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Comparison of the population structure and dynamics of *Aristeus antennatus* (Risso, 1816) between exploited and unexploited areas in the Mediterranean Sea

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Abstract

Data on the size distribution and population biology of the deep-water shrimp *Aristeus antennatus* were collected during four trawl surveys carried out along the Italian coasts (exploited area) and off north-western Greece (unexploited area). Comparison between the sampled populations was carried out in the 500–800 m depth range where trawl fishing, targeting deep-water shrimps (*A. antennatus* and *Aristaeomorpha foliacea*), occurs only along the Italian coasts. Some explorative hauls were also made as deep as about 1200 m. *A. antennatus* was collected down to 1122 m in the Italian area and 1174 m in Greek waters. It was found to be more abundant in the former area than in the latter. In both areas, the sex ratio was largely in favour of females and changed with depth. Maturity process by size was found to be similar in the two areas. Even though the median carapace lengths computed for the Greek samples were significantly greater than those for the Italian ones, a wide size range with superimposed modal components was found on both sides of the Ionian Sea. The estimated growth performance was the same in the two areas. In the Greek sampled population, the total mortality rates generally coincided with the natural mortality rates. No significant differences in the total mortality rates were detected between the Italian and Greek stock. The application of the yield per recruit model to the exploited stock, according to different scenarios, indicated conditions close to optimal harvesting. These results are discussed considering all the features which reduce vulnerability to fishing and favour recovery of the *A. antennatus* stock, thus blunting the differences in the population structure between the exploited and unexploited areas.

Keywords: *Aristeus antennatus*; Distribution; Maturity; Size structure; Population dynamics; Exploitation rate; Mediterranean Sea

1. Introduction

The blue-and-red shrimp *Aristeus antennatus* (Risso, 1816) represents one of the most important deep-water resources of the Mediterranean Sea,

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exploited by trawl fishing from the westernmost side throughout the basin as far as the western Ionian Sea (Bianchini and Ragonese, 1994). Considering the multispecies nature of Mediterranean fisheries, *A. antennatus* is caught together with many other species both by-catch and discards. According to the official Italian statistics (ISTAT), *A. antennatus* is landed together with other deep-water shrimps, mostly *Aristaeomorpha foliacea*, as the commercial category of "red shrimps". In the 1990s, the total Italian landings of "red shrimps" were between 3000 and 6000 t/year (Relini et al., 1999). Although their catches fluctuate largely according to the season and area, thousands of tonnes of "red shrimps" are landed along the Mediterranean coasts of the western and central basin (Fiorentino et al., 1998; Carbonell et al., 1999; Bas et al., 2003; Sardà et al., 2004).

The biology and ecology of *A. antennatus* have been much investigated in the last 20 years (Bianchini and Ragonese, 1994 and references therein; Cau et al., 2002 and references therein). However, several aspects of its population dynamics and exploitation condition remain vexed questions. Concerning population dynamics, the main uncertainties regard recruitment, for which very little information is available (Orsi Relini and Relini, 1988, 1998; D'Onghia et al., 1997; Mura et al., 1997; Sardà and Cartes, 1997), the growth parameter estimates, which are greatly affected by the size structure of the sampled population, and the mortality rate estimates, which are largely influenced both by growth parameter estimates and methods used (Orsi Relini and Relini, 1998). With regard to the exploitation condition, there are contrasting assessment results ranging from underexploitation to high overfishing for the different Mediterranean stocks (Fiorentino et al., 1998 and references therein). Indeed, in spite of the growth overfishing detected in most of the demersal Mediterranean resources (Caddy, 1993; Bombace, 1995), *A. antennatus* is probably the only highly exploited commercial species subject to a sustainable harvest rate (Demestre and Martin, 1993; Ragonese and Bianchini, 1996; Relini et al., 1999).

In the Ionian Sea (eastern–central Mediterranean) along the Italian coasts, where both *A. antennatus* and *A. foliacea* have long been intensively fished, the assessment carried out using analytical models indicated optimal exploitation of the former and overfishing of the latter (Matarrese et al., 1997). These authors found that *A. antennatus*, differently from *A. foliacea*, does not show the typical life-history effects of fishing (Jennings and Kaiser, 1998), such as the truncated size/age structure and the decrease in population reproductive potential. On the eastern side of the Ionian Sea along Greek coasts, where the commercial fishery is only carried out down to 400–500 m, recent studies on the population structure and dynamics of *A. antennatus* have detected various quite similar patterns between the study area, where the species is unexploited, and other Mediterranean areas where exploitation occurs (Papaconstantinou and Kapiris, 2001; Kapiris, 2004).

The very wide distribution of *A. antennatus* on bathyal bottoms (Sardà, 1993; Sardà et al., 1994, 2004) seems to play the main role in the recovery of the stock, thus indicating the importance of refuges for sustainable fishing (Gell and Roberts, 2003). However, its high fecundity, up to four times that of *A. foliacea* in the larger females (Orsi Relini and Semeria, 1983), should also be taken into account when considering the population resilience of this shrimp.

With the aim of providing a contribution to the debate regarding population dynamics and exploitation status of *A. antennatus* in the Mediterranean Sea, data collected during some study projects funded by EC and Italian and Greek governments were used. In particular, these data were taken using the same methodology and equipment for trawl fishing during the same periods in border-marker areas of the northern Ionian Sea with different fishing intensity: off the south-eastern Italian coast, where *A. antennatus* is exploited, and off north-western Greece, where there is no deep-water trawl fishing (unexploited area). The aim of this paper is the comparison of the population structure and dynamics of the blue-and-red shrimp between exploited and unexploited areas of the Ionian Sea.

2. Materials and methods

2.1. Areas of investigation

The Italian area is located along the Apulian coast of the north-western Ionian Sea and regards the Gallipoli fishery (Fig. 1). This fishery is mostly characterized by trawlers which exploit demersal resources from Monday to Friday only during day-light hours. The trawlers are smaller than 10 t of gross tonnage and

