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Deep-sea distribution, biological and ecological aspects of *Aristeus antennatus* (Risso, 1816) in the western and central Mediterranean Sea*

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SUMMARY: The object of the DESEAS Project, funded by the EC, was to gather preliminary data on the abundance and maximum depth distribution of the rose shrimp *Aristeus antennatus* in the Mediterranean Sea. An exploratory survey was therefore designed with that goal in mind and conducted on the R/V *García del Cid*, sampling the maximum depths in three specific areas in the central and western Mediterranean, one off Ibiza (Balearic Islands), one off Calabria (western Ionian Sea), and one off the southern Peloponnesian Peninsula (Gulf of Kalamata, eastern Ionian Sea). The depths sampled ranged from 600 to 4000 m, with specimens of *A. antennatus* being collected down to 3300 m. There were three distinct boundaries marking the abundance of this species: < 1000 m, relatively high abundance (up to 1000 ind km^{-2}); 1000-1500 m, relatively moderate abundance (up to 300 ind km^{-2}); and > 1500 m, relatively low abundance (<100 ind km^{-2}). The known population structure of this shrimp species, with increasing proportions of males and juveniles with depth, was also recorded in the deep-sea regions in other areas of the Mediterranean. No evidence of any differences in gonad development or in the presence of spermatophores carried by females was found in any of the three sampling areas. Lastly, a tendency for the relative proportion of juveniles to increase with depth was also observed.

Key words: *Aristeus,* Mediterranean, deep-sea, shrimp, crustaceans.

RESUMEN: DISTRIBUCIÓN PROFUNDA, ASPECTOS BIOLÓGICOS Y ECOLÓGICOS DE *ARISTEUS ANTENNATUS* (RISSO, 1816) EN EL MEDITERRÁNEO OCCIDENTAL Y CENTRAL. – El objetivo del proyecto DESEAS, financiado por la CE, fue obtener datos preliminares de abundancia y distribución de profundidad máxima de la gamba rosada *Aristeus antennatus* en el Mar Mediterráneo. El diseño de la campaña exploratoria fue realizado con este propósito y se desarrolló a bordo del *B/O García del Cid*. Se realizaron muestreos en las máximas profundidades de tres áreas específicas en el Mediterráneo occidental y central: una cerca de Menorca (Islas Baleares), otra frente a las costas de Calabria (Iónico occidental) y la última al sur de la península del Peloponeso (en el Golfo de Kalamata, Iónico oriental). Las profundidades muestreadas fueron las comprendidas entre 600 y 4000 m, obteniendo individuos de *A. antennatus* hasta 3300 m. Se detectaron tres niveles de abundancias diferenciados en esta especie: < 1000 m, relativamente muy abundante (hasta 1000 ind km^{-2}); 1000-1500 m, abundancia relativamente moderada (hasta 300 ind km^{-2}); > 1500 m, relativamente poco abundante (< 100 ind km^{-2}). En las tres áreas estudiadas se confirmó la estructura de la población conocida hasta el momento, es decir, aumento de la proporción de machos y juveniles con la profundidad. No se encontraron evidencias de diferencias en el desarrollo gonadal o en la presencia de espermatóforos de las hembras entre áreas. Finalmente se observó la existencia de una tendencia en el aumento de la proporción de juveniles con la profundidad.

Palabras clave: Aristeus, Mediterráneo, mar profundo, gamba, crustáceos.

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INTRODUCTION

During the last ten years a variety of aspects of *Aristeus antennatus* (Risso, 1816) have been studied in detail in the western and central Mediterranean Sea, such as fisheries (Demestre and Lleonart, 1993; Demestre and Martín, 1993; Bianchini and Ragonese, 1994; Martínez-Baños, 1997; Sardà *et al.,* 1998a; García-Rodríguez and Esteban, 1999; Carbonell, *et al.,* 1999, 2003; Ragonese *et al.,* 2001; Mytilineou *et al.,* 2001; Papaconstantinou and Kapiris, 2001; Cau *et al.*, 2002; Tudela *et al.,* 2003), biology (Matarrese *et al.,* 1992, 1997; Sardà and Cartes, 1993; Ragonese and Bianchini, 1996; Mura *et al.,* 1997; Follesa *et al.*, 1998; Orsi Relini and Relini, 1998; Sardà *et al.,* 1998b; Kapiris *et al.,* 2002; García-Rodríguez, 2003), ecology (Sardà *et al.,*1994; Sardà and Cartes, 1997; D'Onghia *et al.,* 1997; Cartes and Maynou, 1998; Mura *et al.,* 1998; Kapiris *et al.,* 1999), and physiology (Company and Sardà, 1998; Puig *et al.,* 2001). A number of research projects have been carried out on this species recently (RESHIO, COCTEL, DESEAS, INTERREG II, MEDITS, MEDBARI, MED-AQUA...). The species distribution in the Catalan Sea (western Mediterranean) tends to take the form of elongate shoals concentrated at depths between 700 m and 1000 m along the continental slope in winter and spring (Sardà *et al.,* 2003a). The shoals are made up of mature adult females during spring and early summer in deep-waters. From mid-summer and throughout autumn, catches in fishing grounds located on the margins of submarine canyons increase and are made up of smaller individuals (Sardà *et al.,* 1994; Tudela *et al.*, 2003; Sardà *et al.,* 2003b). In the Mediterranean, this species may be fished from depths of 80 m along the Algerian coast at night (Nouar, 2001), with more abundant distribution between 400 m and 800 m in Tyrrhenian waters (Aquastudio, 1996). Its distribution ranges between 100 and 150 m and nearly 1000 m in the western Ionian Sea (south Italy, Tursi, 1996; Relini *et al.*, 2000), down to 800 in the eastern Ionian (Papaconstantinou and Kapiris, 2001; Mytilineou *et al.*, 2001) and between 900 and 1000 m off Catalonia (Tobar and Sardà, 1987; Demestre and Martín, 1993; Sardà *et al.*, 1998a; Tudela *et al.*, 2003). However, experimental catches of this species (Sardà and Cartes 1993; Cartes and Sardà, 1992, 1993) have been made to a depth of 2250 m. This broad depth distribution range for this species has led to a number of hypotheses concerning its ecology and possible relationships between the exploited populations on the upper and middle slope and the non-exploited populations dwelling deeper on the lower slope (Sardà *et al.,* 2003b). In addition, it has raised the need to establish the full depth distribution range for this species, for two reasons: first, to be able to improve the assessment of the resource over its entire habitat and second, to improve the basic knowledge on reproduction and recruitment, which might differ with depth and location. The current status and state of knowledge can be summarised as follows:

