

Depth-size trends in western Mediterranean demersal deep-sea fishes

Constantino Stefanescu, Jaime Rucabado, Domingo Lloris

Institut de Ciències del Mar, Paseo Nacional s/n, E-08039 Barcelona, Spain

ABSTRACT: We analyze the bathymetric trends of demersal deep-sea fishes in the Catalan Sea (NW Mediterranean) between 1000 and 2250 m depth. In the first part of the study, only the pattern shown by the whole fauna ('within-fauna pattern') is considered. At 1200 m there is a significant decrease in fish mean weight, as a consequence of the replacement of the dominant large or medium-sized species by small ones. This faunal shift may be a consequence of the lower trophic availability at greater depths, as shown by an important decrease in megafaunal biomass between 1000 and 2250 m. In the second part, the study focuses on the depth-size trends of the most common species ('within-species pattern'). Results show that the bigger-deeper phenomenon is not a well-established tendency. None of the lower slope species and only 2 of the 5 middle slope species analyzed behave as bigger-deeper species. Moreover, some species which display a bigger-deeper trend in North Atlantic waters do not show any significant trend in the Mediterranean. Considering the recent Atlantic origin of Mediterranean ichthyofauna and the contrasting behaviour in the 2 areas, the hypothesis that mean size increase with depth is the result of inherited ontogenic behaviour can be discarded.

INTRODUCTION

Depth-size trends in deep-sea fishes has been a controversial subject in the last few years (e.g. Haedrich & Rowe 1977, Polloni et al. 1979, Macpherson & Duarte 1991 and references cited therein). Trends have been studied both for individual species ('within-species pattern') and for the whole fauna, analyzing average individual size at different depths ('within-fauna pattern') (cf. Carney et al. 1983). However, the results have been contradictory depending on the areas investigated and the sampling techniques used.

For invertebrates (meio- and macrobenthos) the within-fauna trend is towards a reduction in the organisms' average size with increasing depth (Thiel 1975, 1979, 1983, Gage 1978, Jumars & Gallagher 1982, Carney et al. 1983, Sokolova 1990). Both physiological and ecological reasons have been put forward to explain the observed pattern, but there is still a great deal of speculation on the matter. For demersal deep-sea fishes the results obtained up to now have been contradictory. First results seemed to indicate the opposite tendency to that of the invertebrates, i.e. a bigger-deeper phenomenon (Haedrich & Rowe 1977, Polloni et al. 1979). However subsequent studies have proved that this tendency changes according to the area

studied (Merrett & Marshall 1981, Sulak 1982, Snelgrove & Haedrich 1985, Gordon 1986, Merrett 1987). The confusion has led some authors to suggest that the bigger-deeper phenomenon could be nothing more than a sampling artefact (Percy et al. 1982); in one area, at least, evidence has shown this to be so (Merrett et al. 1991b).

Within-species the observed trend is also variable (Polloni et al. 1979, Mauchline & Gordon 1984, Snelgrove & Haedrich 1985, Middleton & Musick 1986, Gordon & Duncan 1987, Macpherson & Duarte 1991, Merrett et al. 1991b, among others). In some taxonomic groups (e.g. gadiforms) the occurrence of larger individuals in deeper waters is a fairly common pattern. The trend can, however, be erroneously interpreted if phenomena such as ontogenic and sexual migrations are not taken into account (Snelgrove & Haedrich 1985, Middleton & Musick 1986).

In this paper we analyze the bathymetric trends of demersal deep-sea fishes in the Catalan Sea (western Mediterranean) between 1000 and 2250 m depth. In the first part, only the pattern shown by the whole fauna is considered. Contrary to that observed in other areas, fish size decreases with depth and some of the reasons for this anomalous pattern are discussed. In the second part, the study focuses on the most common

species in the area. In some species we find a different behaviour to that shown in Atlantic waters. This means we must discard the idea of a generalized phenomenon (as suggested recently by Macpherson & Duarte 1991) involving an ontogenic migration of individuals to progressively deeper water.

MATERIAL AND METHODS

All the material included in the present paper was collected in the Catalan Sea (NW Mediterranean), off the Iberian coast (38° 45' N to 42° 00' N), during 4 cruises (summer and fall) from July 1987 to October 1988 (Stefanescu et al. 1992b).

The sampling gear used was a semiballoon-otter trawl (OTSB14, headline length 13.7 m) trawled on a single warp. The procedure followed was basically that described by Merrett & Marshall (1981) and Sulak (1982). Each tow usually lasted about 3 h. Depth was measured by a vertical ELAC LZ120 echosounder at intervals of 15 min. The mean assigned depth of each trawl was calculated from arithmetic means of these interval depths.

A total of over 16 000 fishes representing 29 demersal species (Stefanescu et al. 1992b) were collected at ca 50 stations between 984 and 2251 m depth. For each haul individuals were counted and the total weight of the catch was calculated as the sum of fresh weights of species. Both parameters (abundance and biomass) were standardized to a common sampled area of 1000 m², according to the values proposed by Sulak (1982) for an OTSB14 trawled on a single warp at 2.5 knots. The individual mean weight for each sample was calculated by dividing the biomass by the abundance.

A regression analysis was performed to determine any significant change in abundance, biomass and specimen mean weight with changing depth. Scheffé's linear contrast was also employed to test significant differences in the values of these parameters among 6 depth intervals of 200 m, defined between 1000 and 2200 m.

Prior to the calculations and plotting, abundance and biomass (per unit area) and mean fish weight were converted to log-transformed values.

Bathymetric trends within-species were analyzed only for those species with their bathymetric range almost or totally contained within the range 1000 to 2250 m (cf. Stefanescu et al. 1992b). Nine common species with their bathymetric distribution centered below 1000 m were selected. Abundant information for depths less than 1000 m has allowed an accurate definition of upper bathymetric limits of the species (Maurin 1962, Raimbault 1963, Macpherson 1977,

Matallanas 1979, Allué et al. 1981, Allué 1985). Because the maximum depth of our samples (2251 m) is close to the maximum depth of the Catalan Sea (ca 2500 m), the lower bathymetric ranges of the species have been well established.

Preanal length was utilized for macrourids and total length for the remaining species (except in the case of *Bathypterois mediterraneus*, in which standard length was used). To test the null hypothesis 'fish size is depth independent' a regression analysis between both variables was performed. The coefficient of determination (r^2) was also calculated to determine what proportion of the variance of size could be attributed to change in depth. The geometric mean was preferred for calculating the mean fish size of each sample, because the arithmetic mean is susceptible to the influence of a few large specimens and does not represent accurately the mode in fish size at a given station.

