Deep-sea Shrimp *Aristeus antennatus* Risso 1816 in the Catalan Sea, a Review and Perspectives

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Abstract

The shrimp, *Aristeus antennatus*, is a species with a wide depth distribution in the Mediterranean Sea, ranging from 100 m to more than 3 000 m depth. This means that this species colonizes several habitats adapting their population structure and feeding habits to each of them, and finally adapting its life cycle to the colonized habitats (canyons, upper and middle slope – fishing grounds – and lower slope – virgin grounds). After more than 12 years of experience in research of this species in the western Mediterranean, new results are presented about the efficiency of the sampling gears used, and fished and virgin populations are compared. An increase in the abundance at around 1 400–1 500 m depth is also reported. *Aristeus antennatus* is an extraordinarily eurybathic species and was detected down to 3 300 m depth in a recent exploratory survey carried out in the Mediterranean Sea. Based on these observations three hypotheses about the possible exchange of individuals between fishing and virgin grounds are made. In the light of the discussion, new study perspectives are presented.

Key words: *Aristeus antennatus*, deep-sea, fishing grounds, Mediterranean, shrimps, trawling, virgin grounds

Introduction

The rose, blue or red[1] shrimp *Aristeus antennatus* Risso, 1816, is one of the most valued fishery resources in the Mediterranean Sea, and is characterized by a wide bathymetric distribution ranging between *ca.* 100 m and more than 2 200 m (Sardà and Cartes, 1993; Bianchini and Ragonese, 1994). There have been many studies of its biology, ecology and fisheries in the Mediterranean Sea (Bas, 1966; Massutí and Daroca, 1978; Relini Orsi and Relini, 1979; 1987; Orsi Relini and Relini, 1985; 1998; Sardà and Demestre, 1987; Demestre and Fortuño, 1992; Matarrese *et al.*, 1992, 1997; Aquastudio, 1996; Ragonese and Bianchini, 1996; Tursi *et al.*, 1996; Mura *et al.*, 1997; Martínez-Baños, 1997; D'Onghia *et al.*, 1997; García-Rodríguez and Esteban, 1999; Carbonell *et al.*, 1999). Recently, general studies covering its whole bathymetric range have been carried out in the western Mediterranean. (Cartes and Sardà, 1992, 1993; Sardà *et al.*, 1994). The wide bathymetric distribution of this species can be divided in two depth ranges, with well-differentiated characteristics. On the upper and middle slope, between 400 and 800 m deep, this species is under a high level of fishing pressure (fishing grounds) and the population is mainly composed of females (Demestre and Martín, 1993; Martínez-Baños, 1997; Tobar and Sardà, 1987). A well-known seasonal mobility pattern is present in this area (Sardà *et al.*, 1998a). On the lower slope, between 800 and 2 200 m depth, the density is lower, there is no fishing activity (virgin grounds), the sex proportions are not significantly different from 1:1 (Sardà and Cartes, 1993), and no information is available on seasonal population movements at these depths. The study of the life history of *A. antennatus* presents an interesting scenario: the fishing grounds are mainly occupied by females of high-density, large-sized individuals, while the virgin grounds are occupied by smaller-sized individuals at low-density. However, *A. antennatus* does not seem to be overexploited on its fishing grounds (Demestre and Lleonart, 1993; Tursi *et al.*, 1996; Martínez-Baños, 1997; García-Rodríguez and Estaban, 1999). Thus, considering the present status of knowledge of *A. antennatus*, the questions addressed are about the relationship and interaction between the exploited and virgin populations. The grounds below 1 000 m depth are beyond the reach of commercial fishing boats and we can assume that the shrimp populations are virgin at these depths.

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[1] The most common name in Spanish waters is rose shrimp (*gamba rosada*) (FAO, 1987).

These virgin populations have lower densities and higher proportion of males than the exploited populations.

After 12 years of experience in deep-sea biological studies of *A. antennatus*, the aim of this paper is to review the published data considering experimental catches below 1 000 m depth in the western Mediterranean (Catalan and Balearic Seas), to use all this knowledge in a comparative manner among depth intervals and discuss some new ideas about deep-sea *A. antennatus* populations. Three hypotheses about the relationship between the two populations are presented. The three scenarios are first set up and then discussed. Then with the application of a simulated analysis of the abundance and biomass of both populations, we suggest future perspectives of study.