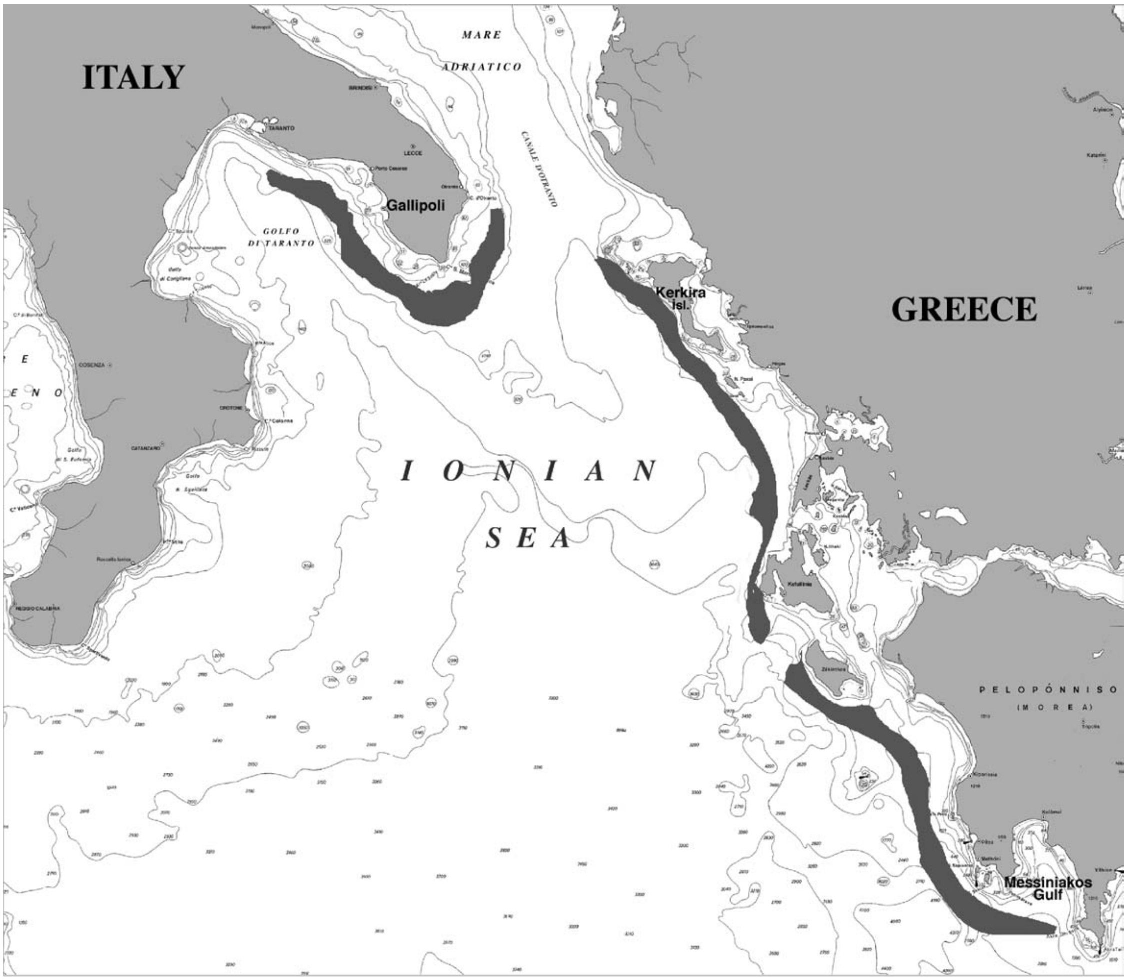

Fig. 1. Map of the study areas in Italian and Greek waters of the Ionian Sea.

are equipped with an Italian type otter trawl net with 40 mm stretched mesh size in the codend. Trawlers generally go out on daily trips; they set off at 3–4 a.m. and return to the harbour at 3–4 or 5–6 p.m. during wintertime and summertime, respectively. The commercial hauls vary in duration, from 1 h to about 4 h and may regard different depths, from 300 to 700 m, in the same tow. Fishing is not allowed at night or weekends. The red shrimps fishing grounds are between 350–400 and 700–750 m in depth. These bottoms are about 15–22 nautical miles from Gallipoli harbour and are mainly sought from spring to autumn. During 1998–1999, the red shrimp CPUE ranged from 5 to 48 kg/boat per day and its contribution to the total catch made up 58.6% in weight and 66.1% in economic value (Carlucci et al., 2003).

The Greek areas involved in this study are between Kerkira Island and the Messiniakos Gulf (Fig. 1). The commercial fishery in Greece is carried out down to about 400–500 m. That means that large marine grounds remain unexploited, since the Greek continental shelf has a reduced extension. Sometimes, Italian fishermen extend their fishing activity into areas close to Greek waters, since in these areas they can find unexploited resources, the abundance, geographical distribution or exploitation of which their Greek counterparts are not aware of. For the first time, in 1996, a research project concerning the fishery in the deep waters of the southern Greek Ionian Sea showed the presence of the red shrimps, *A. foliacea* and *A. antennatus*, in important quantities (Petrakis and Papaconstantinou, 1998). However, this research was carried out in a small geographical area. Further research projects were carried out later in order to explore the deep-water resources of the Greek northern Ionian Sea, focusing on the localization and estimation of the abundance and catch per unit effort of the red shrimp stocks (Kapiris et al., 2001; Politou et al., 2003, 2004; Mytilineou et al., in press).

2.2. Data collection

Data were collected during three trawl surveys (April–May, July–August and September–October 2000) carried out both off the south-eastern Italian coast (north-western Ionian) and off north-western Greece, between Kerkira Island and northern Zakinthos (north-eastern Ionian) (Fig. 1), as part of the study projects GRUND (Relini, 1998), MEDITS (Bertrand et al., 2002) and INTERREG II Italy–Greece (Politou et al., 2003). Further data from the Italian study area and another area further south along the Greek coast were collected during another survey carried out in July–August 2001 as part of the RESHIO project (Exploration of pristine red shrimp resources and comparison with exploited ones in the Ionian Sea. EEC Research Programme 99/29). This latter area in Greek waters extends from southern Zakinthos Island to the Messiniakos Gulf (Fig. 1).

A commercial motor powered vessel, equipped with an otter trawl net, with stretched mesh of 40 mm in the codend, was hired for the GRUND, INTERREG II and RESHIO cruises. During the MEDITS survey an especially designed net with a stretched mesh of 20 mm in the codend was used (Bertrand et al., 2002). However, it has been shown that no selection occurs for *A. antennatus* even using the stretched mesh of 40 mm in the codend (D'Onghia et al., 1998a, 2003a; Imperatrice et al., 2003). The horizontal and vertical opening of the two types of net, measured by the SCANMAR acoustic system, depended on depth, wire length, towing speed, etc. (Fiorentini et al., 1994, 1999). The sampling design adopted in each study project was depth stratified. The hauls were carried out from dawn to dusk and had an average duration of 1 h. The number of the sampled specimens was standardized to hour and square kilometre for subsequent numerical processing. The vessel speed, measured using GPS, was maintained at 2.5–3.0 knots. In this study, only the hauls carried out at depths greater than 500 m have been considered. The comparison of the population structure and dynamics between Italian and Greek areas has only been made for a depth range of 500–800 m where *A. antennatus* is exploited in the Italian waters. For this purpose, a comparable number of hauls between the study areas was randomly selected from the various projects. Samples at depths below 800 m as far as 1174 m were only taken during the INTERREG II project which had an explorative character since it sought unknown zones. Only one haul at a depth of 810 m was carried out during the RESHIO project. Some analyses were also performed using data collected during these explorative hauls. The date and number of hauls carried out in each cruise, above and below 800 m, are reported in Table 1.