It is a eurybathic species, with a known depth range prior to this study ranging between 80 and 2250 m, and with high abundances around 700 m.

It is known that carry out temporal movements between the open slope and the margins of submarine canyons.

Its biology (reproduction, sex-ratio, feeding habits, and population dynamics and fisheries) is relatively well known down to 800 m, where fishery occurs.

As a result, the distribution and population dynamics for this species are well known within its area of exploitation, but they are very poorly understood in other. Still, it is quite clear that there is interaction between the exploited stock and the virgin stock (Sardà, 2003b) and that this aspect needs to be addressed for proper overall management of the resource. However, the energy requirements necessary to support the life cycle of this species in each of the habitats in which it dwells are completely unknown. These requirements are most likely the ultimate cause of the spatio-temporal fluctuations recorded in the margin of the canyons and the characteristics of the population structure of this species in the bathyal deep-sea grounds (Puig *et al.,* 2001).

The first objective of this paper is to determine the maximum depth distribution of *Aristeus antennatus* and compare its abundance between different Mediterranean areas. A second objective is to compare biological aspects among these distant populations in order to determine latitudinal effects on structure of populations. The last objective tries to establish a relationship between the environmental parameters, temperature and salinity in the water column and the density of shrimps from the different three areas explored: the Balearic, western Ionian and eastern Ionian Seas.

An exploratory survey in these three areas, was therefore designed with these objectives in mind. This paper presents the results of the survey and dis-

TABLE 1.- Haul characteristics.

Area	Haul	Date	Depth (m)	Initial position Latitude	Longitude	Haul duration (h)
Balearic	0	06.06.01	1200	40º48'30"	1º48'13"	1.30
	1	07.06.01	600	38º36'51"	1º53'29"	1.16
	2	08.06.01	800	38º30'13"	1º49'12"	1.06
	3	08.06.01	1000	38º28'47"	1º53'20"	1.40
	4	08.06.01	1500	38º17'15"	1º48'10"	1.13
	5	09.06.01	2500	38º15'57"	2º21'10"	2.28
	6	10.06.01	2800	38º04'01"	5º27"04"	2.30
W. Ionian	7	14.06.01	600	38º18'50"	16º37'28"	1.11
	8	14.06.01	800	38º16'56"	16º37'32"	0.95
	9	15.06.01	1000	38º15'11"	16º34'44"	1.48
	10	15.06.01	1500	38º10'16"	16º38'34"	2.00
	11	16.06.01	2000	37º42'18"	16º40'07"	1.16
	12	17.06.01	1500	38º12'07"	16º43'52"	1.08
	13	18.06.01	1200	32º13'58"	16º35'17"	0.33
	14	18.06.01	1700	38º06'13"	16º42'10"	1.45
Abyssal	24	01.07.01	4000	35º41'51"	17º47'00"	3.00
	25	02.07.01	3300	36º08'21"	16º32'09"	2.00
E. Ionian	15	22.06.01	600	36º47'46"	22º04'29"	1.00
	16	22.06.01	800	36º51'52"	22º06'16"	1.05
	17	22.06.01	1300	36º42'52"	22º10'25"	1.00
	18	23.06.01	2200	36º32'17"	22º01'46"	2.15
	19	23.06.01	2600	36º21'05"	22º00'06"	1.30
	20	24.06.01	1100	36º44'49"	22º07'32"	1.15
	21	25.06.01	1700	36º24'06"	22º14'06"	1.30
	22	26.06.01	800	36º51'39"	22º06'12"	1.15
	23	26.06.01	600	36º47'43"	22º04'28"	1.30

cusses the ecological implications for this singular eurybathic species in the Mediterranean.

MATERIALS AND METHODS

An international exploratory fishing survey (DESEAS) was carried out on board the R/V *García del Cid* from 6 June to 2 July 2001. The research vessel measured 38 m in length and had a power rating of 1500 HP. A total of 25 effective hauls were completed in three areas in the western and central Mediterranean Sea (Table 1, Fig. 1). These areas were the Balearic Sea (southeast of the Island of Ibiza); the western Ionian Sea off Calabria, in Italy; and the Gulf of Kalamata in the eastern Ionian Sea, off the southern Peloponnesian Peninsula. Two additional exploratory hauls were carried out in the abyssal trench in the western Ionian Sea at depths of 3300 and 4000 m. Fishing was

