

## INTRASPECIFIC AGGREGATION STRUCTURE OF A SHOAL OF A WESTERN MEDITERRANEAN (CATALAN COAST) DEEP-SEA SHRIMP, *ARISTEUS ANTENNATUS* (RISSO, 1816), DURING THE REPRODUCTIVE PERIOD

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**ABSTRACT** The deep-sea rose shrimp, *Aristeus antennatus*, constitute an important fishery resource in the Western Mediterranean Sea. The spatio-temporal behavioral pattern of *A. antennatus* is well-known, with the species forming seasonal aggregations on the middle slope at depths between 400 and 900 m. These aggregations form between late winter and early summer. The object of the present study is to determine the internal structure of shoals of the western Mediterranean (Catalan coast) rose shrimp along the slope on the grounds where the species is fished (from 400 to 1000 m) at the time of peak density during the reproductive period. Interactions between fishing and research vessel have been used to sample synchronically and bathymetrically the shoals of the deep-sea shrimp to determine intra and interspecific shoal structures. The results of this study on *A. antennatus* have specifically shown that (1) The pattern shrimp shoal distribution is such that density rises rapidly in the portion located in the shallower distribution range of this species and then gradually decreases at greater depths; (2) the distribution of this resource straddles both sides of the ecological boundary located at 900 m, though with changes in the sex-ratio and individual size; (3) species coexisting with this shrimp species are concentrated at depths other than the depths of peak shrimp density; (4) commercial trawlers deploy according to the abundance pattern of the resource; and (5) the reproductive portion of the stock is heavily exploited.

**KEY WORDS:** *Aristeus antennatus*, Mediterranean Sea, population structure, aggregation, sex ratio, size frequencies, fisheries, shoals

### INTRODUCTION

The deep-sea rose shrimp, *Aristeus antennatus* (Risso, 1816) (Crustacea, Decapoda, Dendrobranchiata, Aristeidae), represents an important fishery in the Western Mediterranean Sea (Sardà & Martín 1986, Demestre & Lleonart 1993, Bianchini & Ragonese 1994, Carbonell et al. 1999). This species is a characteristic component of the demersal muddy bottom community on the middle slope at depths between 400 and 1,200 m (Cartes & Sardà 1993), where Cartes & Sardà (1992) and Maynou & Cartes (2000) have defined it as a nektonic species of moderate-to-high swimming mobility. However, the distribution of this species is also fished frequently between 400 and 800 m in other Mediterranean areas (Bianchini & Ragonese 1994, Carbonell et al. 1999, Papaconstantinou & Kaporis 2001, Cau et al. 2002). The distribution of this species is nonetheless considerably broader, reaching at least to depths of 2250 m (Sardà & Cartes 1992, 1993), indicating that the species is eurybathic with a distribution considerably broader than that of other decapod crustacean species.

The spatiotemporal behavioral pattern of *A. antennatus* is well known, with the species forming seasonal aggregations on the middle slope at depths between 400 and 900 m. These aggregations form between late winter and early summer (Tobar & Sardà 1987, Demestre & Martín 1993, Sardà et al. 1994). Towards the end of summer, the shrimp shoals tend to break up and move inside submarine canyons, with the shrimp being fished at shallower depths (400–700 m) along the margins of the canyons, locations that are less accessible to trawlers (Sardà 1993, Sardà et al. 1994, Sardà et al. 1997).

During the period in which this species forms aggregations (late winter to early summer), shoals consist of reproductive adult females. Copulation takes place at the start of the aggregation stage (Relini Orsi, 1980, Sardà & Demestre 1987) with a percentage of

males in the population of less than 20% (Sardà & Cartes 1992, Demestre & Martín 1993, Sardà et al. 1994). Tursi et al. (1996) reported that during copulation in late winter, males can be 50% of the population in Ionian Sea. Studies conducted on the catchability of shoals of this species (Sardà & Maynou 1998) have suggested that the shoals take on an elongate shape parallel to the coast. It is exactly at this time when the shrimp stock bears the brunt of fishing effort (Tudela et al. 2003), because shoal formation is at its peak on the part of the slope most readily accessible to trawlers and females attain maximum size, that is, biomass concentration is also at its peak. In addition, marketability of this species is also highest at this time.

Studies on schooling in pelagic species (Swartzman et al. 1994, Nonacs et al. 1994, Nottestad et al. 1996) particularly using echosounding, and in species in captivity (Pitcher 1983, Pitcher et al. 1985), have been common, but there have been very few such studies on benthic or benthopelagic species. Gordo & Duarte (1991) considered some *Merluccius* species and reported size-dependent schooling behavior. Macpherson & Duarte (1991) also related size and depth for different fish species and discussed the possible existence of a general size-depth relationship. On the whole, studies on schooling and shoaling behavior have been quite diverse in terms of methodology used, and they have also dealt with a range of different aspects. Furthermore, although shoaling of coastal prawns and migratory displacements relating to their life cycles are well known (García & Le Reste 1987), our literature review has not disclosed any similar studies on shoaling patterns for species dwelling at depths below the margin of the continental shelf.

Accordingly, the object of the present study was to determine the depth structure of shoals of the Catalan coast rose shrimp, *Aristeus antennatus* (Risso, 1816), along the slope on the grounds where the species is fished (from 700 to 1000 m) at the time of peak density (aggregation). Bearing in mind, however, that the depth distribution for this species extends across several community boundaries (down to at least 3000 m in depth; Sardà 2001), the

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role of the noncommercially exploited portion of the population on the population as a whole has also been discussed. Shoaling structure has been considered in terms of both intraspecific aspects, such as density, size range, and sex ratio, and interspecific aspects, i.e., density relationships between the rose shrimp and other fish and crustacean species dwelling in the same faunal assemblage, on the basis of depth. Our goal has been to underscore the importance of understanding the intra and interspecific structure of aggregations of marine species as a significant factor in establishing the actual level of vulnerability to exploitation by fisheries. In addition, over and above a simple discussion of the results presented here, this article aspires to be an example of studies of this kind and thus also includes a consideration of ecological and fisheries aspects in the discussion, relating them to the specialized literature.

#### MATERIAL AND METHODS

A study was conducted jointly by the *R/V García del Cid* and commercial trawlers on 21 to 23 June 2000 on the "Serola" fishing grounds located off Barcelona (Northwest Mediterranean Sea), where mature females of the deep-sea rose shrimp typically aggregate at that time of year (Fig. 1).

To be able to obtain an instantaneous view of the aggregation structure of a shoal of this deep-water species, operations must be completed in the shortest possible time to avoid variations in response to sudden environmental changes affecting community structure. The weather was sunny and good over the 48 h in which sampling was performed and remained stable over the course of the survey.

