Reproductive patterns and population characteristics in five deep-water pandalid shrimps in the Western Mediterranean along a depth gradient (150–1100 m)

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ABSTRACT· Reproductive patterns and populations characteristics of 5 deep-water pandalid shrimp species of the genus *Plesionika* (Decapoda: Caridea) were studied between 150 and 1100 m depth in the Western Mediterranean Sea over the period 1991 to 1994, including monthly samples taken from November 1992 to October 1993. With the aim of establishing interspecific relationships among reproductive biology and population characteristics 2831 individuals of *Plesionika heterocarpus*, 1787 of *P. edwardsi*, 1601 of *P. gigliolii*, 3888 of *P. martia* and 928 of *P. acanthonotus* were analysed. Results show an increasing seasonality in reproductive periods from the shallowest species, *P. heterocarpus* (distributed between 82 and 699 m depth) with ovigerous females present throughout the year, to the deepest species, *P. acanthonotus* (distributed between 165 and 1550 m) with ovigerous females present only in late spring and early summer months. A possible link was hypothezised between deep-water pandalid shrimp breeding period and sinking particulate matter from primary production. A significant decrease in relative brood size (number of eggs per 'standard' 20 mm carapace length female) with increasing depth distribution of each species was found. No significant relationship between egg size and depth distribution was apparent. In 4 of the 5 species studied a differential depth distribution based on sex-ratio and intraspecific size composition by depth was found. The only species where no significant trend was found in sex-ratio by depth, *P. acanthonotus*, did not show differences in size composition by depth. A slight interspecific size overlap was observed. Sex-ratio and size composition by depth distribution are discussed in the light of trophic and reproductive behaviour of each species.

KEY WORDS: Reproduction · Population characteristics · Deep-water · Depth gradient · Pandalid shrimps · Decapoda Caridea · Western Mediterranean

INTRODUCTION

The patterns of deep-sea reproductive biology—length of breeding period, brood size, egg size—have been studied in the last 2 decades, mainly with reference to the presence of seasonally (Tyler 1988, Gage & Tyler 1991). Based on the hypothesis that the deep-sea is a physically seasonless environment, Orton (1920) hypothesised that the breeding period of deep-sea species ought to be continuous throughout the year.

Thorson (1950) predicted that benthic deep-sea invertebrates would show low fecundity, and large egg size with larvae lacking pelagic development, in contrast to their shallow-water congenerics. Several studies have been carried out on the reproductive biology of deep-sea species to test Orton's and Thorson's ideas. Deep-sea echinoderms are the taxon for which most information is available on reproductive biology, showing continuous reproduction, larger eggs and low fecundity as dominant reproductive patterns (Gage & Tyler 1991). Nevertheless some deep-sea echinoderm species show seasonal reproductive cycles. Schoener (1968) was the first to report seasonality in the reproductive patterns of *Ophiura ljungmani* and *Ophiomu-*

sium lymani. Three species from the Rockall Trough (NE Atlantic) also showed seasonal breeding periods, viz. *O. ljungmani, Plutonaster bifrons* and *Echinus affinis* (Tyler 1986). Small egg size and high fecundity is a general feature in these seasonal breeding echinoderms. Rokop (1974, 1977), in studies at a bathyal station in the San Diego Trough off California at 1240 m depth, found no evidence of reproductive seasonality for species belonging to various taxa (3 species of bivalves, 2 ophiuroids, 2 isopods, 1 amphipod and 1 polychaete) and only 1 brachiopod and 1 scaphopod spawned seasonally. Crustaceans form a very diverse group, morphologically and ecologically, and this is reflected in the variety of reproductive patterns encountered. Omori (1974) described continuous reproductive patterns for lower meso- and bathypelagic decapods and fewer and larger eggs were the general trend. The same pattern was found in 2 polychelids, *Stereomastis nana* and *S. sculpta*, by Wenner (1978). However, seasonal reproductive patterns have been found in some species of bathyal and abyssal crustaceans. Evidence for seasonal reproductive patterns was described in some abyssal isopod species (George & Menzies 1967, 1968, Harrison 1988), in the abyssal cumacean *Leucon profundus* (Bishop & Shalla 1994) and in the bathyal decapod *Dorhynchus thomsoni* (Hartnoll & Rice 1985). Although seasonal reproduction have been observed in different deep-sea taxa, the predominant pattern commonly reported in deep-sea animals is continuous reproduction (Tyler 1986). Nevertheless, the scarce and geographically disperse data are not adequate to define a general pattern of reproductive biology in deep-sea species (Tyler 1988, Gage & Tyler 1991).

