

Relationship between size and depth in decapod crustacean populations on the deep slope in the Western Mediterranean

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Abstract—The size distribution of decapod crustaceans in relation to depth between 900 and 2200 m on the slope in the Catalan Sea (Western Mediterranean) was analysed in a series of four surveys carried out in 1988–1989. Regression analysis and multivariate cluster analysis were applied to data matrices relating size frequency to depth for each species. The results indicated a tendency for size to decrease significantly with depth in the most abundant species in the decapod communities studied (*Aristeus antennatus*, *Acantheephyra eximia*, *Pontophilus norvegicus* and *Polycheles typhlops*). Mean weight calculated for all the species combined also decreased significantly with depth. In addition, major changes in size frequency structure were observed at around 1400 and 2000 m for certain species, coinciding with the results for community structure in the same zone. Trophic aspects would appear to be an important cause of these phenomena for deep-water decapods in the Mediterranean.

INTRODUCTION

RELATIVELY few studies have been carried out concerning the size frequency structure of deep-water marine fauna, particularly in decapod crustacean species. The basic literature deals with the community structure and distribution of biomass of various megafaunal groups (ROWE and MENZIES, 1969; GRASSLE *et al.*, 1977; HAEDRICH and ROWE, 1977; POLLONI *et al.*, 1979; WENNER and BOESCH, 1979; HAEDRICH *et al.*, 1980; MERRETT and MARSHALL, 1981; SMITH and HAMILTON, 1983; LAMPITT *et al.*, 1986; MARKLE *et al.*, 1988). The size–depth phenomenon has been studied mainly in fishes (HAEDRICH *et al.*, 1980; SNELGROVE and HAEDRICH, 1985; GORDON and DUNCAN, 1987; MACPHERSON and DUARTE, 1991; STEFANESCU *et al.*, 1992; and others) and to a lesser extent in other mega and macrobenthic groups (JONES, 1969; THIEL, 1975; POLLONI *et al.*, 1979; REX, 1979).

The literature contains practically no information of the size–depth relations for decapod crustaceans. Changes in the structure of deep-sea communities are conditioned by such physicochemical limiting factors as light, temperature, pressure, sediment type, bottom topography, currents, and distribution of water masses, all of which exert a direct influence on the distribution and intensity of other biological parameters such as organic matter content and detritus in the bottom sediment (SOKOLOVA, 1972), and on the distribution of energy and trophic relationships (ROWE and MENZIES, 1969; REX, 1973, 1977; SOMERO, 1978; HAEDRICH *et al.*, 1980; CHILDRESS *et al.*, 1990). The primary objective of this work has been to establish the possible causes responsible for changes in deep-sea

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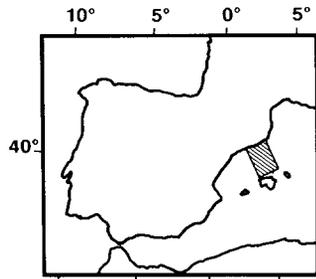


Fig. 1. Map of the study area.

communities. The next step would be to analyse to what extent these various aspects influence biological factors, such as size, in deep-water species. A number of authors (THIEL, 1973; POLLONI *et al.*, 1979; REX, 1979; SMITH and HAMILTON, 1983; THIEL, 1983; and others) have attempted to explain the causes underlying the size–depth relationship, scarcity of food being the most commonly proposed cause.

Different aspects of decapod crustacean fauna and community structure have been studied in the Western Mediterranean (ABELLÓ *et al.*, 1988; ABELLÓ and VALLADARES, 1988; CARTES, 1991). CARTES and SARDÀ (1993) detected changes in decapod communities at around 1300 m and 2000 m and identified species that, because of their broad depth distribution ranges, might be suitable targets for studying depth-related differences in population structure.

The object of the present paper is to analyse and discuss the relationship between size and depth of decapod crustacean species that occupy broad depth distributions below 1000 m in the Western Mediterranean, and also to detect possible changes in the size distributions of such species.

MATERIALS AND METHODS

Samples were collected by the research trawler *García del Cid* (38 m in length, 1500 HP) using an OTSB-14 type bottom trawl (MERRETT and MARSHALL, 1981). The sampling area was located between the coast of Catalonia and the Balearic Islands (Fig. 1, Table 1), where maximum depth reaches nearly 2300 m.

Based on the distribution and abundance of decapod crustaceans collected in the samples, the following species were selected for study: the aristeid *Aristeus antennatus* (Risso, 1816); the carideans *Acantheephyra eximia* S. I. Smith, 1884, *Nematocarcinus exilis* (Bate, 1888), *Plesionika acanthonotus* (S. I. Smith, 1880) and *Pontophilus norvegicus* (M. Sars, 1861); the polychelids *Polycheles typhlops* Heller, 1862 and *Stereomastix sculpta* (S. I. Smith, 1880); the galatheid anomuran *Munida tenuimana* G. O. Sars, 1872; and the geryonid brachyuran *Geryon longipes* A. Milne Edwards, 1881. All specimens examined were in either benthic or suprabenthic stages (adults and juveniles). No information is available on deep-sea decapod larvae and post-larvae in the area.