The fishing vessels operating in this area are trawlers from the port of Barcelona specialized in the shrimp fishery, with engine power ratings ranging between 800 and 1100 horsepower and lengths between 17 and 21 m. Five fishing trawlers conducted fishing operations during their normal operating hours at depths

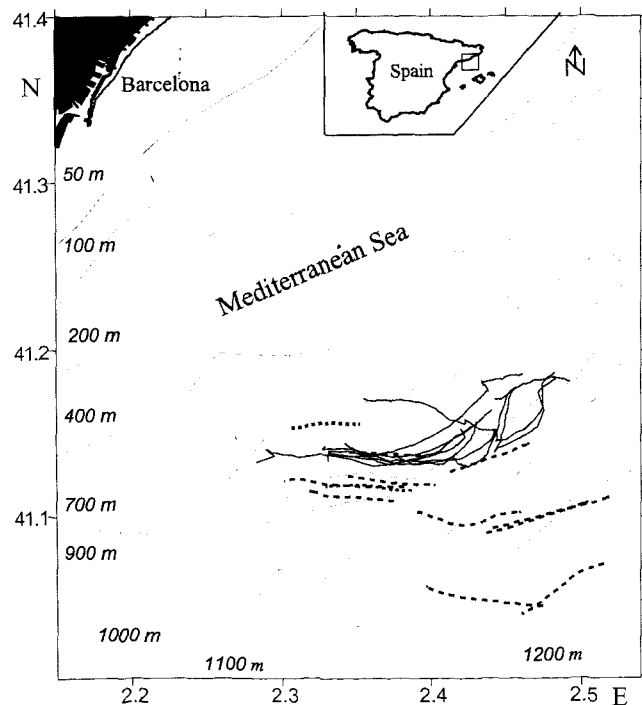


Figure 1. Study area showing the transects on which hauls were performed by the research vessel (dotted lines) and the trawlers (solid lines).

between 780 and 850 m. Haul duration was typical for the fishery, namely, two hauls daily lasting about 3.5 h each. Landings by these trawlers were recorded on June 22, 2000, by a surveyor at the wharf. Trawler headings and locations were monitored continuously using the Automatic Radar Plotting Aid (ARPA) radar system on board the research vessel, which made it possible to follow the courses of their hauls from start to finish (Fig. 1).

The *R/V García del Cid* is 38 m in length with an engine power rating of 1100 horsepower. It operated concurrently with the trawlers in the same area, but over a broader depth range, between 700 and 1 200 m (Fig. 1). A total of 11 daytime and nighttime hauls were conducted on June 21 to 23, 2000, at least two hauls in each of the 700-, 800-, 900-, 1000-, and 1200-m depth intervals. Depths, towing speed, starting time, and ending time were recorded for each haul (Table 1). The horizontal mouth opening of the gear between the wings (13.5 m) was also recorded using remotely operated Scanmar sensors.

Haul duration was 1 h to ensure that the sampling data would be discrete and suitable for use in discriminatory analysis. Biologic data collected consisted of the number and individual weight of all specimens caught. Standard carapace length (CL in mm), individual weight in g, sex, and maturity stage were recorded for all rose shrimp specimens. The data from fishing trawlers and the data from the research vessels are not directly comparable and only relative comparisons were undertaken. These data were presented in different graphics and with different units. Only biologic data and size frequencies obtained on board the research vessel were used in data treatment to avoid potential deviations. Only those females in an advanced gonad maturity stage (maturity stages IV and V according to the gonad coloration scale published by Relini & Relini (1979) as expanded by Demestre & Fortuño (1992) were classified as mature). Percentage size frequency values were compared using multivariate analysis to evaluate similarity of the surface areas of the bars and using the Kolmogorov-Smirnov test ( $P < 0.05$ ) to compare the cumulative frequency values.

The sampling protocol used, using short hauls yielding data that were highly discrete in terms of time, provided a "snapshot" of the resource. This strategy has furnished good results when used in studies of the density and spatial distribution of benthic (González-Gurriarán et al. 1993, Maynou et al. 1996) and benthopelagic (Carter et al. 1993) crustaceans. Samples of longer duration would have entailed the risk of introducing new variables, principally in relation to changes in weather, which would definitely be a potential source of noise in the data analysis. On the basis of the results of previous work conducted in this same area published by Tobar & Sardà (1987), Demestre & Martín, (1993), Sardà et al. (1994), and Sardà et al. (1998), shoals of *A. antennatus* are continuously present at the sampling depths from late winter to early summer.

Biomass in number and individual weight standardized to  $\text{km}^2$ , on the basis of the area swept by each haul, have been graphically represented using the sampling data collected by the research vessel. Measurements were effected individually and overall and on the total of fish and other shrimp species. In the case of the commercial trawlers, which were not equipped with remotely controlled monitoring systems, shrimp landings ( $\text{kg}\cdot\text{h}^{-1}$ ) were weighted on the basis of the length of the working day ( $7\text{ h}\cdot\text{d}^{-1}$ ). Specialized personnel was on board of each commercial vessel weighting the shrimp caught. Also bills of sales in auction was collected to compare data on board. Figure 1 includes trend lines fit visually to facilitate interpretation and discussion of the data.

TABLE 1.  
List of hauls effected.

Haul Code	Depth (m)	D/N	Local Starting Time (h)	Local Ending Time (h)	Starting Position	Ending Position	Swept Area (km <sup>2</sup> )
H1	700	D	15:03	16:05	41° 09' 01" N 02° 18' 04" E	41° 08' 42" N 02° 22' 01" E	0.06290
H2	800	D	17:52	18:47	41° 08' 08" N 02° 20' 32" E	41° 08' 27" N 02° 16' 49" E	0.06806
H3	900	N	21:43	22:56	41° 07' 44" N 02° 21' 37" E	41° 07' 43" N 02° 25' 43" E	0.08001
H4	1000	N	3:53	5:20	41° 06' 07" N 02° 23' 06" E	41° 08' 16" N 02° 29' 13" E	0.09779
H5	1200	D	8:03	9:16	41° 05' 53" N 02° 28' 56" E	41° 04' 06" N 02° 25' 42" E	0.06826
H6	750	D	12:17	13:18	41° 08' 30" N 02° 21' 21" E	41° 08' 40" N 02° 17' 50" E	0.06645
H7	1000	D	15:32	16:33	41° 07' 08" N 02° 24' 34" E	41° 08' 15" N 02° 28' 51" E	0.09005
H8	1200	N	19:33	21:09	41° 04' 23" N 02° 27' 05" E	41° 05' 04" N 02° 21' 55" E	0.08116
H9	750	N	0:18	1:42	41° 08' 38" N 02° 21' 01" E	41° 08' 51" N 02° 16' 09" E	0.07038
H10	800	N	3:44	4:40	41° 08' 18" N 02° 20' 36" E	41° 08' 14" N 02° 23' 58" E	0.07006
H11	900	D	6:52	7:54	41° 07' 34" N 02° 24' 44" E	41° 08' 40" N 02° 27' 59" E	0.06714

D/N, day-night hauls.