Materials and Methods

A total of 196 hauls from thirteen exploratory surveys (twelve in the Catalan and Balearic sea and one including the Ionian deep-sea waters) on board of the R/V *García del Cid* (38 m length and 1 200 HP) between 1987 and 2001 (Table 1) were used in this review. Two trawl systems were used: OTSB-14 (Marinovich model, used by Haedrich and Horn, 1970 and Sulak, 1984, among others) for the five first cruises; and OTMS (used by Sardà *et al.*, 1998b) for the others. Both gears were trawled by means of a single cable. The OTSB-14 and OTMS have similar

overall dimensions, and a codend of 15 mm (stretched mesh) was used in both gears. Nevertheless, OTMS has a more modern design in terms of hydrodynamics. The main differences are lateral opening (OTMS: 13 m; OTSB-14: 8m), height (OTMS: 1.8 m; OTSB-14: 0.8 m), and length of bridles (OTMS: 32 m; OTSB-14.3 m). These dimensions were measured *in situ* with the remote acoustic system SCANMAR. The duration of the hauls was 1 hr or 1.5 hr. Because of the lack of SCANMAR at the beginning of the study the catch rates were standardized by hour of effective trawling for the comparison between OTSB-14 and OTMS. The data obtained with the OTSB-14 were only used to study biological parameters. Only quantitative OTMS trawl data was used to compare the abundance between exploited and virgin grounds, because this trawl system was considered more effective for the capture of this species (Sardà, 1998b). This avoided the calibration problems that arise when comparing different gears. The mouth opening of the OTMS trawl was measured using SCANMAR and the area swept by the trawl was computed. For the cruises using OTMS the results were expressed as standaridzed abundance as number of individuals per square nautical mile (nm^2). The standard biological measures taken as size (CL mm), weight (g), sex-ratio or maturity stages have been explained in previous papers (see Sardà and Demestre, 1987; Demestre and Fortuño, 1992). The overall data presented in this work have been obtained from: a) The previous publications of Sardà and Demestre, 1987; Sardà *et al.*,

TABLE 1. Sampling cruises and gears used in this study.

Gear-Cruise	Date	No. of hauls	Number ind. Caught	Sea of study
OTSB-14				
BATHOS II	September 1987	4	72	Catalan
BATHOS III	June 1988	23	151	Catalan
BATHOS IV	July 1988	11	147	Catalan
BATHOS V	October 1988	17	127	Catalan
ZONAP I	May 1992	23	405	Catalan
OTMS				
RETRO I	April 1991	8	1 745	Catalan
RETRO II	December 1991	9	1 021	Catalan
RETRO III	March 1992	9	732	Catalan
RETRO IV	July 1992	9	2 200	Catalan
BATMAN I	March 1994	26	2 696	Catalan
QUIMERA I	October 1996	21	1 724	Balearic
QUIMERA II	May 1998	11	1 219	Balearic
DESEAS	June 2001	25	483	Balearic and Ionian
Total	13 cruises	196	12 722	

1994; Sardà and Cartes 1992 and Sardà and Cartes, 1997; b) The results have been re-worked and combined with a view to obtaining new perspectives of study. The present work has involved the data from different cruises, combining them by depth strata or season and presenting them in comparative graphs. Only data taken on the same boat and with the same fishing gear have been used; c) The significance of the results has been tested by the appropriate statistical procedure, such as Student's *t*-test, ANOVA or Kolmogorov-Smirnov tests. The tests were not applied when the number of available individuals was very low. Data were mostly lacking in some deep strata, due to the low density of individuals in the bathyal zone or due to the difficulty of obtaining replicate samples at great depths.

An approximate estimation of the deep-sea shrimp abundances by means of the swept area method has been made using abundances from OTMS only. For this purpose a specific area has been defined in Catalan Sea, occupying a total surface of 1 740 nm^2 (Fig. 1). The surface of the fishing grounds (middle slope) has been estimated at 120 nm^2 and the surface of the virgin grounds (lower slope) at 1 620 nm^2. Estimates of the number of individuals were obtained from calculations of the mean densities obtained by commercial ships on the fishing grounds (between 400

and 800 m depth) and from the mean densities obtained by the research vessel on the virgin grounds (between 800 and 2 200 m depth). The biomass and density were referred to nm^2 extrapolated from the commercial boats on the fishing grounds and from the experimental OTMS surveys on the virgin grounds. The same methodology and proportional swept area were applied to both fishing gears because the OTMS, used by the research vessel, is a replicate of the gear used by commercial trawls in the region. The use of the research vessel for sampling below 1 000 m is obligatory, because, unlike to commercial fishing vessels, it is technologically adapted to work at these depths.