Table 1
List of cruises, sampling date and number of hauls in which *A. antennatus* was collected by depth in the two study areas of the Ionian Sea

Survey	Date	No. of hauls	
		500–800 m	>800 m
Italian area			
MEDITS	May 2000	9	–
INTERREG	August 2000	9	2
GRUND	September–October 2000	9	–
RESHIO	July 2001	10	–
Greek area			
INTERREG	April 2000	10	4
INTERREG	July 2000	10	4
INTERREG	September 2000	10	2
RESHIO	July–August 2001	10	1

2.3. Methods

Using the number of individuals for each haul swept area, the average density was computed and expressed as number per square kilometre ($N\,\text{km}^{-2}$). The swept area was estimated according to the wing spread of the net (horizontal opening) and the speed of the vessel (Pauly, 1983). Changes in density with depth were tested by means of regression analysis. Differences in density between the two areas were evaluated using the non-parametric test of Kruskal–Wallis (Conover, 1980).

For each specimen of *A. antennatus*, the carapace length (CL) was measured to the nearest millimetre, from behind the orbit of the eye to the posterior border of the cephalothorax. Sex was determined macroscopically and maturity stage of gonads in females was evaluated according to the scale proposed by Orsi Relini and Relini (1979) (four stages). However, only the relevant results are reported here considering immature (first and second stages) and mature (third and fourth stages) females. Sex ratio for each area was estimated by survey and depth. Statistical differences between changes in the number of females and males by depth were determined using the *G*-test (Sokal and Rohlf, 1969).

The change in size with depth was statistically tested in each area by means of regression analysis, using the median carapace length of each haul for the two sexes separately. The median length was adopted in order to minimize the effect due to the extreme values and asymmetric distributions. Since the decrease in body size may be an indicator of effects of fishing (Haedrich and Barnes, 1997), differences in the median carapace length between the samples collected in Italian and Greek waters, between 500 and 800 m, were evaluated using the non-parametric test of Kruskal–Wallis (Conover, 1980). The median value was estimated starting from the smallest length of individuals that are fully represented in catch samples (L') in order to avoid the influence of recruitment. The L' value adopted was 30 mm CL (D'Onghia et al., 1998a, 2003a).

The size distributions were calculated for each area and sex. Comparison between the distributions in the two areas, for the 500–800 m depth stratum, was carried out using the percentage of similarity (Kohn and Riggs, 1982). The significance in the differences was determined by the Kolmogorov–Smirnov test (Conover, 1980).

Gaussian components in the female length–frequency distributions by survey and area (500–800 m) were separated with the Bhattacharya method by means of the FiSAT program (Gayanilo et al., 1995). Each representative component, with a separation index greater than 2, was assumed to be a single cohort. Differences between observed and expected length–frequency distributions were evaluated using the χ^2 method. Growth parameters of the Von Bertalanffy equation were estimated using the "mean length-at-age" derived from the Bhattacharya analysis of which differences between observed and expected length–frequency distributions were not significant. The growth performance index Φ' (Munro and Pauly, 1983) was also estimated for comparison purposes.

Two different approaches were followed for the computation of the total mortality rate (Z) taking into consideration the differences in the exploitation pattern occurring on the two sides of the Ionian Sea. Since for *A. antennatus* an almost discrete recruitment was shown in the north-western Ionian Sea (D'Onghia et al., 1997, 1998b) the total mortality rate (Z) was computed according to the Beverton and Holt (1957) and Hoenig (1987) methods. Both methods require as input the Von Bertalanffy growth parameters (L_∞ and k), the smallest length of individuals that are fully represented in catch samples (L') and the mean length in the catch starting from L'. The L' value adopted was 30 mm CL (D'Onghia et al., 1998a, 2003a).

The total mortality rate in the Greek area was considered to be approximately equal to the natural mortality rate (M), since no commercial deep-water trawl fishing occurs in this area. Thus, Z would be equal to M, being $F = 0$. For this reason, in the Greek area the natural mortality rate was also estimated using the Hoenig (1983) empirical regression which relates M to life-history parameters. In the Italian area, the total mortality was considered as the sum of the natural and fishing mortality rates ($Z = M + F$). The value of the natural mortality rate estimated in Greek waters was adopted for the Italian stock. Differences in the total mortality values between the two areas were evaluated using the non-parametric test of Kruskal–Wallis (Conover, 1980).

The exploitation condition of the Italian stock was assessed by means of the yield per recruit model of Beverton and Holt (1957). Considering the underlying variability in the stochastic processes, such as recruitment, growth and mortality, most probably the steady state conditions required for the application of the yield per recruit model are not satisfied. However, this model was employed in order to compare the results with other Mediterranean areas where trawl fishing occurs and similar studies have been carried out. Since females are bigger and found shallower than males, representing the most exploited fraction of the stock (Sardà, 1993), the population dynamics and exploitation conditions were only studied for them.

3. Results

3.1. Distribution pattern

The blue-and-red shrimp was caught as far as the deepest bottoms investigated, between 503 and 1122 m in the Italian area and between 528 and 1174 m in Greek waters (Table 2). The density values ranged from 22.5 to 5878.2 $N\,\text{km}^{-2}$ in the former and from 10.4 to 2658.4 $N\,\text{km}^{-2}$ in the latter. Within the depth range 500–800 m, density was significantly higher in Italian than in Greek waters ($p = 0.0029$). Considering the depth range of 500–800 m, no significant changes in density with depth were shown in either area ($p > 0.05$). For the whole depth range investigated in Greek waters, a slight increasing trend was shown up to 650–700 m and a clear decreasing one after this depth range, as demonstrated by a significant non-linear regression analysis ($F = 12.71$; $p < 0.01$; d.f. = 48) (Fig. 2). In the Italian area, no significant variations were observed across the whole depth range probably as a consequence of the only two hauls carried out beyond 800 m.

The sampled population consisted mainly of females in both the north-western and north-eastern Ionian Sea. Higher percentage values of males were found between 500 and 800 m during May 2000 in Italian waters and at depths greater than 800 m during almost all surveys in both areas (Table 3). Apart from the first survey in the eastern Ionian, the changes in the sex ratio with depth were statistically significant (Italian area, August 2000: $G = 22.09$, $p < 0.01$; Greek area, July 2000: $G = 13.31$, $p < 0.01$; September 2000: $G = 18.62$, $p < 0.01$; July–August 2001: $G = 31.46$, $p < 0.01$).

