Marine Biology (2002) 141: 527–539
DOI 10.1007/s00227-002-0851-4

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Life-history traits of *Plesionika martia* (Decapoda: Caridea) from the eastern-central Mediterranean Sea

Received: 20 April 2001 / Accepted: 23 March 2002 / Published online: 23 May 2002

Abstract Life-history traits of *Plesionika martia* (Milne Edwards, 1883) were studied through data collected during six seasonal trawl surveys carried out in the Ionian Sea (eastern-central Mediterranean) between July 1997 and September 1998. *P. martia* was found at between 304 and 676 m depth, with the highest density in the 400–600 m range. Intraspecific, size-related depth segregation was shown. Recruitment occurred in summer at the shallowest depths. Juveniles moved to the deepest grounds as they grew. The largest female and male were 26 and 25 mm carapace length, respectively. The sex ratio was slightly in favour of females at depths >400 m. Although a seasonal spawning peak was shown, the reproduction appears to be rather prolonged throughout the year. Females with ripe gonads were found from spring to autumn. Ovigerous females with eggs in late maturity stage were found year round. Large females could spawn more than one time within their annual reproductive cycle. The size at first maturity (50% of the ovigerous females) was 15.5 mm CL. Average brood size of eggs with a well-developed embryo was 2,966 ± 1,521. Iteroparity, low fecundity and large egg size patterns were observed. Brood size increased according to the carapace length. Two main annual groups were found in the field population of the Ionian Sea. Estimates of the Von Bertalanffy growth parameters are: $L_\infty = 30.5$ mm, $k = 0.44$ year^{-1} in females; $L_\infty = 28.0$ mm, $k = 0.50$ year^{-1} in males. A negative allometry was detected mostly in the ovigerous females. The life cycle of *P. martia* is discussed in the light of life-history adaptations shown in other deep-water shrimp species.

Communicated by R. Cattaneo-Vietti, Genova

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Keywords Crustacea Decapoda · *Plesionika martia* · distribution · reproduction · fecundity · population structure · growth · life cycle · Mediterranean Sea

Introduction

The golden shrimp *Plesionika martia* (Milne Edwards, 1883) is a demersal species with a worldwide distribution in tropical and temperate ocean waters (Holthuis 1980). In the Mediterranean it is found along the continental shelf edge and slope, where it is more common in the western basin than in the eastern and absent in the northern and central Adriatic Sea (Relini et al. 1999).

Although the occurrence of *P. martia* in the Mediterranean has been recorded since the beginning of deep-water fishing (Brian 1931, 1942), most of the studies only regard its depth distribution and abundance within the crustacean communities of the western Mediterranean (Maurin 1961, 1965; Audouin 1965; Lagardère 1972; Orsi Relini 1973; Relini et al. 1986; Mura 1987; Abelló et al. 1988; Righini and Auteri 1989; Cartes and Sardà 1992; Mura and Cau 1992; Cartes et al. 1994; Carbonell and Abelló 1998; Cuccu et al. 1998). On the western side of the basin, feeding habits have also been investigated (Lagardère 1972; Cartes 1993), and, only recently, an insight has been provided into the reproductive biology, population characteristics and growth of the species (Company and Sardà 1997, 2000). Reproductive studies have also been undertaken in the Sardinian seas (Campisi et al. 1998).

Concerning the rest of the Mediterranean, information on the bio-ecology of *P. martia* is rather scant, and generally refers to the presence, depth distribution and abundance. Arena and Li Greci (1973) reported data for Sicilian waters; Froglia (1972), Bombace and Froglia (1973), Vaccarella et al. (1992) and Marsan et al. (2000) for the South Adriatic; Katagan et al. (1988) for the west coast of Turkey; Koukouras et al. (1992, 1998) for the Aegean Sea and Politou et al. (2000) for the east side of the Ionian Sea. On the west side of this latter basin

P. martia can play, together with other pandalid shrimps, an important role as bycatch of the deep bottom trawling, mainly in relation to the abundance changes of the target species *Aristeus antennatus* and *Aristaeomorpha foliacea* (Tursi et al. 1993). A recent investigation on the demersal fish assemblages in the western Ionian Sea indicates the golden shrimp to be among the dominant species of the bathyal grounds (D'Onghia et al. 1998a).

The increasing exploitation of deep-sea resources (down to 800 m) in the eastern-central Mediterranean and the lack of scientific knowledge on the golden shrimp in this area, led the authors to investigate its depth distribution pattern, reproduction, fecundity, population structure and growth. The aim of the present paper was to provide information on the life-history traits of *P. martia* in the western Ionian Sea.

Materials and methods

Sampling

Samples were collected during six experimental bottom trawl surveys carried out in the western Ionian Sea (Fig. 1) from July 1997 to September 1998 as part of three study projects: DEEP-FISHERIES (Gordon 1998), MEDITS (Bertrand et al. 2000) and GRUND (Relini 1998). In these surveys a total of 153 h of sampling was conducted between 200 and 750 m. A total of 19,635 specimens was sampled from 304 to 676 m of depth (Table 1).

A professional motor-powered vessel, equipped with Italian-type nylon otter trawl net with stretched mesh of 40 mm in the codend, was hired during DEEP-FISHERIES and GRUND cruises. A cover with stretched mesh of 20 mm was employed on the codend with the aim of sampling small specimens. During the MEDITS survey an especially designed net with a stretched mesh of 20 mm in the codend was used (Bertrand et al. 2000). The horizontal and vertical opening of the two nets, 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 research cruise was depth stratified. The hauls were carried out from dawn to dusk, with a duration of 3 h during DEEP-FISHERIES surveys and 1 h during GRUND and MEDITS surveys. The vessel speed, measured using a global positioning system, was maintained at 2.5–3.0 knots.

Data collection

For each defrosted specimen of *P. martia* the following data were recorded in the laboratory.

- Carapace length, CL, was measured from the post-orbital socket to the posterior-median edge of the cephalothorax, to the nearest millimetre.
- Body weight, BW, was taken to the nearest 0.1 g.
- Sex was determined under a binocular microscope, observing the shape of the endopodite in the first pair of pleopods and the presence or absence of the male appendix in the second pair of pleopods (Zariquiey Alvarez 1968; King and Moffitt 1984). Considering that both during hauling and sorting on board and after defrosting in the laboratory a large number of specimens was damaged and without pleopods, the sex was determined in 15,174 individuals (8,231 females and 6,943 males).
- Four stages of gonadal development in females were defined according to the relative intensity of the colour and size of the gonads. Stage 1 refers to immature and resting individuals with white-transparent gonads. Stages 2 (light green–blue, early maturity), 3 (dark green–blue, advanced maturity) and 4 (blue, full maturity) represent three successive phases of gonadal activity (Company 1995).