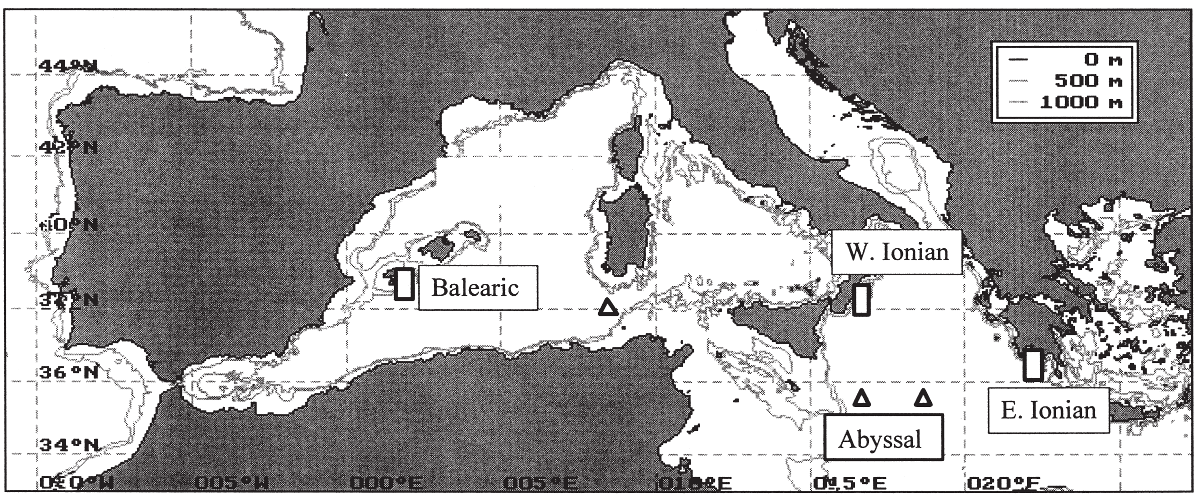

FIG. 1. – Sampling locations in the Mediterranean Sea.

carried out using a *Maireta* (OTMS) trawl gear towed by a single 12 mm-diameter warp ending in a crowfoot which was connected to two bridles (100 m), each of which was in turn connected to an otter board weighing 340 kg and measuring 205 cm x 120 cm (Sardà *et al.,* 1998c). Codend mesh size was 40 mm stretched covered by a codend cover with a mesh size of 12 mm stretched. Trawling depths were selected based on the topography of the bottoms available for trawling, and a previous exploration with a sounder was necessary since most trawls were carried out in unexplored areas for which no prior fishing experience was available. Because the bottom is volcanic in the central Mediterranean, it proved extremely difficult to find areas of bottom suitable for trawling.

The specimens making up the catches were counted, separated by sex, and measured at cephalothorax length (CL mm). Sexual development stage was assessed according to the gonad colour using the scale proposed by Demestre and Fortuño (1992) based on gonad colour, and recorded. Towing time varied according to depth and the projected yield for each haul. Density (number km^{-2}) and biomass (g km^{-2}) were calculated by the swept area method based on measurements of gear opening width obtained using remotely controlled SCANMAR sensors and the mean speed for each haul, down to a depth of 1500 m, depth on which the sensors fail because of the hydrostatic pressure. Gear opening width was assumed to be the same below that depth, because previous measurements showed that there were no variations in width between 600 and 1500 m, most likely due to the action of the crowfoot (Engas and Ona, 1991). Haul depths were previously selected in 500 m depth. Though some species occur in very low numbers, these specimens are of great importance due to the paucity of individuals in the bathyal and abyssal zones. Density and biomass were plotted by depth and area, as were the percentage size, sex-ratio, and gonad maturity stage values. The Kruskal-Wallis non-parametric test was used to demonstrate significant abundance differences between strata, and a post hoc test was used to identify differences between adjacent depth intervals. In the plots, individuals smaller than 20 mm CL were considered juveniles for both sexes, since these lengths encompass immature males and females as a compromise between the opinions of different authors (Demestre and Fortuño, 1992; Sardà and Cartes, 1997; Mura *et al.,* 1997).

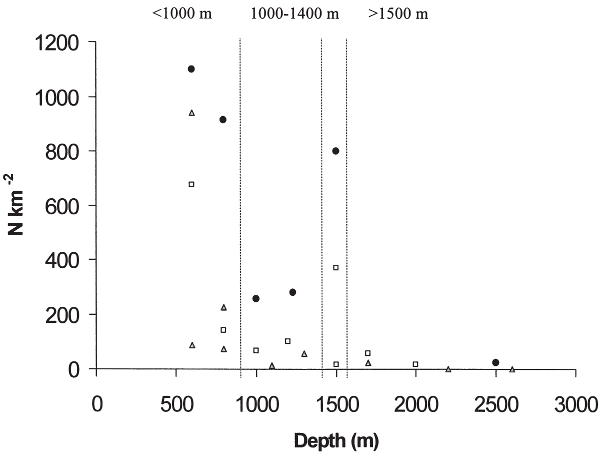

FIG. 2. – Density of *A. antennatus* by depth for all samples combined. Broken lines separate the depth ranges compared. Circle, Balearic Sea; square, western Ionian Sea; triangle, eastern Ionian Sea.

Temperature and salinity profiles were obtained at each haul using a CTD. These data are presented and discussed in Politou *et al.,* (2004), together with data on *Aristaemorpha foliacea*.