For all these species, carapace length (CL, in mm) was measured from the orbit of the eye to the posterior margin of the cephalothorax, and sex was recorded. The data employed were absolute values by 200-m depth stratum between the 1000- and 2200-m isobaths. All the samples were collected during a series of four surveys carried out in the

Table 1. Location and depth of trawls

Date	Depth (initial–final)	Location	
25/06/88	1823–1773	40°26.7'N	2°00.4'E
26/06/88	2163–2039	40°45.4'N	3°09.7'E
26/06/88	2266–2239	40°37.2'N	3°38.0'E
27/06/88	1857–1819	40°28.9'N	2°42.0'E
27/06/88	1621–1539	40°06.1'N	2°51.2'E
28/06/88	1737–1720	40°18.2'N	2°59.9'E
30/06/88	2211–2193	40°35.8'N	3°32.3'E
02/07/88	1520–1429	40°58.4'N	2°24.2'E
02/07/88	1680–1574	40°52.6'N	2°23.9'E
03/07/88	1011– 946	40°48.9'N	1°35.7'E
04/07/88	1249–1193	40°49.2'N	1°50.9'E
04/07/88	1434–1319	40°43.2'N	1°44.6'E
04/07/88	1753–1779	40°38.6'N	2°06.0'E
05/07/88	1827–1883	40°31.9'N	2°16.0'E
05/07/88	1772–1899	40°17.2'N	2°07.2'E
06/07/88	1735–1680	40°13.2'N	2°25.6'E
06/07/88	1631–1578	40°05.8'N	2°04.9'E
06/07/88	1439–1394	40°02.9'N	2°14.3'E
07/07/88	980–1019	39°52.8'N	2°24.3'E
07/07/88	1224–1184	39°57.5'N	2°18.1'E
08/07/88	1752–1737	40°19.9'N	1°53.3'E
10/07/88	1069–1062	41°11.1'N	2°32.1'E
11/07/88	1927–1820	40°20.2'N	2°43.6'E
26/07/88	1029– 908	41°22.4'N	3°11.6'E
26/07/88	2107–1941	41°13.5'N	3°23.4'E
27/07/88	2188–2156	41°05.3'N	3°21.2'E
28/07/88	2071–1880	40°56.7'N	3°00.7'E
28/07/88	1900–1746	41°12.6'N	3°07.5'E
29/07/88	2221–2196	41°11.2'N	3°36.9'E
29/07/88	1916–1762	41°06.5'N	2°59.4'E
30/07/88	1816–1796	40°49.6'N	2°32.5'E
30/07/88	1284–1246	40°52.6'N	2°03.1'E
31/07/88	1531–1446	40°59.3'N	2°26.4'E
31/07/88	1358–1247	41°06.0'N	2°32.6'E
25/10/88	1609–1562	40°20.5'N	1°42.5'E
25/10/88	1779–1744	40°28.5'N	1°58.4'E
26/10/88	1100–1054	39°54.5'N	2°21.6'E
26/10/88	1800–1694	40°09.4'N	1°59.0'E
27/10/88	1754–1698	40°19.3'N	1°53.3'E
27/10/88	1680–1575	40°30.7'N	1°47.6'E
27/10/88	1234–1196	40°39.4'N	1°36.4'E
27/10/88	1014–1004	40°50.6'N	1°44.1'E
28/10/88	1036– 994	40°53.3'N	1°44.6'E
28/10/88	961–1087	40°59.5'N	1°58.5'E
28/10/88	1158–1034	40°56.2'N	2°06.5'E
29/10/88	1110–1035	41°01.2'N	2°13.2'E
29/10/88	1120–1008	41°04.2'N	2°20.2'E
29/10/88	861–1100	41°07.5'N	2°27.3'E
29/10/88	1524–1479	41°02.9'N	2°35.9'E
30/10/88	1795–1740	41°04.1'N	2°53.4'E
16/10/89	862– 989	40°49.8'N	1°33.8'E
17/10/89	1772–1808	40°25.8'N	1°59.8'E
18/10/89	1478–1547	40°12.1'N	1°39.7'E

same season (summer–autumn). Each survey sampling covered depth intervals ranging from 900 to 2200 m (Table 1).

The relationship between mean size and depth was analysed using linear regression for each species individually (following logarithmic transformation). Regression also was applied to analyse the relationship between mean weight (biomass in g/no. of individuals) and depth, by sample. The size frequency distribution by depth interval was established for each species. For analysis of the size associations, a data matrix presenting the values for the variables size frequency and depth was constructed for each of the selected species. Size frequency values in the matrices were grouped by 2-mm size interval. Multivariate cluster analysis was applied to each data matrix after standardization to number of individuals per sample and log transformation of the values, and the linear correlation coefficient was employed as the quantitative index of association using the UPGMA aggregation algorithm. Only data for species abundant along broad depth distributions (*A. antennatus*, *A. eximia*, *N. exilis*, *P. norvegicus*, *M. tenuimana* and *S. sculpta*) were considered. *P. acanthonotus*, *P. typhlops* and *G. longipes* were only abundant in a narrow depth range between 900 and 1300 m (CARTES, 1991) and therefore were excluded from the cluster analysis. Males and females were considered together except for *A. antennatus*, in which size-related sexual dimorphism is pronounced and both sexes are abundant in samples.