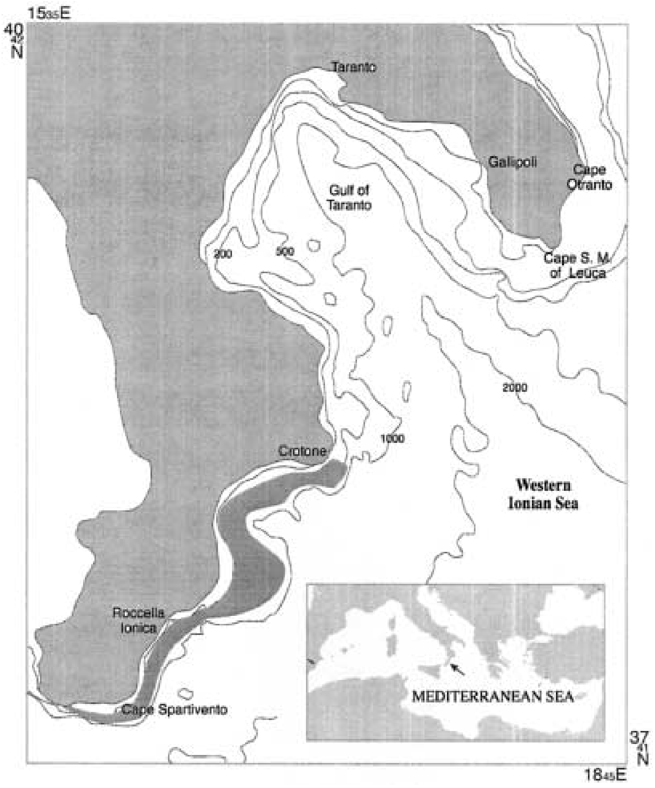


Fig. 1. Map of the western Ionian Sea with indication of the area (*shaded*) investigated from July 1997 to September 1998

- Three stages of egg development were considered on ovigerous females: early stage (1), eggs of recent spawning with intense sky-blue colour and no embryo pigmentation visible; middle stage (2), pale-green coloured eggs with slight embryo eye pigmentation; late stage (3), colourless eggs with embryo eye pigmentation well visible and embryo well developed (Company and Sardà 1997).
- Gonad weight, GW, was taken to the nearest 0.001 g, on a subsample of females ($n = 505$).
- Egg number was counted on a subsample of ovigerous females with eggs in different stages of development under a binocular microscope. The egg size, to the nearest 0.01 mm, was measured for each stage of egg development. The major and minor axes of ellipsoidal eggs were measured under a binocular microscope using a micrometer lens.

Data processing

Using the number of individuals for the swept area of each haul, the average abundance, expressed as the number per square kilometre (± SD), by depth was computed in order to define the depth of the highest concentration of *P. martia* in the Ionian Sea. The swept area was estimated according to the wing spread of the net (horizontal opening) and the speed of the vessel (Pauly 1983).

Sex ratio by depth was computed for the population sampled throughout the research. Statistical differences between the number of females and males by depth were determined using the *G*-test (Sokal and Rohlf 1969). The change in carapace length with depth was statistically tested by means of linear regression.

The size distributions of the females in each maturity stage of the gonads and the size distributions of ovigerous females were calculated for each survey. Moreover, the length-frequency distributions by maturity stage of the gonads were computed for ovigerous females with eggs in the late maturity stage, in order to

Table 1. List of cruises, with relative date, number of sampling hours, depth of occurrence and number of *Plesionika martia* caught in the Ionian Sea

Cruise	Date	No. of sampling hours	Depth (m)	No. of specimens
DEEP-FISHERIES	Jul 1997	34	360–676	1,904
GRUND	Sep 1997	18	417–606	3,762
DEEP-FISHERIES	Dec 1997	32	304–673	2,628
DEEP-FISHERIES	Mar 1998	35	314–673	5,287
MEDITS	May 1998	17	385–562	916
GRUND	Sep 1998	17	401–599	5,138

evidence the link between gonad activity and spawning. According to King and Butler (1985) and Caldentey et al. (1990a), the size at first maturity was considered to be the size at which 50% of the females in the population were ovigerous. In fact, in pandalid shrimps, the final phase of the reproductive cycle is characterised by the presence of eggs between the pleopods. The size at first maturity was determined, for the pooled data from May, July and September (main reproductive season), using the asymmetric function reported in Sardà et al. (1993). Since the larger females in a cohort could spawn earlier in a definite reproductive season, mean, minimum and maximum sizes were recorded considering all ovigerous females during each month.

The gonadosomatic index (GSI) was computed: gonad weight/total body weight (without eggs)×100. The mean size of the eggs was computed using the arithmetic mean between major and minor axes according to Company and Sardà (1997). The average brood size was estimated for each stage of egg development. Statistical differences between the number of eggs in each stage by month were determined using the *G*-test (Sokal and Rohlf 1969). The relationship between carapace length and brood size was evaluated by regression analysis (King and Butler 1985; Company and Sardà 1997). The annual and monthly (for May, July and September) reproductive effort (RE) were estimated as the ratio between the weight of the eggs and the body weight (King and Butler 1985).

The length-frequency distributions (1 mm size classes) of the whole sampled population, females and males, were performed for each month. The modal components in the size-frequency distributions were separated by means of the Bhattacharya method as reported in the FiSAT program (Gayanilo et al. 1995). Each representative component, with a separation index >2, was assumed to be a single cohort and then utilised to identify the modal progression. Growth was treated as a continuous function (Garcia and Le Reste 1981). The Von Bertalanffy growth parameters were estimated separately for females and males using ELEFAN in the FiSAT program (Gayanilo et al. 1995).

The "overall growth performance" ϕ' (Munro and Pauly 1983) was computed in order to compare the growth rates of the two sexes and those of the western Mediterranean population (Company and Sardà 2000). The carapace length–body weight relationship was computed according to the power curve function, log-transformed: $\ln BW = \ln a + b(\ln CL)$, where ln*a* is the intersect and *b* the allometric coefficient (or slope). This was calculated for females (non-ovigerous, ovigerous with eggs removed, non-ovigerous plus ovigerous) and for males. The linear regression equations for the two sexes were compared statistically using the Chow-test (Koutsoyiannis 1977). This test verifies whether there is a significant difference between both the slope (*b*) and the intersect (*a*) of the two regression lines estimated from two different samples.

Results

Distribution pattern

Plesionika martia was found between 304 and 676 m of depth, with the highest density in the 400–600 m range (Table 2). Although the species was caught in almost 100% of the hauls carried out at depths >400 m, great changes were shown in the number of specimens collected. This is also evident in the scatter plot of the logarithm of density versus depth (Fig. 2). The relationship between density and depth was not statistically significant ($P>0.05$).

The sex ratio by depth, for the entire dataset, was slightly in favour of females at depths >400 m (Fig. 3). The difference in the change between the number of females and males across the vertical gradient was statistically significant ($G_2=52.64$, $P<0.01$).

Both females and males showed a significant increase in size with depth ($P<0.01$), resulting in the following relationships:

- $CL_{females} = -1.2463 + 0.0363 depth$; $r=0.857$, $r^2=0.735$
- $CL_{males} = 0.9794 + 0.0305 depth$; $r=0.854$, $r^2=0.730$

The trend of increasing size by depth was slightly steeper for females than for males (Fig. 4).