The life histories of deep-water pandalid shrimps are practically unknown, which contrasts with the high diversity and high biomass observed for this taxon, along with their potential as a fishery resource in tropical and subtropical bathyal environments (Zariquiey Alvarez 1968, Crosnier & Forest 1973, King 1981, 1984, 1987, Abelló et al. 1988, Cartes & Sardà 1992, Thessalou-Legaki 1992, Cartes et al. 1994, Sardà et al. 1994). Some of the deep-water pandalid species found in the Mediterranean Sea have an extensive geographical distribution, which includes tropical Atlantic and Pacific areas (González et al. 1990, King 1984, 1987). The only work carried out on the comparative life-histories of deep-water pandalid shrimps is that reported by King & Butler (1985), on Pacific pandalids off Fiji. However, a study by Cartes (1993) is available on the interspecific trophic relationships among the 3 deepest pandalid shrimps in the Western Mediterranean, *Plesionika edwardsi, P. martia* and *P. acanthonotus.*

Depth represents a multicomponent factor related to one of the major biotic and abiotic gradients found in the oceans. Light, temperature, pressure, food availability and predator density are some of the factors which influence species distribution and life-histories. Five species of *Plesionika* are widely distributed in the study area, the Catalan Sea (Western Mediterranean), although restricted to different depth ranges where abundance is maximum (Abelló et al. 1988, Cartes & Sardà 1992, authors' own unpubl. data). Taking into account these considerations, the objective of this paper is to make interspecific comparisons, along a depth gradient (150 to 1100 m), of the reproductive period length, brood size, egg size, sex ratio and size composition of the 5 most abundant deep-water pandalid shrimp species in the Western Mediterranean Sea, viz. *Plesionika heterocarpus* (Costa, 1871), *P. edwardsi* (Brandt, 1851), *P. gigliolii* (Senna, 1903), *P. martia* (A. M. Edwards, 1883) and *P. acanthonotus* (S. I. Smith, 1882).

MATERIALS AND METHODS

We obtained samples for the 5 pandalid species by trawling over suitable shelf and slope grounds, from 150 to 1100 m. The trawl was fitted with a 6 mm mesh cod-end liner Samples were taken from 1991 to 1994, including a period of continuous sampling between November 1992 and October 1993 during which samples were obtained once a month. The number of individuals studied and depth parameters per species are given in Table 1.

Table 1. Number of individuals measured and sexed, depth range distribution and depth of maximum abundance of the 5 species of pandalid shrimps studied

Species	Species codes	No. of individuals measured	No. of individuals sexed			Depth range (m)	Depth of maximum abundance (m)
			Females	Males	Indeterminate		
Plesionika heterocarpus	Ph	2831	1373	1446	12	82–699	250
Plesionika edwardsi	Pe	1787	822	596	8	256–512	300
Plesionika gigliolii	Pg	1601	828	523	2	100–748	350
Plesionika martia	Pm	3888	1657	1597	76	165–871	600
Plesionika acanthonotus	Pa	928	492	368	68	165–1550	650

Specimens of each species were measured (carapace length, CL. from the post orbital socket to the posterior median edge of the cephalothorax) to the nearest 0.1 mm. Sex was determined under a binocular microscope, based on presence or absence of the male appendix in the second pair of pleopods (Zariquiey Alvarez 1968, King & Moffitt 1984).