A matrix consisting of species (columns) and hauls (rows) was constructed for community analysis. Species that occurred only in a single haul and species occasionally represented by only a single individual in some hauls have not been included. The data were log transformed  $\ln(x+1)$  and used in multivariate cluster analysis. The linear correlation value was used as the similarity index and UPGMA as the aggregation algorithm.

The abundance ratios for rose shrimp to other crustacean and fish species were calculated by dividing the number of rose shrimp individuals by the total number of individuals of all species in the other two groups, crustaceans and fishes, respectively. Diversity was calculated using Simpson's index, a good discriminator for indicating dominance by a given species or group of species (May, 1975), which is the case of the rose shrimp here, the predominant species in the present study. This diversity index has been recommended for use in comparisons of marine communities (Lambhead et al. 1983).

## RESULTS

### Abundance and Distribution

Shrimp abundance on the basis of the samples collected by the research and commercial vessels have been depicted in biomass (Fig. 2a and b) and number of individuals (Fig. 3). These figures show that the lowest catches, with densities of about 20 ind. km<sup>-2</sup>, were made at around 700 m in depth, whereas the highest catch densities, of around 1700 ind. km<sup>-2</sup>, were made at 800 m. Individual density levels then tapered off progressively with increasing depth. These results clearly define a specific structure across the shoal with depth, with rose shrimp density augmenting sharply in the shallowest portion of the shoal and then gradually falling off towards the deepest portion.

The yields obtained by the trawler that effected tows at a depth of around 800 m (Fig. 2b) were 2-fold those of the three trawlers operating at greater depths and 5-fold those of the trawler operating at a shallower depth. Trawler deployment thus mirrored the distribution of the shrimp resource being fished: one vessel operating at 700 m, where shrimp density was lowest; one vessel operating at 800 m, where shrimp density was highest; and three vessels operating at more than 800 m, where biomass began to taper off. This spatial deployment of the fishing trawlers was dictated by the amount of space that had to be left between them to

ensure proper maneuverability. The first vessel to reach the fishing grounds begins to work at the depth the skipper deems best to achieve the highest yields. Vessels arriving later will then take up a position next to the vessels already present, though always on the deeper side, where rose shrimp density will tend to be lower still profitable.

### Day-Night Shoal Structure

Figures 2a and 3 depict the hauls conducted in the daytime (hollow circles) and nighttime (solid circles). The distribution pat-

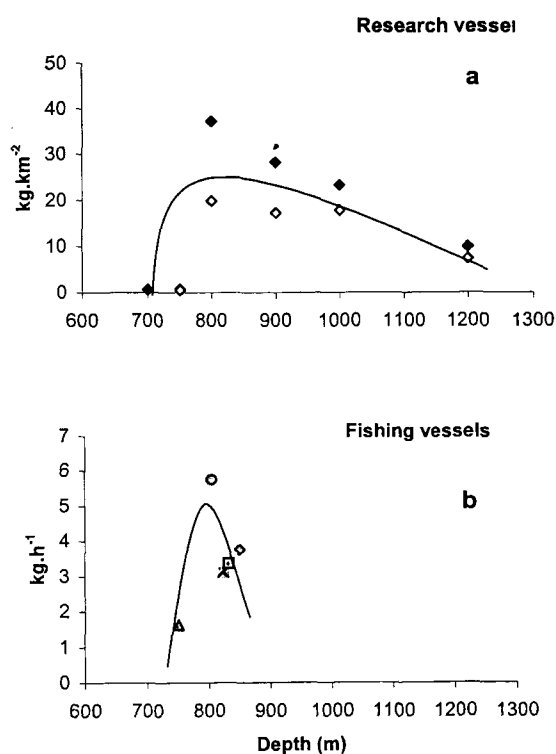


Figure 2. Catches in weight by depth taken by the research vessel (a) and the trawlers (b). Hollow symbols, day samples. Solid symbols, night samples. Grey points, different fishing vessels.

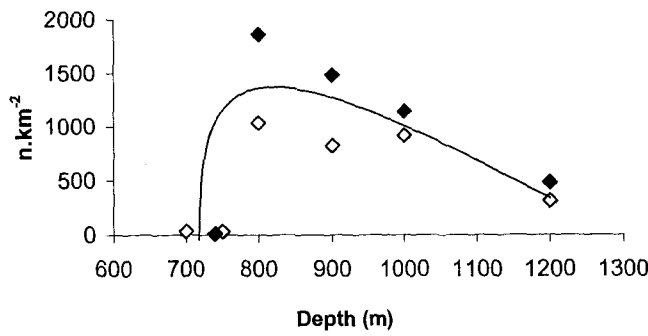


Figure 3. Densities by depth made by the research vessel. Hollow symbols, day samples. Solid symbols, night samples.

tern can be observed to differ according to depth. In the depth range between 750 and 900 m catches were higher at night than in the daytime, which suggests that part of the population migrate to the upper portion of the slope at night. The low individual densities at 700 m were insufficient to allow any reliable inferences concerning daytime-nighttime movements. Differences between daytime and nighttime catches appeared to decrease with depth; however, it should be noted that commercial day-night catch data were

unavailable for comparison with the experimental catch data, because commercial trawlers are not allowed to operate at night. This observations coincides with the migrations of decapods suggested by Cartes et al. (1993).

**Size Frequencies**

Figure 4 shows the size frequencies for females at the different sampling depths. The bell-shaped size frequency curves tended to flatten out and have wider tails with depth both in the daytime and at night. At depths around 800 m the population tended to consist of females with a modal mean size of 40 mm CL, ranging from a minimum of 20 mm CL to a maximum of 51 mm CL. A similar structure was observed at 1000 m. However, from 1000 m, there was a change in the size frequency distribution, with the proportions of both the smallest sizes and the largest sizes increasing. This trend was quite distinct at 1200 m, despite the low number of individuals, however due to the low occurrence of *A. antennatus* in this depth, the number of individuals caught was considered sufficient for a good size spectrum on this depth. Because of the small number of individuals caught at 700 m, it was not possible to construct a sufficiently representative size structure for that depth.