Finally, it must be remembered that the phenomenon of size increase with depth is highly complex and could be related to reproductive or seasonal migrations, both horizontal and vertical (cf. Gordon 1979, Snelgrove & Haedrich 1985, Middleton & Musick 1986), which can be masked if the sampling period is not adequate. The problem is enhanced at depths subject to the influence of environmental variation (photoperiodicity, pulses in surface productivity, periodic cycles in water temperature, etc.). These aspects can lead to erroneous conclusions when not properly considered.

RESULTS

Within-fauna pattern

Bathymetric trends in abundance, biomass and mean fish weight are shown in Fig. 1.

Abundance (Fig. 1A) does not change significantly with depth ($r = 0.21$, 46 df, $p < 0.05$). There are, however, important oscillations in the mean values over the whole range considered. Therefore, increasing depth is not related to decreasing fish abundance in the Catalan Sea (Table 1), as occurs in other Atlantic areas for the same depth range (Grassle et al. 1975, Cohen & Pawson 1977, Merrett & Marshall 1981, Sulak 1982, Merrett & Domanski 1985, Merrett et al. 1991a).

Biomass does decrease significantly with depth ($r = 0.59$, 46 df, $p < 0.05$), although a large part of this variation can be attributed to the sharp decrease in values around 1200 m (Fig. 1B; Table 1). At greater depths the trend is less pronounced and no significant difference is found among the mean values for the depth intervals considered.

Mean fish weight shows a marked and uniform decrease from 1000 m to the deepest level sampled

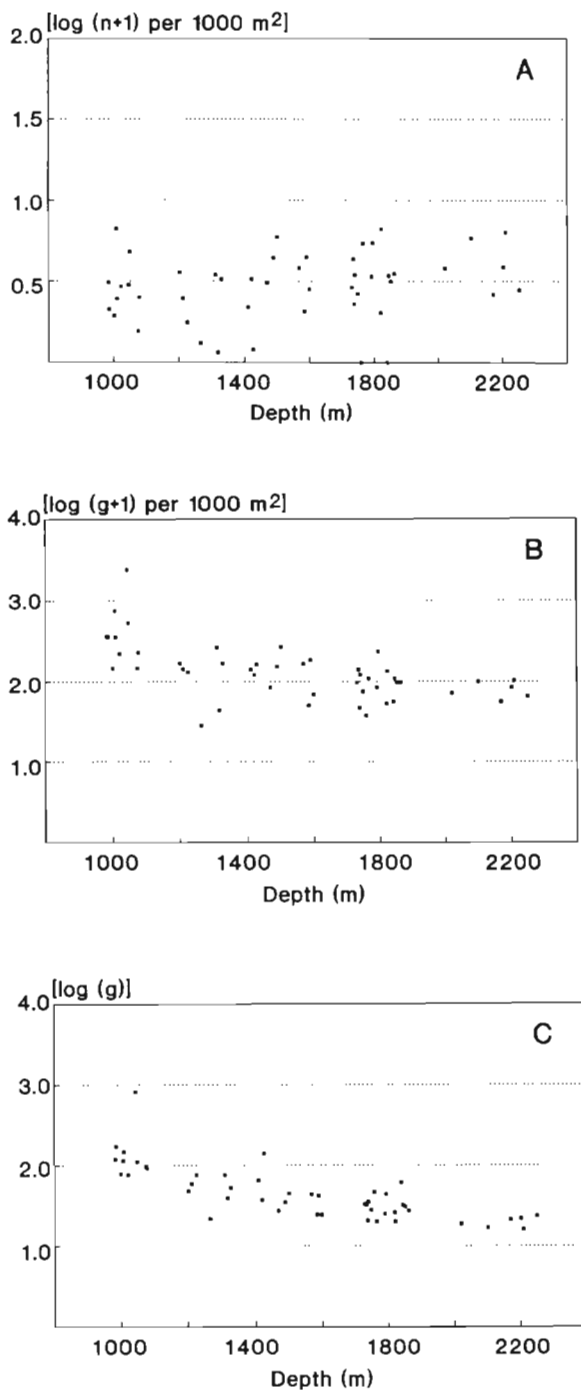


Fig. 1. Bathymetric distribution of 3 faunal parameters of the demersal deep-sea fish fauna in the Catalan Sea (NW Mediterranean). (A) Abundance; (B) biomass; (C) mean fish weight

(Fig. 1C). The 2 variables show a strong correlation ($r = 0.77$; 46 df, $p < 0.001$) and fit a linear regression of equation $[Y (\log \text{ mean weight}) = -0.0007 X (\text{depth}) + 2.7027]$. Mean values differ significantly between the

first depth interval sampled and the other intervals. However at greater depths, although values continue decreasing markedly, differences are not significant.

Within-species pattern

The analysis of the size-depth trend for each species is detailed in Table 2. Of the 9 species studied, 6 (*Bathypterois mediterraneus*, *Polyacanthonotus rissoanus*, *Coryphaenoides guentheri*, *Chalinura mediterranea*, *Mora moro* and *Cataetyx alleni*) do not show any specific trend, individuals of varying size and age being distributed over the whole range occupied by the species.

The bathymetric ranges of *Bathypterois mediterraneus*, *Polyacanthonotus rissoanus*, *Coryphaenoides guentheri* and *Chalinura mediterranea* in the Catalan Sea were almost totally covered by the sampled depths (Stefanescu et al. 1992b). *Cataetyx alleni* can be found occasionally at lesser depths (Matallanas 1983, author's unpubl. data). However, the few specimens captured there are of sizes distributed over the whole range shown by the species (3 to 13 cm). For *Mora moro* the only available data correspond to large adults (≥ 24 cm). The absence of young individuals in our samples could be the result of a pelagic existence (as Gordon & Duncan 1985 suggested for *Lepidion eques*, a very common morid in Rockall Trough). Therefore, it is not possible to know with certainty how the size distribution of this species is influenced by depth.

In contrast, *Alepocephalus rostratus*, *Coelorhynchus labiatus* and *Lepidion lepidion* do show significant size-depth changes. For *A. rostratus* and *L. lepidion* mean size increases with depth while for *C. labiatus* the opposite trend occurs (Table 2).