RESULTS

Total abundance in number of individuals of *Aristeus antennatus* per km^2 exhibited peaks between 600 and 800 m and then fell off sharply below 1000 m (Fig. 2). Between 600 and 800 m there were large fluctuations in abundance from 1100 ind km^{-2} to 38 ind km^{-2}. Abundance did not exceed 300 ind km^{-2} from 1000 to 1500 m, where it increased again to 800 ind km^{-2}. Below 1500 m the number of individuals dropped appreciably, and abundance did not exceed 50 ind km^{-2} down to 3300 m, where estimated abundance was 11 ind km^{-2}. At

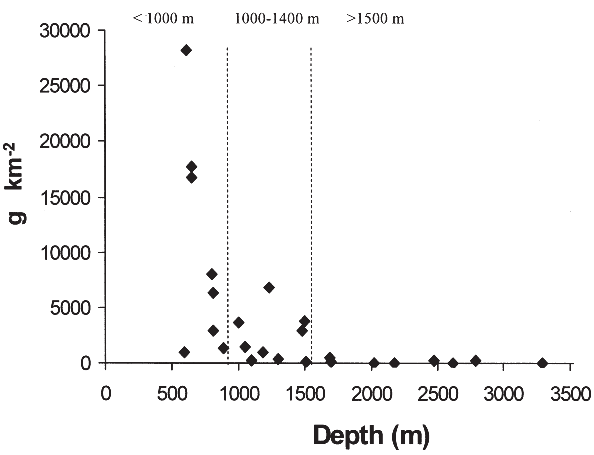

FIG. 3. – Biomass of *A. antennatus* by depth. Broken lines separate the depth ranges compared.

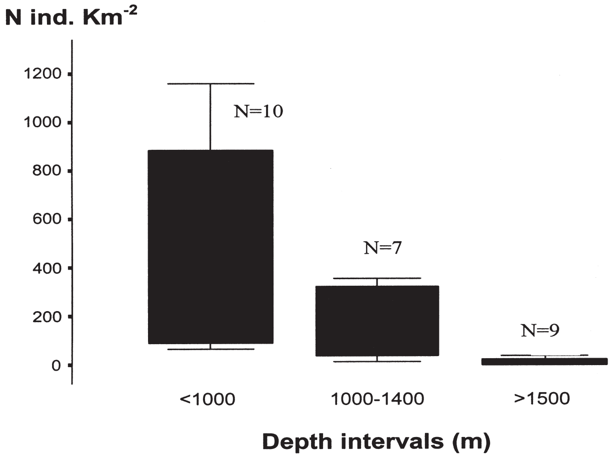

FIG. 4. – Box-plot diagram for the Kruskal-Wallis significance test for the depth ranges compared for all samples combined (X^2 = 14.645; $p < 0.05$). Thick black line, average; rectangle, 75% of the standard deviation; horizontal lines, standard deviation. N, number of samples

1500 m a peak of abundance was detected, as previously found by Sardà *et al.* (2003).

Biomass distribution followed a similar pattern, except at 1500 m, where the weight of the individuals captured was lower than that of individuals taken on the middle slope (Fig. 3).

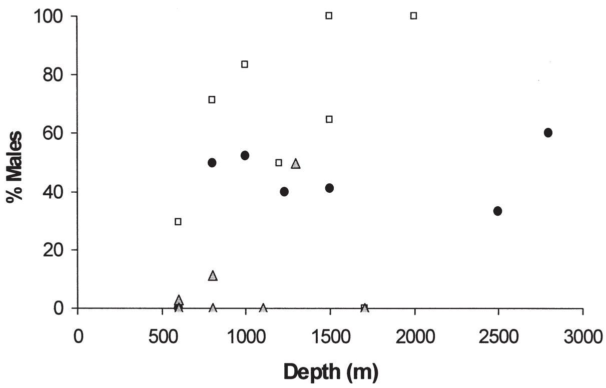

FIG. 5. – Percentage of males by depth for the three sampling areas. Circle, Balearic Sea; square, western Ionian Sea; triangle, eastern Ionian Sea.

The Kruskal-Wallis test yielded significant differences of abundance between the three strata (X^2 = 14.645; $p < 0.05$) (Fig. 4). The overall distribution pattern for males and females separately was similar to the pattern reported for total abundance (Fig. 5). Females outnumbered males at the shallower depths, with the numbers of males increasing to a sex-ratio around 1:1 at depths below 1000 m. The figure reveals a mean percentage of males of around