Reproduction

Apart from December, females in reproductive activity (stages 2 + 3 + 4) were collected during each survey, with the highest percentage of fully mature ovaries (stage 4) during July (Fig. 5). The smallest specimens with active

Table 2. Total number of hauls, percentage of hauls in which the species was found, number of sampling hours and mean number per square kilometre (N km^{-2}), with relative standard deviation (*SD*), computed for *Plesionika martia* caught in the Ionian Sea from July 1997 to September 1998

Depth (m)	No. of hauls	Species found (% hauls)	No. of sampling hours	*P. martia* (N km^{-2})	
				Mean	SD
200–400	24	38	43	186	319
400–600	58	97	85	2,000	2,233.3
600–750	10	100	25	477	306.8

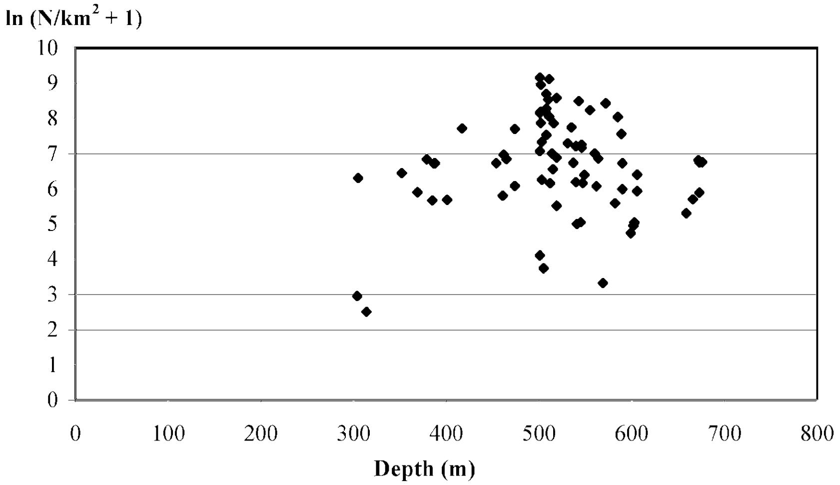


Fig. 2. *Plesionika martia.* Scatter plot of logarithm of numerical abundance by depth of shrimp caught in the Ionian Sea

gonads measured 12 mm CL. Immature specimens were found rather uniformly spread over the length range, due to the presence of both juveniles and resting individuals. The trend of the GSI by survey confirmed the above evidence on gonad activity (Fig. 6). As expected, the mean GSI value increased according to the maturity stage of the gonads, confirming macroscopic observations (Fig. 7).

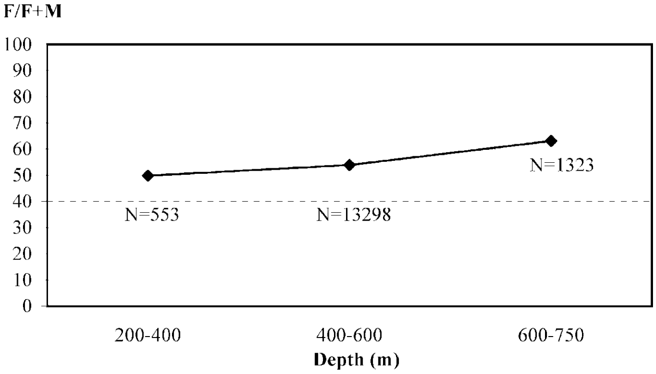


Fig. 3. *Plesionika martia.* Sex ratio by depth, with indication of total number (*N*), computed for shrimp caught in the Ionian Sea

Ovigerous females with the three egg development stages were found each month and mostly during May, July and September (Fig. 8). The highest percentages of females without eggs were shown for all sizes in December and March. In these 2 months, only the largest females were ovigerous. The sharp separation between juveniles and spawners was evident in the size structure of July 1997 and September 1998.

From May to October a noteworthy fraction of the female population bore eggs in the late stage (egg development stage 3), and most had gonads in advanced and full maturity. During December and March only large females were found with eggs in the late maturity stage; their gonads were almost exclusively immature in the former month and were in all maturity stages in the latter (Fig. 9).

The smallest female bearing eggs had a carapace length of 12 mm. The smallest one with eggs of stage 3 measured 15 mm CL. The size at attainment of 50% maturity was 15.5 mm CL (Fig. 10). For sizes greater than this, the highest percentages of ovigerous females

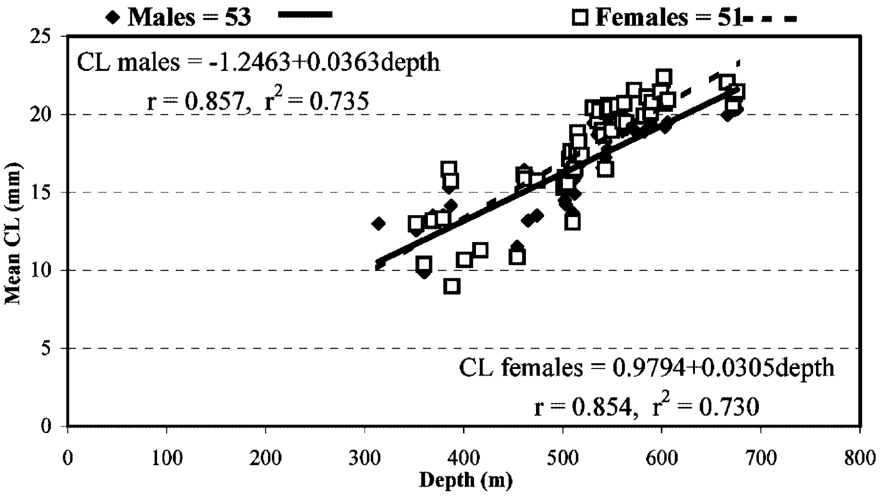


Fig. 4. *Plesionika martia.* Mean carapace length (*CL*) by depth, with regression lines, computed for males and females caught in the Ionian Sea

