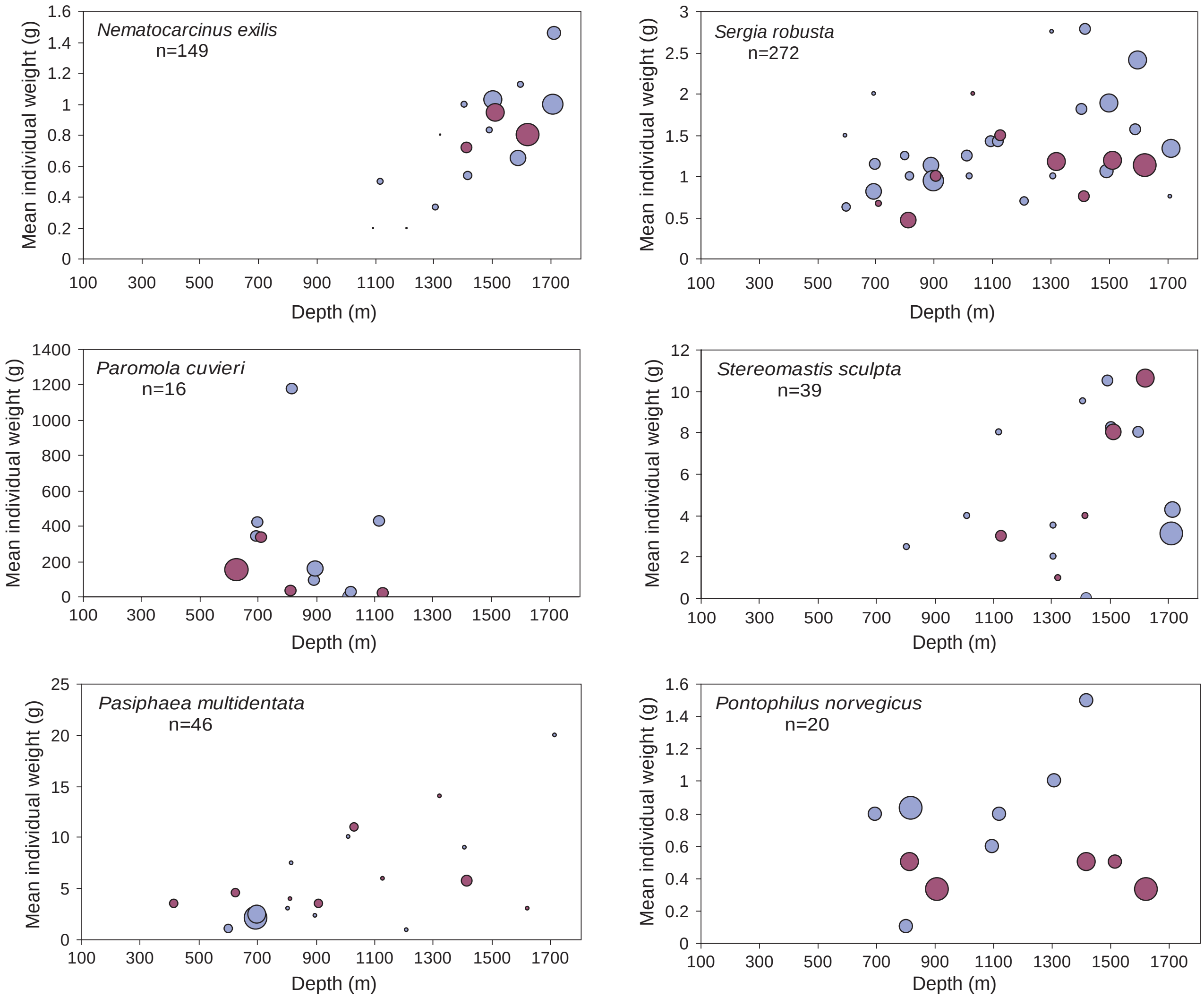

Fig. 8. (Continued). Bubble plot showing the depth distribution of the mean individual weight of the decapod crustaceans predominant at higher depths. *n* = number of analyzed individuals. The size of the bubble is proportional to the number of individuals present. Blue corresponds to Quimera-I and red to Quimera-II cruises, respectively.