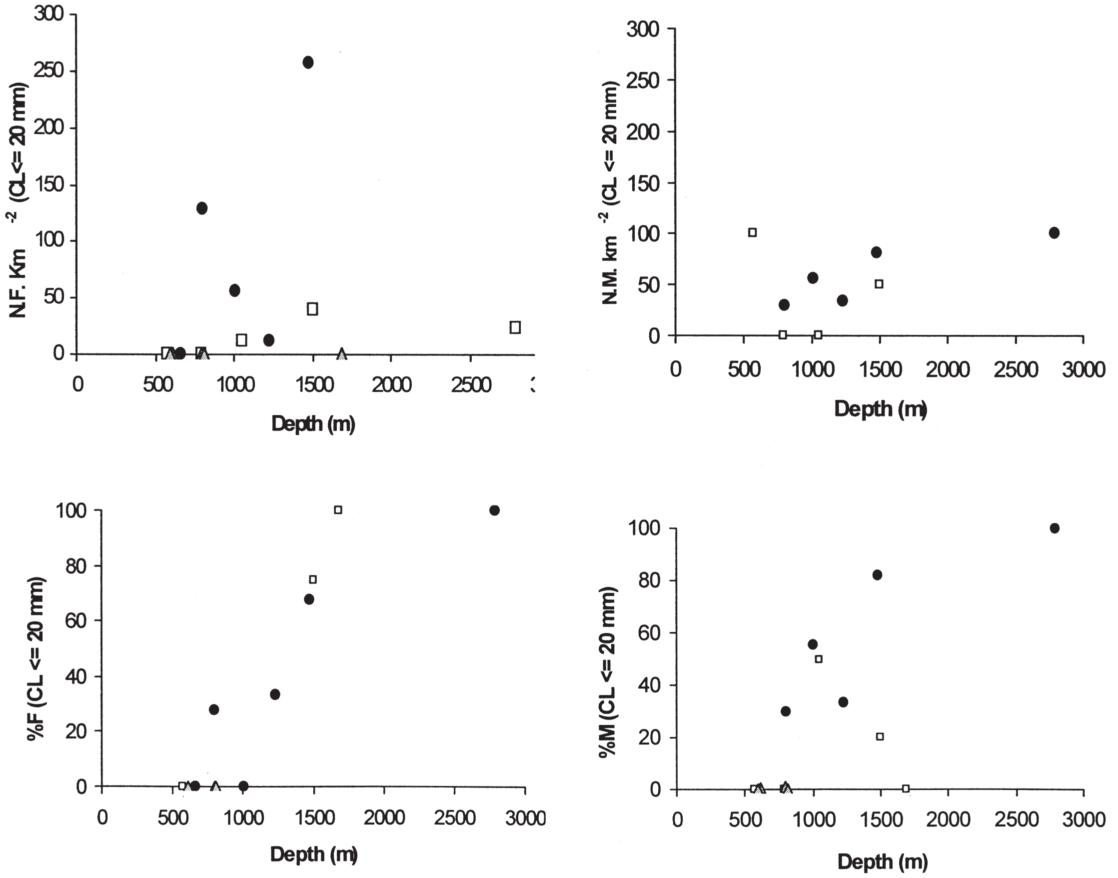

FIG. 6. – Density and percentage of juveniles (CL < 20 mm) by depth for the three sampling areas. Circle, Balearic Sea; square, western Ionian Sea; triangle, eastern Ionian Sea.

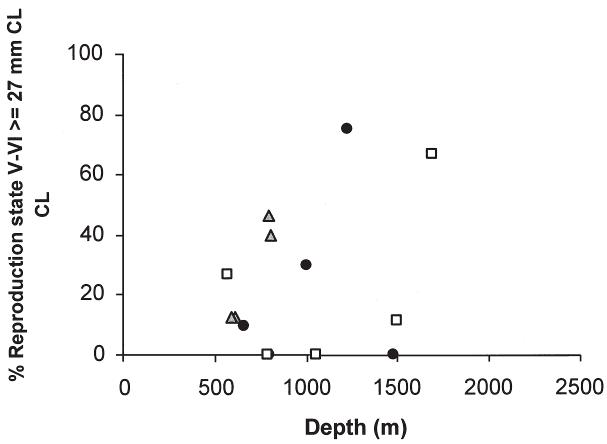

FIG. 7. – Percentage of mature females by depth for the three sampling areas. Circle, Balearic Sea; square, western Ionian Sea; triangle, eastern Ionian Sea.

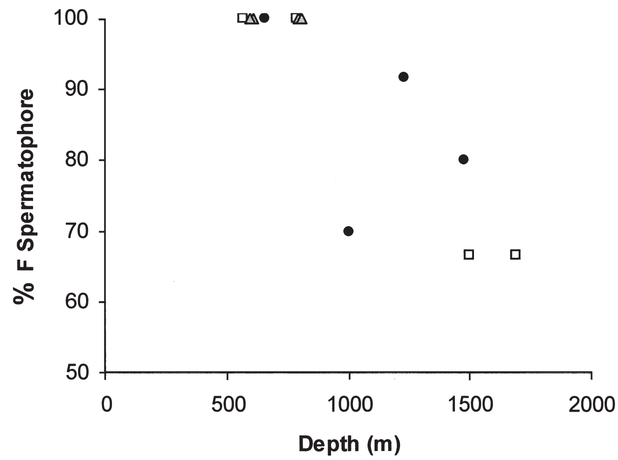

FIG. 8. – Percentage of spermatophore-bearing females by depth for the three sampling areas. Circle, Balearic Sea; square, western Ionian Sea; triangle, eastern Ionian Sea.