The similarity analysis for the size frequencies (Table 2) indicated significant differences ( $P < 0.05$ ) between the size frequen-

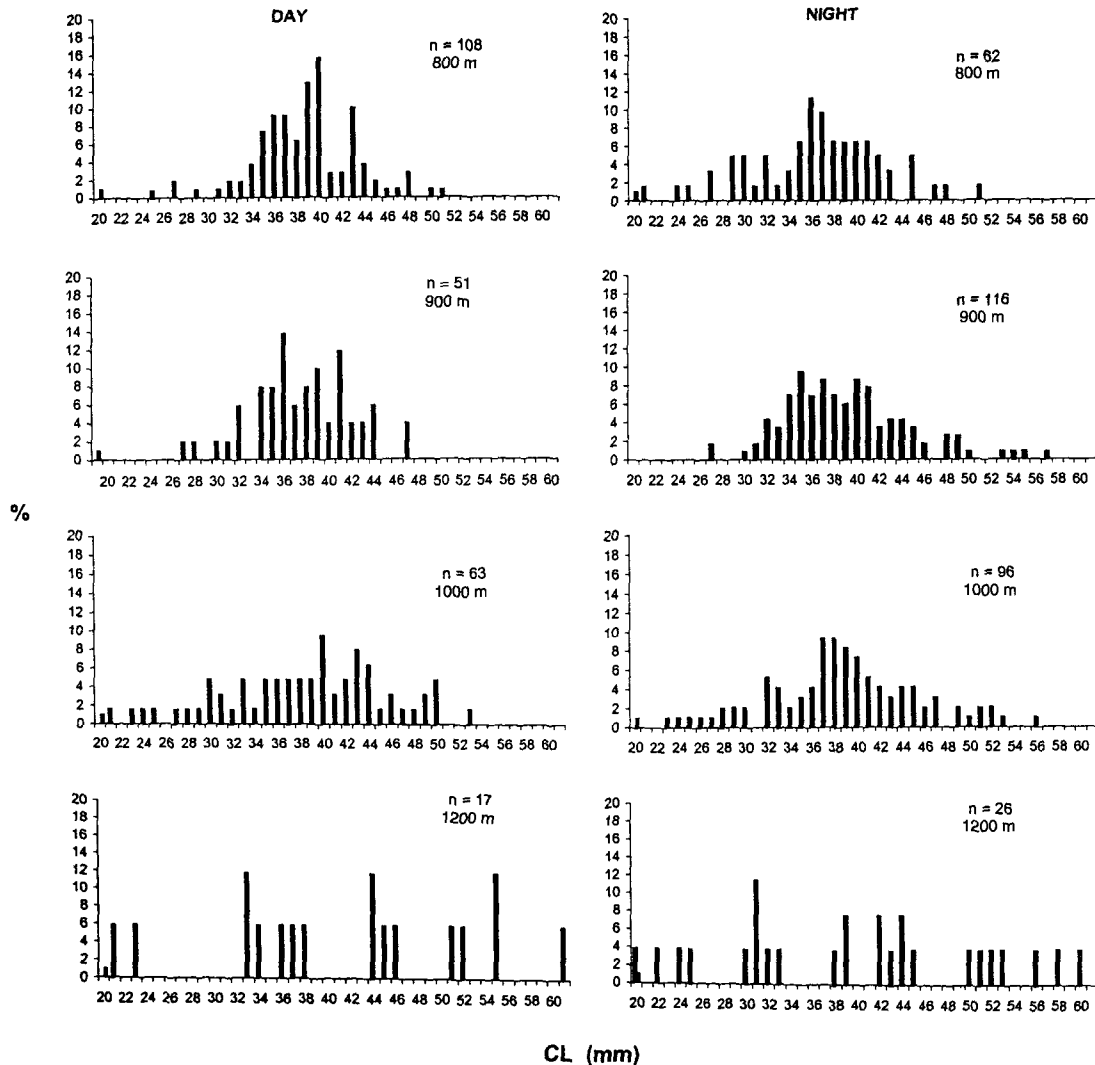


Figure 4. Size frequencies for females by depth and by daytime-nighttime. CL, carapace length.

TABLE 2.  
Similarity between frequency values.

H3	900 m	N	0.724						
H4	1000 m	N	0.717	0.728					
H5	1200 m	D	0.306*	0.373*	0.378*				
H7	1000 m	D	0.653	0.677	0.697	0.349			
H8	1200 m	N	0.380*	0.365	0.460	0.469	0.426		
H10	800 m	N	0.694	0.736	0.649	0.305*	0.657	0.310*	
H11	900 m	D	0.683	0.723	0.670	0.333*	0.638	0.386*	0.711
			H2	H3	H4	H5	H7	H8	H10
			800 m	900 m	1000 m	1200 m	1000 m	1200 m	800 m
			N	N	N	D	D	N	N

H, haul code; D, day; N, night.

\* Significant differences ( $P < 0.05$ ) Kolmogorov-Smirnov test.

cies for the 800–900 m and 1000–1200 m depth intervals but not between daytime and nighttime. There was a tendency towards greater spread of the sizes at deeper depths, with higher proportions of both juvenile and larger individuals. It is interesting to note that the most relevant changes in the size structure of the *A. antennatus* population were linked to the community boundary (below 900 m) for the species, as will be discussed in the following section. Males exhibited a trend similar to that of the females, with greater proportions of the extreme sizes (small and large individuals) at depths greater than 900–1000 m (Fig. 5). However, because of the low occurrence of males in the population at the time of year when the study was carried out, no reliable analysis of the level of significance was possible.

#### Sex Ratio

The sex ratio (Fig. 6) was characterized by the low presence of males at depths of 800 m (<20%) and 900 m (<5%). The proportion of males increased progressively from 1000 m, gradually rising to nearly 40%. Virtually 100% of the adult females were mature, and all bore a spermatophore on the telum, which confirms that the shoal was at the spawning stage, as demonstrated in various earlier papers (Sardà & Demestre 1987, Demestre & Fortuño 1992, Sardà et al. 1994).

#### Assemblages Differences

The increase in biomass with depth (Figs. 7 and 8) was caused principally by the presence of very large species, e.g., *Alepocephalus rostratus*, *Mora moro*, and *Lepidion lepidion*, which are typical of the community below 900 m, and their occurrence also raised abundance levels (Table 3). According to the results of the cluster analysis, the main discriminating factor was the presence of deep-water fish and crustacean species in the depth interval considered in this study, such as *Bathypterois mediterraneus*, *Mora moro*, *Nezumia aequalis*, *Acanthephyra eximia*, *Geryon longipes*, *Munida tenuimana*, *Paromola cuvieri*, and *Sergestes arcticus*, as opposed to species that are characteristic of shallower depths, such as *Hymenocephalus italicus*, *Phycis blennoides*, *Trachyrhynchus scabrus*, *Schylliorhinus canicula*, *Aristeus antennatus*, *Pasiphaea multidentata*, *Pasiphaea sivado*, and *Polycheles typhlops* (Fig. 9). Trawls nos. 1, 2, 9, 6, and 10 made up a group comprising the 700- and 800-m depth intervals. Trawls nos. 3, 5, 4, 7, 11, and 8 made up a group comprising the depth intervals between 900 and 1200