(mainly euphausiids), while on the lower slope zooplankton are the dominant food source of the dominant species, *Alepocephalus rostratus* (Carrasón, 1994). The deep-sea communities of the study area depend on plankton productivity as the main source of energy (Polunin *et al*., 2001).

The hypothesis that faunal renewal intensity (zonation) depends on the individual size of taxa/ species (Gage and Tyler, 1991) has been tested for the dominant components of the deep-Mediterranean, fish and crustacean decapods. Our results show that this hypothesis seems too simple to explain the zonation in size by depth of the vagile megafauna captured by the trawl. Most fishes and crustaceans are grouped together with a complexity of patterns suggesting that life histories are more important than depth in their size distribution. This complex distribution might be more influenced by the trophic aspects and other biological factors, such as physiology (sensory organs, depth adaptations) and biological characteristics, such as the dispersion capability of the species, than by depth. The oligotrophy of the Mediterranean might also be determinant in the complex partitioning of resources by the megafauna, which exploit different fractions of the food resource depending of the taxa and consequently show different response patterns to the depth gradient.

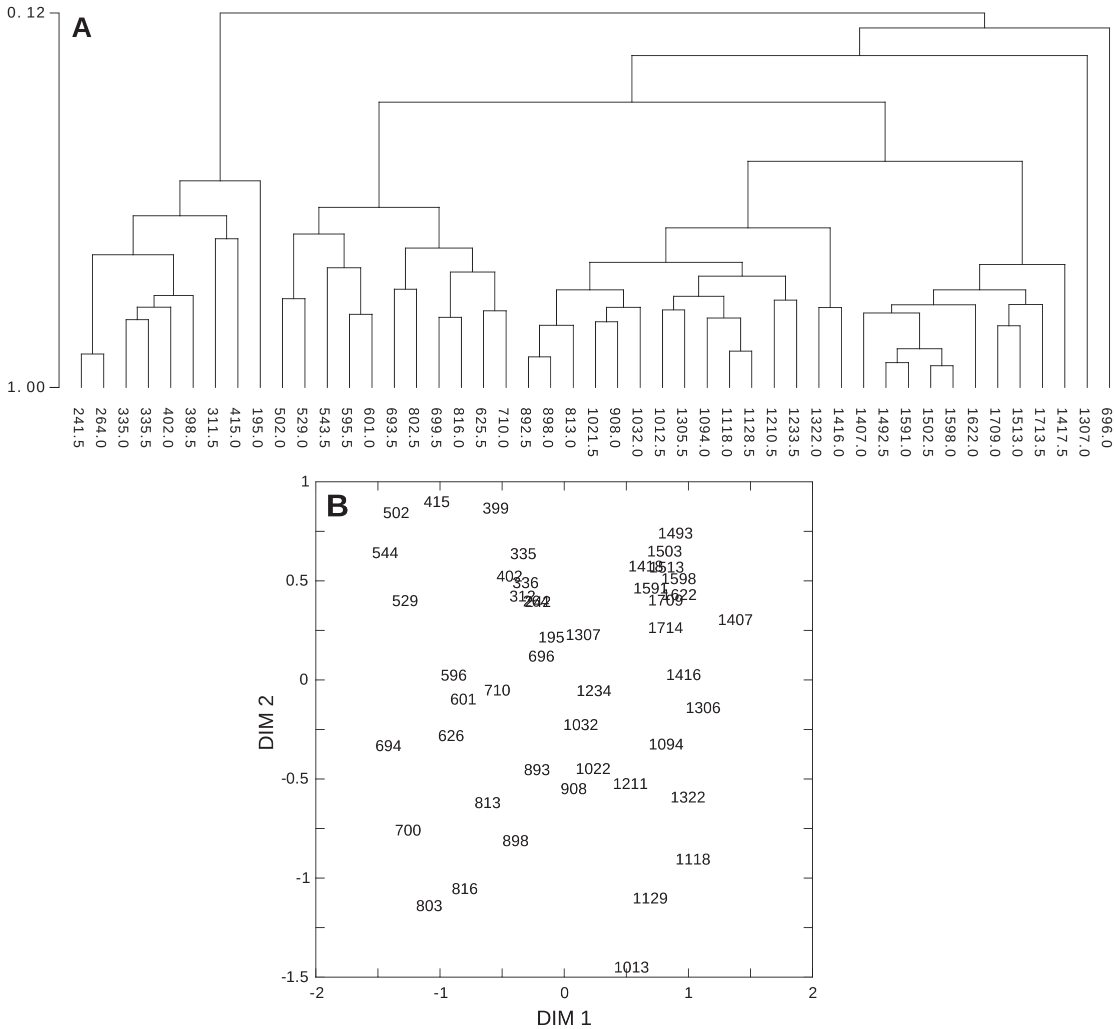

Fig. 9. (**A**) Cluster of the trawl hauls as a function of the mean weight of fish and decapod crustaceans, and (**B**) Multi-dimensional scaling showing the grouping of the depth of the trawling hauls.

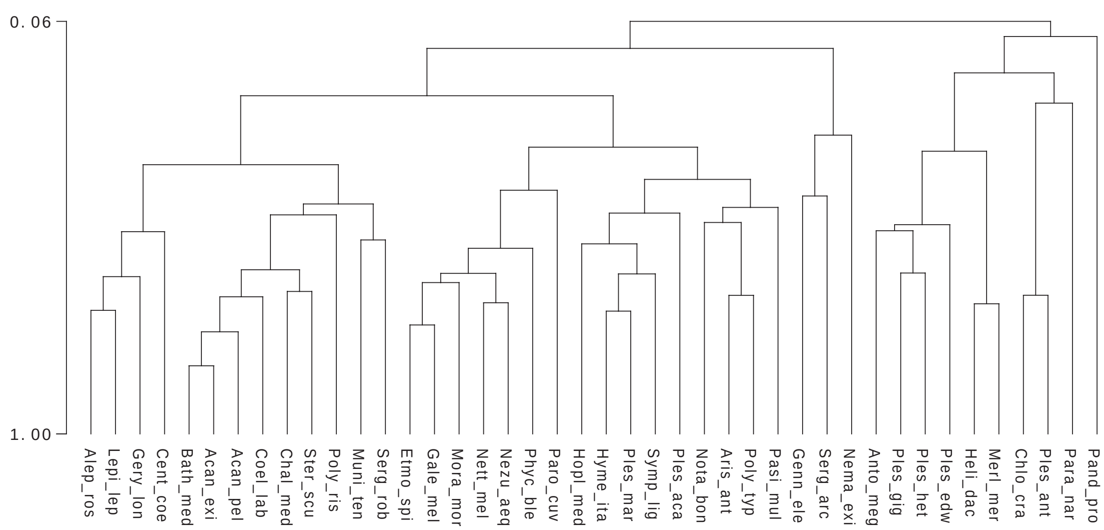

Fig. 10. Cluster showing the ordination of fish and decapod crustaceans species as a function of their mean weight. Species full names in Tables 1 and 2.