However, correct interpretation of depth-size data also requires, as noted by Middleton & Musick (1986), information on bathymetric distribution as size frequencies of the population. Thus, an increase in mean fish size with depth can be attributed to a 'bigger-deeper' phenomenon (maximum fish size correlated with maximum depth) or a 'smaller-shallower' phenomenon (individuals of maximum size are uniformly distributed along the whole range shown by the species, while the smaller individuals are concentrated in shallower water).

In the Catalan Sea *Alepocephalus rostratus* exhibits a smaller-shallower trend (Fig. 2); for all depths at which the species is abundant (1000 to 2000 m) the dominant size class is 24 to 28 cm (4 to 6 yr old specimens, according to Morales-Nin 1990). Moreover, there is a complete absence of 0 to 1 yr old individuals (≤ 17 cm) at depths below 1400 m and a paucity of 2 yr old individuals (around 20 cm) at depths greater than

Table 1. Summary of mean values (\pm SD) for the parameters abundance [$\log(n + 1)$ per 1000 m²], biomass [$\log(g + 1)$ per 1000 m²] and mean fish weight [$\log(g)$] for 6 depth intervals of 200 m between 1000 and 2200 m. Scheffe's linear contrast showed no significant differences for abundance values but a large difference for biomass and mean fish weight ($p < 0.01$) between the values for 1000 to 1200 m and the rest

Parameter	Depth interval (m)					
	1000–1200	1200–1400	1400–1600	1600–1800	1800–2000	2000–2200
Samples	10	7	10	9	6	6
Abundance	0.45 \pm 0.18	0.35 \pm 0.19	0.48 \pm 0.19	0.48 \pm 0.23	0.44 \pm 0.26	0.60 \pm 0.14
Biomass	2.56 \pm 0.35	2.03 \pm 0.33	2.10 \pm 0.21	1.96 \pm 0.23	1.93 \pm 0.15	1.89 \pm 0.10
Mean weight	2.12 \pm 0.28	1.69 \pm 0.17	1.62 \pm 0.21	1.49 \pm 0.12	1.49 \pm 0.15	1.29 \pm 0.06

1600 m. Only for larger individuals (> 20 cm) does the distribution become uniform along the whole bathymetric range shown by the species. Considering the likely demersal spawning of alepocephalids (Crabtree & Sulak 1986), these data suggest the existence of a reproductive migration to shallower water (1000 to 1200 m), with younger individuals living at this depth and to a lesser extent at 1200 to 1400 m. After 2 yr an ontogenic migration to greater depths occurs. This migration affects only a part of the population and 2 yr old individuals rarely exceed the 1600 m level.

Contrary to the above, *Lepidion lepidion* is a bigger-deeper species (Fig. 3), with individuals of 6 to 15 cm dominating at 1000 to 1400 m and individuals of 19 to 20 cm at depths of 1400 to 1600 m. Below 1600 m the size classes less than 15 cm are poorly represented and, although individuals of 20 cm dominate, those of > 25 cm regularly appear. The few specimens trawled by fishing boats (author's unpubl. data) at 600 to 800 m have all been small; so we can expect a similar pattern at 800 to 1000 m. This species thus shows an ontogenic migration towards progressively increasing depths.

Analysis of the data for *Coelorhynchus labiatus* reveals a smaller-deeper phenomenon (Table 2). This is rather surprising considering the opposite tendency

observed in the western North Atlantic (Mauchline & Gordon 1984, Merrett et al. 1991b). These results should, however, be interpreted with caution as the data are limited and the mean number of individuals per sample is low.

DISCUSSION

Within-fauna pattern

In the Catalan Sea, the mean fish weight of the whole fauna shows a decreasing tendency below a depth of 1000 m. When abundance (no. per 1000 m²) and biomass (g per 1000 m²) are taken into account simultaneously an important faunal shift is evident between 1000 and 2250 m. At 1200 m there is a significant decrease in the fish mean weight, as a consequence of the replacement of the dominant large or medium-sized species (e.g. gadiforms such as *Mora moro*, *Phycis blennoides*, *Trachyrhynchus trachyrhynchus* and sharks such as *Hexanchus griseus*), by small ones (such as the macrourids *Coryphaenoides guentheri* and *Chalinura mediterranea* and the chlorophthalmid *Bathypterois mediterraneus*; cf. Stefanescu et al. 1992b). It can be

Table 2. Results of regression analysis for the 2 variables size vs depth for demersal deep-sea fishes in the Catalan Sea, with bathymetric range totally or almost covered by the depth interval 1000 to 2250 m. a and b are the major axis regression coefficients for the equation $Y(\log \text{ size}) = a + bX(\text{depth})$. Regression significant at * 95 %, *** 99.9 %; NS: not significant; r^2 : determination coefficient; TL: total length; SL: standard length; PAL: preanal length; depth shows extreme ranges of species capture; Ns: number of samples analyzed; Ni: number of individuals analyzed

Species	a	$b \times 10^{-2}$		r^2	Length (mm)	Depth (m)	Ns	Ni	Trend
<i>Alepocephalus rostratus</i>	159.9	7.6	***	0.33	40–480 (TL)	984–2133	42	787	Smaller-shallower
<i>Bathypterois mediterraneus</i>	102.2	0.9	NS	0.15	45–180 (SL)	1308–2251	9	994	
<i>Polyacanthonotus rissoanus</i>	62.7	-0.4	NS	0.15	37–70 (PAL)	1225–2251	12	102	
<i>Coelorhynchus labiatus</i>	144.9	-5.7	*	0.41	33–94 (PAL)	1153–1588	14	78	Smaller-deeper
<i>Coryphaenoides guentheri</i>	53.5	-0.5	NS	0.03	13–70 (PAL)	1409–2201	16	544	
<i>Chalinura mediterranea</i>	43.2	0.1	NS	0.00	15–102 (PAL)	1409–2251	12	203	
<i>Lepidion lepidion</i>	21.7	10.0	***	0.86	60–370 (TL)	984–2251	40	2972	Bigger-deeper
<i>Mora moro</i>	325.7	2.9	NS	0.05	240–510 (TL)	984–1326	15	240	
<i>Cataetx alleni</i>	72.9	0.9	NS	0.04	30–130 (TL)	1008–1790	18	352	