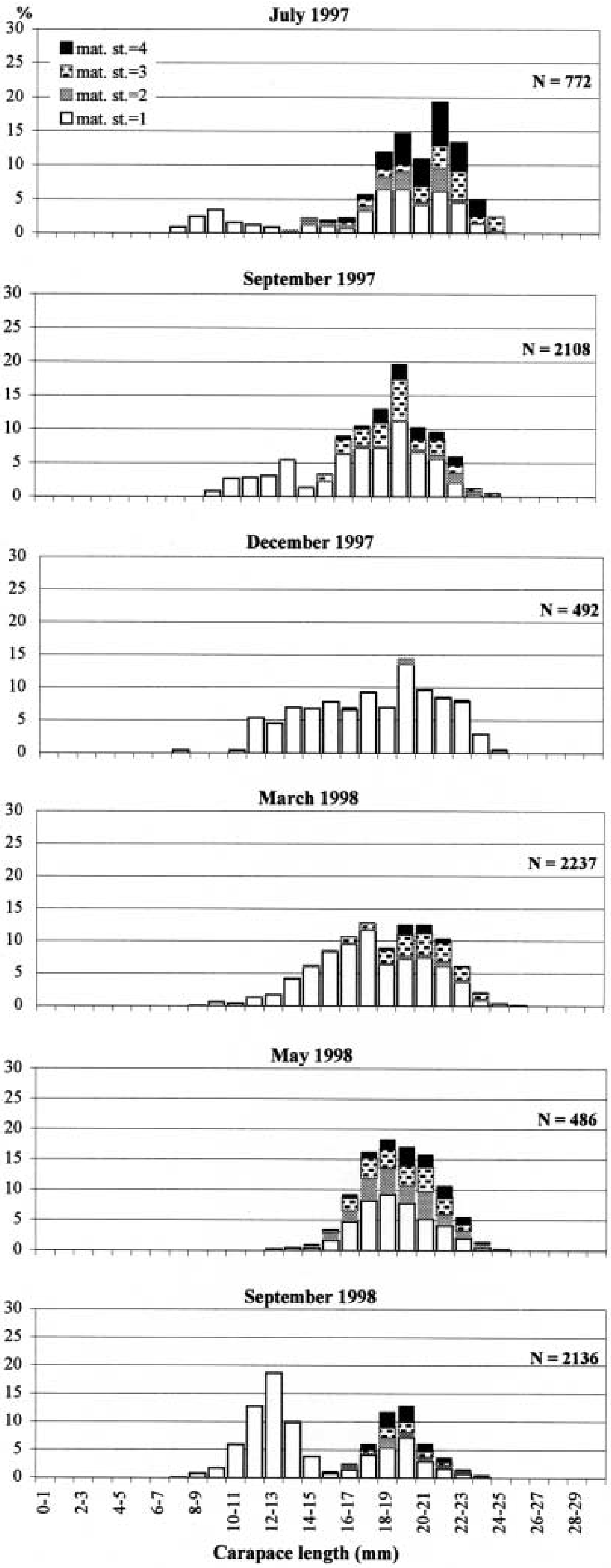


Fig. 5. *Plesionika martia.* Length-frequency distributions by maturity stage of gonads (*mat. st.*) of female shrimps caught in the Ionian Sea

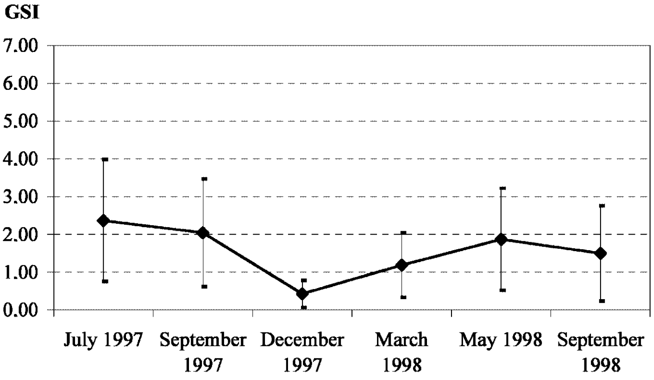


Fig. 6. *Plesionika martia.* Mean gonadosomatic index (*GSI*) by survey, with relative standard deviation, computed for female shrimps caught in the Ionian Sea

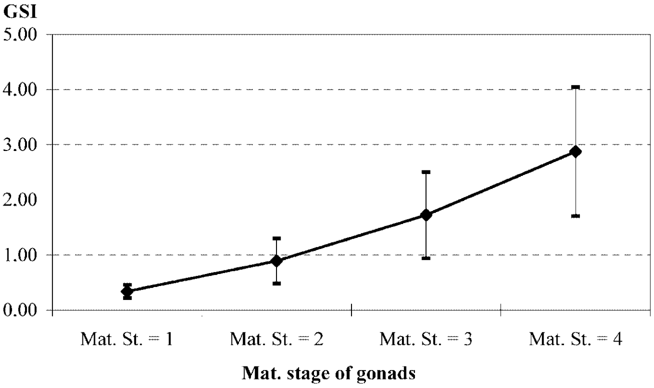


Fig. 7. *Plesionika martia.* Mean gonadosomatic index (*GSI*) by maturity stage, with relative standard deviation, computed for female shrimps caught in the Ionian Sea

(>90%) were found in July 1997 and September 1998 (Fig. 11). High percentage values (>70%) were also shown during September 1997 and May 1998. The values were around 10% in December and March. As suggested in Figs. 8 and 9, during these 2 months an increase in both minimum and mean sizes of ovigerous females was observed.

Fecundity

The brood size and egg sizes of each egg development stage are reported in Table 3. The brood size varied greatly in each stage (mean CV around 45%). On average, survival from the second development stage to the third (86%) was higher than that from the first development stage to the second (61%). This was confirmed by the analysis carried out for the months when the highest percentage of ovigerous females were found (Fig. 12). The change in the average number of eggs in each stage during the 3 months was statistically significant ($G_4 = 775.37$, $P < 0.01$). The annual reproductive effort was 0.121 ± 0.023, while during May, July and

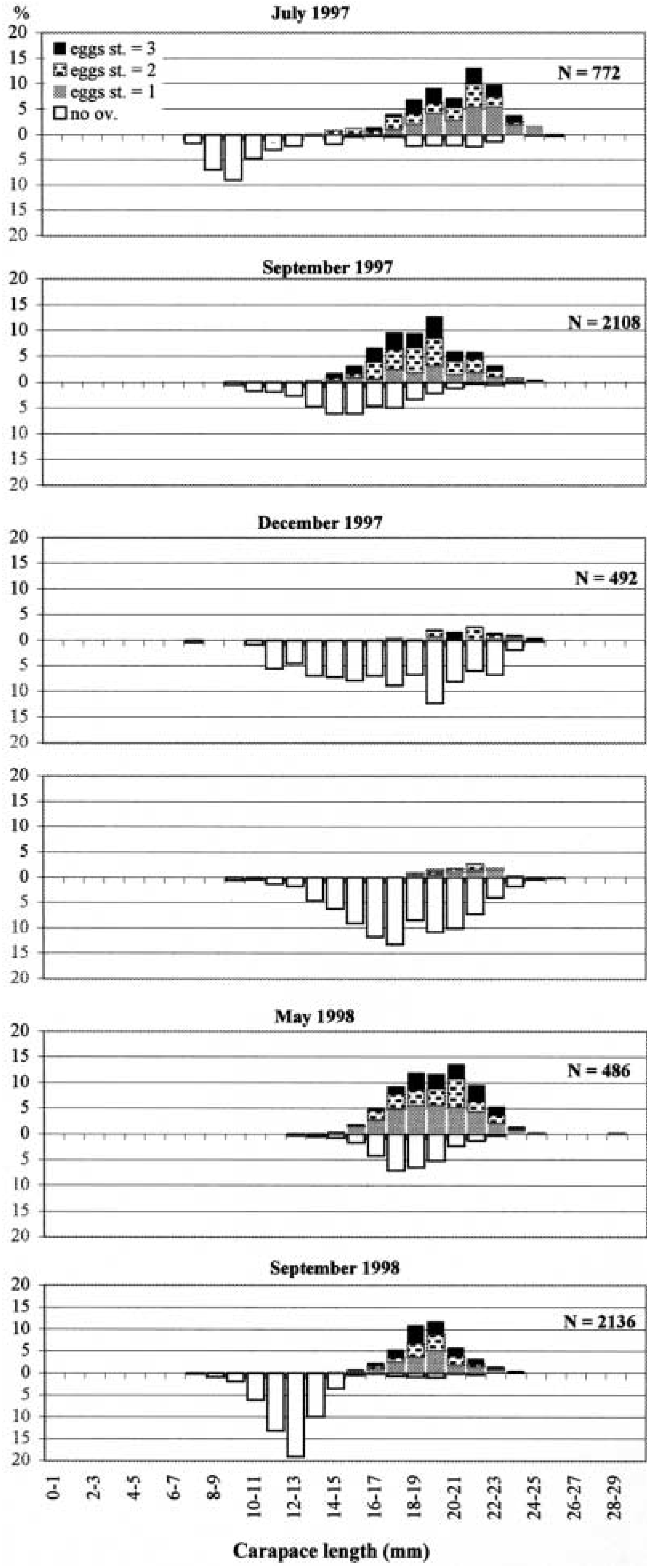


Fig. 8. *Plesionika martia.* Length-frequency distributions by development stage of eggs (*eggs st.*) for ovigerous females and non-ovigerous females (*no ov.*) of shrimp caught in the Ionian Sea