Due to the low density of individuals below 1 000 m and to the difficulty of sampling at great depths, samples were selected from cruises in different years corresponding to the months of gonadal development to build a composite year of monthly data. Combining consecutive months from different cruises to determine the percentage of mature females and size frequencies by depth stratum was the only way to compare successive time samples and to obtain preliminary results for these depths. The individuals caught in cruises made with the research vessel only were used to obtain biological data. In all cases, only representative samples have been used and small
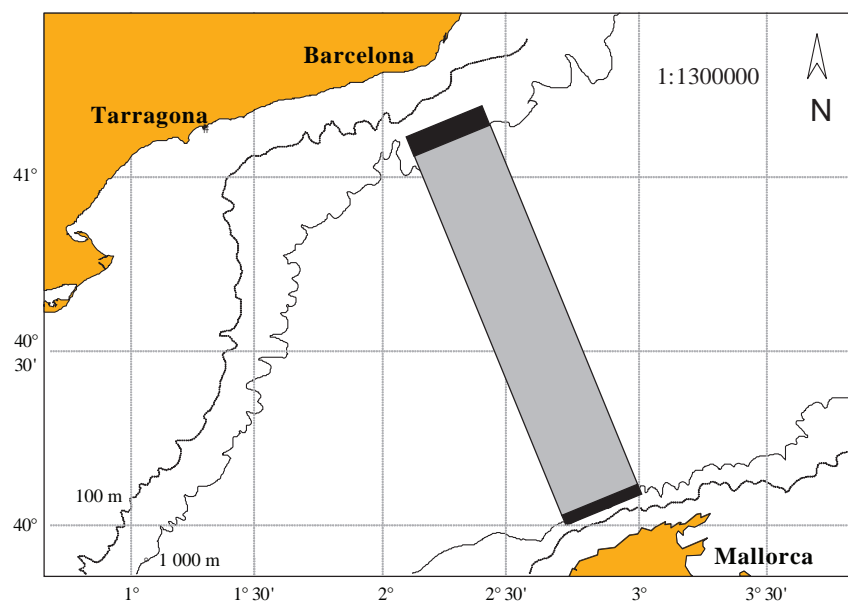

Fig. 1.   Study area on the Western Mediterranean. Rectangle represents the area where simulated abundances have been estimated. Grey rectangle, virgin grounds; black rectangles, fishing grounds.

dividuals of indeterminate sex have been excluded
from the analyses.

Results

The importance of the trawl system

The first deep-sea research cruises in the West-
ern Mediterranean used the OTSB (Marinovich) as
sampling gear and later this was replaced by the
OTMS. (Fig. 2, comparison between A–B and C–D).
The density estimates in Fig. 2A and B correspond to
catches obtained with the OTMS in the Catalan sea
from cruises shown in Table 1. A comparison between
the catches of the two sampling gears in the same
study area and the same season (Spring) showed that
the catch obtained with the OTMS gear was >5 times
greater than those obtained by the OTSB gear (corre-

sponding to the differences observed in Fig. 2, be-
tween A–C and B–D). The use of the OTMS on
Quimera II cruise (Spring, Balearic sea) identified an
important increase in the abundance of *A. antennatus*
at around 1 500 m (Fig. 2E). Deeper than 1 000 m
there is an overall decrease in biomass with depth (Fig.
2F). Correspondingly, the mean size decreases dras-
tically, such that different size frequencies can be ex-
pected to be present in the two populations. Despite
these interesting findings, these data need to be cor-
roborated with future sampling to determine if this is
a permanent phenomenon of this region.

Does female maturity change with depth?