Five stages of gonadal development were established for females. The stages (immature, resting and 3 stages of gonadal activity) were defined according to the relative intensity of the color and size of the gonad (Company 1995). The monthly samples taken between November 1992 and October 1993 were used to study reproductive periods. In order to estimate and compare the length of the annual reproductive cycle, we present the monthly percentage of females with active gonads and ovigerous females in relation to total female numbers. Three stages of egg development were defined based on ovigerous females: eggs of recent spawning with intense colour and no embryo pigmentation visible, early stage (1); pale egg colour with slight embryo eye pigmentation, middle stage (2); total loss of egg colour with embryo eye pigmentation well visible and embryo well developed, late stage (3).

Samples of ovigerous females with eggs in different stages of development were taken to estimate the brood size and the egg size for each species. All the eggs carried by each female were counted under a binocular microscope. The relative brood size was calculated by taking the relationship between CL and the number of eggs carried by each female, according to King & Butler (1985). The egg mean size was computed by the arithmetic mean between the major and the minor axes of the ellipsoidal egg, using a binocular microscope with a calibrated eyepiece.

The sex-ratio (as proportion of females) and the mean CL was calculated for all individuals in each sample with 10 or more individuals per species; in 70% of the cases 25 or more individuals of each species were studied. The number of individuals per species and sample varied between 11 and 383. For each sample the significance ($p < 0.05$) of the deviation from the expected sex-ratio percentage (50:50) was tested by means of the G-test, using Williams' correction. The sex-ratio variation with depth was tested by the Mann-Whitney test between samples from different depth ranges (Sokal & Rohlf 1981). The relationship between size (mean CL) and depth was analysed by linear regression.

RESULTS

Reproductive biology

The percentage of females with active gonads and ovigerous females of the 5 pandalid species is shown in Fig 1 Females of the shallowest species (see Table 1), *Plesionika heterocarpus*, were in reproductive activity throughout the year, with a percentage of females with active gonads over 20% at any given month (Fig 1A) and a percentage of ovigerous females always higher than 60% (Fig. 1B). *P. edwarsi*, *P. gigliolii* and *P. martia*, species with a depth range intermediate between the shallowest and the deepest species, showed a shorter reproductive cycle, with maximum presence of females with active gonads and ovigerous females during spring and summer months. Their reproductive activity is less pronounced during the fall and winter months, when compared with *P. heterocarpus*. Finally, the deepest pandalid species, *P. acanthonotus*, showed an even shorter reproductive period restricted to the late spring-early summer months.
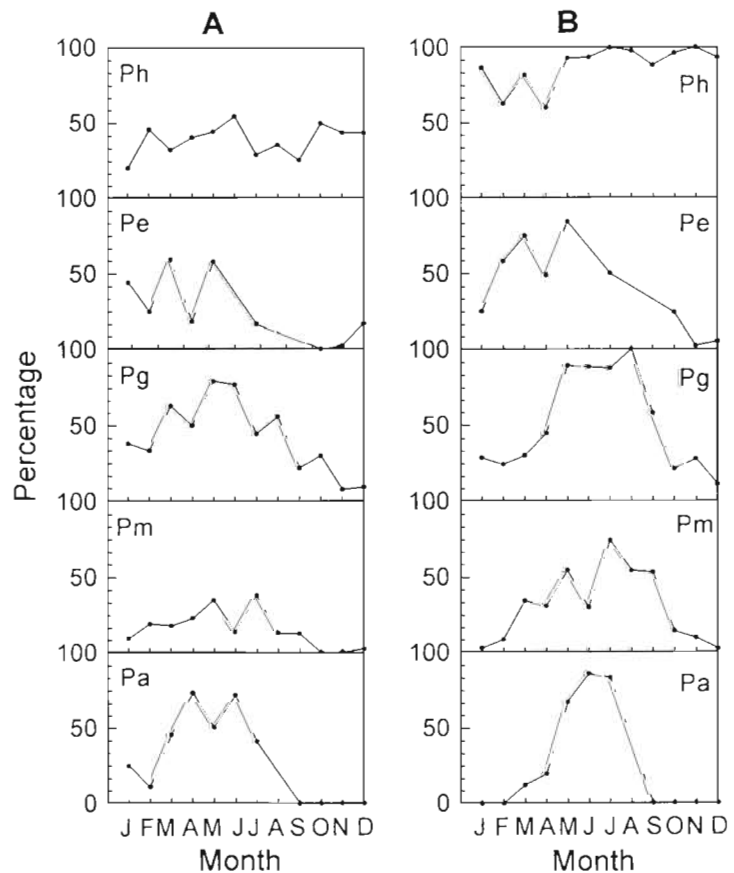