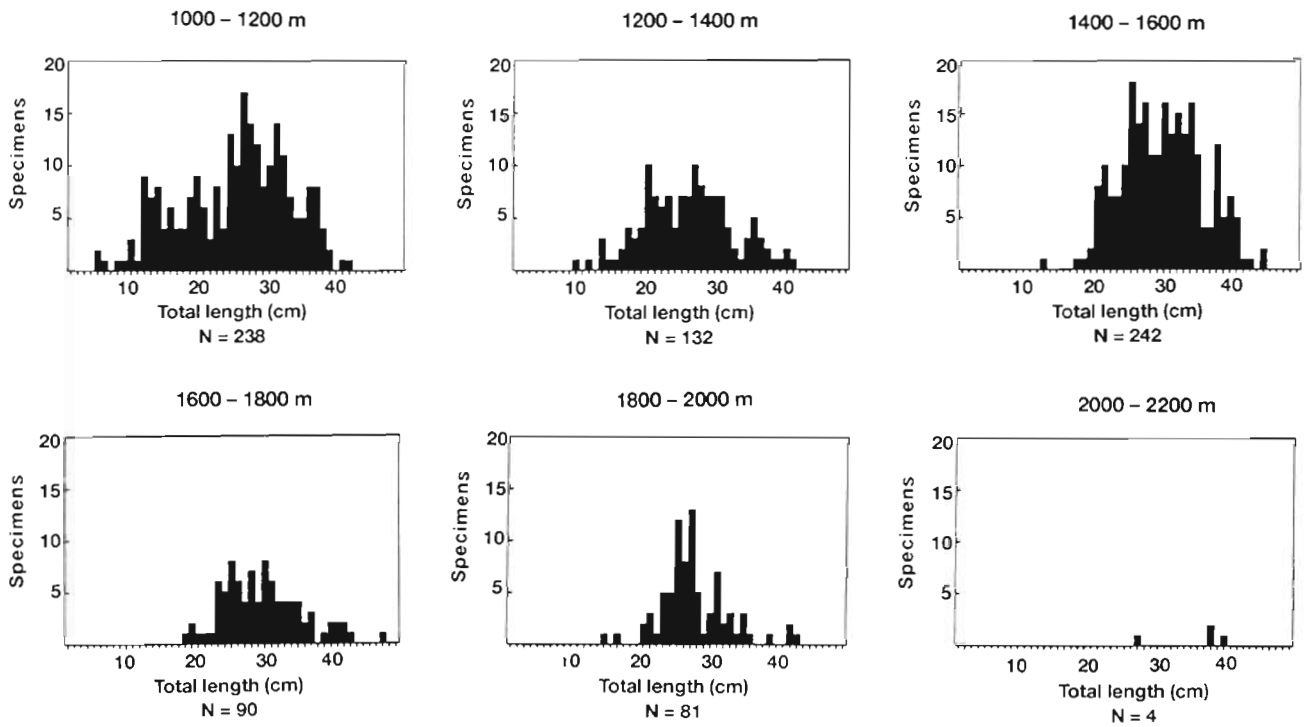


Fig. 2. *Alepocephalus rostratus*. Length-frequency distributions at different depth intervals

said, therefore, that demersal ichthyofauna shows a smaller-deeper trend below 1000 m depth.

In our opinion, this faunal shift is a consequence of

the impossibility of large or medium-sized species to satisfy their energetic requirements in an environment progressively more tropically restrictive. The increas-

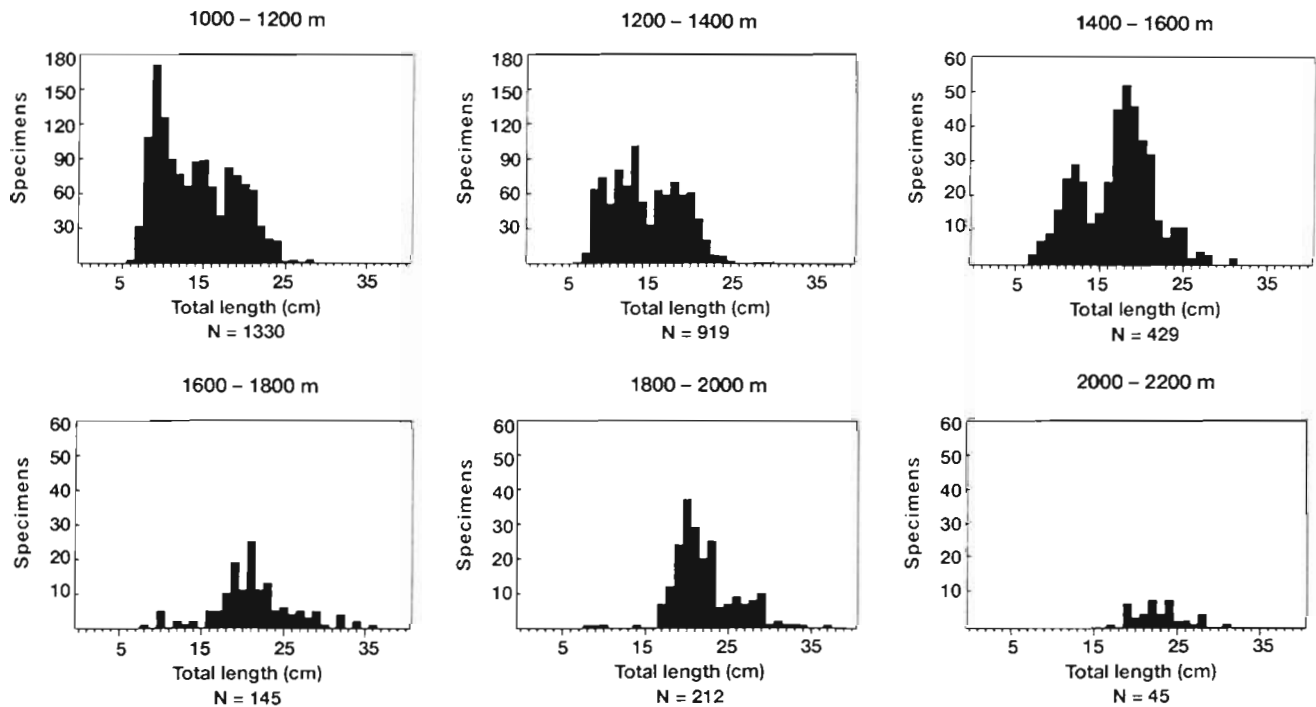


Fig. 3. *Lepidion lepidion*. Length-frequency distributions at different depth intervals

ing oligotrophy with increasing depth is shown by an important drop in megafaunal biomass between 1000 and 2250 m (fish: present work; decapod Crustacea: Cartes 1991).