The proportion of mature females by size-class
intervals, using data from all cruises in order to cover
different months between May and August, and only
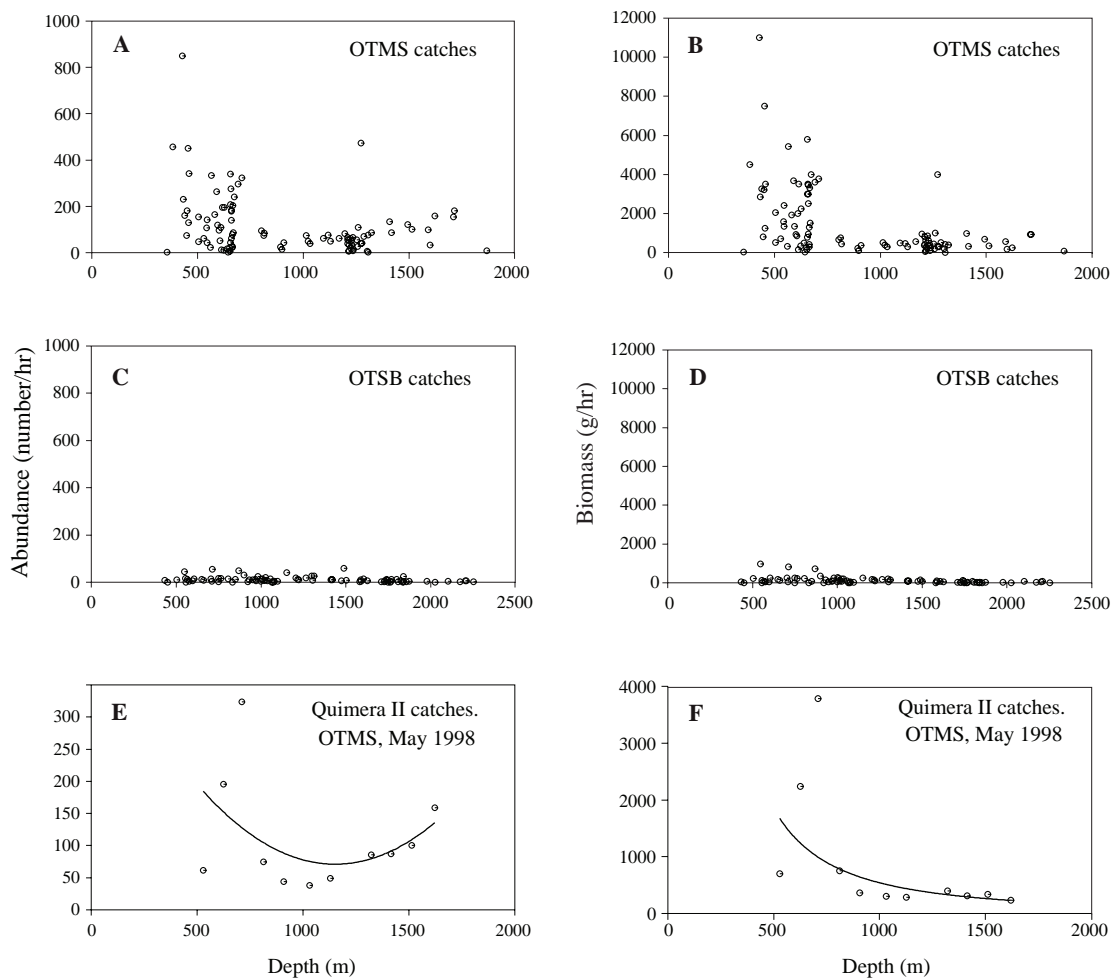considering maturity stages IV, V and VI, are shown

Fig. 2.   Bathymetric abundance and biomass of *A antennatus* captured by different gears. See letter references
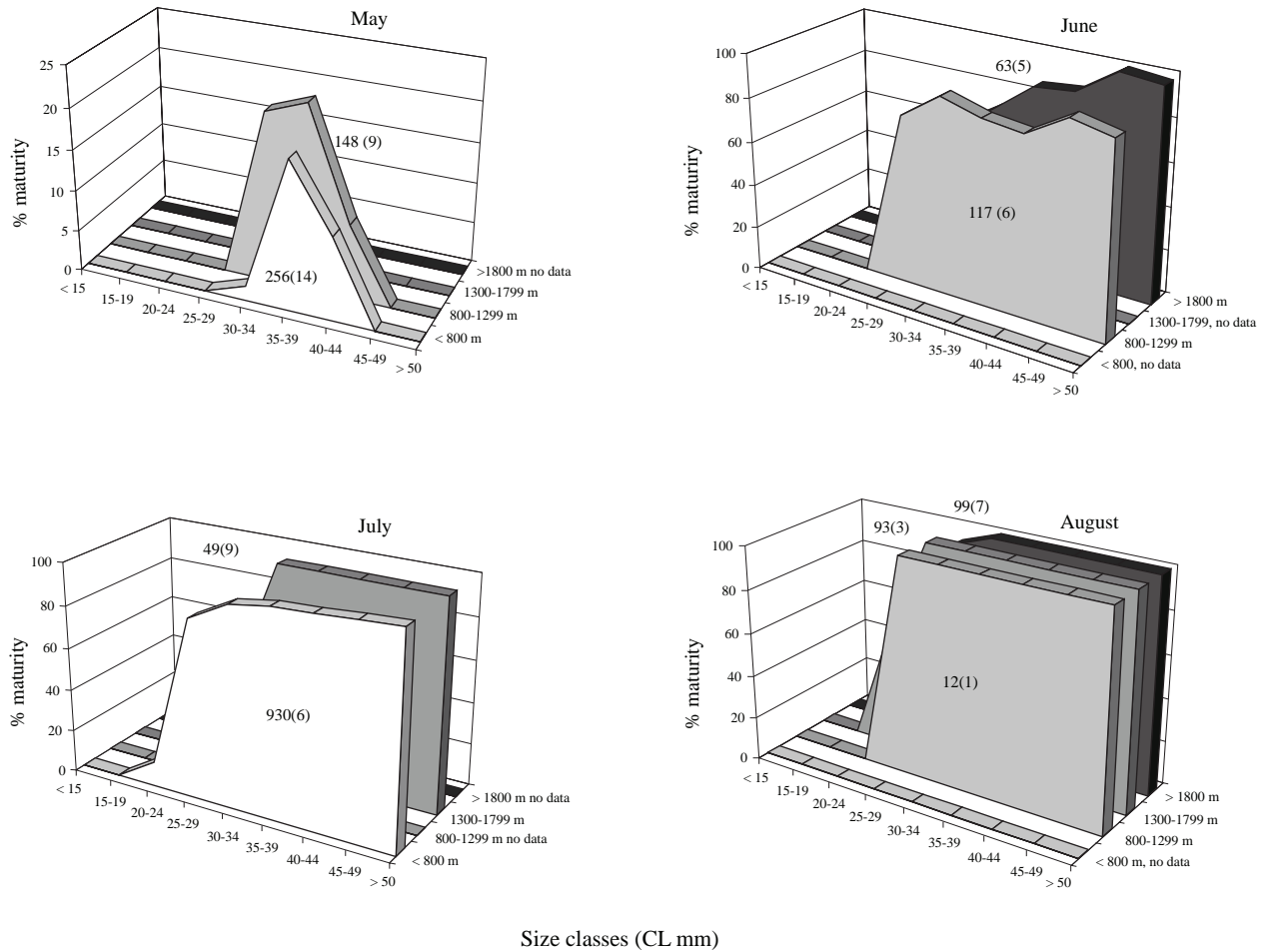in the text.