Fig. 1 Monthly percentages of (A) females with active gonads, and (B) ovigerous females, in 5 deep-water pandalid species. Species codes as in Table 1
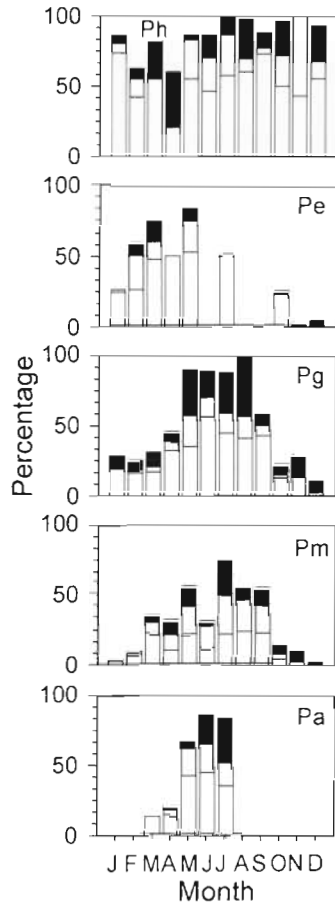
Fig. 2. Monthly percentages of ovigerous females in each egg development stage. White bars: recently spawned eggs (stage 1); grey bars: intermediate egg development (2); and black bars: embryo well developed (3). Species codes as in Table 1

Fig. 3. Relationship between carapace length (CL) and brood size. Parameters of regression curves (RC, $Y = aX^b$) and correlation coefficients are: Ph (a = 1.78; b = 2.70; r = 0.65); Pe (a = 113.17; b = 1.26; r = 0.47); Pg (a = 0.00; b = 4.69; r = 0.43); Pm (a = 27.24; b = 1.67; r = 0.38); Pa (a = 4.79; b = 2.17; r = 0.64). Species codes as in Table 1

The percentage of ovigerous females in each of the egg developmental stages is shown in Fig 2. Ovigerous females with eggs in late maturity stage (stage 3) were found year round, suggesting the existence of more than one spawning in the same annual reproductive cycle.