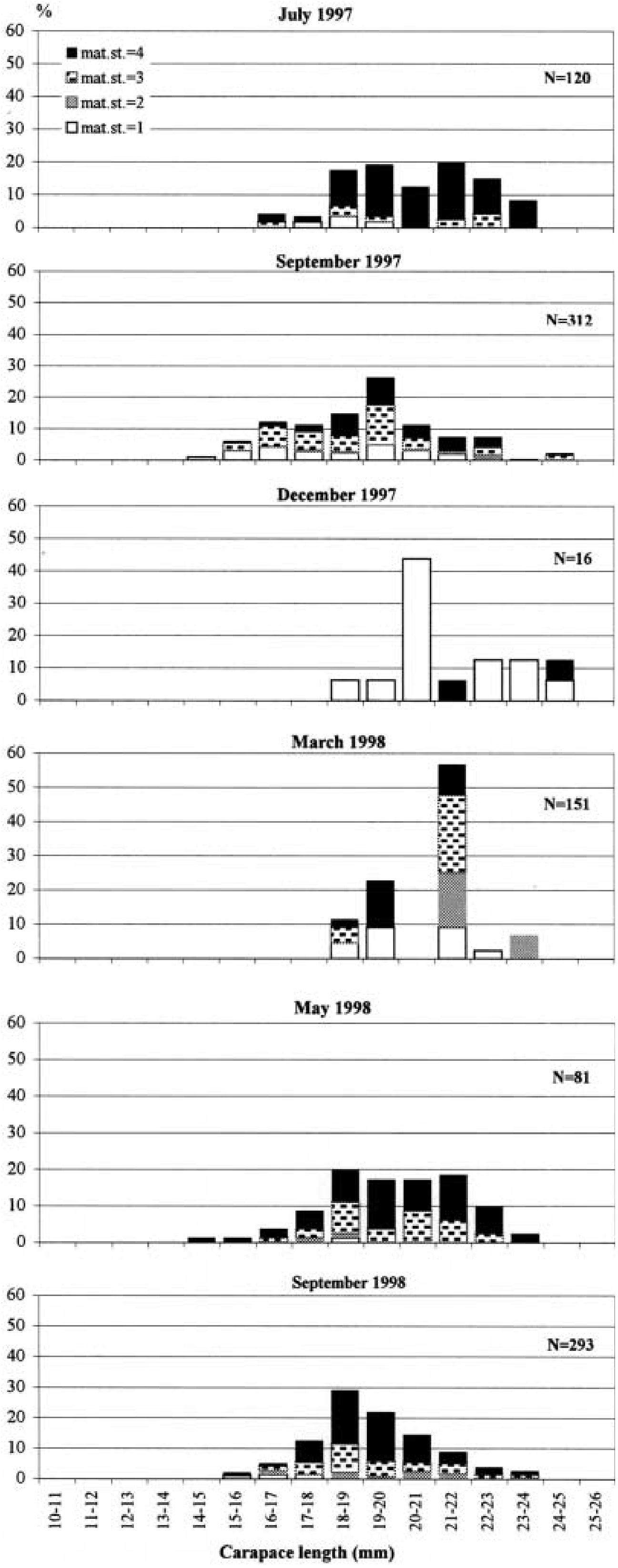


Fig. 9. *Plesionika martia.* Length-frequency distributions by maturity stage of gonads (*mat. st.*) of female shrimps with eggs in late development stage (*3*)

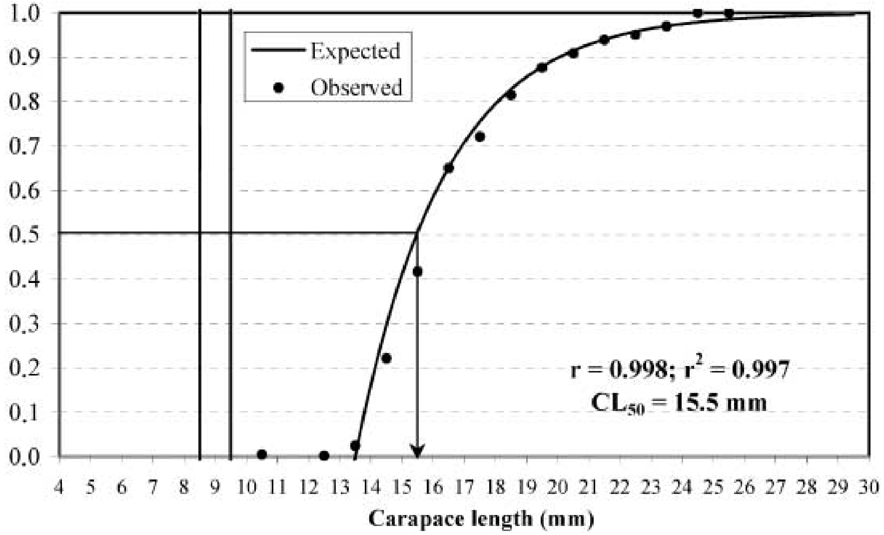


Fig. 10. *Plesionika martia.* Expected and observed percentage by size of ovigerous female shrimps, with size at first maturity (CL_{50})

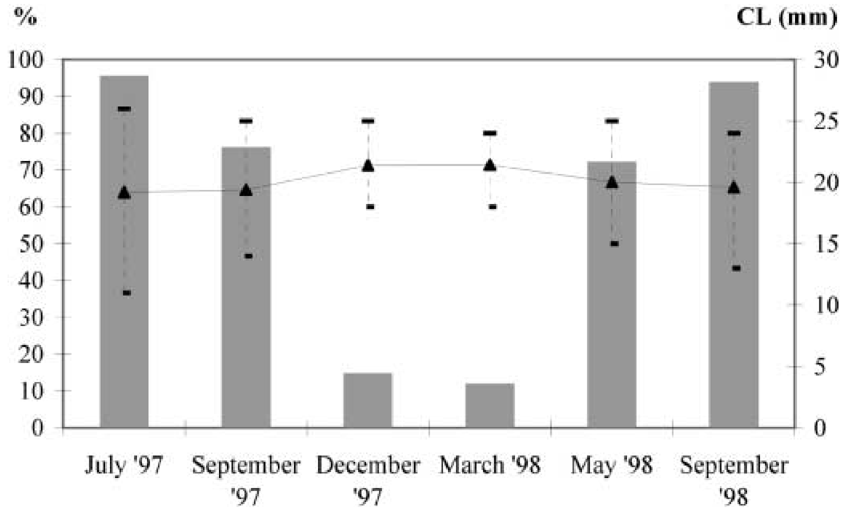


Fig. 11. *Plesionika martia.* Percentage of ovigerous females ($CL > CL_{50}$) and trend of minimum, mean and maximum carapace length by survey computed for all ovigerous females *P*

Table 3. *Plesionika martia.* Minimum, mean with relative standard deviation (*SD*) and maximum values of brood size and of the mean diameter for different egg development stages of shrimp in the Ionian Sea

	Min.	Mean ± SD	Max.
Stage 1 ($N = 33$)			
Brood size	1,800	5,653 ± 2,410	11,200
Mean diameter (mm)	0.39	0.61 ± 0.05	0.65
Stage 2 ($N = 24$)			
Brood size	1,440	3,450 ± 1,489	7,269
Mean diameter (mm)	0.65	0.75 ± 0.05	0.78
Stage 3 ($N = 64$)			
Brood size	650	2,966 ± 1,521	6,627
Mean diameter (mm)	0.65	0.78 ± 0.02	0.79

September it was 0.120 ± 0.024, 0.156 ± 0.070 and 0.118 ± 0.013, respectively.