The sex ratio (males:females) was calculated for *A. antennatus*, *A. eximia*, *N. exilis*, *P. typhlops*, *S. sculpta* and *M. tenuimana* within each depth interval, to see if size variations with depth are related with sex ratio changes. To test sex-ratio results for each species, a G-test of samples proportion heterogeneity (SOKAL and ROHLF, 1979) was applied. The sex ratios were not calculated for the other species attending to different particular aspects. Thus, in *P. norvegicus* nearly all the collected specimens were females, whereas in *G. longipes* males were highly predominant. *P. acanthonotus* was abundant only within a narrow depth range.

RESULTS

Figure 2 depicts the size frequencies for each species over the depth range considered. The modal size shifted towards the smaller sizes with depth in *Aristeus antennatus*, *Acantheephyra eximia*, *Pontophilus norvegicus* and *Polycheles typhlops*. Size frequency of *Munida tenuimana* also decreased below 1400 m. The slopes of the regression lines for the mean size of *A. eximia*, *A. antennatus*, *P. typhlops* and *P. norvegicus* versus depth were significantly non-zero. In these species (half of the species considered) mean size tended to decrease with depth (Table 2). *M. tenuimana* followed an opposite trend, mean size increasing from 1000 to 1400 m and then decreasing down to 1900 m (Fig. 4). A similar situation occurred for *P. norvegicus* (Fig. 4). Between 1000 and 1400 m, large individuals predominated for both *A. eximia* and *A. antennatus*. Below 1400 m, the few *P. typhlops* specimens were almost exclusively immature individuals. In summary, size differences were accentuated in those species with the broadest depth distributions (*A. antennatus*, *A. eximia*, *P. typhlops*). In these latter species, the general pattern involved a reduction in mean size with depth.

Cluster analysis (Fig. 3A, B) also reflected a decreasing size trend with depth for *A. eximia* and *A. antennatus* (males and females). In both these species there was a discontinuity in the size associations near 1400 m (Fig. 3A); a second discontinuity

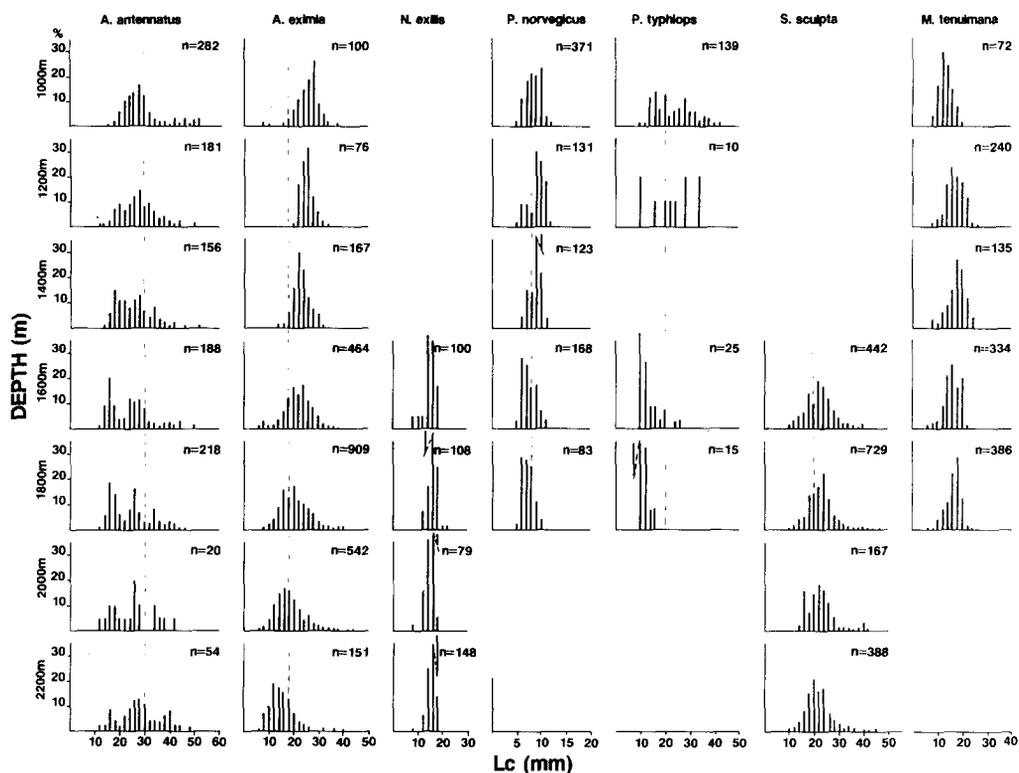


Fig. 2. Size frequencies by species on depth. *n*: number of individuals.

Table 2. Parameters for the regression of mean size on depth by species. *r*: size–depth correlation coefficient (*c.c.*) (+: significant *c.c.*, $P < 0.05$; *: significant *c.c.*, $P < 0.01$; -: non-significant *c.c.*, $P > 0.05$); *a*: y-intercept; *b*: slope; *d.f.*: degrees of freedom; *n*: total number of individuals

Species	<i>r</i>	Depth range (m)	<i>b</i>	<i>a</i>	<i>d.f.</i>	<i>n</i>
<i>A. antennatus</i>	0.40+	969–2209	–0.0045	32.85	32	1099
<i>A. eximia</i>	0.81*	969–2253	–0.0076	34.09	38	2409
<i>N. exilis</i>	0.24–	1586–2253	–0.0010	17.06	11	435
<i>P. acanthonotus</i>	0.39–	926–1265	0.0037	9.74	12	311
<i>P. norvegicus</i>	0.48+	979–1874	–0.0012	10.17	18	876
<i>P. typhlops</i>	0.87*	926–1874	–0.0186	44.05	12	189
<i>S. sculpta</i>	0.07–	1489–2253	0.0007	20.80	28	1726
<i>M. tenuimana</i>	0.48*	926–1839	0.0028	11.37	32	1167
<i>G. longipes</i>	0.10–	926–1642	–0.0029	49.73	9	127
Mean weight	0.52*	926–2253	–0.0058	13.93	46	8339