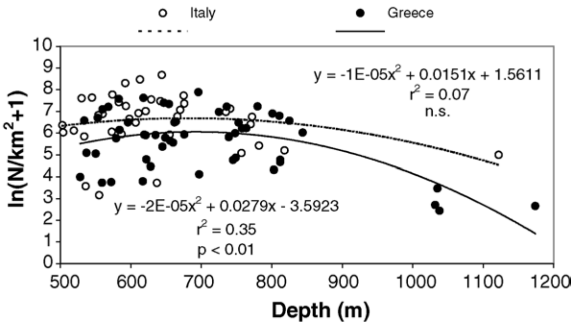

Fig. 2. Relationship between density and depth in *A. antennatus* caught in each study area.

The median carapace lengths of the samples collected in the whole investigated depth range are shown in Fig. 3. No significant changes in the median lengths with depth were detected in either sex and area ($p > 0.05$) while, considering the 500–800 m depth range, a significant increasing trend with depth was only shown for females in the Italian area ($\text{CL} = -110.56 + 0.4078\,\text{depth} - 0.0003\,\text{depth}^2$; $r^2 = 0.5$; $p < 0.01$). Within the 500–800 m depth range,

Table 2
Depth range of finding, average density ($N\,\text{km}^{-2} \pm$ S.D.), minimum and maximum carapace length (CL) of *A. antennatus* specimens collected in the two study areas in each investigated period

Date	500–800 m				>800 m			
	Depth range (m)	$N\,\text{km}^{-2} \pm$ S.D.	CL Minimum	CL Maximum	Depth range (m)	$N\,\text{km}^{-2} \pm$ S.D.	CL Minimum	CL Maximum
Italian area								
May 2000	534–772	1337 ± 1759.58	15	59	–	–	–	–
August 2000	555–782	1468 ± 1772.04	20	59	818–1122	164 ± 24.90	22	52
September–October 2000	503–607	1085 ± 814.80	20	65	–	–	–	–
July 2001	583–735	1180 ± 668.47	16	63	–	–	–	–
Greek area								
April 2000	534–753	470 ± 405.08	23	61	803–1174	207 ± 336.18	24	60
July 2000	553–764	583 ± 596.62	22	61	811–1038	355 ± 397.21	25	59
September 2000	528–749	335 ± 330.69	20	56	810–1032	65 ± 72.43	29	52
July–August 2001	568–780	1226 ± 803.21	17	63	810	986	20	56

Table 3
Females (*F*) and males (*M*) percentage *of A. antennatus* by survey and depth

Area	Survey	Depth 500–800 m *F* (%)	*M* (%)	>800 m *F* (%)	*M* (%)
Italian area	May 2000	42.94	57.06	–	–
	August 2000	77.83	22.17	36.45	63.55
	September–October 2000	87.86	12.14	–	–
	July 2001	69.77	30.23	–	–
Greek area	April 2000	84.83	15.17	83.61	16.39
	July 2000	93.10	6.90	82.26	17.74
	September 2000	92.09	7.91	40.65	59.35
	July–August 2001	90.47	9.53	64.29	35.71

the median carapace lengths computed for the samples collected in Greek waters were significantly greater than those calculated for the samples in the Italian area, both in females ($p = 0.0202$) and males ($p = 0.0299$).

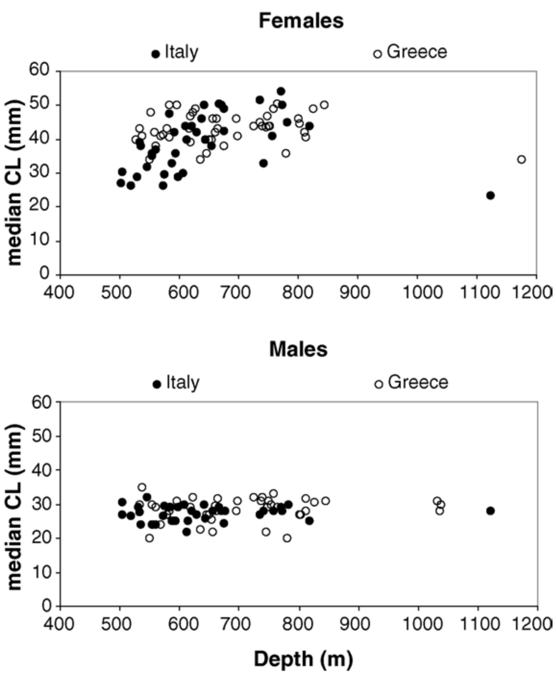

Fig. 3. Relationship between median carapace length and depth in *A. antennatus* by sex and area.

3.2. Reproductive pattern

The pattern of the reproductive condition of *A. antennatus* females on the two sides of the Ionian Sea is reported in Table 4 and presented in Fig. 4. During spring, mature specimens were only found on the north-western side. In the second and fourth survey (July and August in both areas) mature specimens were found to be rather uniformly spread over the sampled length range of both areas, indicating the spawning peak of the species within its reproductive cycle. During September and September–October, a progressive decrease in mature specimens confirmed the conclusion of the reproductive season, particularly in Italian waters. The smallest ripe female measured 20 mm CL in the Italian area and 25 mm CL in Greek one.

3.3. Population structure

The minimum and maximum sizes found in the study areas are reported in Table 2. Size distributions of females and males are shown in Figs. 5 and 6, respectively. Multimodal distributions were detected in females caught in each study area and cruise. Their sizes ranged from 15 to 65 mm CL in the Italian area and from 17 to 63 mm CL off Greece. The abundance of the different size classes changed from survey to survey. The individuals from depths greater than 800 m had similar size range as those from shallower waters.

Size distributions of males, within a smaller range of sizes, showed a bimodal trend in each area. The specimens measured between 16 and 39 mm CL in Italian

Table 4
Percentage of immature and mature females of *A. antennatus* collected in each investigated period in the two study areas of the Ionian Sea

Date	*N*	Immature (%)	Mature (%)
Italian area			
May 2000	442	92.53	7.47
August 2000	971	36.05	63.95
September–October 2000	695	97.99	2.01
July 2001	613	12.07	87.93
Greek area			
April 2000	393	100	0
July 2000	535	31.96	68.04
September 2000	281	82.56	17.44
July–August 2001	798	28.32	71.68

N, total number of females.

waters and between 17 and 36 mm CL in Greek ones. The most abundant individuals had sizes between 26 and 32 mm CL on both sides of the Ionian Sea. As shown for females, the sizes of males sampled at depths greater than 800 m were in the size range observed within the 500–800 m depth stratum.