Considerable changes in brood size were also shown within and between carapace length classes (Fig. 13). The relationship between brood size of the third egg development stage and CL was highly significant ($P < 0.01$): $BS_3 = -5{,}508.5 + 408.72CL$; $r = 0.495$, $r^2 = 0.245$; $n = 64$. On average, the increase in size between the first and second development stage was greater than that between the second and the third.

Population structure

P. martia was sampled during each survey with a wide range of sizes (Table 4). The smallest unsexed individual

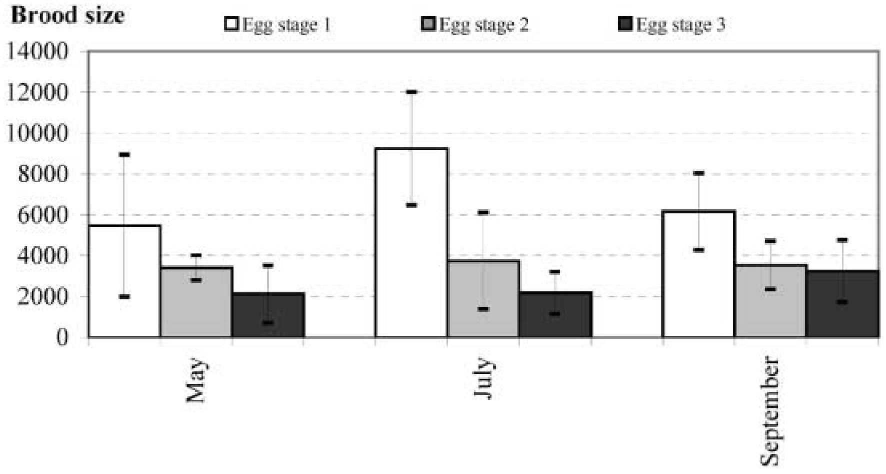


Fig. 12. *Plesionika martia.* Mean brood size, with relative standard deviation, computed by egg development stage and by month for shrimp in the Ionian Sea

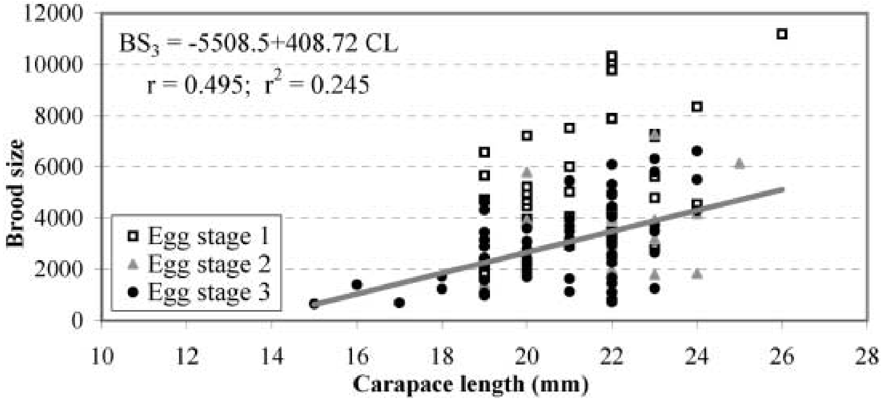


Fig. 13. *Plesionika martia.* Relationship between brood size and carapace length, by different egg development stages, computed for female shrimps caught in the Ionian Sea (the regression line applies only to the third stage)

Table 4. *Plesionika martia.* Total number of individuals, size of the smallest unsexed specimen (*I*), and minimum, maximum and mean carapace length (*CL*) with relative standard deviation (*SD*), computed by sex and survey for shrimp caught in the Ionian Sea

Cruise	Total *N*	I CL (mm)	Females				Males			
			N	CL (mm)			*N*	CL (mm)		
				Min.	Mean ± SD	Max.		Min.	Mean ± SD	Max.
Jul 1997	1,904	6	772	8	17.9 ± 5.1	26	481	8	14.9 ± 4.8	24
Sep 1997	3,762	7	2,108	10	18.1 ± 2.9	25	1,347	10	17.0 ± 2.7	23
Dec 1997	2,628	8	492	8	18.2 ± 3.5	25	645	10	17.6 ± 3.0	25
Mar 1998	5,287	9	2,237	9	18.7 ± 2.9	26	1,937	10	17.6 ± 2.6	24
May 1998	916	8	486	13	19.6 ± 2.0	25	399	10	18.8 ± 2.0	24
Sep 1998	5,138	6	2,136	8	15.9 ± 3.7	24	2,134	8	15.7 ± 3.2	23
Total	19,635		8,231	8	17.7 ± 3.58	26	6,943	8	16.8 ± 3.2	25

had a carapace length of 6 mm. The largest female and male measured 26 and 25 mm CL, respectively. The mean carapace length of females was always greater than that of males. The highest standard deviation values were obtained when the smallest mean sizes of both sexes were estimated (July 1997 and September 1998), indicating the occurrence of both very small and large specimens in the sampled population. The mean size in both sexes increased slightly from July 1997 to May 1998, becoming smaller again in September 1998. This aspect is also evident from the length-frequency distributions presented in Figs. 5 and 8 for females and in Fig. 14 for males, showing several modal components throughout the research period in the sampled population.

The recruitment pulse was shown during July 1997 and, after 1 year, during September 1998. Analysis of the size composition by depth during July, when the highest percentage of juveniles was found, confirmed the relationship between size and depth (Fig. 15).

Apart from December 1997 and September 1998, females were more abundant than males. The sex composition by size changed throughout (Fig. 16). It was generally around 50% at < 20 mm CL, and increasingly