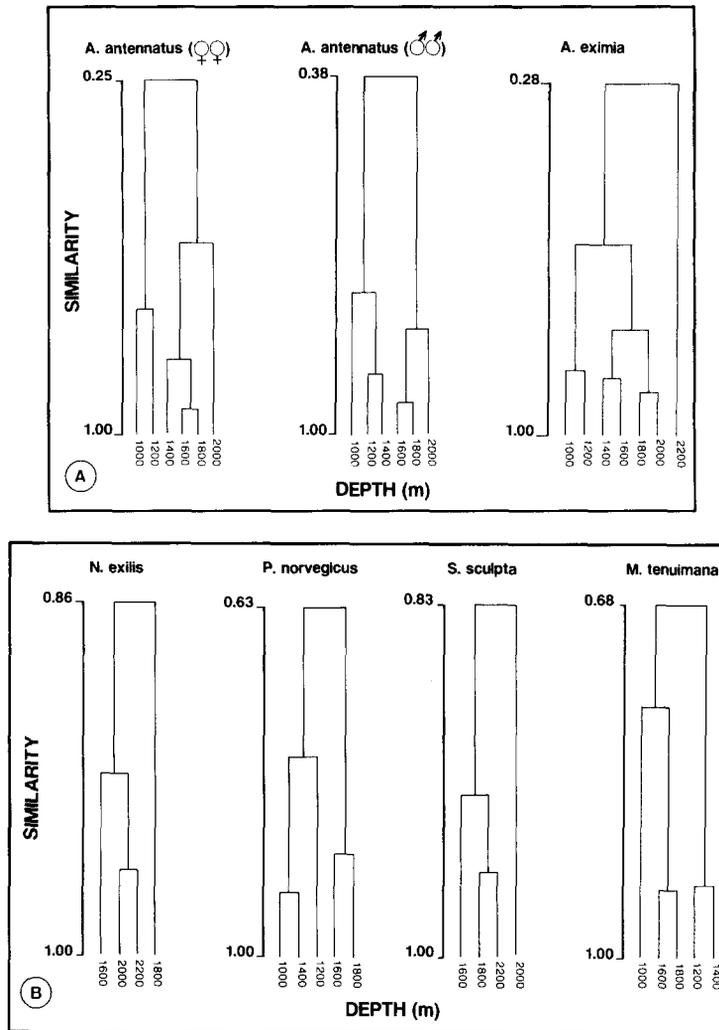


Fig. 3. Diagrams for the cluster analysis by depth (linear correlation—UPGMA).

occurred in the deepest depth interval at around 2000 m. In *M. tenuimana* and *P. norvegicus* the size trend was reversed in various depth intervals (Fig. 3B), which is attributable to the two opposing trends in the size–depth relationship in these two species referred to above. A reversal in the size–depth relationship took place in the 1200 to 1400 m depth stratum (Fig. 4). The cluster analysis did not disclose any clear trend for *N. exilis* and *S. sculpta*.

A reduction in mean weight (biomass) was recorded with depth for all the combined species (Fig. 5), which agrees with the results for decapod crustaceans reported by POLLONI *et al.* (1979).

Non-significant differences ($P > 0.001$) were observed on sex-ratio values when depth increased (G-test of homogeneity) for *Nematocarcinus exilis*, *Polycheles typhlops*, *Stereomastis sculpta* and *Munida tenuimana* (Fig. 6), whereas *Aristeus antennatus* and *Acanthe-*

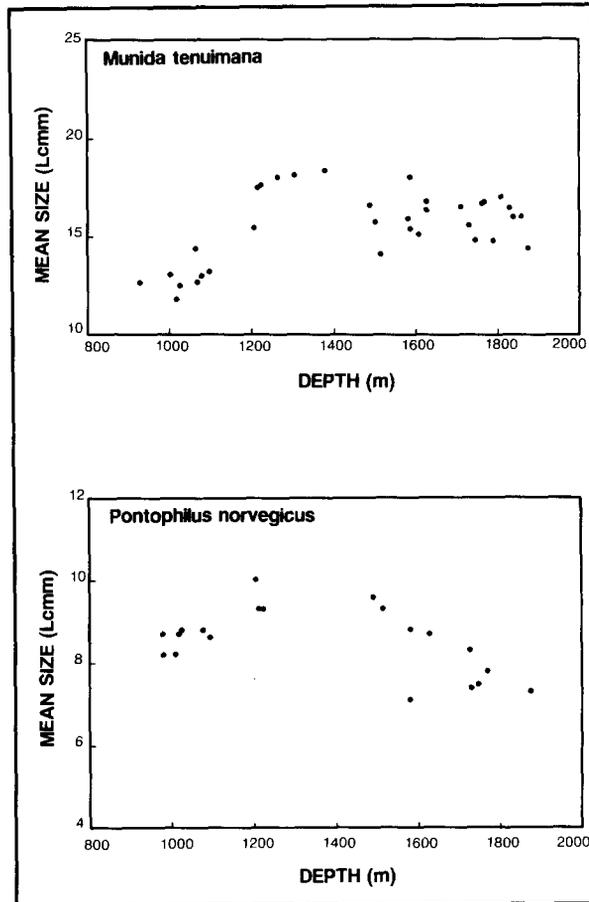


Fig. 4. Relationship between mean size and depth in *Munida tenuimana* and *Pontophilus norvegicus*.