There are no data on meio- and macrofauna; however, an exponential decrease in abundance with depth has been recorded off northwestern Mediterranean areas (Carpine 1970, Thiel 1983, Pérès 1985, among others).

Considering the notably scarce resources appearing to predominate in the Catalan Sea at 1200 m, the disappearance of large species would seem to agree with the hypothesis of Mahaut et al. (1990). These authors distinguished 2 demersal deep-sea fish groups characterized by distinct trophic strategies: (1) species feeding on the epibenthos and infauna, and indirectly dependent on organic particles sedimenting down from shallower levels (termed 'microphagous' by Hureau et al. 1979); and (2) species feeding directly on megafauna carcasses deposited in a more unpredictable and limited manner. The latter group can be amplified when not only necrophagous species but also those feeding actively on large pelagic and benthopelagic prey are considered. In this category are included the species termed 'predators' by Hureau et al. (1979). Preponderant in this second class will be the sharks and some macrourids which, to a lesser extent, also display necrophagous habits (cf. Desbruyères et al. 1985).

Mahaut et al. (1990) suggest that species from the second group are not present in those areas where 'large carcasses never reach the seafloor', this being the case in oligotrophic seas. A current analysis of the diet of *Centroscymnus coelolepis* (Carrassón et al. 1992), the only shark abundant on the lower slope, has revealed the practical non-existence of carrion remains. This is in sharp contrast to findings in the North Atlantic (Clarke & Merrett 1972, Sedberry & Musick 1978, Mauchline & Gordon 1983) and could serve as evidence in favour of the hypothesis of Mahaut et al. (1990).

Moreover, the scarcity of large prey on the lower slope (sensu Haedrich & Merrett 1988) of the Catalan Sea seems to be in agreement with the existence of a demersal fish community dominated by small species feeding almost exclusively on small epibenthic and benthopelagic invertebrates (Carrassón & Matallanas 1990, M. Carrassón pers. comm.).

An additional factor to explain the observed smaller-deeper trend is the significant size reduction, when compared to Atlantic populations, found in the Mediterranean populations of many species, especially those of the lower slope. In *Polyacanthonotus rissoanus*, for example, the differences are particularly remarkable (Fig. 4). For the macrourids *Coryphaenoides guentheri* and *Chalinura mediterranea*

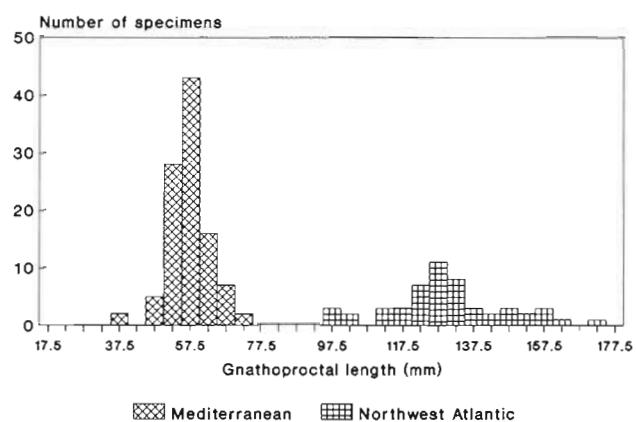


Fig. 4. *Polyacanthonotus rissoanus*. Length-frequency distributions in 2 populations, one from the Mediterranean (Catalan Sea) and the other from the western North Atlantic (Middle-Atlantic Bight). [Modified after Crabtree et al. (1985) and authors' data]

maximum sizes as observed in the Atlantic (Geistdoerfer 1986) compared with those found in the present study are, respectively, 48 cm TL and 22 cm TL for *C. guentheri* and 73 cm TL and 34 cm TL for *C. mediterranea*. *Centroscymnus coelolepis* showed a maximum size of 114 cm in the Atlantic (Compagno 1984) compared with the 63 cm observed in this study. Our data for these species are in complete agreement with previous Mediterranean data (Roule 1912, Geistdoerfer & Rannou 1971, 1972, McDowell 1973, Sulak et al. 1984).

It is evident that this phenomenon is very complicated and is undoubtedly the result of a combination of factors of disparate origin (e.g. latitudinal gradients on fish size, cf. Lindsey 1966; ecological factors affecting body size, cf. Peters 1983). More limited resources (a striking difference exists between Mediterranean and Atlantic waters) and an elevated temperature can both be assumed to play an important part (cf. Margalef 1982, pp. 273–278), and have already been advocated (Tortonese 1960) as determinant in reducing size in Mediterranean deep-sea fish.

From these data it is evident we cannot generalize the idea, first proposed by Dayton & Hessler (1972) and subsequently developed by Haedrich & Rowe (1977), Polloni et al. (1979), Haedrich et al. (1980) and Carney et al. (1983), of an evolutionary tendency to select for increased size in demersal fish when confronted with the limited resources of the deep sea. According to these authors advantages associated with a large size would play a key part in explaining the bigger-deeper phenomenon observed in the North Atlantic. Greater mobility and the consequent increased ability to catch pelagic prey and feed on widely dispersed corpses (cf. Haedrich 1974, Haedrich & Henderson 1974, Percy 1976, Sedberry & Musick 1978), along with decreased

metabolic cost per unit weight and a higher nutrient storage capacity (Peters 1983), would all play an important role.

Subsequent studies carried out in other areas have shown that the described bigger-deeper phenomenon cannot be considered universal (Sulak 1982), even in highly productive seas (Merrett & Marshall 1981, Snelgrove & Haedrich 1985). It has even been suggested (Percy et al. 1982, Gordon 1986) and demonstrated by Merrett et al. (1991b) that the phenomenon is the result of sampling artefacts, given the greater difficulty larger fish experience in avoiding the sampling gear at increased depths where their metabolism is slower. The possibility that the results presented in this paper are a sampling artefact can be rejected. Of the different benthic sampling gears used in deep-sea fish studies (e.g. Gordon 1986, Merrett et al. 1991a) the OTSB14 will, if anything, tend to enhance any bigger-deeper trend in the ichthyofauna. It is obvious, therefore, that this explanation does not suffice for the Catalan Sea where the reverse trend occurs.