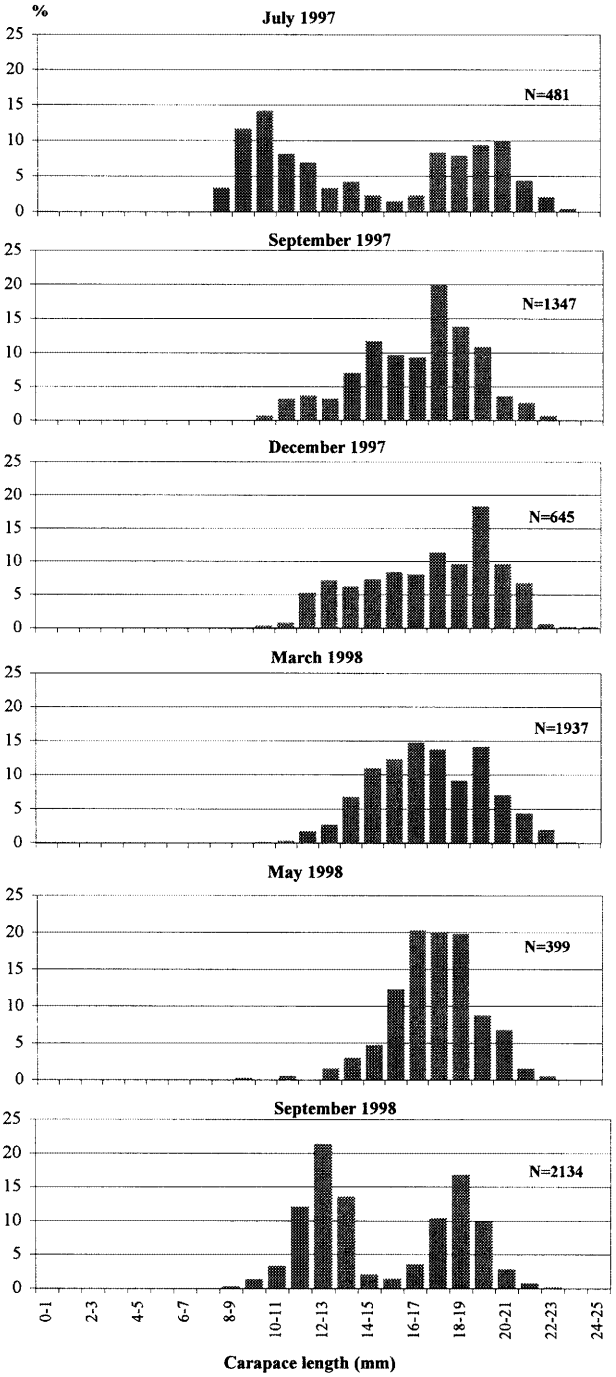


Fig. 14. *Plesionika martia*. Length-frequency distributions of male shrimps caught in the Ionian Sea

in favour of females from 20 mm to the largest shrimp size measured. Since these results were otherwise clear, statistical processing was considered inappropriate and unnecessary for the type of data presented.

Growth

By using the Bhattacharya method, it was possible to separate, both in females and males, four modal components in July 1997, one in May 1998 and three in September 1998 (separation index >2). In fact, only during these months, no significant differences between the observed and expected size frequencies were detected ($\chi^2 <$ critical values, $P > 0.05$). In the other months the expected size distributions of the various modes were statistically different from those observed, and thus they were not utilised to perform ELEFAN.

Assuming that the first modes of 9.93 ± 1.35 and 9.33 ± 1.05 mm CL identified in females and males, respectively, during July progressed in length up to those of 19.36 ± 1.23 and 18.43 ± 1.12 mm CL, respectively, detected in September, the following Von Bertalanffy growth parameter estimates were computed:

- Females: $CL_\infty = 30.5$ mm, $k = 0.44$ year^{-1}; $Rn = 0.340$
- Males: $CL_\infty = 28.0$ mm, $k = 0.50$ year^{-1}; $Rn = 0.262$

The growth performance index ϕ' was 2.61 for females and 2.59 for males, which, as observed in the size distributions, confirmed a slightly higher growth rate in females than in males.

Considering the growth in weight, the size–weight relationship was computed for the carapace length (CL, in mm) and body weight (BW, in g). The functions were as follows:

- Non-ovigerous females: $BW = 0.000889 \times CL^{2.89}$; $r = 0.97$; $n = 3{,}831$; confidence limits of the slope $(b) = 2.866$–2.914
- Ovigerous females: $BW = 0.00207895 \times CL^{2.62}$; $r = 0.92$; $n = 217$; confidence limits of the slope $(b) = 2.468$–2.768
- Females (non-ov. plus ov.): $BW = 0.00100098 \times CL^{2.85}$; $r = 0.96$; $n = 4{,}048$; confidence limits of the slope $(b) = 2.830$–2.876
- Males: $BW = 0.001045 \times CL^{2.84}$; $r = 0.95$; $n = 6{,}540$; confidence limits of the slope $(b) = 2.814$–2.860

The Chow-test gave results significantly different only between the length–weight relationship of the ovigerous females and males ($F^* = 242.01$, $P < 0.01$) while the differences between males and the two other categories of females were not statistically significant ($P > 0.05$).

Discussion and conclusions

Life-history traits shown in *Plesionika martia* from the Ionian Sea can be included in the patterns described for deep-water caridean shrimps (King and Butler 1985; King 1987) and are in agreement with observations on the species from the western Mediterranean (Company and Sardà 1997, 2000; Campisi et al. 1998; Carbonell and Abelló 1998; Cuccu et al. 1998).

The intraspecific size-related depth segregation appears to conform to a distribution pattern that would reduce competition for space and food resources among size classes (Gage and Tyler 1991; Cartes 1993). The high variability in the numbers found during sampling could be related to the high degree of patchy distribution

Fig. 15. *Plesionika martia*. Length-frequency distribution by depth stratum for all specimens of *P.* shrimps caught in the Ionian Sea during July 1997

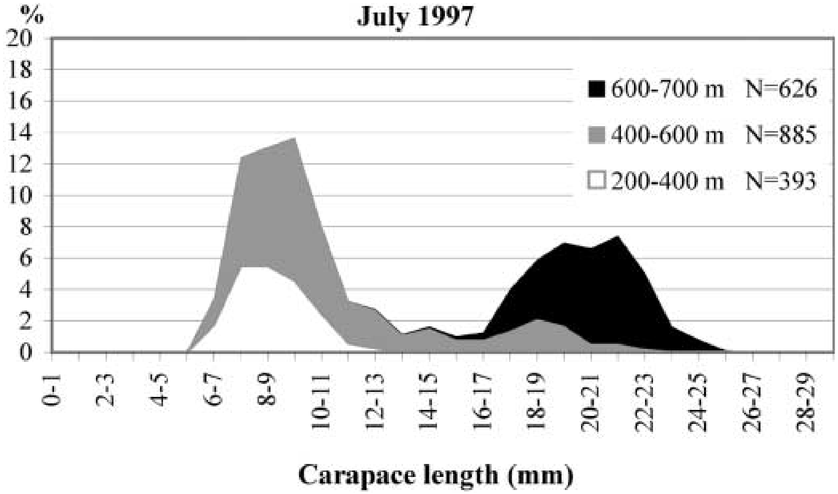
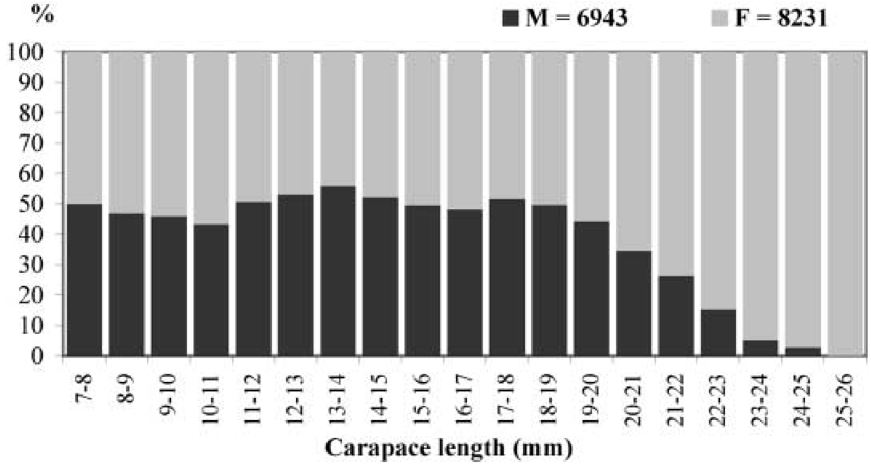


Fig. 16. *Plesionika martia*. Sex ratio by carapace length of shrimp caught in the Ionian Sea



of shrimps (Omori 1974), highlighted for *P. martia* and *P. heterocarpus* in the north-western Mediterranean (Maynou et al. 1996). Although the depth distribution range of the species, both the upper and lower limit, may change between the various Mediterranean areas (Company and Sardà 1997; Carbonell and Abelló 1998; Cuccu et al. 1998; Marsan et al. 2000; Politou et al. 2000), in the Ionian Sea the highest densities were also shown between 400 and 600 m.