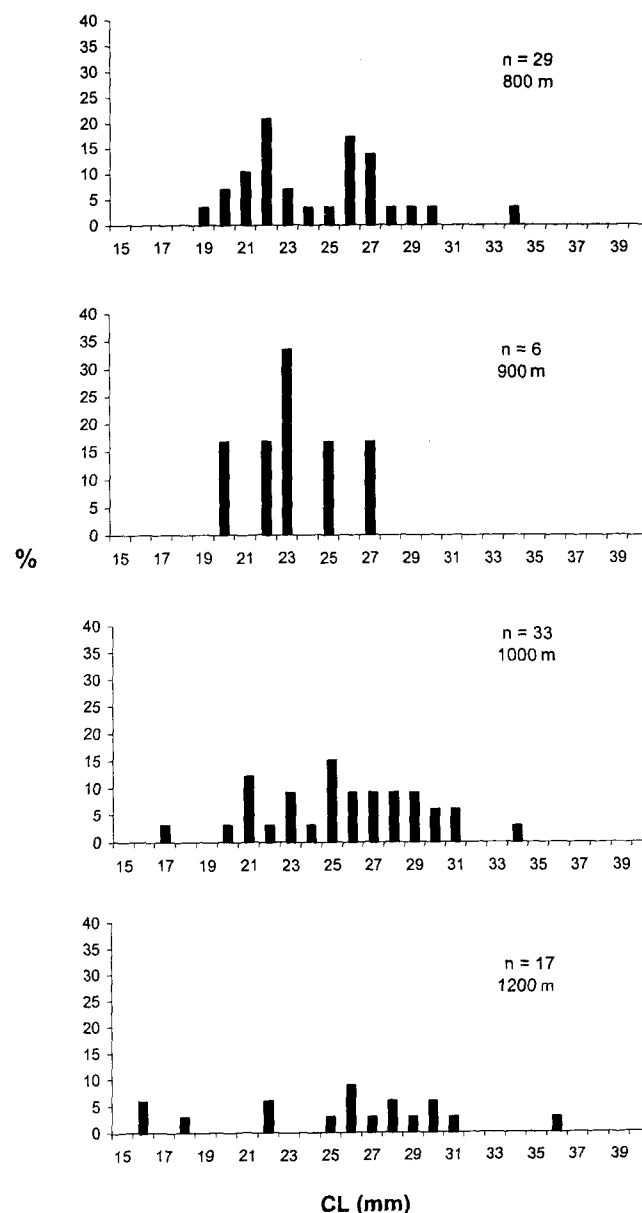


Figure 5. Size frequencies for males by depth. CL, carapace length.

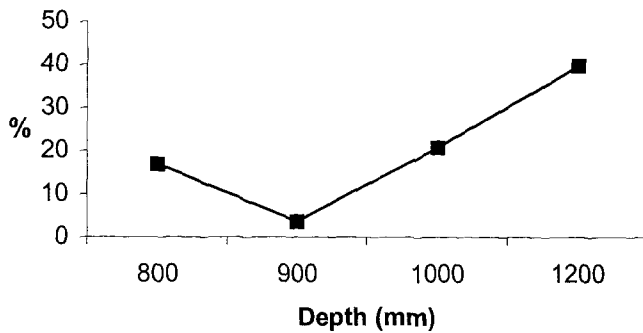


Figure 6. Sex ratio by depth expressed as the percentage of males.

m. It is important to bear in mind that, unlike most other species, distribution of the deep-water rose shrimp is virtually continuous from 700–800 m to more than 1200 m (Fig. 2). Accordingly, this species is represented and attains high abundance levels in both of the assemblages revealed by the cluster analysis.

#### Density-Dependent Exclusion

The density of other species was lowest between 800 and 1000 m, where shrimp shoal density was highest. As *A. antennatus* density decreased with depth, the density of other species increased progressively (Fig. 10), which suggests a high degree of density-dependent exclusion between the shoal of shrimps, the dominant species, and the distribution of other species at the same depth. This was also reflected by diversity, which displayed little variation between trawls, with Simpson index values between 0.09 and 0.19 (Fig. 11). High index values are indicative of lower diversity due to dominance by one or just a few species. Index values were highest (reflecting single species abundance and low diversity) and displayed less dispersion for the depth intervals between 800 and 1000 m, as a consequence of the greater occurrence of shrimps in those intervals. Diversity index values were most variable for the extreme depth intervals sampled (700 and 1200 m), bearing out the preceding results.

#### DISCUSSION

A number of workers have described the composition of the community supporting the deep-sea rose shrimp, *Aristeus antennatus*, fishery in the Western Mediterranean Sea separately for crustaceans and for fish (Abelló et al. 1988, Stefanescu et al. 1992, Cartes & Sardà 1993, Stefanescu et al. 1994). This community, dwelling over muddy bottoms on the middle slope, is composed

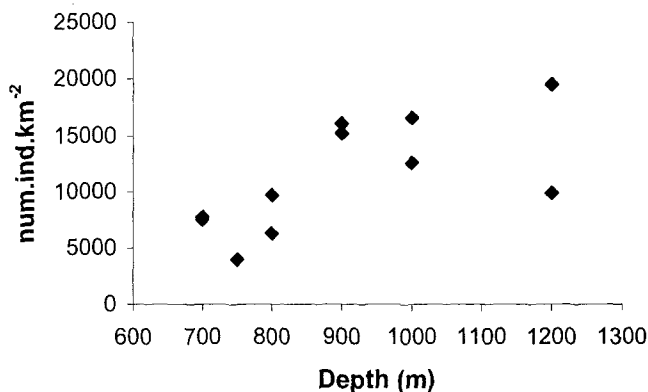


Figure 7. Individual abundance by depth.

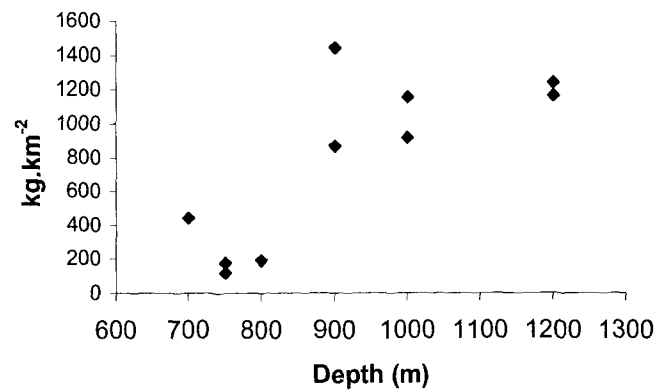


Figure 8. Biomass by depth.