Brood size and egg size

The relationship between CL and brood size was significant (p < 0.05) in all 5 species (Fig. 3). It is not adequate to directly compare brood sizes among species given that the CL of the smallest ovigerous females and the CL of the largest ovigerous females are different for each species (Table 2). From the regression lines between CL and brood size, a relative brood size was computed for a standard female of 20 mm CL. Relative brood size and egg size in relation to the depth of maximum abundance of each species is
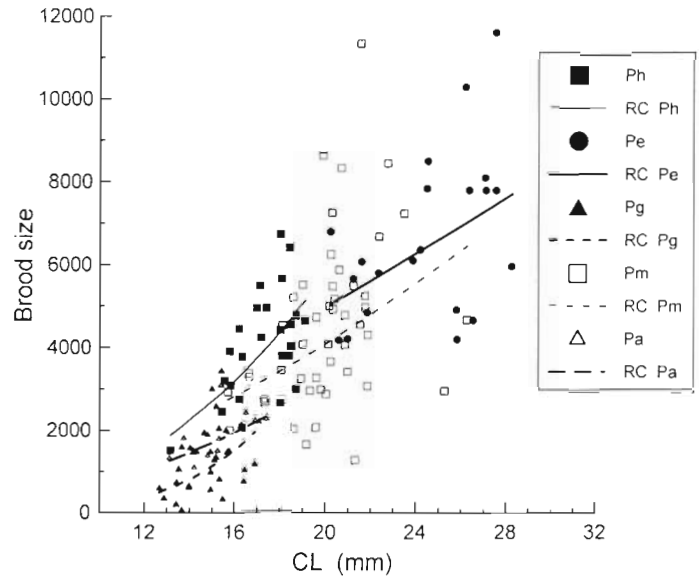
shown in Fig. 4. Egg size has been plotted in the late stage of egg development (3), because this is the stage which offered the most precise information of the initial larval size and, therefore, of its survival probability (Thorson 1950, Todd 1979, McEdward 1986). The relative brood size and the depth of maximum abundance were negatively correlated (r = –0.89, p < 0.05), with a slope significantly different from zero (p = 0.044). Egg size in the late stage of development was very similar among species and no significant relationship was found between egg size and depth of maximum abundance.

Sex-ratio as a function of depth

In 4 of the 5 species studied, significant (p < 0.05) variations were found in the distribution of sexes by depth (Fig. 5). The shallowest species, *Plesionika heterocarpus*, presented a significantly (p = 0.026) larger proportion of males in its deepest range distribution. The 3 intermediate depth species, *P. edwardsi*, *P. gigliolii* and *P. martia*, showed a significant (p = 0.045, p = 0.024 and p = 0.015 respectively) differentiation with depth in sex distribution, with a high proportion of females in samples at around 400 m depth. In *P. edwardsi* samples with a high proportion of females corresponded to its deepest distribution range (>400 m), in *P. gigliolii* to its intermediate depth distribution

Table 2. Egg size in each developmental stage. Length of the smallest female carrying eggs (mm CL), length of the biggest female, relative brood size. Standard deviations are in parentheses

Species	Egg developmental stage	No. of individuals studied	Egg size (mm)	Relative brood size	Female ovigerous (CL min.)	Female (CL max.)
Plesionika heterocarpus	1	25	0.44 (0.04)	5851	11.0	20.2
	3	19	0.53 (0.04)			
Plesionika edwardsi	1	21	0.51 (0.07)	4986	18.3	29.0
	3	16	0.59 (0.09)			
Plesionika gigliolii	1	29	0.48 (0.04)	4294	9.3	18.6
	3	13	0.55 (0.05)			
Plesionika martia	1	47	0.45 (0.05)	4105	14.2	26.7
	3	21	0.55 (0.06)			
Plesionika acanthonotus	1	16	0.48 (0.03)	3156	9.6	17.9
	3	6	0.53 (0.03)			