Fig. 3.   Percent of maturity stages (IV, V and VI) of *A. antennatus* during the maturity period by depth and size intervals.
Numbers are individuals analyzed. Between brackets, number of hauls by depth intervals.

in Fig. 3. The graphic shows that the percentages of mature individuals are similar at all depths. No significant differences were observed among them (Kolmogorov-Smirnov test, $p<0.05$). Due to the difficulties of obtaining these deep samples with a sufficient number of individuals for all months, some gaps at some depth intervals exist. However, these results did not reveal evidence of any variation on the reproductive pattern with depth, because they coincide with the reproductive period indicated by Sardà and Demestre (1987) for individuals at depths shallower than 800 m.

Sex-ratio

Shallower than 800 m depth the population is dominated by females (around 70%, Fig. 4A). Below 1 000 m, the sex-ratio changes and males dominate the population in a proportion of approximately 2:1, although this proportion is very variable. On the other

hand, shallower than 800 m (Fig. 4B), there are indications of seasonal variations. During the summer there was a major prevalence of females on the upper slope (400 m) and the middle slope (600-700 m). The different sex ratios shallower and deeper than 800 m were so large, that a statistical test was not considered necessary.

Size distributions: are there different growth patterns with depth?

The preliminary study of the modal progression in the size distribution with depth (Fig. 5) indicates that the larger individuals were concentrated in shallower waters (<800 m) and consisted mainly of adult females with a wide and frequently unimodal size distribution. The largest proportion of small individuals (<20 mm CL) were most frequently on the deepest grounds (>1 000 m depth), and the highest concentration of smallest sizes (<15 mm CL) were at depths
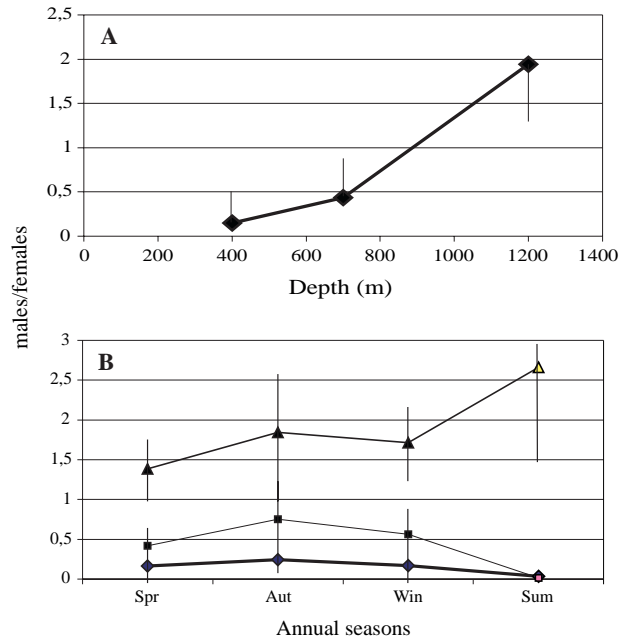
Fig. 4.   **A**) sex-ratio of *A. antennatus* by different depth intervals. **B**) sex-ratio by different seasons and depths: diamonds, 400 m; squares, 700 m; and triangles, 1 200 m.

below 1 500 m. The modal progression of females can be followed by eye through different depths zones (Fig. 5), and no evidence of different growth patterns of females among the depth zones was observed. A progression line can be drawn that follows the first cohort until it attains 24 mm CL. However, the small number of individuals in some samples (due to the low density and sampling difficulties at the greatest depths), precludes the application of a statistically valid modal size frequency analysis. Nevertheless, it provides the opportunity to study the size frequency over a very wide range distribution and for previously unknown depths.