Within-species pattern

The basic component of the phenomenon we have been discussing can be described as a substitution of one species for another along a bathymetric gradient. We now consider the size distribution as shown by individual species. It is well known, and has often been taken as a rule (Heinke's law) by some authors (cf. Cushing 1982), that in many demersal fish species older specimens are found at greater depth. This has recently been discussed at some length by Macpherson & Duarte (1991), albeit over a restricted depth range and number of species. After an analysis of size-depth relations (maximum depth 750 m) in Namibia and the Catalan Sea they conclude that the bigger-deeper phenomenon is a common characteristic of the demersal ichthyofauna. The proposed mechanism involves an ontogenic migration to deeper waters, where the adults benefit from a reduced basal metabolic rate and increased life expectancy at lower temperatures (Love 1970, 1980). As in the Mediterranean the water temperature remains constant (ca 13°C) below 160 to 200 m (Salat & Font 1987), Macpherson & Duarte (1991) suggest that this behaviour represents an inherited evolutionary response and is, therefore, of a genetic nature.

Present results contradict this hypothesis. The lack of a specific trend below 1000 m means it is not possible to consider the idea of a bigger-deeper phenomenon as a well-established tendency. Thus, for example, none of the exclusively lower slope species (*Polyacanthonotus rissoanus*, *Bathypterois mediterraneus*, *Coryphaenoides guentheri*, *Chalinura mediterranea*) showed

any significant size-depth variation. This had been noted for *B. mediterraneus* in a previous study (Rannou & Gaborit-Rezzouk 1976). Moreover, although data for the other exclusive lower slope species (*Centrosymnus coelolepis*, *Lepidion guentheri* and *Cataetyx laticeps*) were not sufficient to allow statistical analysis, the available data indicate no particular pattern (Stefanescu et al. 1991, 1992a, Carrassón et al. 1992).

Of the 5 middle slope species which were statistically analyzed (*Alepocephalus rostratus*, *Coelorhynchus labiatus*, *Lepidion lepidion*, *Mora moro* and *Cataetyx alleni*) only *A. rostratus* and *L. lepidion* behave as bigger-deeper or smaller-shallower species.

Thus, it is evident from our results that the majority of demersal species with bathymetric ranges comprised between 1000 and 2250 m do not show any clear size-depth trend. This is particularly surprising for the macrourids *Coelorhynchus labiatus*, *Coryphaenoides guentheri* and *Chalinura mediterranea* which display a bigger-deeper trend in North Atlantic waters (Mauchline & Gordon 1984, Gordon & Duncan 1987, Merrett et al. 1991b). In the case of *Polyacanthonotus rissoanus* the results are contradictory depending on the prospected areas. Crabtree et al. (1985) did not find any relation in the western North Atlantic, but N. R. Merrett (pers. comm.) found a slight bigger-deeper trend in the Porcupine Bight (eastern North Atlantic).

Considering the relatively recent Atlantic origin of Mediterranean ichthyofauna (Fredj & Maurin 1987), and the contrasting behaviour shown in the 2 areas, we can discard the hypothesis that mean size increase with depth is a result of inherited ontogenic behaviour. This theory may have resulted from the restricted number of species (31 in the Mediterranean) and depth range investigated (20 to 750 m) (Macpherson & Duarte 1991). In fact, many of the species considered by these authors are known at depths up to, and far greater than, 1000 m (Fischer et al. 1987, Stefanescu et al. 1992b). In the light of these factors we are inclined to view any generalization of this phenomenon with reservation. We believe any further study on this subject should narrow its perspectives and centre on the autoecology of each individual species, as the complexity of links established by a species with its surrounding environment will result in highly variable and specific adaptive responses in each case, as has been indicated here.

Acknowledgements. We are grateful to N. R. Merrett (Natural History Museum, London), J. E. Cartes and F. Sardà (Institut de Ciències del Mar, Barcelona), for their comments on the manuscript. Comparative unpublished data from the North-east Atlantic were generously provided by N. R. Merrett and J. D. M. Gordon (Dunstaffnage Marine Laboratory, Oban). Susan Watt prepared the English version. This work was supported by the research program BATIMAR (CSIC-CAICYT; reference PAC 86-008/ID 821).