With regard to the comparison between the size distributions, in females, both the lowest (45%) and

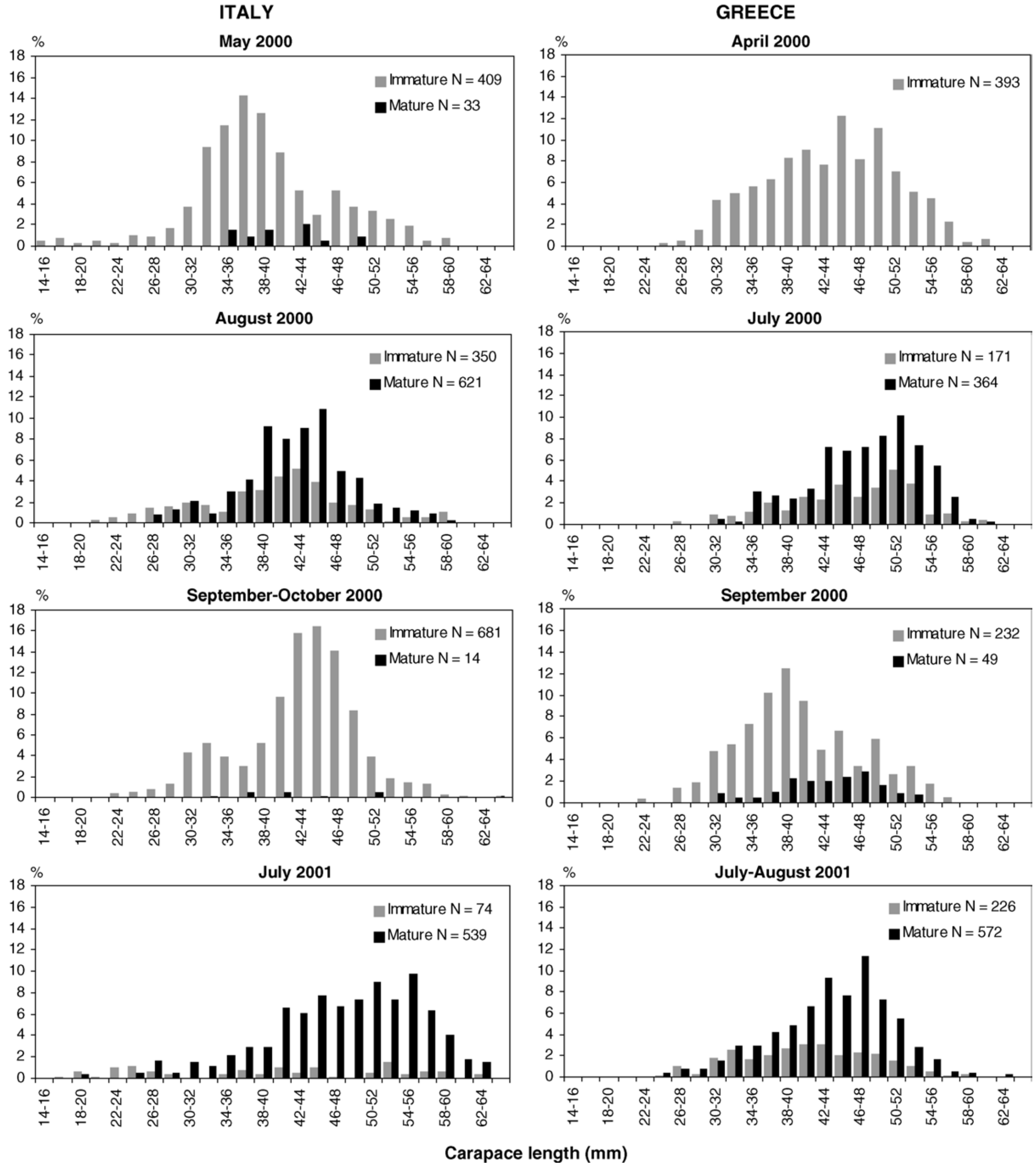

Fig. 4. Length–frequency distributions by area and maturity in *A. antennatus* females caught in the Ionian Sea.

the greatest (85%) percentages of similarity were shown between a survey in Italy and one in Greece, indicating a greater variation by season in the same area than between the two areas. In males, the lowest (8%) and highest (79%) percentages of similarity were also detected between Italy and Greece (Table 5). The Kolmogorov–Smirnov test provided significant differences both between areas in each

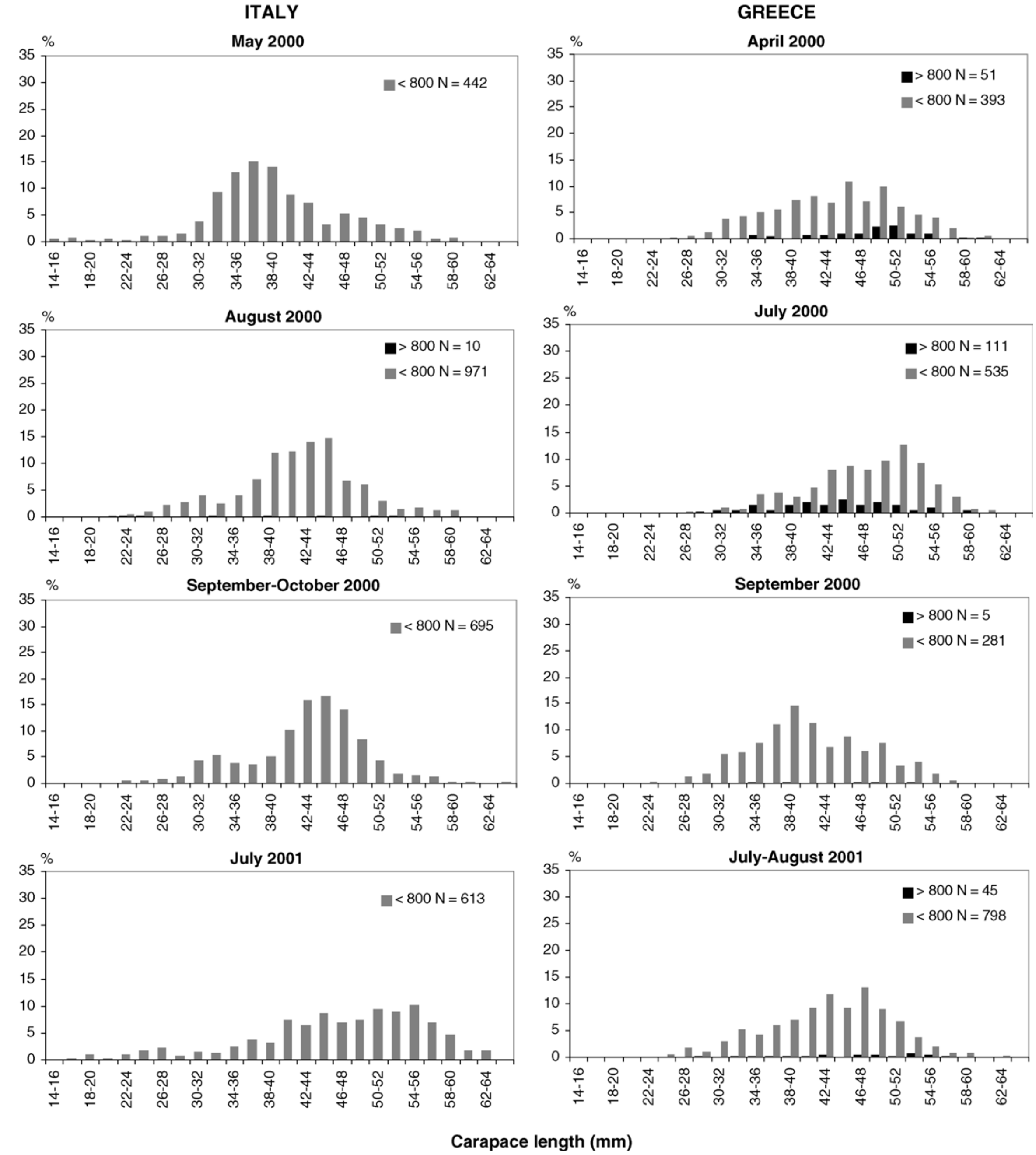

Fig. 5. Length–frequency distributions by area and depth in *A. antennatus* females caught in the Ionian Sea.

season and between seasons within each study area ($p < 0.01$).