What do we know about recruitment?

The first recruitment signal was observed in March, at around 1 200 m depth, with the occurrence of individuals between 11 and 12 mm CL (Fig. 5). They probably correspond to the individuals of 6 mm of CL that can be caught in December (Sardà and Cartes, 1997) at 1 200 m depth; the peaks can be followed in females through time until the individuals attain sizes of 22–24 mm CL, which correspond approximately to one-year old. The pattern appears very marked in the deep-sea (dotted and black histograms), differentiating their distributions from the individuals from the fishing grounds (unshaded histogram)

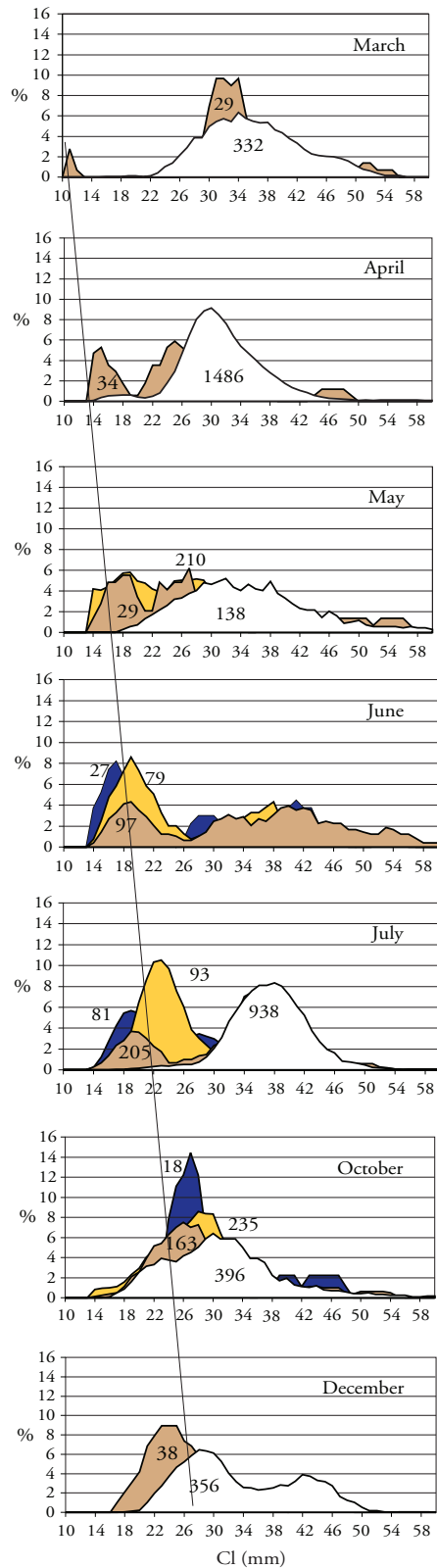Fig. 5.   Female size frequencies distribution of *A. antennatus* by depth. White, <800 m; tan, 800–1 299 m; yellow, 1 300–1 799 m; and navy, >1 800 m. Number represents individuals measured.
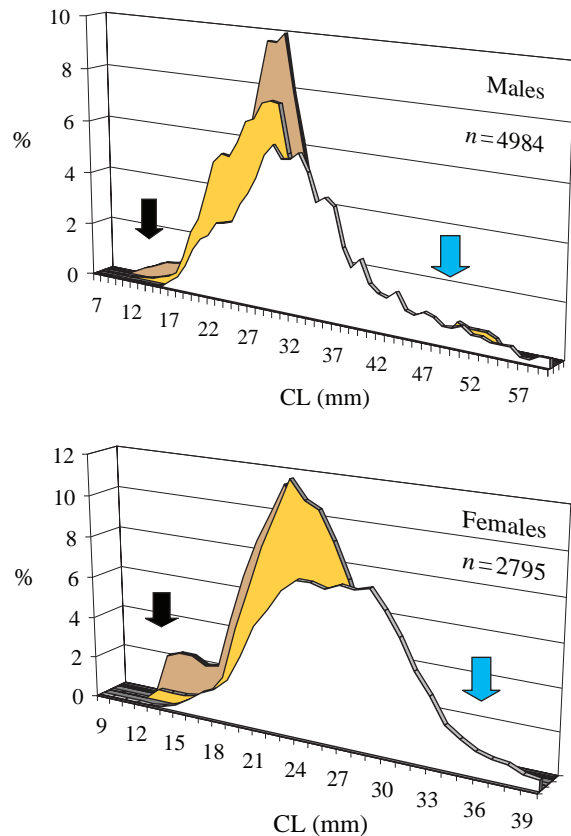
Fig. 6.   Total size frequency distributions of *A. antennatus* by depth and sex. Unshaded, <1 000 m; yellow, 1 000–1 500 m; tan, >1 500 m. Black arrow, juvenile in deep samples. Blue arrow, adult individuals in shallow waters.