As shown in Sardinian waters (Campisi et al. 1998; Cuccu et al. 1998), in Albanian waters of the southern Adriatic Sea (Marsan et al. 2000) and in some Spanish areas (Carbonell and Abelló 1998), the sex ratio was in favour of females. Males were also found to be less abundant than females among *P. gliglioli* from the Sardinian Channel (Mura 1995) while small changes in the sex ratio were observed among *P. edwardsii* from the Spanish western Mediterranean (Garcia-Rodriguez et al. 2000).

Since there are positive relationships both between size and depth and brood size and carapace length, most of the eggs are spawned at the greatest depth of species' habitat. In addition, the largest proportion of females seems to occur at the greatest depth, while juveniles have the shallowest distribution in the depth gradient. Thus, considering that pelagic development is fairly common in the bathyal zone, both for invertebrates (Mileikovsky 1971) and fish (Merrett and Haedrich 1997), and is known for deep-water pandalids (King and Butler 1985; King 1987; Pessani 1993), planktonic larvae of *P. martia* migrate upwards and develop in or just below the euphotic zone, where there is a rich supply of food, phytoplankton and suspended matter (Omori 1974). Large eggs produced by spawners would increase the probability of larval survival in the journey within the water column, which, as discussed by Company and Sardà (1997), in the Mediterranean, is carried out within isothermal conditions. Indeed, brood size and egg size as well as the brood size–carapace length relationship confirm the pattern observed in the western Mediterranean (Company and Sardà 1997).

After metamorphosis the juveniles move deeper, reaching the bottoms on the upper slope. The most abundant occurrence of recruits during summer could be the consequence of the reproductive peak occurring in the same season as the previous year, as shown in the western Mediterranean (Company and Sardà 1997; Campisi et al. 1998). In fact, the highest percentages of fully mature and ovigerous females were shown in July, when the highest reproductive effort was also observed. The values of the reproductive effort of *P. martia* in the Ionian Sea are coherent with the pattern reported for deep-water caridean shrimps (King and Butler 1985; King 1987).

Although, the spawning of *P. martia* in the Ionian Sea showed a peak during summer, it appears to be rather prolonged year round, as observed by Company and Sardà (1997) and Campisi et al. (1998). Moreover, since females bearing eggs in the late maturity stage were found with ripe ovaries, at least two spawning events could be possible for them within their annual reproductive cycle. In fact, the same females with well-developed embryos and already mature ovaries found in May–July can spawn again from September to October or December, while the occurrence of large ovigerous individuals with immature gonads would indicate a resting phase in the reproductive cycle. Indeed, as the planktonic larvae migrate upwards, crossing an environment where survival is rather variable, natural selection should favour a reproductive pattern characterised by iteroparity (Murphy 1968).

The sizes of the ovigerous females recorded in the Ionian Sea indicated that during the reproductive peak all females > 12 mm CL could be involved in spawning, while only the largest individuals are berried throughout the year. Even in *P. giglioli* within the prolonged reproductive season observed in the Sardinian Channel, the minimum size of ovigerous females decreased during the spawning peak (Mura 1995).

The length-frequency distributions of the berried females in *P. martia* showed that individuals start to spawn only in the second year, after they reach the size of 12 mm CL. The fact that data on the percentage of ovigerous females by size class fitted an asymmetric curve highlights the abrupt beginning of spawning activity in the individuals.

Considering that a spawning peak takes place in July, the young-of-the-year found in the same month could be around 1 year old. Juveniles of *P. martia* (< 12 mm CL) in the study area during July and October were previously reported in D'Onghia et al. (1998b). These specimens, being recruits, carry out inverse ontogenetic migration, moving towards the deepest zones as they grow and completing their second year of life at a size of about 18–19 mm CL. Modal groups of 18 and 19 mm CL were also found in the southern Adriatic Sea for males and females, respectively (Marsan et al. 2000). The existence of more than one spawning in the same annual reproductive cycle could explain the presence of overlapping microcohorts in the length-frequency distributions.

Average absolute and specific growth rates within the first 2 years were 0.80 and 0.082 mm CL month^{-1}, respectively in females and 0.77 and 0.080 mm CL month^{-1}, respectively, in males. Taking into account that females attain maturity in their second year of life, the growth slows down and individuals complete their third year of life when they reach around 23 mm CL (females) and 22 mm CL (males). The estimated Von Bertalanffy parameters, modelling such a growth pattern, are in agreement with those computed by Company and Sardà (2000). According to these authors the two sexes showed comparable overall growth performance, and exhibited no more than two or three annual groups in the field population.

The slope of the size–weight relationship suggests the existence of a negative allometry in the growth of *P. martia*. In particular, the presence of eggs causes a more marked effect. This negative allometry seems to be due to the abrupt onset of maturity and spawning, and is in agreement with the slope values reported for *P. edwardsii* by Caldentey et al. (1990b) (ovigerous females = 1.9861–2.2595; males = 2.5953) and by Garcia-Rodriguez et al. (2000) (ovigerous females = 2.597; males = 2.805). Although Company and Sardà (2000) reported slope values around 3 for both females and males of *P. martia*, they did not compute the size–weight relationship for ovigerous females only. In addition, these authors reported a negative allometry for other nektobenthic pandalid species, and a negative allometry is well known in other nektobenthic shrimps living in the same environment, such as *Aristaeomorpha foliacea* (Ragonese et al. 1997) and *Aristeus antennatus* (Carbonell et al. 1999).

The population structure of *P. martia* in the Ionian Sea seems to be markedly influenced by recruitment and growth pattern. However, even though analysis of mortality was not carried out, fishing mortality seems to assume an important role in regulating the size structure of the field population, according to Barry and Tegner (1990). In fact, specimens > 19 mm CL were rather scarce in the length-frequency distributions. Considering that the golden shrimp in the Ionian Sea, as in many Mediterranean areas (Barry and Tegner 1990), is intensively captured as a bycatch species by deep-water bottom trawling, its population structure is the result of both the life-history traits shown and the "top down" effect of fishing.

Acknowledgements This work was supported by DG XIV of the European Commission as part of the projects DEEP-FISHERIES (Developing deep-water fisheries: data for their assessment and for understanding their interaction with and impact on a fragile environment) and MEDITS (International bottom trawl survey in the Mediterranean Sea) and by the Italian government in the context of the research "Valutazione delle Risorse Demersali" (GRUND).

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