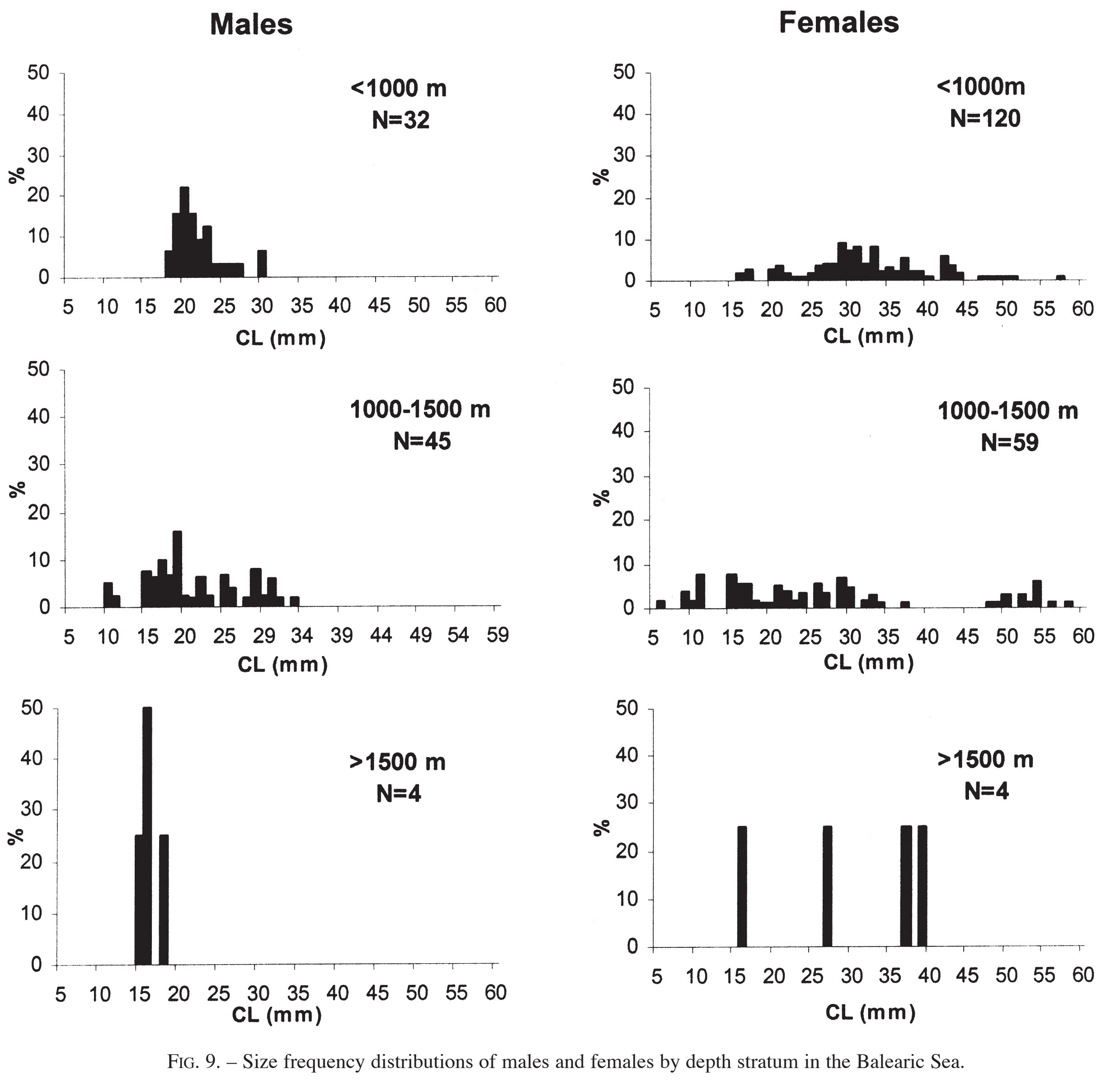

FIG. 9. – Size frequency distributions of males and females by depth stratum in the Balearic Sea.

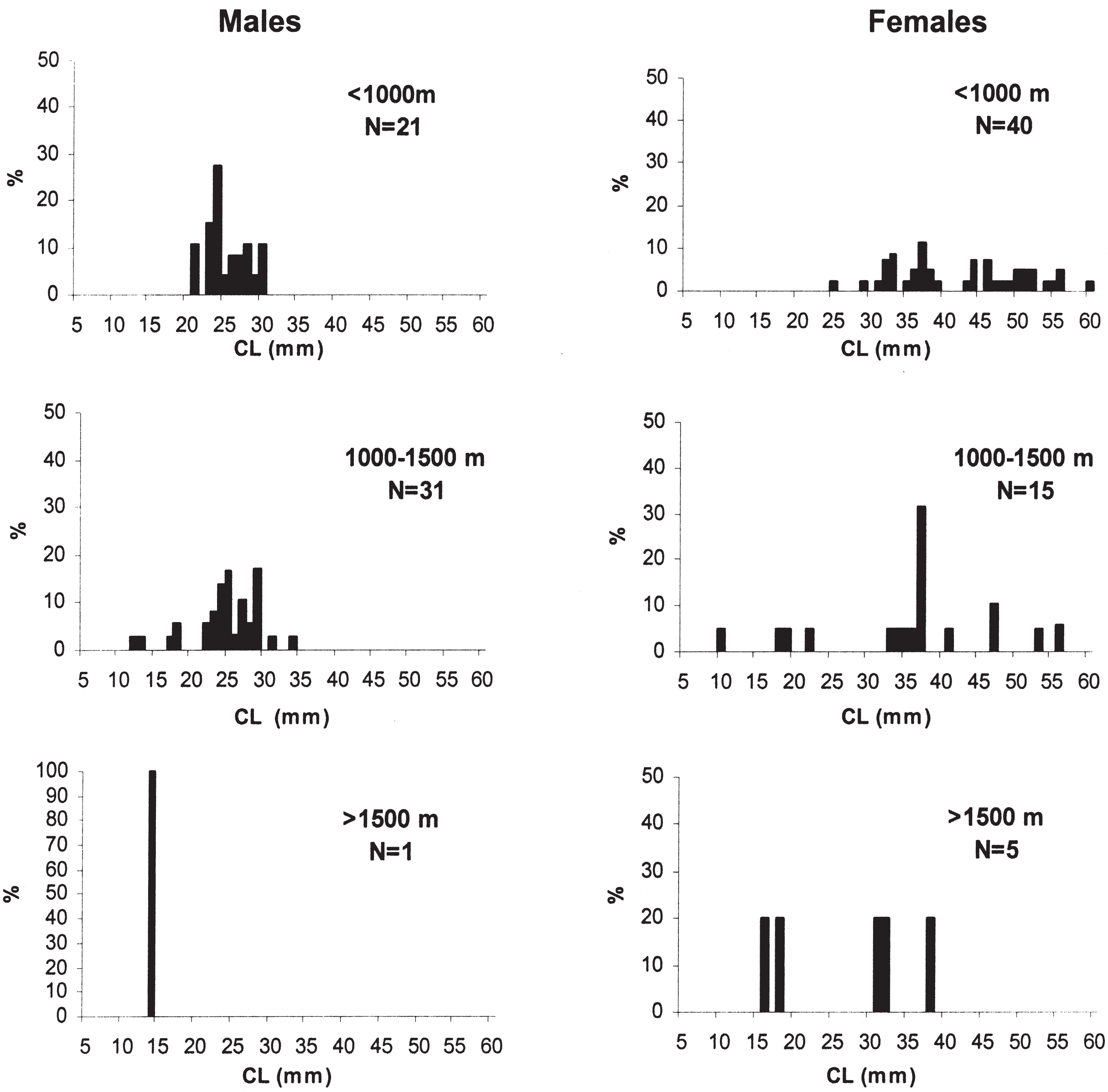

FIG. 10. – Size frequency distributions of males and females by depth stratum in the western Ionian Sea.