range (between 350 and 450 m) and in *P. martia* to its shallowest distribution range (<450 m). In the deepest species, *P. acanthonotus*, no significant trend between sex-ratio and depth was found, and only in its deepest distribution range (>800 m) was a slight tendency (not significant; $p = 0.900$) towards a higher proportion of females encountered. Summarizing our findings, there is no clear parallelism in the sex distribution by depth in the 5 species studied, and only the 3 species with an intermediate depth range showed a higher proportion of females at around 400 m, but with different patterns of distribution by depth.
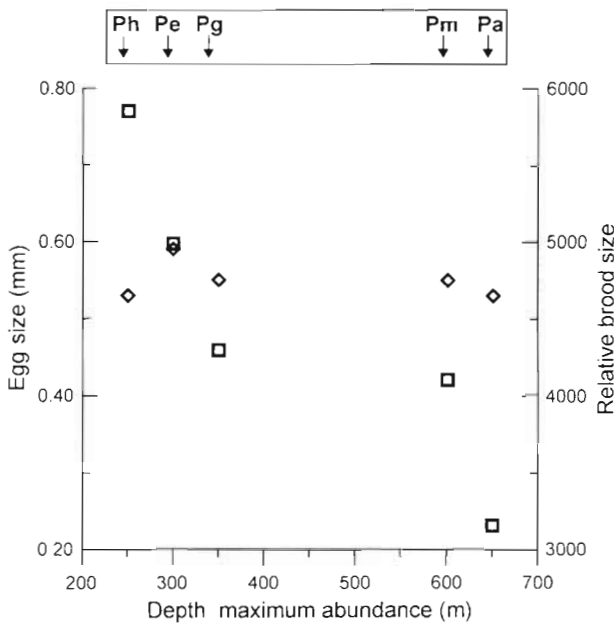

Fig. 4. Relation of egg size (embryo well developed, stage 3) and relative brood size to depth of maximum abundance. (◇) Egg size; (□) relative brood size. Species codes as in Table 1
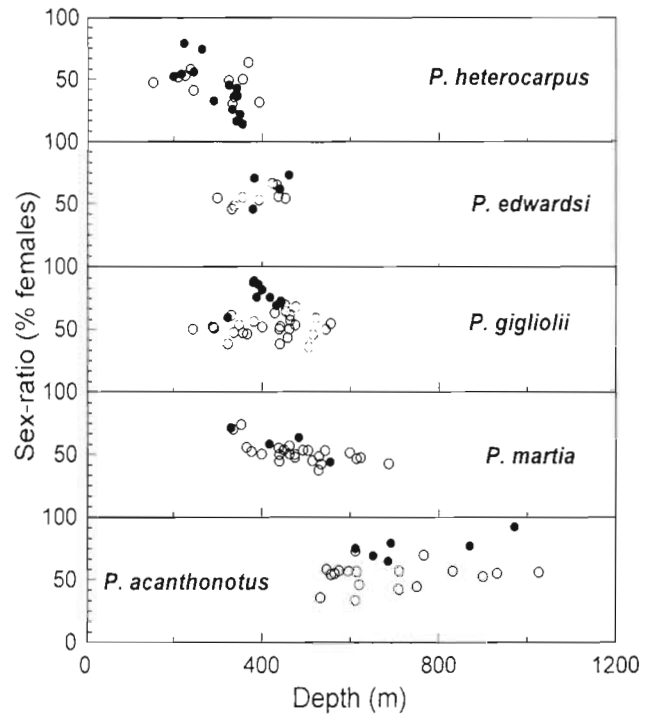