phyra eximia presented significant differences ($P < 0.001$). In *A. eximia* a G-test of goodness fit to sex-ratio proportion of 2:3 was applied, and no significant differences ($P > 0.001$) were found. In *A. antennatus*, data were presented separately by sexes because of the sexual dimorphism and differences in sex ratio recorded with depth. Variations observed in depth–size relations therefore are not attributable to changes in sex-ratio values with depth.

DISCUSSION

Considerable efforts have been made to elucidate the structure of deep-water communities (ROWE and MENZIES, 1969; HAEDRICH *et al.*, 1975, 1980; WENNER and BOESCH, 1979; STEFANESCU, 1993; and others). Most of these authors agree that major ecological boundaries occur within the depth range considered in the present study, at between 1200 and 1400 m and then again between 1900 and 2000 m. This finding appears to be common to several regions in different seas. Recent results obtained for the Western Mediterra-

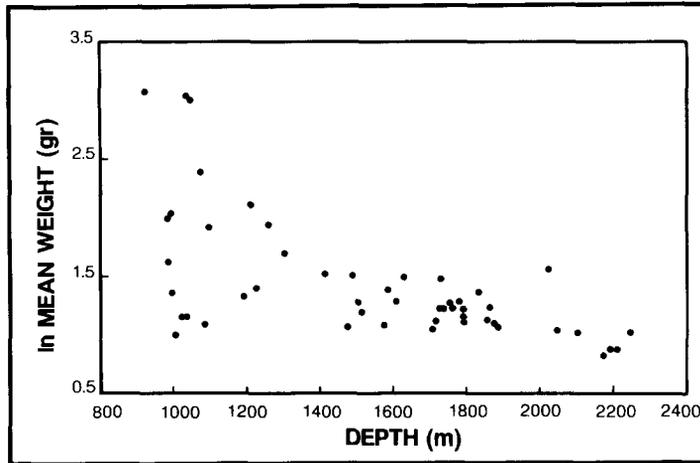


Fig. 5. Relationship between mean weight and depth.

near Sea are in agreement with respect to the first boundary in the case of fish communities (STEFANESCU *et al.* 1993) and both boundaries in the case of decapod crustaceans (CARTES and SARDÀ, 1993). These findings coincide with the downward trend in mean size of the dominant species in deep-sea bathyal decapod communities with depth and the existence of distinct boundaries shared by certain species.

The most interesting questions focus on which factors are actually responsible for these boundaries and how they affect different species. The commonly accepted cause is that

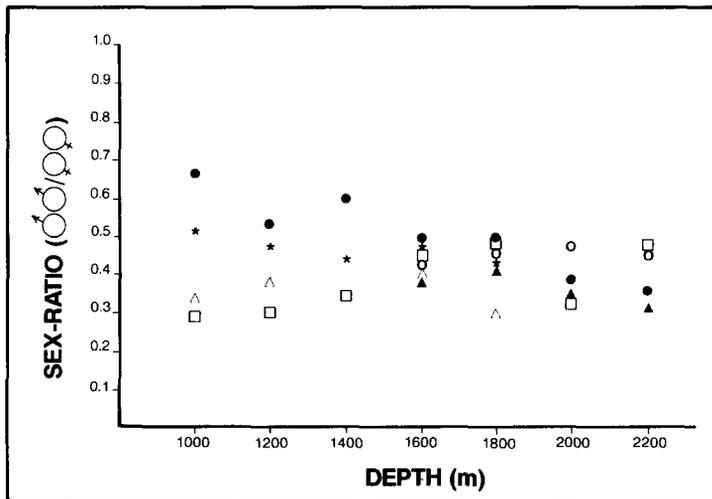


Fig. 6. Sex ratio for the main species considered (● = *A. antennatus*; □ = *A. eximia*; ▲ = *N. exilis*; △ = *P. typhlops*; ○ = *S. sculpta*; ★ = *M. tenuimana*).

food availability, coupled with how species exploit existing food resources and patterns of energy distribution with their overall life strategies, is responsible for the size distribution within a given habitat (ROWE, 1971; HESSLER and JUMARS, 1974; THIEL, 1975, 1979; CAREY, 1981). Since the overall structure of communities changes with depth, it seems logical to expect the internal structure of the distributions of species to be affected as well. Certain species of decapod crustaceans would appear to be ideally suited for proving such an hypothesis because they are readily captured and hence are good sources of data for the requisite calculations, inasmuch as, theoretically, they are less mobile than fish and their diet consists largely of infauna or epifauna (LAGARDÈRE, 1977; CARTES and SARDÀ, 1989; CARTES, 1991). CARTES (1991) also reported differences in the composition of the diet of such species within these same depth intervals. Thus, the ecological changes taking place with depth should be directly reflected in specific aspects of population structure.