60% (between 42 and 84 %) below 1000 m. At 600 m the proportion of males remained below 40%.

Both abundance and proportion of juveniles displayed a tendency to increase with depth in all three sampling areas (Fig. 6). On the whole, the lowest abundance were recorded on the middel slope. These results could indicate a relationship between recruitment and depth jointly with the decrease of large individuals.

High proportions of mature females at maturity stages V and VI were recorded at depths > 1000 m (around 70% females) (Fig. 7). Again, on account of the small number of individuals available, a certain trend towards a drop in the proportion of mature females carrying a spermatophore with depth can only be tentatively suggested (Fig. 8), also considering that the size of females and proportion of mature females decreases with depth.

The maximum and minimum sizes in the size frequency distributions increased with depth for both males and females (down to 1500 m), and this tendency was observed in all three areas (Figs. 9, 10 and 11). Here again, data for depths below 1000 m were not available (very scarce) for the eastern Ionian Sea, and hence this finding cannot be corroborated in that area.

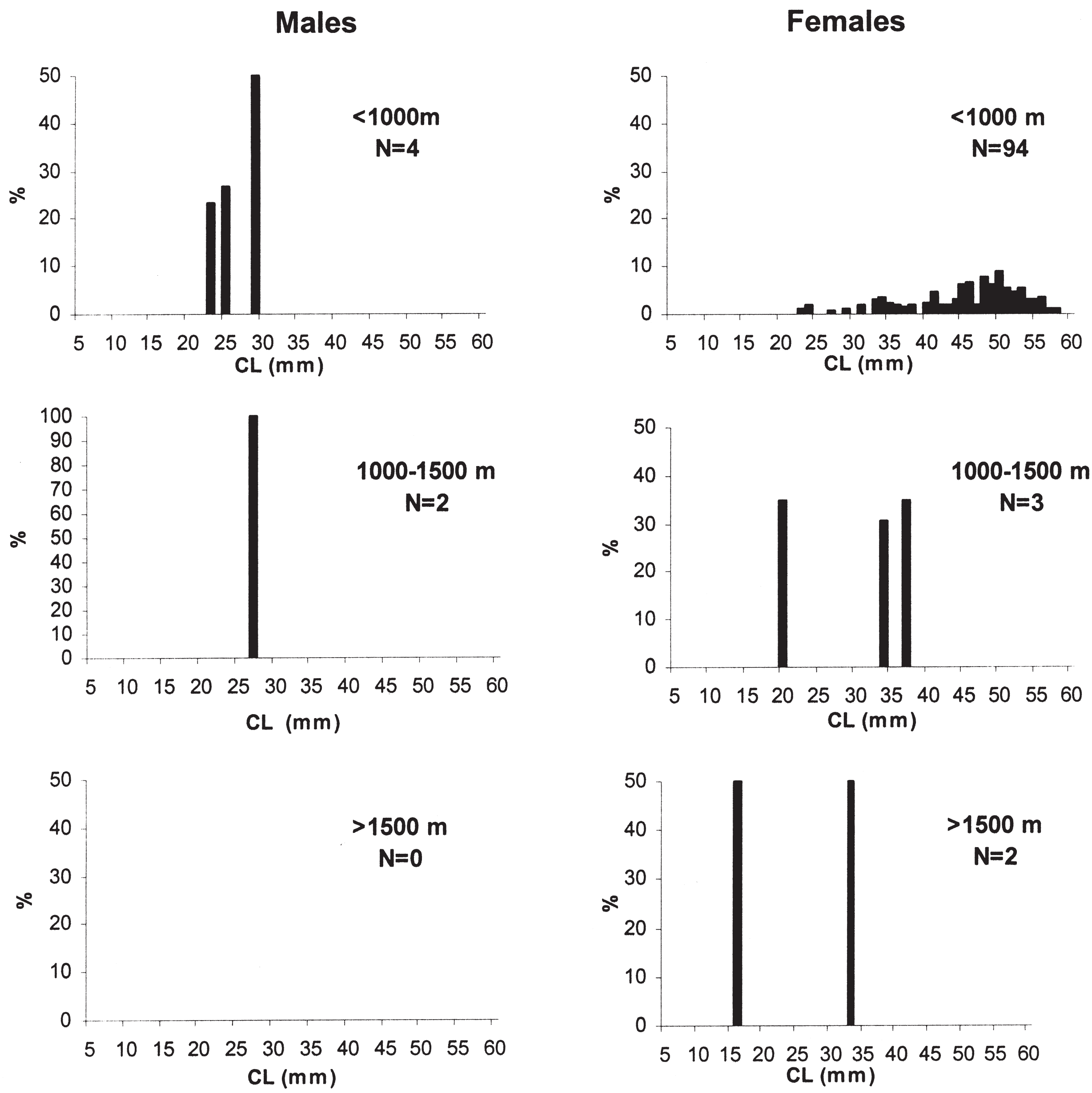

FIG. 11. – Size frequency distributions of males and females by depth stratum in the eastern Ionian Sea.