LITERATURE CITED

- Allué, C. (1985). Composición y estructura de la comunidad de peces demersales frente a Barcelona (Años 1980–1981). *Thalassas* 3 (1): 57–90
- Allué, C., Leonart, J., Lloris, D., Macpherson, E., Rucabado, J., Sánchez, P., Sardá, F. (1981). Campaña Mediterráneo II. Pescas de arrastre. Datos Informativos Inst. Inv. pesq. (Barcelona) 8: 115–240
- Carney, R. S., Haedrich, R. L., Rowe, G. T. (1983). Zonation of the fauna in the deep sea. In: Rowe, G. T. (ed.) *The sea*, Vol. 8, Deep-sea biology. John Wiley & Sons, New York, p. 371–398
- Carpine, C. (1970). *Ecologie de l'étage bathyal dans la Méditerranée occidentale*. Mém. Inst. océanogr. (Monaco) 2: 1–146
- Carrassón, M., Matallanas, J. (1990). Preliminary data about the feeding habits of some deep-sea Mediterranean fishes. *J. Fish. Biol.* 36: 461–463
- Carrassón, M., Stefanescu, C., Cartes, J. (1992). Diets and bathymetric distribution of two bathyal sharks of the Catalan deep sea (Western Mediterranean). *Mar. Ecol. Prog. Ser.* 82: 21–30
- Cartes, J. E. (1991). Análisis de las comunidades y estructura trófica de los crustáceos decápodos batiales del mar Catalán. Ph. D. thesis, Univ. Politècnica de Catalunya
- Clarke, M. R., Merrett, N. R. (1972). The significance of squid, whale and other remains from the stomachs of bottom-living deep-sea fishes. *J. mar. biol. Ass. U.K.* 52 (3): 599–603
- Cohen, D. M., Pawson, D. L. (1977). Observations from the DSRV ALVIN on populations of benthic fishes and selected larger invertebrates in a near Deep Water Dumpsite-106. N.O.A.A. Dumpsite Evaluation Report 77-1 2: 423–458
- Compagno, L. J. V. (1984). *FAO species catalogue*. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of sharks species known to date. Part 1. Hexanchiformes to Lamniformes. *FAO Fish. Synop.* 125
- Crabtree, R. E., Sulak, K. J. (1986). A contribution to the life history and distribution of Atlantic species of the deep-sea fish genus *Conocara* (Alepocephalidae). *Deep Sea Res.* 33 (9): 1183–1201
- Crabtree, R. E., Sulak, K. J., Musick, J. A. (1985). Biology and distribution of species of *Polyacanthonotus* (Pisces: Notacanthiformes) in the western North Atlantic. *Bull. mar. Sci.* 36 (2): 235–248
- Cushing, D. H. (1982). *Climate and fisheries*. Academic Press, London
- Dayton, P. K., Hessler, R. R. (1972). Role of biological disturbance in maintaining diversity in the deep-sea. *Deep Sea Res.* 19: 199–208
- Desbruyères, D., Geistdoerfer, P., Ingram, C. L., Khrpounoff, A., Lagardère, J. P. (1985). Répartition des populations de l'épibenthos carnivore. In: Laubier, L., Monniot, Cl. (eds.) *Peuplements profonds du golfe de Gascogne*. Ifremer, Brest, p. 233–254
- Fischer, W., Bauchot, M.-L., Schneider, M. (ed.) (1987). *Fiches FAO d'identification des espèces pour les besoins de la pêche (Révision 1). Méditerranée et Mer Noire. Zone de pêche 37 Vol. II*. FAO, Rome
- Fredj, G., Maurin, C. (1987). Les poissons dans la banque des données MEDIFAUNE. Application à l'étude des caractéristiques de la faune méditerranéenne. *Cybium* 11 (3): 219–299
- Gage, J. D. (1978). Animals in the deep sea sediments. *Proc. R. Soc. Edinb.* 76 (B): 77–93
- Geistdoerfer, P. (1986). Family Macrouridae. In: Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E. (eds.) *Fishes of the North-eastern Atlantic and the Mediterranean*, Vol. 2. UNESCO, Bungay, p. 644–676
- Geistdoerfer, P., Rannou, M. (1971). A propos des *Chalinura* méditerranéens (Téléostéens, Macrouridae). *Bull. Mus. natn. Hist. nat., Paris, 2ème sér.* 42 (5) (1970): 1009–1018
- Geistdoerfer, P., Rannou, M. (1972). Poissons benthiques récoltés en Méditerranée occidentale par le N.O. 'Jean Charcot' (campagne Polymède). *Bull. Mus. natn. Hist. nat., Paris, 3ème sér.* 25: 101–110
- Gordon, J. D. M. (1979). Lifestyle and phenology in deep sea anacanthine teleosts. *Symp. zool. Soc. Lond.* 44: 327–359
- Gordon, J. D. M. (1986). The fish populations of the Rockall Trough. *Proc. R. Soc. Edinb.* 88 (B): 191–204
- Gordon, J. D. M., Duncan, J. A. R. (1985). The biology of fish of the family Moridae in the deep water of the Rockall Trough. *J. mar. biol. Ass. U.K.* 65: 475–485
- Gordon, J. D. M., Duncan, J. A. R. (1987). Deep-sea bottom-living fishes at two repeat stations at 2200 and 2900 m in the Rockall Trough, northeastern Atlantic Ocean. *Mar. Biol.* 96 (3): 309–325
- Grassle, J. F., Sanders, H. L., Hessler, R. R., Rowe, G. T., McLellan, T. (1975). Pattern and zonation – a study of the bathyal megafauna using the research submersible ALVIN. *Deep Sea Res.* 22: 457–481
- Haedrich, R. L. (1974). Pelagic capture of the epibenthic rattail *Coryphaenoides rupestris*. *Deep Sea Res.* 21: 977–979
- Haedrich, R. L., Henderson, N. R. (1974). Pelagic food for *Coryphaenoides armatus*, a deep benthic rattail. *Deep Sea Res.* 21: 739–744
- Haedrich, R. L., Merrett, N. R. (1988). Summary atlas of deep-living demersal fishes in the North Atlantic Basin. *J. nat. Hist.* 22: 1325–1362
- Haedrich, R. L., Rowe, G. T. (1977). Megafaunal biomass in the deep-sea. *Nature, Lond.* 269: 141–142
- Haedrich, R. L., Rowe, G. T., Polloni, P. T. (1980). The megabenthic fauna in the deep-sea south of New England, USA. *Mar. Biol.* 57: 165–179
- Hureau, J.-C., Geistdoerfer, P., Rannou, M. (1979). The ecology of deep-sea benthic fishes. *Sarsia* 64 (1–2): 103–109
- Jumars, P. A., Gallagher, E. (1982). Deep-sea community structure: three plays on the benthic proscenium. In: Ernst, W. G., Morin, J. G. (eds.) *The environment of the deep sea*. Prentice-Hall, New Jersey, p. 217–255
- Lindsey, C. C. (1966). Body sizes of poikilotherm invertebrates at different latitudes. *Evolution* 20: 456–465
- Love, R. M. (1970). *The chemical biology of fishes*. Academic Press, London
- Love, R. M. (1980). *The chemical biology of fishes*. Vol. 2: *Advances 1968–1977*. Academic Press, London
- Macpherson, E. (1977). Estudio sobre las relaciones tróficas en peces bentónicos de la costa catalana. Ph. D. thesis, Univ. Barcelona
- Macpherson, E., Duarte, C. M. (1991). Bathymetric trends in demersal fish size: is there a general relationship? *Mar. Ecol. Prog. Ser.* 71: 103–112
- Mahaut, M.-L., Geistdoerfer, P., Sibuet, M. (1990). Trophic strategies in carnivorous fishes: their significance in energy transfer in the deep-sea benthic ecosystem (Meriadzeck Terrace – Bay of Biscay). *Prog. Oceanogr.* 24: 223–237
- Margalef, R. (1982). *Ecología*. Omega, Barcelona
- Matallanas, J. (1979). Contribución al estudio de la ictiofauna de la zona explotada por las barcas de pesca de Blanes (Mar Catalana). *Bol. Soc. Hist. Nat. Baleares* 23: 127–145
- Matallanas, J. (1983). Primera captura de *Cataetys alleni*