principally of the target species, *Aristeus antennatus*, along with other species of no commercial interest, e.g., *Geryon longipes*, *Polycheltes typhlops*, *Lepidion lepidion*, *Alepocephalus rostratus*, and *Trachyrhynchus scabrus*. In any case, *A. antennatus* is an interesting species as compared with the other species dwelling in the community because of certain specific biologic characteristics, namely, (1) its broad depth distribution, making it a highly eurybathic species, and (2) even though fishing pressure has been extremely high over the past 40 y, the population seems to be in a healthy state of exploitation. Cartes & Sardà (1993) defined three main zonation for the deep-sea decapod fauna in the Western Mediterranean: the upper middle slope above 670 m; the lower middle slope between 850 and 1200 m; and, below this last-mentioned depth, a transition zone to the lower slope community (down to 2000 m). However, sampling between 650 and 900 m in that study was inadequate, and the depth limit between the upper middle slope and lower middle slope assemblages could not be accurately determined. Based on the samples collected in the present study, the boundary between the upper middle slope and the lower middle slope would appear to be more exactly situated at around 900 m related exclusively for *A. antennatus*. The above-mentioned boundaries represent genuine barriers to distribution for different decapod crustacean and fish species, but not for *A. antennatus*, which enjoys a continuous distribution from 550 and at least 3000 m (Sardà et al. 1993, Sardà 2001). However, we must consider here that the definition of boundary is a controversial question, often depending on the sampling adequacy and data used in the analysis. Haedrix & Merret (1990) and Koslow (1993) and Stefanescu et al. (1993) and Moranta et al. 1998, provided respectively different results investigating in the same areas, however only fishes are considered in these studies. In this paper we present clusters including crustacean and fishes, reaching similar results as Morales-Nin et al. (2003) with a first boundary around 800 m depth. However, as has been observed in the present study, changes in the internal population structure of this species are apparent, linked to a community boundary existing at around 900 m. Similarly, the findings presented here have demonstrated that the main stock, in terms of fishable biomass, is distributed chiefly between 700 and 1,000 m during the period of gonadal maturation from late winter to early summer. This portion of the *A. antennatus* population consists primarily of females, with low proportions of males (<10%) and medium-sized individuals. The highest fishing effort is expended during the reproductive period of females. All these aspects would appear to suggest that this species can be expected to quickly become overexploited, but this does not seem

TABLE 3.  
Species abundances (number individuals km<sup>-2</sup>).

Species	Haul Code Depth (m)	1 700	9 700	6 750	2 800	10 800	11 900	3 900	4 1000	7 1000	5 1200	8 1200
Pisces												
<i>Alepocephalus rostratus</i>		0	0	60	0	0	3098	462	2516	2254	689	4731
<i>Antonogadus megalokynodon</i>		97	71	0	15	14	0	0	0	0	0	0
<i>Bathypterois mediterraneus</i>		0	0	0	0	0	0	0	20	11	0	123
<i>Benthocometes robustus</i>		0	0	0	0	300	0	0	0	11	0	12
<i>Coelorhynchus coelorhynchus</i>		0	782	301	44	414	0	50	0	0	234	554
<i>Chauliodus sloani</i>		16	14	0	0	29	0	0	0	0	0	0
<i>Epigonus telescopus</i>		48	14	0	15	0	0	0	0	0	0	0
<i>Hymenocephalus italicus</i>		403	85	45	29	0	0	0	0	0	0	0
<i>Lampanyctus crocodilus</i>		48	71	15	73	29	119	37	10	111	73	0
<i>Lepidion lepidion</i>		113	384	150	191	271	1162	1850	1391	1199	1143	1799
<i>Myctophidae</i>		16	57	15	0	43	0	0	0	11	0	0
<i>Mora moro</i>		0	171	120	59	157	149	75	61	477	308	308
<i>Nettastoma melanurum</i>		0	0	0	0	0	0	25	61	0	29	25
<i>Nezumia aequalis</i>		16	28	0	88	29	447	612	654	644	293	357
<i>Notacanthus bonapartei</i>		64	355	75	59	71	60	137	1023	167	15	74
<i>Phycis blennoides</i>		225	57	120	59	29	149	137	20	44	15	0
<i>Symphurus nigrescens</i>		48	14	30	0	14	0	0	0	0	0	0
<i>Trachyrhynchus scabrus</i>		1208	298	316	720	571	1549	2125	1166	655	469	789
Selaceans												
<i>Etmopterus spinax</i>		0	0	0	0	0	30	0	0	11	59	74
<i>Galeus melanostomus</i>		113	242	241	309	200	387	525	123	144	322	308
<i>Scyliorhinus canicula</i>		48	28	0	15	0	0	0	0	0	0	0
Crustaceans												
<i>Acanthephyra eximia</i>		0	14	15	0	0	119	62	757	155	483	838
<i>Aristeus antennatus</i>		32	568	30	1028	1856	819	1350	1135	888	308	456
<i>Geryon longipes</i>		113	43	45	88	143	194	187	317	122	132	271
<i>Monodaeus couchi</i>		0	0	0	0	14	0	0	0	0	0	271
<i>Munida tenuimana</i>		16	227	0	59	200	89	37	61	33	293	961
<i>Paromola cuvieri</i>		16	43	0	15	57	209	50	51	67	88	99
<i>Pasiphaea multidentata</i>		129	28	150	59	29	30	87	20	0	29	49
<i>Pasiphaea sivado</i>		0	0	15	0	0	0	175	0	0	15	0
<i>Plesionika acanthonotus</i>		0	57	0	0	14	119	0	20	67	0	25
<i>Plesionika martia</i>		741	28	211	59	29	30	50	0	0	0	0
<i>Polycheles thyllops</i>		290	227	75	176	428	179	137	102	144	44	25
<i>Pontophilus norvegicus</i>		0	0	0	0	57	89	87	41	144	59	25
<i>Sergestes arcticus</i>		0	0	0	0	14	30	0	0	56	147	0
<i>Sergia robusta</i>		16	0	0	0	0	89	0	0	11	59	0

to be the actual condition of the stock (Demestre & Lleonart 1993). Accordingly, perhaps the biology and internal population structure of this species may somehow include the necessary features to avert potential overexploitation.

The community boundary at around 900 m described here is mainly the result of the upper limit to the depth distribution range for such species as *Alepocephalus rostratus*, *Lepidion lepidion*, *Nezumia aequalis*, *Acanthephyra eximia*, and *Geryon longipes*, species with high abundance and biomass levels. Also, the ARPA log system results indicate that this same depth is the maximum fishing depth at which commercial trawlers operate following the *A. antennatus* shoals. Therefore, this community boundary could be a direct effect of the high fishing pressure down to the said depth of 900 m. On the other hand, at the present time no technical constraints preventing fishing operations at deeper depths exist, yet fishermen seem to be aware that there is a community boundary at that level and thus do not operate at deeper depths, in the knowledge that yields of *A. antennatus* there will be insufficient.