DISCUSSION

The most novel aspect is the collection of new data of this study at depths below 1100 m in regions where this resource has not yet been exploited. By way of a general conclusion, the results would indicate that population structure follows a similar pattern down to 2200 m throughout the Mediterranean, as previously suggested by Sardà *et al.* (2003b). Also it can be concluded that in the Mediterranean the depth distribution for *A. antennatus* extends at least to 3300 m. The abundance of this species has three distinct boundaries: < 1000 m, with relatively high abundance (up to 1000 ind km^{-2}); 1000-1500 m, with relatively moderate abundance (up to 300 ind km^{-2}), and > 1500 m, with relatively low abundance (< 50 ind km^{-2}). Variations in abundance at depths < 1000 m are common in the fishery of this species, with abundance being dependent on local and seasonal depth distributions (Tobar and Sardà, 1987; Demestre and Martín, 1993; Tudela *et al.*, 2003). The peak of abundance observed at 1500 m was previously found by Sardà *et al.* (2003b) in the northwestern Mediterranean. Now, a similar pattern in the Balearic Sea and western Ionian was also observed. Unfortunately, bottoms suitable for trawling at that depth were not found in the eastern Ionian Sea and the tendency could not be confirmed in this area.

The same population structure already described in the western Mediterranean, with an increasing proportion of males and juveniles with depth, has now been recorded in the other parts of the Mediterranean. This finding was postulated earlier by Sardà *et al*. (2003b) in the western Mediterranean. At around 500 m the proportion of males remained below 40%, as observed previously by Bas (1965), Sardà and Demestre (1987), Carbonell *et al*. (1999), and García-Rodríguez and Esteban (1999), among others. No evident differences in gonad maturity stage or in the proportion of females with spermatophores were observed between the three areas sampled.

Also, different hydrological conditions (i.e. temperature and salinity and productivity) between the western and central Mediterranean (Hopkins, 1989; D'Onghia *et al.,* 2003) have been reported to affect the species distribution (Politou *et al*., 2004). Few papers discuss the depth distribution of *Aristeus* in Atlantic waters (Ribeiro-Cascalho, 1988), though the temperature of Atlantic deep-sea waters decreases several degrees below that of Mediterranean waters, where temperature is constant between 12.8 and 14.1 ºC. According to this author, the distribution of *Aristeus* occurs in Atlantic Portuguese waters at the same depth and temperature as in Mediterranean. Additionally, oxygen does not seem to be a limiting factor for *Aristeus* depth distribution because Mediterranean deep-waters are relatively rich in oxygen at all depths (Miller *et al*., 1970).

Lower density at greater depths, together with the relative reduction of larger males, may diminish the opportunities to mate at these depths. Smaller female size at these depths may also play a role in this finding. In addition, as is the case for the populations dwelling on the slope, smaller females undergo a larger number of moults and are thus more likely to lose the spermatophore. The presence of mature females at great depths, at which the photoperiod exerts no direct influence, suggests that mechanisms for the induction of gonad development are related to quality of the food becoming available via energy fluxes. As reproductive females in advanced maturity stages occur at all depths, larvae shift up across the water column to surface during pelagic development phases. Post-larvae would go to deeper waters, but the scarcity of food in open waters and during its return to the bottom in deep-waters probably produce little success on settlement during sinking. However, the presence of mature females in stage V, females with spermatophores and small individuals found in deep-waters demonstrate that a minimum reproductive process can occur in deep-sea waters.

The higher proportions of juveniles of *A. antennatus* in the deeper zone suggest a response to food competition or predation by other shrimp species (e.g. *Plesionika* spp.) on the continental slope. Howevere, also a large presence of juveniles is detected everywhere along the depth distribution of large individuals of *Aristeus* (Mura *et al.,* 1997; Tursi *et al.,* 1996; Sardà *et al.,* 1994; García-Rodríguez and Esteban, 1999). On the other hand, Sardà and Cartes (1997), Cartes and Demestre (2003) and Sardà *et al.* (2003b) and the present results indicate that juveniles also occur in deep-water, and their proportion increases with depth, probably due the high success or adaptability of the smaller individuals to deep-sea waters. In this paper we can see that higher abundance of juveniles is more frequently found below 800 m, which could mean that recruitment occurs in deeper waters. However, further studies need to be made to elucidate the recruitment process of deep-sea shrimps.

Based on the above findings (Gage and Tyler, 1990), a hypothesis can be put forward as a topic for future study: *Aristeus antennatus* populations respond to ecological changes (and low food availability) with depth due to changes in the size frequency structure, sex-ratio, and density—and therefore in the biomass and recruitment strategy—but the individual metabolism does not vary.

In relationship to the increase in abundance at 1500 m to levels close to the density levels at shallowest depth, no explanation has been found. Our hypothesis suggests that characteristic environmental features at these depths should be similar to those in shallower waters on the upper and middle slope. Unknown energetic fluxes probably develop near 1500 m in the western Mediterranean due to geomorphological processes that have not yet been studied.

Consequently, future studies should focus on determining the "*food indicators*" (organic carbon, organic nitrogen and particulate carbon) (De Bovée *et al.,* 1990) associated with deep-sea shrimp distributions. Certain evidence in this respect was published by Puig *et al.* (2001) and suggested a correlation between different deep nepheloid layers and the depth distribution of juveniles and mature females of *Plesionika* spp. The following factors should be considered as possible principles of ecological interaction between the environment and *Aristeus antennatus*: i) concentrations of organic compounds decrease considerably with depth, indicating depletion of trophic resources in the bathyal zone (Tselepides *et al.,* 2000); ii) deep-sea sediments tend to be environments with limited food resources, and the abundance and distribution of benthic organisms can be expected to be directly related to the amounts and quality of the food reaching the surface of the sediment (Gooday and Turley, 1989); iii) carbohydrates, lipids, and proteins are indicators of the labile fraction of organic matter in the sediment ingested by organisms as part of the diets of megafaunal organisms such as deep-sea shrimps (Danovaro, 1999; Grèmare *et al.*, 1997).

Finally, the data presented here correspond to an exploratory survey that in some cases based the conclusions on few samples from different areas. The authors wish to express the idea that this paper can suggest an initial hypothesis, but further investigations integrating western, central and eastern Mediterranean environments are needed in order to improve the knowledge of deep-sea shrimps.

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