- (Byrne, 1906) (Pisces, Bythitidae) en el Mediterráneo español. *Inv. pesq.* 47 (3): 413–418
- Mauchline, J., Gordon, J. D. M. (1983). Diets of the sharks and chimaeroids of the Rockall Trough, northeastern Ocean. *Mar. Biol.* 75: 269–278
- Mauchline, J., Gordon, J. D. M. (1984). Diets and bathymetric distribution of the macrourid fish of the Rockall Trough, north eastern Atlantic Ocean. *Mar. Biol.* 81: 107–121
- Maurin, C. (1962). Etude des fonds chalutables de la Méditerranée occidentale (Ecologie et Pêche). Résultats des campagnes des navires océanographiques 'Président Théodore-Tissier', 1957 à 1960, et 'Thalassa', 1960 et 1961. *Rev. Trav. Inst. Pech. marit.* 26 (2): 163–218
- McDowell, S. B. (1973). Order Heteromi (Notacanthiformes). *Mem. Sears Fdn mar. Res.* 1 (6): 1–228
- Merrett, N. R. (1987). A zone of faunal change in assemblages of abyssal demersal fish in the eastern north Atlantic: a response to seasonality in production? *Biol. Oceanogr.* 5: 137–151
- Merrett, N. R., Marshall, N. B. (1981). Observations on the ecology of deep-sea bottom living fishes collected northwest Africa (08°–27°N). *Prog. Oceanogr.* 9: 185–244
- Merrett, N. R., Domanski, P. A. (1985). Observations on the ecology of deep-sea bottom living fishes collected off northwest Africa: II. The Moroccan slope (27–34°N), with special reference to *Synaphobranchus kaupii*. *Biol. Oceanogr.* 3 (4): 349–399
- Merrett, N. R., Gordon, J. D. M., Stehmann, M., Haedrich, R. L. (1991a). Deep demersal fish assemblage structure in the Porcupine Seabight (eastern north Atlantic): slope sampling by three different trawls compared. *J. mar. biol. Ass. U.K.* 71: 329–358
- Merrett, N. R., Haedrich, R. L., Gordon, J. D. M., Stehmann, M. (1991b). Deep demersal fish assemblage structure in the Porcupine Seabight (eastern north Atlantic): results of single warp trawling at lower slope to abyssal soundings. *J. mar. biol. Ass. U.K.* 71: 359–373
- Middleton, R. W., Musick, J. (1986). The abundance and distribution of the family Macrouridae (Pisces: Gadiformes). *Fish Bull. U.S.* 84 (1): 35–62
- Morales-Nin, B. (1990). A first attempt at determining growth patterns of some Mediterranean deep-sea fishes. *Scient. Mar.* 54 (3): 241–248
- Pearcy, W. G. (1976). Pelagic capture of abyssobenthic macrourid fish. *Deep Sea Res.* 23: 1065–1066
- Pearcy, W. G., Stein, D. L., Carney, R. S. (1982). The deep-sea benthic fish fauna of the northeastern Pacific Ocean on Cascadian and Tufts Abyssal Plains and adjoining continental slopes. *Biol. Oceanogr.* 1: 375–428
- Pérès, J. M. (1985). History of the Mediterranean biota and the colonization of the depths. In: Margalef, R. (ed.) *Key environments. Western Mediterranean*. Pergamon Press, Oxford, p. 198–233
- Peters, R. H. (1983). *The ecological implications of body size*. Cambridge University Press, Cambridge
- Polloni, P., Haedrich, R. L., Rowe, G., Clifford, C. H. (1979). The size-depth relationship in deep ocean animals. *Int. Revue ges. Hydrobiol.* 64 (1): 39–46
- Raimbault, R. (1963). Notes sur certains espèces ichtyologiques capturées au cours des campagnes de l'Institut des Pêches en Méditerranée (1957–1961). *Rev. Trav. Inst. Pech. marit.* 27 (1): 161–171
- Rannou, M., Gaborit-Rezzouk, M. (1976). Contribution à l'étude des Bathypteroidae (Pisces: Iniomi) de l'Atlantique et de la Méditerranée. *Bull. Mus. natn. Hist. nat., Paris*, 3ème sér., (375), *Zool.* 263: 453–466
- Roule, L. (1912). Notice sur les Sélacies conservés dans les collections du Musée Océanographique. *Bull. Inst. océanogr.* 243: 36 pp.
- Salat, J., Font, J. (1987). Water mass structure near and offshore the Catalan coast during the winters of 1982 and 1983. *Ann. Geophys.* 198 (5B): 49–54
- Sedberry, G. R., Musick, J. A. (1978). Feeding strategies of some demersal fishes of the continental slope and rise off the mid-Atlantic coast of the USA. *Mar. Biol.* 44: 357–375
- Snelgrove, P. V. R., Haedrich, R. L. (1985). Structure of the deep demersal fish fauna off Newfoundland. *Mar. Ecol. Prog. Ser.* 27: 99–107
- Sokolova, N. N. (1990). On size of the deep-sea macrobenthic invertebrates. *Prog. Oceanogr.* 24: 251–252
- Stefanescu, C., Lloris, D., Rucabado, J. (1991). A propos de la présence de *Lepidion guentheri* (Giglioli, 1880) (Moridae) en Méditerranée occidentale ibérique. *Cybium* 15 (2): 139–146
- Stefanescu, C., Lloris, D., Rucabado, J. (1992a). Primeras citas de *Cataetx laticeps* (Osteichthyes: Bythitidae) y *Dysomma brevirostre* (Osteichthyes: Synaphobranchidae) en el mar Catalán (Mediterráneo Ibérico). *Misc. zool.* 14: 135–143
- Stefanescu, C., Lloris, D., Rucabado, J. (1992b). Deep-living demersal fishes in the Catalan Sea (Western Mediterranean) below a depth of 1000 m. *J. nat. Hist.* 26: in press
- Sulak, K. J. (1982). A comparative taxonomic and ecological analysis of temperate and tropical demersal deep-sea fish faunas in the Western North Atlantic. Ph.D. thesis, University of Miami
- Sulak, K. J., Crabtree, R. E., Hureau, J.-C. (1984). Provisional review of the genus *Polyacanthonotus* (Pisces, Notacanthidae) with description of a new atlantic species, *Polyacanthonotus merretti*. *Cybium* 8 (4): 57–68
- Thiel, H. (1975). The size structure of the deep-sea benthos. *Int. Rev. ges. Hydrobiol.* 60: 575–606
- Thiel, H. (1979). Structural aspects of the deep-sea benthos. *Ambio Spec. Rep.* 6: 25–31
- Thiel, H. (1983). Meiobenthos and nanobenthos of the deep sea. In: Rowe, G. T. (ed.) *The sea*. Vol. 8, Deep-sea biology. John Wiley & Sons, New York, p. 167–230
- Tortonese, E. (1960). General remarks on the Mediterranean deep-sea fishes. *Bull. Inst. océanogr.* 1167: 14 pp.

This article was submitted to the editor

Manuscript first received: October 21, 1991

Accepted: February 11, 1992