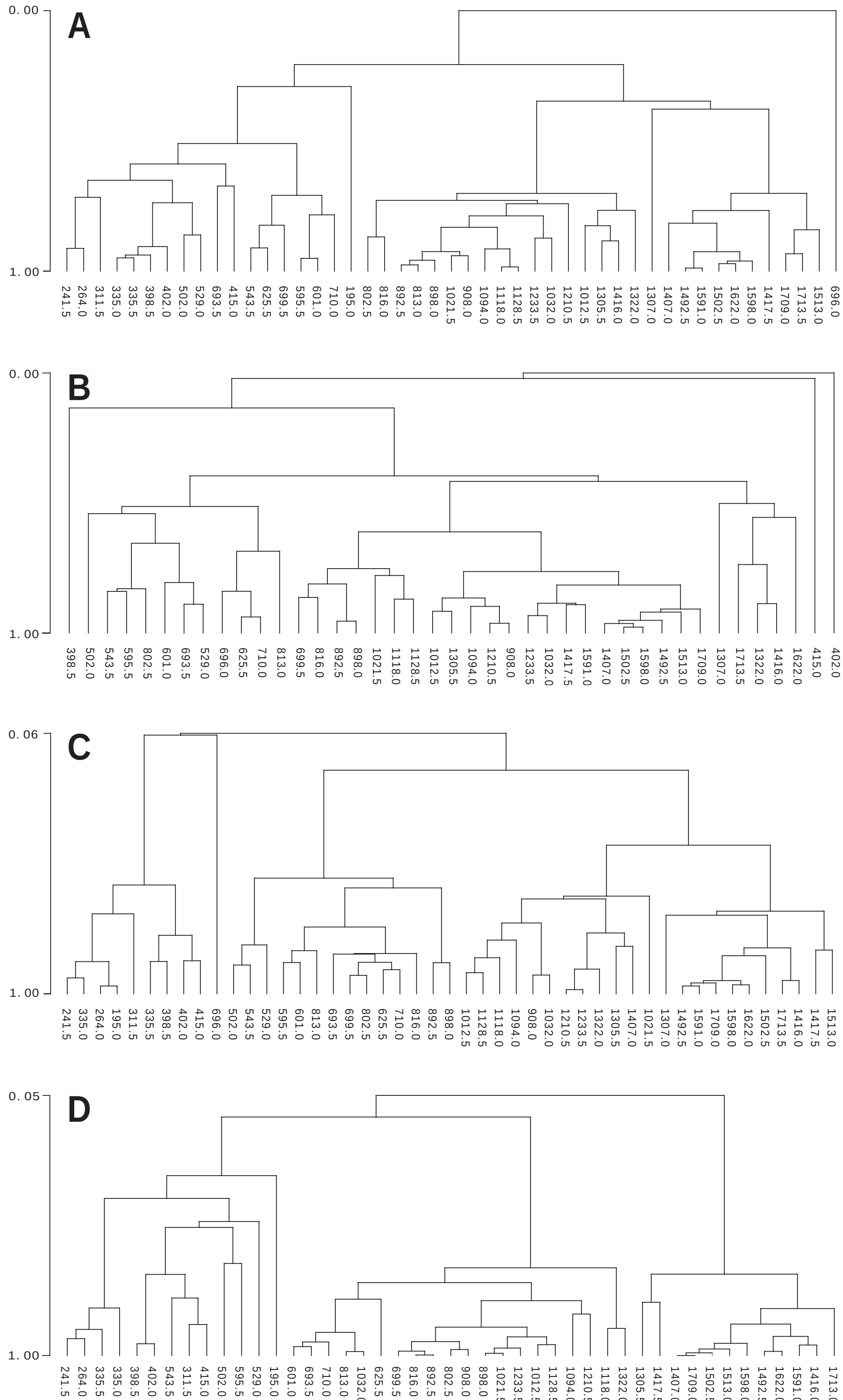

Fig. 11. Ordination in function of the mean weight (**A**) below the median weight (MDS) of fishes, (**C**) decapod crustaceans, (**B**) over the MDS for fishes and (**D**) decapod crustaceans.

Acknowledgements

The Quimera cruises were funded in the framework of the research project 'Deep-sea fisheries' (ref.FAIR CT95-0655).

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