Fig. 5. Sex-ratio (as percentage of females) by sample depth. (●) Samples with sex-ratio significantly ($p < 0.05$) different from the theoretical percentage 50:50; (○) not significantly different from 50:50. *P. heterocarpus*: samples shallower than 350 m depth have a significantly greater proportion of females than those deeper than 350 m ($p = 0.026$, Mann-Whitney U-test); *P. edwardsi*: samples shallower than 400 m have a significantly lower proportion of females than those deeper than 400 m ($p = 0.045$); *P. gigliolii*: samples shallower than 350 m and deeper than 450 m have a significantly lower proportion of females than those at their intermediate depth distribution, 350 to 450 m ($p = 0.024$); *P. martia*: samples shallower than 450 m have a significantly higher proportion of females than those deeper than 450 m ($p = 0.015$); *P. acanthonotus*: samples shallower than 700 m and deeper than 700 m are not significantly different ($p = 0.900$)
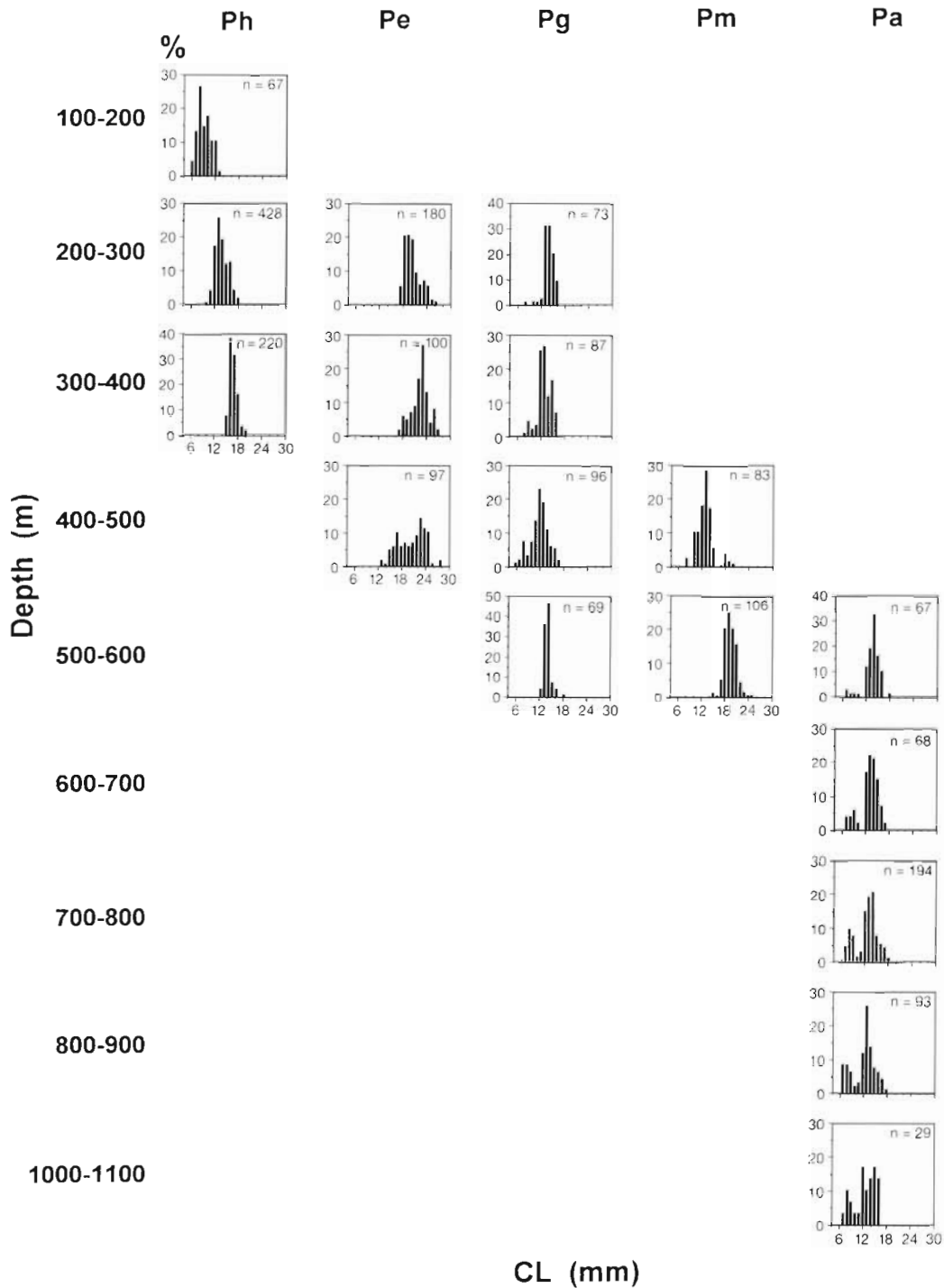
Fig. 6. Size frequency histograms by species at different depth intervals. Histograms correspond to April samples, in which the presence of smaller individuals is maximum. Species codes as in Table 1. n = number of individuals

Intra- and interspecific relationships between size distribution and depth

Length frequency histograms by depth range and species for April samples, in which the number of smaller individuals is maximum, are shown in Fig. 6.