Most size–depth relationship studies on decapods have been limited to relatively shallow-dwelling species, such as *Parapandalus narval* (THESSALOU-LEGAKI *et al.*, 1989) and *Parapenaeus longirostris* (ARDIZZONE *et al.*, 1990). The mean size of these species increases with depth. This change has been associated with evidence of migrations in *P. longirostris*. However, below 1000 m environmental conditions are completely different. THIEL (1975) suggested that, from a metabolic standpoint, smaller size would be more profitable at greater depths, where food resources are less plentiful in the meio- and macrobenthos. CHILDRESS *et al.* (1990) reported a relationship between decapod crustacean metabolism and depth in the Pacific, noting that metabolic rates decrease as temperature decreases, and hence with depth. However, in the Mediterranean temperature remains constant at around 13°C below about 200 m (HOPKINS, 1985), indicating that this hypothesis is not applicable in our case.

No information is available on deep-sea decapod larvae in the Mediterranean Sea. The larvae of the deep-sea species considered in this paper are not present in the neritic zone (FUSTER, 1987). Migration to shallower depths for reproduction has been suggested only for *Polycheles typhlops* (ABELLÓ and CARTES, 1992), though the smallest immature individuals were collected on the slope. In the other deep-sea species considered, mature females (Panaeoidea) or ovigerous females were collected in all depth strata between 900 and 2200 m (unpublished data). Consequently, a generalized pattern of migrations for reproductive purposes appears unlikely. Recruitment thus probably takes place throughout the entire sampling area on the slope for all the species considered. However, the samples in the present study were collected during a specific time of year, and hence only inferences can be drawn with respect to these questions.

The factors affecting the size frequency distributions of individual species may differ substantially, probably in response to different biological or metabolic processes (absolute growth, moult frequency, moult increment, spawning cycle and spawning synchronism, incubation or shedding of eggs, etc.). However, the most common trend recorded for deep-sea decapods in the Western Mediterranean (decreasing mean size with depth) is, in the authors' opinion, related to trophic aspects, as suggested by other researchers (THIEL, 1975; REX, 1979). In this respect, ROWE (1983), THIEL (1983) and JUMARS and GALLAGHER (1982) have pointed out the quantitative decrease in the macrobenthos over the entire slope with increasing depth. PÉRÈS (1985) reported a similar trend in the Mediterranean. In addition, CHARDY *et al.* (1973), JUMARS and GALLAGHER (1982), PÉRÈS (1985) and SOKOLOVA (1990) recorded a general decrease in the size of the macrobenthos with increasing depth. In our study area, CARTES (1991) also recorded a decrease in the trophic

resources in the endobenthic macrofauna and the macroplankton (euphausiids and mesopelagic fishes) from 1300 to 1400 m. Such factors cause species to alter their feeding strategies. Crustaceans feed primarily on the infauna and epifauna; in other words, a substantial portion of their diet is based on organisms that dwell directly in or on the substrate and are subject to horizontal transport through the food chain (CAREY, 1981; SMITH and HAMILTON, 1983; LAMPITT *et al.*, 1986).

Another possible factor to be considered is trophic pressure exerted by other megabenthic groups (fishes, cephalopods) in their capacity as predators on decapod crustaceans. Accepting the hypothesis that recruitment takes place over the entire slope, smaller individuals would benefit from lower trophic pressure at greater depths (lower slope below 1300–1400 m). In this respect STEFANESCU *et al.* (1993) point out that in the Mediterranean the diversity of fish species, potential predators on crustaceans, declines with depth, which in turn favours the survival of the smaller size groups of decapod crustaceans at greater depths. Dominant fish species on the lower slope are small in size and prey mainly on copepods and peracarid crustaceans (CARRASSON and MATALLANAS, 1990; STEFANESCU and CARTES, 1992).

In conclusion, a series of biological factors may be regarded as common to certain decapod crustaceans in relation to depth in the Western Mediterranean. Thus, the mean size of most of the decapod crustacean species with broad depth distributions decreases over the 900–2000 m depth range. Certain of these species may form associations based on their size frequency distributions with depth, thereby giving rise to groups whose distributions in turn conform closely to the boundaries separating bathyal communities reported in the same area. Such variations in size cannot be considered an effect of sexual dimorphism or sex-ratio variations. In our opinion, various trophic aspects would seem to be determining factors both for the distribution pattern and zonation as well as for the decreases in the size range observed in the internal structure of the decapod crustacean populations in the Western Mediterranean.

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REFERENCES

- ABELLÓ P. and F. J. VALLADARES (1988) Bathyal decapod crustaceans of the Catalan Sea (northwestern Mediterranean). *Mesogee*, **48**, 97–102.
- ABELLÓ P., F. J. VALLADARES and A. CASTELLÓN (1988) analysis of the structure of decapod crustacean assemblages of the Catalan coast (North-West Mediterranean). *Marine Biology*, **98**, 39–49.
- ABELLÓ P. and J. E. CARTES (1992) Population characteristics of the deep-sea lobsters *Polycheles typhlops* and *Stereomastis sculpta* (Decapoda: Polychelidae) in a bathyal mud community of the Mediterranean Sea. *Marine Biology*, **114**, 109–117.
- ARDIZZONE G. D., M. F. GRAVINA, A. BELLUSCIO and P. SCHINTU (1990) Depth–size distribution pattern of *Parapenaeus longirostris* (Lucas 1846) (Decapoda) in the Central Mediterranean Sea. *Journal of Crustacean Biology*, **10**, 139–147.