The deep-sea rose shrimp presents a well-defined distribution

pattern across this boundary at 900 m. The number of individuals making up the shoal rose sharply from 750 to 800 m, that is, over a depth interval of around 500 m, spatially equivalent to about one mile, given the bottom configuration at the study location. From 900 m shrimp abundance fell off gradually over a distance of about 5 or 6 miles down to a depth of around 1200 m, though shrimp distribution continues over a distance of several dozen miles out to the bathyal zone (Sardà et al. 1993, Maynou & Cartes 2000). Shoals were tongue-shaped situated parallel to the depth profile, with peak abundance in the shallower portion (Sardà & Maynou 1998). Small daily or weekly variations in shoal location caused the fishing trawlers to relocate operations over the depth of peak shrimp abundance (Sardà & Maynou 1998). To date trawlers have not undertaken shrimp fishing operations at deeper depths for technical reasons: insufficiently large winch size, distance to the fishing grounds offshore, unfamiliarity with the bottoms, etc.; even so, in recent years trawlers have been observed to expand their fishing depth gradually down to 1000 m. Nevertheless, shrimp specimens caught experimentally at depths below 1000 m have been shown to

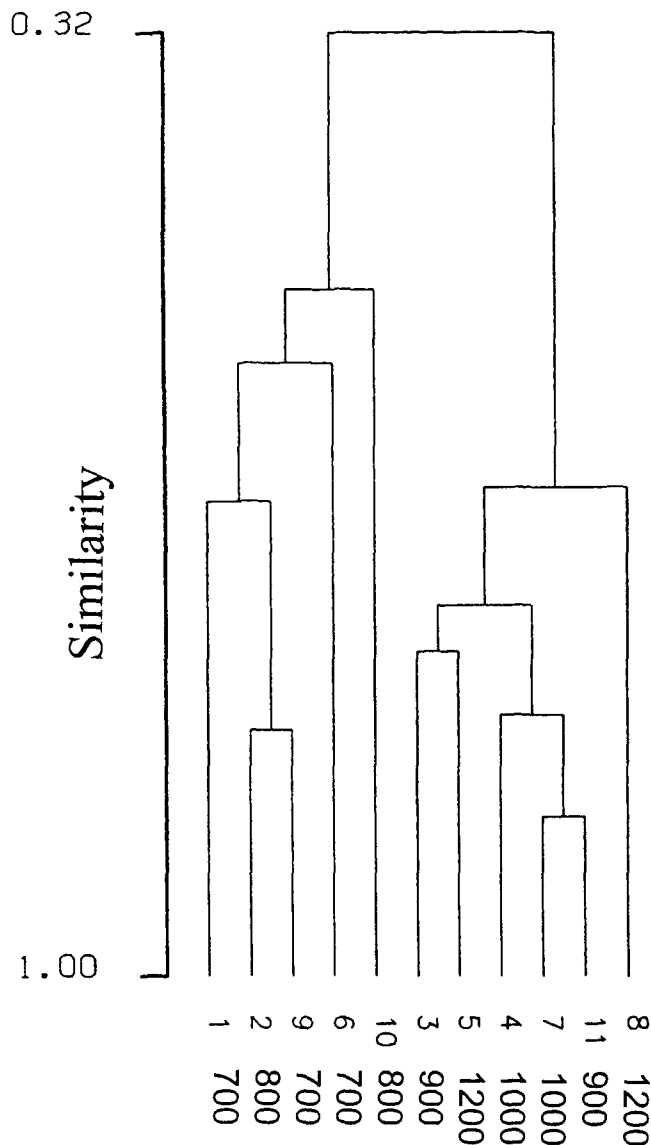


Figure 9. Cluster illustrating the similarity between hauls carried out at different depths.

be, on average, smaller in size (Sardà et al. 1994). The size frequencies set out herein bear out that observation. Furthermore, the proportion of males increases (Sardà et al. 1993), with males being smaller than females as a consequence of this species' sexual dimorphism, as illustrated in Figure 5. These features lower the commercial attractiveness of the deeper shoals and cause the fishing trawlers to stay within the more commercially profitable depth range. Trawlers have never been recorded on the deeper portion of these fishing grounds (Sardà et al. 1998), suggesting that the shoal structure described here remains unchanged at this time of year. The literature contains no discussion of the role of this unexploited or pristine portion of the stock (below 1000 m) in relation to the exploited portion of the stock at shallower depths. Furthermore, stock assessment studies (Demestre & Leonart 1993, Martínez-Baños 1997, García-Rodríguez & Esteban 1999) have suggested that despite the high level of fishing pressure to which they are subjected as a target species, shrimp stocks are not overexploited. The stability of the population in the face of fishing pressure would seem to support the assumption that the stocks are replenished by

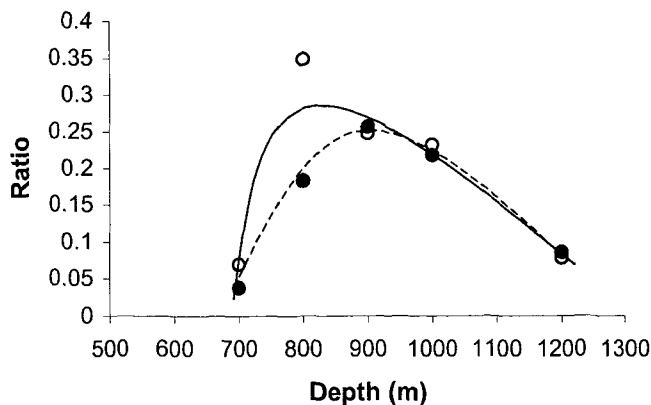


Figure 10. Ratios for the number of shrimp individuals in relationship to other species. Hollow circles, fishes (solid line); solid circles, crustaceans (dotted line).

an influx of individuals from the pristine populations located in deeper waters.

Based on the size frequency data, modal size at first maturity for males would appear to be in the neighborhood of 21 mm CL (Sardà & Demestre 1987, Sardà & Cartes 1997). Mean size of males appeared to be located mainly in the 800 m depth interval, where they coexist with sexually mature females. The implication is that mating takes place principally between adult females and two-year-old males around the time of first maturity (Demestre & Fortuño 1992), with smaller and larger males being less aggregated and mainly present at deeper depths, down to 1200 m (Sardà & Cartes 1997). To date there is no further evidence to suggest that these depths are recruitment zones or are subject to lower predation and thus are more conducive to juvenile development, as postulated for deep-water species by Gage & Tyler (1990).