In the female length–frequency distributions, up to five and four modal components were detected in Italian and Greek waters, respectively (Table 6). The occurrence of small specimens in Italian waters during May 2000 and July 2001 allowed the identification of a modal group with mean length-at-age

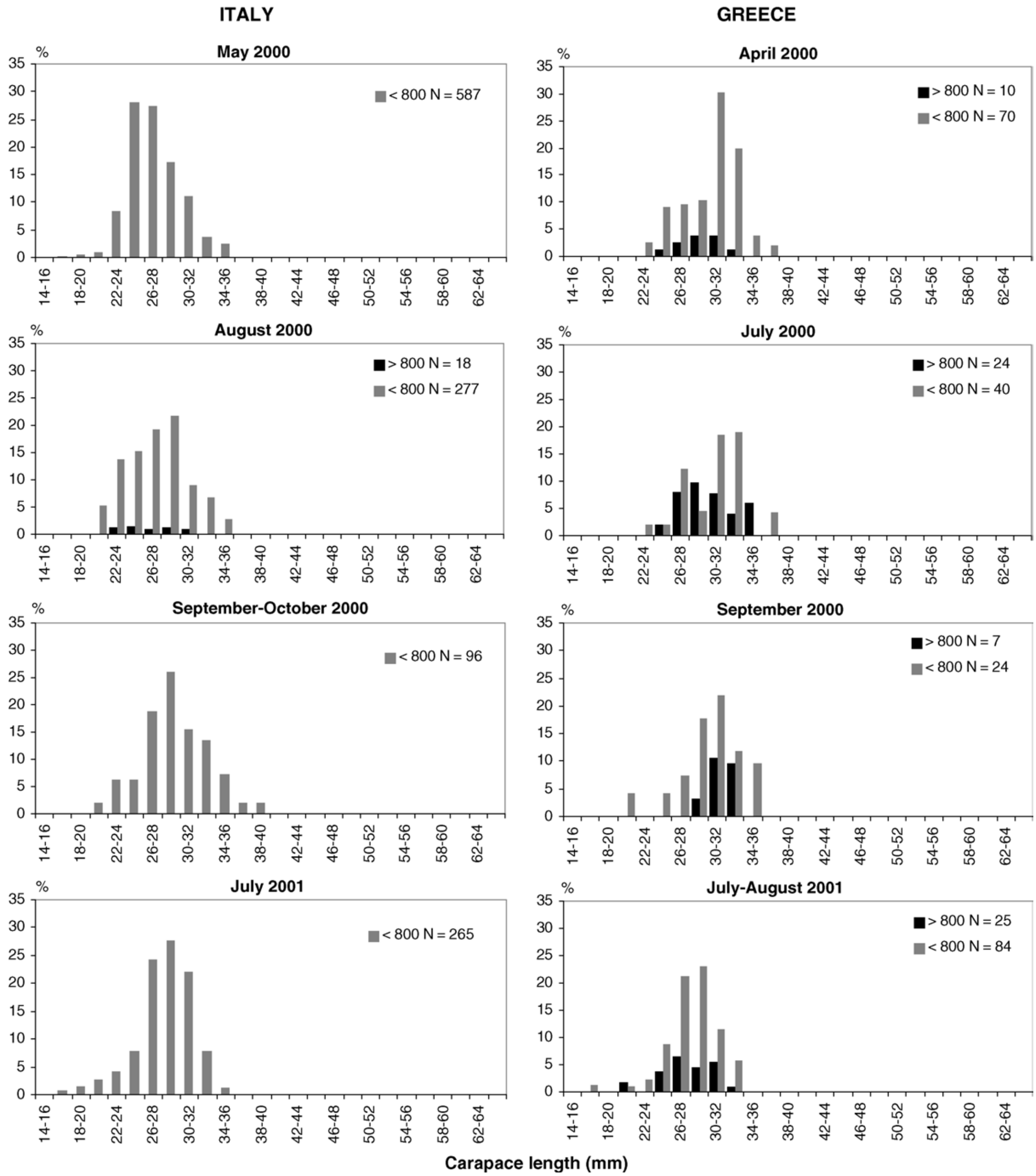

Fig. 6. Length–frequency distributions by area and depth in *A. antennatus* males caught in the Ionian Sea.

Table 5
Percentage similarity matrices for size distribution by sex

	Italy 1	Italy 2	Italy 3	Italy 4	Greece 1	Greece 2	Greece 3	Greece 4
Females								
Italy 1	100							
Italy 2	57	100						
Italy 3	58	78	100					
Italy 4	50	54	59	100				
Greece 1	69	56	69	70	100			
Greece 2	50	54	64	80	74	100		
Greece 3	75	45	55	51	78	55	100	
Greece 4	63	76	85	63	65	67	52	100
Males								
Italy 1	100							
Italy 2	62	100						
Italy 3	27	49	100					
Italy 4	62	77	49	100				
Greece 1	21	40	68	41	100			
Greece 2	12	23	58	24	70	100		
Greece 3	8	16	40	17	48	53	100	
Greece 4	24	44	79	47	57	50	39	100

of 16.54 and 19.00 mm CL, respectively. Apart from some exceptions, an overlapping pattern in the mean length-at-age was observed in the study areas.