(Fig. 6 shows the annual size frequencies). On the other hand, Mura *et al.* (1997) found small individuals between 500 and 550 m depth, but these authors did not work at greater depths and thus could not study the complete size frequency in the Tyrrhenian Sea or the relative importance of small individuals at greater depths.

Discussion and Conclusions

Aristeus antennatus is a eurybathic species with the widest depth distribution observed in the Mediterranean for any megafaunal species, including fishes and cephalopods (Sardà, 2001). This species must have a strong adaptative plasticity, adapting its life cycle to different habitats where energetic supply diminishes with depth. Although some biological parameters such as reproduction and growth can be similar at different depths, other parameters such as density, mean size or sex-ratio vary greatly. In this context, we suggest that the physiology of this species

(growth, reproduction) does not vary in the different habitats occupied (i.e. no evidence of local adaptations). However, this species is adapted to the energy available at different depth ranges by adapting its population structure, density and individual size, and also concentrating its reproductive potential and recruitment to specific depth ranges, more favourable to the success of specific processes of its life cycle (population adaptations).

On the other hand, considering the existence of an exploited population shallower than 1 000 m depth (fishing grounds) and a virgin population below this depth, it is worthwhile to investigate the relationships between the different bathymetric populations of this species and whether there is exchange among the populations. Three simple hypotheses for the exchange of individuals between fishing grounds and virgin grounds are presented, assuming that there are different levels of exchange between both populations and that fishing mortality is constant for the fished populations:

Hypothesis 1: The number of individuals on the fishing grounds is larger than the number of individuals on the virgin grounds.

- The exchange of individuals flows from fishing grounds to virgin grounds.
- The virgin population from the lower slope grounds does not contribute to the maintenance of the fishing population.
- The fished population would ultimately become overexploited

Hypothesis 2: The number of individuals on the fishing grounds is equal to the number of individuals on the virgin grounds.

- There is an exchange of individuals between fishing grounds and virgin grounds in both directions. Each population contributes to their mutual maintenance.
- The fished population would be in equilibrium.

Hypothesis 3: The number of individuals on the fishing grounds is smaller than the number of individuals on the virgin grounds.

- The exchange of individuals flows from virgin grounds to fishing grounds
- The virgin population from the lower slope grounds contributes to the maintenance of the fishing population
- The fished population would be permanently underexploited

In order to determine which of the three hypotheses is more likely to correspond to the current situation, an approximate estimation of the shrimp biomass and abundance over the fished grounds (total area: 120 nm^2) and in the wide virgin area between Barcelona coast and Mallorca, Balearic Islands (total area: 1 620 nm^2) was made (see further details on Materials and Methods section). According to previous results, we took into account the fact that it is in the exploited areas where most of the adults and reproductive females occur (Sardà *et al.*, 1994). A very approximate average trawl catch was estimated. The catch rates were 200 individuals/h (183 kg/nm^2 and approximately 4 000 ind/nm^2) on the fishing grounds and 70 individuals/h (12 kg/nm^2 and approx. 1 000 ind/nm^2) on the virgin grounds. Therefore the overall number of individuals occupying the whole area of the non-exploited grounds is about three times the magnitude (1 000 ind/nm^2 per 1 620 nm^2 equals at approx. 1 620 000 individuals) when compared with the number of individuals of the whole surface area covered by the fishing grounds (4 000 ind/nm^2 per 120 nm^2 equals at approx. 480 000 individuals; see Fig. 7), but the total biomass is similar between the two areas (virgin grounds: 19 440 kg; fishing grounds: 21 960 kg; Fig. 7).

This represents a situation closely resembling hypothesis 3. However, the female proportion and the female mean size, as indicated in the previous results of this study, decrease drastically with depth. Note that these estimations are very approximate and do not have any statistical significance. They must be interpreted as a general approximation to the reality while more accurate data are expected. Nevertheless, this data have the importance to be the first data available on deep-sea densities.