- CAREY A. G. (1981) A comparison of benthic infaunal abundance on two abyssal plains in the Northeast Pacific Ocean. *Deep-Sea Research*, **28**, 467–479.
- CARRASSON M. and J. MATALLANAS (1990) Preliminary data about the feeding habits of some deep-sea mediterranean fishes. *Journal of Fish Biology*, **36**, 461–463.
- CARTES J. (1991) Análisis de las comunidades y estructura trófica de los crustáceos decápodos batiales del Mar Catalán. Tesis Doctoral, Universidad Politécnica de Barcelona, 627 pp.
- CARTES J. E. and F. SARDÀ (1989) Feeding ecology of the deep-water aristeid crustaceans *Aristeus antennatus*. *Marine Ecology Progress Series*, **54**, 229–238.
- CARTES J. E. and F. SARDÀ (1993) Patterns of zonation of the deep-sea decapod fauna in the Catalan Sea (Western Mediterranean). *Marine Ecology Progress Series*, **94**, 27–34.
- CHILDRESS J. J., D. L. COWLES, J. A. FAVUZZI and T. J. MICKEL (1990) Metabolic rates of benthic deep-sea decapod crustaceans decline with increasing depth primarily due to the decline in temperature. *Deep-Sea Research*, **37**, 929–949.
- DAILEY M. D. and S. RALSTON (1986) Aspects of the reproductive biology, spatial distribution, growth, and mortality of the deepwater Caridean shrimp, *Heterocarpus laevigatus*, in Hawaii. *Fishery Bulletin*, **84**, 915–933.
- EITNER R. J. and M. A. REX (1990) Population differentiation decreases with depth in deep-sea gastropods. *Deep-Sea Research*, **37**, 1251–1261.
- FASHAM M. J. R. and P. FOXTON (1979) Zonal distribution of pelagic Decapoda (Crustacea: Natantia) in the Eastern North Atlantic and its relation to the physical oceanography. *Journal of Experimental Marine Biology and Ecology*, **37**, 225–253.
- FOXTON P. (1971–1972) Observations on the vertical distribution of the genus *Acanthephyra* (Crustacea: Decapoda) in the eastern north Atlantic with particular reference to species of the “*purpurea*” group. *Proc. RSE, (B)*, **73**, 301–313.
- FUSTE X. (1987) Distribución de larvas de crustáceos decápodos en la costa de Cataluña. *Investigación Pesquera*, **51**, 277–284.
- GORDON J. D. M. (1986) The fish population of the Rockall Trough. *Proceedings of the Royal Society of Edinburgh*, **88**, 121–204.
- GORDON J. D. M. and J. A. R. DUNCAN (1985) The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, Northeastern Atlantic. *Progress in Oceanography*, **15**, 37–69.
- GORDON J. D. M. and J. A. R. DUNCAN (1987) Deep-sea bottom-living fishes at two repeat stations at 2000 and 2900 m in the Rockall Trough, Northeastern Atlantic Ocean. *Marine Biology*, **96**, 309–326.
- GRASSLE J. F., H. L. SANDERS, R. R. HESSKERM, G. T. ROWE and M. CHELLAN (1975) Pattern and zonation: a study of the bathyal megafauna using the research submersible *Alvin*. *Deep-Sea Research*, **22**, 457–481.
- HAEDRICH R. L. and G. T. ROWE (1977) Megafaunal biomass in the deep-sea. *Nature*, **269**, 141–142.
- HAEDRICH R. L., G. T. ROWE and P. T. POLLONI (1975) Zonation and faunal composition of epibenthic populations on the continental slope south of New England. *Journal of Marine Research*, **37**, 191–211.
- HAEDRICH R. L., G. T. ROWE and P. T. POLLONI (1980) The megabenthic fauna in the deep sea south of New England, USA. *Marine Biology*, **57**, 165–179.
- HARGREAVES P. M. (1984) The distribution of Decapoda (Crustacea) in the open ocean and near-bottom over an adjacent slope in the northern north-east Atlantic Ocean during autumn 1979. *Journal of Marine Biology*, **64**, 829–857.
- HESSLER R. R. and P. JUMARS (1977) Abyssal communities and radioactive waste disposal. *Oceanus*, **20**, 41–46.
- HINES A. H. (1989) Geographic variation in size at maturity in brachyuran crabs. *Bulletin of Marine Science*, **45**, 356–368.
- HOPKINS T. S. (1985) Physics of the Sea. In: *Key environments. Western Mediterranean*, R. MARGALEF, editor, Pergamon, Oxford, pp. 100–125.
- JONES N. S. (1979) The systematics and distribution of Cumacea from depths exceeding 200 meters. *Galathea Report*, **10**, 99–180.
- KERR S. R. (1974) Theory of size distribution in ecological communities. *Journal of the Fishery Research Board of Canada*, **31**, 1859–1862.
- KING M. G. (1984) The species and depth distribution of deep-water Caridean shrimps (Decapoda, Caridea) near some southwest Pacific Islands. *Crustaceana*, **47**, 174–190.
- KING M. G. and A. J. BUTLER (1985) Relationship of life-history patterns to depth in deep-water caridean shrimps (Crustacea: Natantia). *Marine Biology*, **86**, 129–138.
- LAGARDÈRE J. P. (1977) Recherches sur la distribution verticale et sur l'alimentation des crustacés decapodes