3.4. Population dynamics

No significant differences between observed and expected length–frequency distributions ($p > 0.05$)

Table 6
Mean values of the modal components of the length–frequency distributions in *A. antennatus* females caught in the Ionian Sea

Modal components	May 2000, $N = 442$			August 2000, $N = 971$			September–October 2000, $N = 695$			July 2001, $N = 613$		
	Mean CL	S.D.	SI	Mean CL	S.D.	SI	Mean CL	S.D.	SI	Mean CL	S.D.	SI
Italian area												
1	16.54	1.63	–	–	–	–	–	–	–	19.00	1.06	–
2	26.00	1.70	5.68	30.91	2.22	–	32.96	2.29	–	25.84	2.28	4.10
3	37.10	3.50	4.27	41.93	3.92	3.59	–	–	–	37.55	2.95	4.48
4	47.81	2.06	3.85	49.71	1.30	2.98	44.94	3.88	3.88	45.26	2.60	2.78
5	52.93	2.16	2.42	55.18	3.03	2.53	56.32	1.50	4.23	53.99	3.73	2.76
	April 2000, $N = 393$			July 2000, $N = 535$			September 2000, $N = 281$			July–August 2001, $N = 798$		
	Mean CL	S.D.	SI	Mean CL	S.D.	SI	Mean CL	S.D.	SI	Mean CL	S.D.	SI
Greek area												
1	–	–	–	–	–	–	–	–	–	–	–	–
2	32.24	2.07	–	–	–	–	32.11	1.90	–	27.36	1.43	–
3	40.68	4.13	2.72	37.11	2.19	–	39.21	3.15	2.81	33.52	2.35	3.26
4	49.18	1.94	2.80	45.24	3.18	3.02	48.50	2.03	3.59	43.03	2.85	3.66
5	54.55	1.82	2.86	52.05	2.47	2.41	52.67	2.05	2.04	52.11	2.52	3.38

S.D., standard deviation; SI, separation index.

were only shown during April 2000 for the population sampled in Greek area and during May and September–October 2000 for the Italian stock. The following Von Bertalanffy growth parameters were obtained:

Italian area

$$L_\infty = 79.39\,\text{mm CL};\quad k = 0.219\,\text{year}^{-1};$$
$$t_0 = -0.225;\quad \Phi' = 3.141$$

Greek area

$$L_\infty = 81.82\,\text{mm CL};\quad k = 0.203\,\text{year}^{-1};$$
$$t_0 = -0.457;\quad \Phi' = 3.132$$

Given the similar pattern in the mean length-at-age, the growth performance in the two study areas also appears to be the same. Furthermore, even though the maximum age in the sampled population corresponds to 5 years, considering the maximum sizes shown in both areas and the growth parameters estimated, the longevity of *A. antennatus* females in the Ionian Sea might be realistically assumed to be in the range of 7–9 years. Using this longevity value and the Hoenig (1983) empirical regression for crustacean species, the natural mortality rate (M) was estimated to be 0.469 and 0.376 year^{-1} for 7 and 9 years of longevity, respectively.

Considering the influence of the Von Bertalanffy growth parameters in the total mortality rate (Z) estimation, this rate was computed according to the Beverton and Holt (1957) and Hoenig (1987) equations using both the above reported growth parameters. The Z/year values computed considering the first three surveys, in order to average the seasonal changes in the same year and the same sampling area, ranged from 0.435 to 0.887 in Italian waters and from 0.327 to 0.781 in Greek ones (Table 7). No significant differences were detected between the two areas using the Kruskal–Wallis test ($p > 0.05$). Estimates from the Beverton and Holt equation were always greater than those provided by the Hoenig (1987) method. The values estimated in the Greek area, during September 2000, were even greater than those obtained for the Italian stock, during September–October 2000, using both growth parameters and estimation methods.

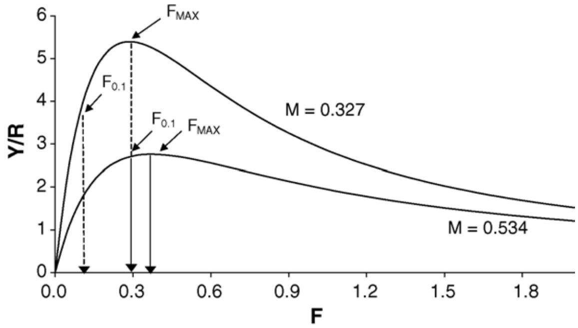

Fig. 7. Yield per recruit curves with indication of F_{max} and $F_{0.1}$ corresponding to different natural mortality rates.

3.5. Exploitation rate

Since Z is equal to M for an unexploited stock, the values obtained from the Hoenig (1987) method are comparable to those obtained for the natural mortality rate estimates using the Hoenig (1983) empirical regression. Following different scenarios, the fishing mortality rate (F) for the Italian stock was estimated by adopting the smallest (0.327) and the greatest (0.534) natural mortality rate estimated for the Greek sampled population using the Hoenig methods (1983, 1987) and the mean Z value (0.608 ± 0.152) computed for the Italian stock. Thus, the F values were equal to 0.281 and 0.074 year^{-1}, respectively, and the exploitation rate estimates ($E = F/Z$) were 0.462 and 0.122, respectively. In other words, such outcomes would indicate that in Italian waters the mortality on *A. antennatus* stock due to the fishing is between 46.2 and 12.2% of the total mortality.

The Beverton and Holt (1957) model was applied with the abovementioned estimates and the age at first capture (t_c) of 0.42, corresponding to the size of about 10 mm CL obtained from selectivity experiments with 40 mm stretched mesh size codend (Ragonese et al., 1994). The model provided the values of $F_{max} = 0.27$ and $F_{0.1} = 0.12$ for $M = 0.327$, and $F_{max} = 0.39$ and $F_{0.1} = 0.27$ for $M = 0.534$, indicating slight overfishing and underexploitation, respectively (Fig. 7).

4. Discussion

Although several studies on the distribution, abundance and population biology of *A. antennatus* have

Table 7
Total mortality rate (Z) estimated for *A. antennatus* females caught in the Ionian Sea

	Italy			Greece		
	May 2000	August 2000	September–October 2000	April 2000	July 2000	September 2000
Beverton and Holt (1957)						
Italian parameters	0.887	0.670	0.617	0.585	0.436	0.781
Greek parameters	0.873	0.661	0.610	0.579	0.434	0.769
Hoenig (1987)						
Italian parameters	0.588	0.472	0.442	0.424	0.331	0.534
Greek parameters	0.576	0.464	0.435	0.415	0.327	0.523

been carried out on both sides of the Ionian Sea (e.g. Matarrese et al., 1992; Tursi et al., 1993; D'Onghia et al., 1997, 1998b; Kapiris et al., 1999, 2001; Papaconstantinou and Kapiris, 2001; Politou et al., 2003; Mytilineou et al., in press), this is the first work which compares the population biology and dynamics of the blue-and-red shrimp in border-marker areas characterized by different fishing pressure on their bathyal bottoms.

Apart from the fact that *A. antennatus* has been found to be more abundant along the Italian coast than in Greek waters, confirming the observations reported in D'Onghia et al. (2003b), the different aspects examined in the present study show generally the same pattern between the population sampled on the two sides of the Ionian Sea.