The data presented in this review give a global picture of the population structure of the deep-sea shrimp over its whole depth distribution in the Catalan Sea. The aim was to compile information from differ-

ent research cruises, which when considered separately yield limited results, but when combined, can provide interesting insights and suggest future research lines. Future studies should be focused towards the following topics, among others:

1) In spite of important structural differences in the mean size (decrease with depth) and in the sex-ratio (proportion of males increasing with depth) in the deepest populations, there are no isolated populations with differentiated growth patterns and there is no evidence of non-coincident reproductive periods. It is therefore assumed that the pattern of metabolic processes responsible for the growth and control of reproduction does not vary with depth.

2) The authors suggest that there is a population adaptation in terms of abundance and size composition to the energy available on the sea floor (Company and Sardà, 1998 and Puig *et. al.*, 2001). The shrimp population from the upper slope (fishing grounds) receives five times more energy input (of organic carbon) than the individuals inhabiting the virgin grounds (5 g org C m^{-2} y^{-1} to 200 m; 1.2 g m^{-2} y^{-1} to 2 000 m in Western Mediterranean) (Miquel *et al.*, 1994). The distribution of the quality and quantity of the scarce food resources in the deeper waters is not enough to modify the reproductive endogenous rhythm or the growth rate. It is suggested that a density-dependent compensation exists, in the sense that the available food can maintain enough basal metabolism to complete the vital cycles in the individuals that inhabit the virgin grounds, at the expense of small size and lower density.

3) It is suggested that the deep-sea shrimp follows the general models reported by Gage and Tyler (1990), that prevents competitive exclusion, by promoting high size diversification to resource partitioning, or that the juvenile individuals are subject to low predator pressure. This could ex-
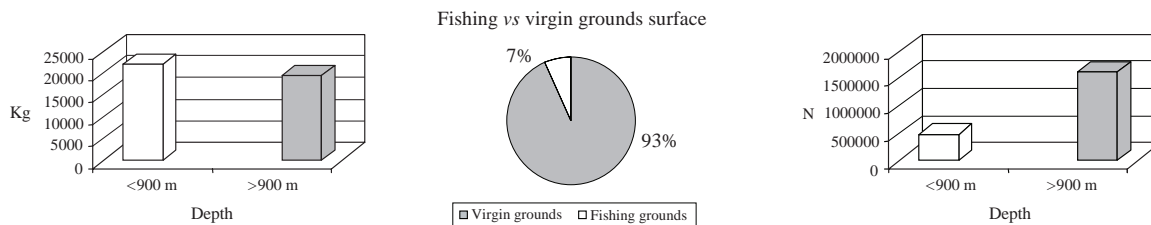

Fig. 7.   Total biomass (kg) and total abundance (N) of *A. antennatus* over the fishing grounds (total surface: 120 nm^2) and over the virgin grounds (total surface: 1 620 nm^2) (see also Fig. 1).

plain the high abundance of small individuals at the greatest depths, jointly with the energetic hypothesis presented by Puig *et al.* (2001).

4) The results of this study appear to support hypothesis 3. However, due to the fact that: i) the maximum reproductive population occurs in the exploited areas, ii) the virgin biomass from the virgin grounds presents very limited reproductive capacity and iii) in the absence of knowledge on migrations between different depths (which have yet not been demonstrated), we should apply the Precautionary Principle to protect exploited populations and avoid exploiting waters deeper than 1 000 m in Mediterranean Sea.

5) The enzymatic analyses carried out by Sardà *et al.* (1998c), provide evidence that there is sufficient genetic flow to consider that *A. antennatus* is a homogeneous population in the whole Mediterranean basin. Therefore, there is no reasonable indication at the moment, to allow us to expect that Mediterranean sub-populations can be considered as a metapopulation, in a global ecological context. Future studies that investigate the flux of individuals among populations should be encouraged.

6) Given the gaps of knowledge in the aspects related to the larval distribution and mobility among virgin and slope grounds, an increase of the scientific effort in these fields should be encouraged in future studies.

We can thus confirm that *A. antennatus* is a deep-sea shrimp with a wide bathymetric range, which can be found from relatively shallow waters (since 80–100 m, FAO, 1987; Relini, *et al*., 2000; Nouar, 2001) to deep-sea waters (at least 2 200 m depth Sardà *et al.*, 1994, and 3 300 m from Sardà, 2001). The Mediterranean has not been adequately sampled at greater depths, and it is possible that it has an even deeper distribution. No reference exists for any other species of crustacean (fish or cephalopods) covering such a huge bathy-metric range. For these reasons, the authors consider this species as of great interest and its scientific study should be given priority for three main reasons: first, for the limited knowledge existing between the exploited and the unexploited population fractions; second, for the existing shortcomings in the knowledge of its real distribution and its ecological role in deep-sea environments, coupled to its contribution to biodiversity in the Mediterranean sea; and third, for the enormous possibilities that the study of

its metabolism can contribute to the knowledge of the adaptive processes in deep-sea organisms.

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