- benthiques de la pente continentale du Golfe de Gascogne. *Bull. Cent. Etud. Rech. scient, Biarritz*, **11**, 367–440.
- LAMPITT R. S., D. S. M. BILLETT and A. L. RICE (1986) Biomass of the invertebrate megabenthos from 500 to 4100 m in the northeast Atlantic Ocean. *Marine Biology*, **93**, 69–81.
- MACPHERSON E. and C. M. DUARTE (1991) Bathymetric trends in demersal fish size: is there a general relationship? *Marine Ecology Progress Series*, **71**, 103–112.
- MARKLE D. F., M. J. DADWELL and R. G. HALLIDAY (1987) Demersal fish and decapod crustacean fauna of the upper continental slope of Nova Scotia from La Have to St. Pierre Banks. *Canadian Journal of Zoology*, **66**, 1259–1960.
- MERRETT N. R. and N. B. MARSHALL (1981) Observations on the ecology of deep-sea bottom-living fishes collected off northwest Africa. (08–27°N). *Progress in Oceanography*, **9**, 185–244.
- POLLONI P., R. HAEDRICH, G. ROWE and C. H. CLIFFORD (1978) The size–depth relationship in deep ocean animals. *Journal of Marine Research*, **33**, 191–212.
- POLLONI P. T., R. L. HAEDRICH and C. H. CLIFFORD (1979) The size–depth relationship in deep ocean animals. *Internationale Revue der Gesamter Hydrobiologie*, **64**, 39–46.
- REX M. A. (1979) *r*- and *K*-selection in a deep-sea gastropod. *Sarsia*, **64**, 29–32.
- REYS J. P. (1976) Les peuplements benthiques (zoobentos) de la region de Marseille (France): aspects methodologiques de la delimitation des peuplements par les methodes mathematiques. *Marine Biology*, **36**, 123–134.
- RICE A. L., R. G. ALDRED, E. DARLINGTON and R. A. WILD (1982) The quantitative estimation of the deep-sea megabenthos—a new approach to an old problem. *Oceanologica Acta*, **5**, 63–72.
- ROWE G. T. (1971) Benthic biomass and surface productivity. In: *Fertility of the sea*, vol. 2, J. D. COSTLOW JR, editor, Gordon & Breach, New York, pp. 441–454.
- ROWE G. T. (1983) Biomass and production of the deep-sea macrobenthos. In: *Deep-sea biology, the sea*, vol. 8, G. T. ROWE, editor, Wiley, New York, pp. 97–122.
- ROWE G. T. and R. J. MENZIES (1969) Zonation of large benthic invertebrates in the deep-sea off the Carolinas. *Deep-Sea Research*, **29**, 257–278.
- SNELGROVE P. V. R. and R. L. HAEDRICH (1985) Structure of the deep demersal fish fauna off Newfoundland. *Marine Ecology Progress Series*, **27**, 99–107.
- SMITH C. R. and S. C. HAMILTON (1983) Epibenthic megafauna of a bathyal basin off southern California: patterns of abundance, biomass, and dispersion. *Deep-Sea Research*, **30**, 907–928.
- STEFANESCU C. and J. E. CARTES (1992) Benthopelagic habits of adult specimens of *Lampanyctus crocodilus* (Risso, 1810) (Osteichthyes, Myctophidae) in the Western Mediterranean deep slope. *Scientia Marina*, **56**, 212–223.
- STEFANESCU C., J. RUCABADO and D. LLORIS (1992) Depth–size trends in western Mediterranean demersal deep-sea fishes. *Marine Ecology Progress Series*, **81**, 205–213.
- STEFANESCU C., D. LLORIS and J. RUCABADO (1993) Deep-sea fish assemblages in the Catalan Sea (Western Mediterranean) below a depth of 1000 m. *Deep-Sea Research*, **40**, 695–707.
- THESSALOU-LEGAKI M., A. FRANTZIS, K. NASSIOKAS and S. HATZINIKOLAOU (1989) Depth zonation in a *Parapandalus narval* (Crustacea, Decapoda, Pandalidae) Population from Rhodos Island, Greece. *Estuarine, Coastal and Shelf Science*, **29**, 273–284.
- THIEL H. (1975) The size structure of the deep-sea benthos. *Internationale Revue der Gesamter Hydrobiologie*, **60**, 575–606.
- THIEL H. (1979) First quantitative data on the deep Red Sea benthos. *Marine Ecology Progress Series*, **1**, 347–350.
- THIEL H. (1983) Macrobenthos and nanobenthos of the deep-sea. In: *The sea*, G. T. ROWE, editor, Wiley, New York, pp. 167–230.
- WARWICK R. M. (1984) Species distribution in marine benthic communities. *Oecologia*, **61**, 32–41.
- WENNER E. L. and D. F. BOESCH (1979) Distribution patterns of epibenthic decapod crustacea along the shelf-slope coenocline middle Atlantic bight, USA. *Bulletin of the Biological Society of Washington*, **3**, 106–133.
- WILLIAMS W. T., G. N. LANCE and STEPHENSON (1970) The macrobenthos of Moreton Bay. *Ecological Monographs*, **40**, 459–494.
- WILSON G. D. (1983) Variation in the deep-sea isopod *Eurycope iptima* (Asellota, Eurycopidae): depth related clines in rostral morphology and in population structure. *Journal of Crustacean Biology*, **1**, 127–140.