There is little information on daytime and nighttime variations in catches, the only data available being provisional data for the Gulf of Taranto (Maiorano et al. 1999 and unpublished data), the area off Sardinia (Sabatini et al. 1999 and unpublished data), and the area off Algeria in North Africa (A. Campillo and A. Nouar,

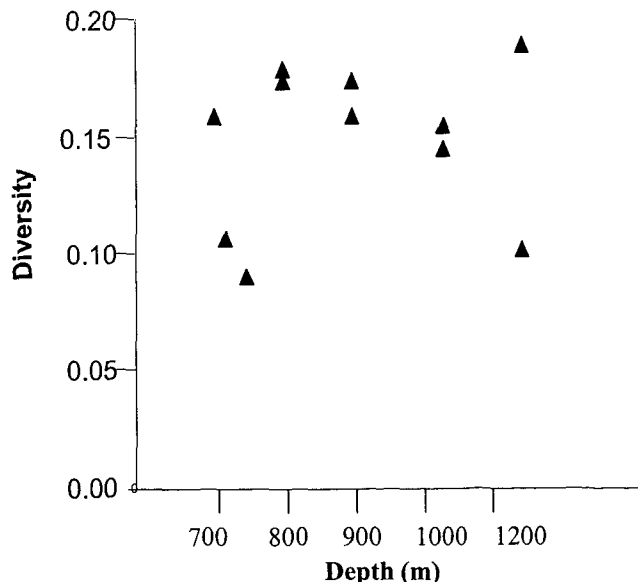


Figure 11. Plot of Simpson's diversity index by depth.



personal communications). The literature reviewed contains no further studies on this topic. According to the researchers just mentioned above, the shrimp population carries out nocturnal migrations up the depth profile and can thus be caught at shallower depths at night. A similar pattern was observed over the depth interval considered in the experiment reported here, with nighttime catches being somewhat higher than daytime catches and the difference peaking in shallower waters at around 800 m. The difference decreased with depth, suggesting the possible involvement of an effect related to light levels (directly or indirectly), with the population located at deeper depths thus being less affected by decreases in luminosity or by the effect of light on migratory mesopelagic organisms dwelling in the higher layers in the water column. Studies of stomach contents would be needed to be able to establish relationships between the vertical migrations of mesopelagic species and food availability at the different depths and in the water column. The present results corroborate the hypotheses described in Cartes et al. (1993). These authors observed that certain nektonic species seem to undergo migrations along the bottom to shallower areas of the slope at night. Moreover vertical migrations into the water column above would seem to be an unlikely explanation, in view of the small share of planktonic prey items in the nocturnal diet of *A. antennatus* (Cartes 1991).

The main question requiring elucidation is why shrimp shoals present the characteristic structure described, in terms of both shoal morphology and size and sex composition. The presence of a lower proportion of larger males and of females of different sizes with increasing depth might be attributable to the adaptation of the metabolisms of large individuals to deeper habitats, which are more oligotrophic and less favorable to high biomass levels composed mainly of reproductive females. An alternative hypothesis could be that adult females in advanced stages of gonadal maturity have certain nutritional requirements that are best filled at depths between 800 and 1000 m, where there may be some sort of environmental features at certain times of year that trigger the population structure observed. Puig et al. (2001) have proved this hypothesis for shrimps of the genus *Plesionika*. They observed characteristic distributions of berried and juvenile females at certain depths, associated with the presence of nepheloid layers in the same area in spring and fall. However, no such relationship has yet been demonstrated for *A. antennatus*.

Cartes & Sardà (1989) and Maynou & Cartes (1997, 1998) consider this species to occupy one of the lower positions in the benthopelagic food chain but to be atypical among deep-sea decapod crustaceans in that it exhibits a relatively high proportion of full stomachs as compared with other deep-sea decapod crustaceans. The high metabolic and growth rate demonstrated for this species by Company & Sardà (1998, 2000) is likewise indicative of this. Furthermore, more mobile species tend to have higher metabolic rates, that is, they have higher energy requirements, which translates into a higher daily ration (Koslow 1996). Given the reduction in food sources in deep-sea habitats, causing dietary overlap and competition for food (Gage & Tyler 1990), it seems reasonable to suppose that *A. antennatus* will have specific nutritional requirements during spawning and will therefore tend to adopt a distribution at optimum depths to fulfill those requirements. This could be one of the main reasons for the high level of dominance found for this species in the depth interval studied. In the Catalán Sea total consumption by bathyal decapod crustacean assemblages is higher on the upper middle slope (400–900 m) than

on the lower middle slope (900–1200 m). The generally lower food consumption by decapod crustaceans with depth is consistent with the commonly accepted notion that food availability also declines with depth, which holds both for the suprabenthos (one of the main sources of food for benthic decapod crustaceans) and for mesopelagic decapods and euphausiid crustaceans and other crustacean taxa (Carpine 1970, Cartes 1998, Cartes & Maynou 1998, Mura et al. 1998). The reduction in food resources takes place around the zonation boundary located at 900 m, with deep-water rose shrimp shoals being located above that depth.

Temperature did not appear to be a determining factor in these processes, in that temperature in the Mediterranean is constant at around  $13 \pm 0.5^\circ\text{C}$  below 200 m (Hopkins 1985), hence the population structure and behavior of *A. antennatus* can be considered temperature-independent. In the deep-water habitat that concerns us here, food availability in the deep-sea food web would seem to be the principal limiting factor (Gage & Tyler 1990).

In conclusion, the results of this study on the Catalan Sea, have specifically shown that the shoals of *A. antennatus* during the reproductive period has the following structure:

- (1) The pattern shrimp shoal distribution is such that density rises rapidly in the portion located in the shallower portion and then gradually decreases with greater depth;
- (2) The distribution of this resource straddles both sides of the ecological boundary located at 900 m, although with changes in the sex-ratio and individual size;
- (3) Species coexisting with this shrimp species are concentrated at depths other than the depths of peak shrimp density;
- (4) Commercial trawlers deploy according to the abundance pattern of the resource;
- (5) The reproductive portion of the stock is heavily exploited;
- (6) There is substantial evidence that ecological aspects need to be taken into account when evaluating the dynamics of exploited populations with a view to sustainable management.

On the whole, the following salient aspects would appear to merit consideration: Fishing on the shrimp stock takes place mainly during the season of aggregation and maturation of reproductive females, which heightens the population's vulnerability to fishing activity. This factor needs to be taken into account for purposes of assessment and management. Nevertheless, studies published by Demestre & Lleonart (1993), Martínez-Baños (1997), and Tursi et al. (1996) have reported the status of exploitation of this species to be near the maximum sustainable yield (MSY) in different parts of the Mediterranean Sea. This is where the unexploited portion of the stock inhabiting the lower-middle slope (from 900 m to at least 2200 m) comes into play. This portion of the stock may act as a reserve, contributing additional biomass to the exploited portion of the stock and thereby preventing overexploitation. However, it should be noted that this hypothesis has not yet been demonstrated and that studies focusing directly on this aspect are needed.

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