The change of the sex ratio with depth as well as the reproductive pattern confirm previous observations in the Ionian (op. cit.) and in the whole Mediterranean (e.g. Bianchini and Ragonese, 1994 and references therein; Cau et al., 2002 and references therein). A decrease in the abundance with depth was only found off Greece due to a greater number of hauls carried out in deeper waters. This trend is well known in *A. antennatus* (Sardà, 1993) for which a non-linear depth-related pattern has been recently reported in Sardà et al. (2003).

Concerning the population structure and dynamics, a common pattern was found in the female length–frequency distributions and growth. Even though the median carapace lengths computed for the Greek samples were significantly greater than those for the Italian ones, most probably as a fishing effect in this latter area, a wide size range with superimposed modal components was found on both sides of the Ionian Sea, in agreement with the trend observed in many Mediterranean basins (Relini et al., 1999; Cau et al., 2002). Quite high similarity percentages were computed between the length–frequency distributions in the two study areas, despite the sensitivity of the Kolmogoroff–Smirnov test to even small percentage differences in the size classes and the fact that it provides statistically significant results. From this point of view, some differences in the size structure between the samples collected in the two border-marker areas were obviously expected in relation to exploitation along the Italian coast as well as to the aleatory character of the sampling, the broad bathymetric distribution of the species (Sardà, 1993) and its displacement capability (Orsi Relini et al., 1986; Matarrese et al., 1995; Sardà et al., 1994; Relini et al., 2000, 2004). In other words, even in the same study area it would be impossible to obtain samples which overlap each other exactly. Therefore, the size–frequency distribution pattern of *A. antennatus* females in the Italian area appears to be comparable to that found in Greek waters, where deep-water bottom trawl fishing does not occur. Such a pattern confirms previous observations on the size structure of *A. antennatus* stock both throughout the western Ionian Sea along the Italian coast (Matarrese et al., 1997) and in the area located along the Apulian coast and regarding the Gallipoli fishery (D'Onghia et al., 1998b). The fact that *A. antennatus* males exhibit a wider depth distribution than females (Sardà, 1993), as also confirmed in this paper, and that only a few explorative hauls were carried out at depths greater than 800 m, prevents the comparison of the sampled male populations between the two areas and between the present and previous studies. For the female populations sampled on the two sides of the Ionian Sea, the size structure analysis produced Von Bertalanffy growth parameters with the same growth performance index, which is in agreement with the very slow scenario reported in Orsi Relini and Relini (1998) and Cau et al. (2002). According to these authors, *A. antennatus* can be considered a shrimp species with a long life span (up to 8–9 years). Recent observations along the western Ionian coasts, both through trawl surveys (Capezzuto et al., 2004) and tagging experiments (Relini et al., 2004), would seem to confirm such a slow growth pattern and longevity.

Irrespective of the growth parameters used in the present study, the total mortality rates were comparable between the two areas. The total mortality rates in Greek waters overlap those of the natural mortality. This confirms the basic hypothesis that the mortality in the Greek population of *A. antennatus* is only due to natural causes, and is in agreement with the results obtained by Papaconstantinou and Kapiris (2001) in a neighbouring area of the eastern Ionian Sea, even though these authors obtained slightly higher values, probably in relation to the different data set and estimation methods. Moreover, the results related to the mortality estimates in the north-western Ionian (Italian sector) are in agreement with a previous study in which a total mortality rate of 0.64 $year^{-1}$ was estimated for the female stock using the Hoenig (1987) method and the following parameters: $L_\infty = 77.18$ mm CL; $k = 0.35$ $year^{-1}$; $t_0 = -0.36$ (Matarrese et al., 1997).

The adoption of two natural mortality rates (0.327 and 0.534) for the further computations carried out in the present paper is in agreement with the lower values of the estimate range reported by several authors (Demestre and Lleonart, 1993; Demestre and Martin, 1993; Ragonese and Bianchini, 1996; Colloca et al., 1998; Carbonell et al., 1999). In addition, Yahiaoui et al. (1986) reported a value of 0.47 for a "virgin" Algerian stock of *A. antennatus* and Fiorentino et al. (1998) proposed the value of $M = 0.3$ as the most realistic estimate of natural mortality rate for this deep-sea shrimp. The adoption of $M = 0.327$ is a conservative choice in estimating fishing mortality rate for the Italian stock, providing an indication of slight overfishing. In contrast, the input of M equal to 0.534 in the Y/R model gives an indication of underexploitation. A value of M higher than this latter would be very close to the total mortality rate in Italian waters and would make the value of fishing mortality nil. This appears to be rather unlikely, considering the fishing pressure exerted along the Italian coasts. According to Ragonese and Bianchini (1996), small changes of M can greatly influence the results of Y/R curves. Indeed, the natural mortality rate represents a major uncertainty in long-term stock assessment using, as in this case, the traditional approach (Gulland, 1988). Therefore, as realistic values of M should be between 0.327 and 0.534, the results related to the exploitation status of *A. antennatus* in Italian waters confirm previous observations of optimal harvesting in the western Ionian Sea (Matarrese et al., 1997) and are in agreement with the results obtained in other Mediterranean areas (Relini et al., 1999; Fiorentino et al., 1998 and references therein). However, taking into account the young age at first capture utilized in the yield per recruit model, the current Y/R could be increased by delaying the entry into the fishery of this shrimp (Ragonese and Bianchini, 1996).

Along the Italian coasts, the female population of *A. antennatus* represents the main exploited stock since they are larger and more abundant than males on the fishing grounds. Although the female stock is exploited for both juveniles and adult individuals, in contrast to the majority of the Mediterranean demersal resources it appears to be close to optimal harvesting. This might be due to its very wide depth distribution on bathyal bottoms and to the fact that part of its population is not vulnerable to trawling (Sardà et al., 2004). During this research, it was sampled as far as the deepest investigated bottoms in both areas. In the western Mediterranean *A. antennatus* was caught down to more than 2000 m (Sardà, 1993) and recently in the Ionian Sea it has been found as deep as 3300 m (Sardà et al., 2004). This shrimp shows a high population mobility, often difficult to follow from the fishery, and displacement in areas, such as canyons, unsuitable for trawling (Orsi Relini et al., 1986; Sardà, 1993; Sardà et al., 1994, 1997; Matarrese et al., 1995). Relini et al. (2000) reported the recapture 1 month after tagging of one specimen about 10 nautical miles from the release point. In addition to its deeper distribution and lower availability to fishing, *A. antennatus* shows a high turnover rate, linked to its early maturity and high fecundity (up to four times that of *A. foliacea* in the larger females, according to Orsi Relini and Semeria, 1983). Thus, all these features seem to play a fundamental role in the stock recovery, blunting the differences in the population structure between exploited and unexploited areas.

Finally, considering the deep distribution and the displacement capability of this shrimp an exchange of specimens between Italian and Greek stocks cannot be excluded and thus the Greek area, where deep-water trawling does not occur, could represent a further refuge for the *A. antennatus* population in the Mediterranean.

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