The smallest individuals of *Plesionika heterocarpus* were encountered at the edge of the shelf and the largest individuals at depths corresponding to the deepest part of its distribution range (300 to 400 m). *P. edwardsi* showed a higher percentage of small individuals between 200 and 300 m, on the shelf-break,

although the smallest individuals were found between 400 and 500 m, at the same depths where the largest individuals were found. At the deepest distribution range of *P. gigliolii* only large individuals were present and between 300 and 500 m depth the smallest individuals were found. In *P. martia* the smallest individuals were mainly distributed between 400 and 500 m. The deepest-ranging species, *P. acanthonotus*, did not show a clear relationship between size composition and depth. Individuals in all depth strata were similar in size composition. Overall, with the exception of *P. acanthonotus*, we found an intraspecific size segregation by depth. As seen in Fig. 5 the smallest individuals of *P. heterocarpus*, *P. edwardsi*, *P. gigliolii* and *P. martia* occurred in the same depth range where the higher percentages of females were found. The only species which did not show a clear size composition with depth, *P. acanthonotus*, also did not show a clear trend between sex-ratio and depth.

The interspecific relationship between mean CL and depth is shown in Fig. 7 and it can be seen that there is practically no overlapping between mean CL and depth among species. The regression line is only given for species in which the slope of the regression between mean CL and depth is significantly different from 0 ($p < 0.05$). *Plesionika edwardsi* is the largest pandalid found in the Western Mediterranean and its mean CL throughout its depth range is clearly larger than the remaining species studied. *P. heterocarpus* had a smaller mean CL than *P. edwardsi* and at depths where its abundance was lower, *P. martia* became

abundant. Thus, segregation by depth exists between the 2 species. Both *P. heterocarpus* and *P. martia* had a positive correlation ($p < 0.05$) between mean CL and depth. The 2 species of similar size, *P. gigliolii* and *P. acanthonotus*, followed the same pattern as the 2 previous species, and at depths where the abundance of the shallower species becomes less, it is substituted by the deeper species. In summary, a clear species-specific segregation by depth was found for species of similar size and, at the same depths, species with differing size were found.

DISCUSSION

The predominant reproductive pattern found in deep-sea animals is continuous reproduction throughout the year, although seasonal reproduction has been found in some taxa (George & Menzies 1967, Tyler 1986, 1988, Harrison 1988, Gage & Tyler 1991, Bishop & Shalla 1994). The pandalid shrimps analysed in this study were distributed at transitional depths between shallow and deep environments. Our results showed an increasing seasonality in the reproductive patterns with depth, with the shallowest species, *Plesionika heterocarpus*, distributed between 82 and 699 m and the deepest species, *P. acanthonotus*, distributed between 165 and 1550 m. This increasing seasonality found in pandalid shrimps of the Mediterranean Sea provides a clear general trend of life-history adaptation with depth.

Little is known in deep-sea animals about the endogenous or exogenous factors which may contribute to controling the reproductive cycle of the species considered, due to the difficulty of performing experimental studies which faithfully reproduce the conditions of the deep-sea environment. Nevertheless, if certain animals have seasonal reproductive patterns, exogenous factors which trigger ovarian development, spawning and/or larval release must exist (Gage & Tyler 1991). Giese (1958) discussed the possibility that larval food availability would determine the breeding period. In this sense, among exogenous factors, sinking organic matter originating from surface primary production has to be considered (Gage & Tyler 1991). Recently, Bishop & Shalla (1994) showed a relationship between phytodetrital sinking and the start of vitellogenesis and larval release in the abyssal cumacean *Leucon profundus* from a station located at 2900 m depth in the Rockall Trough. Some
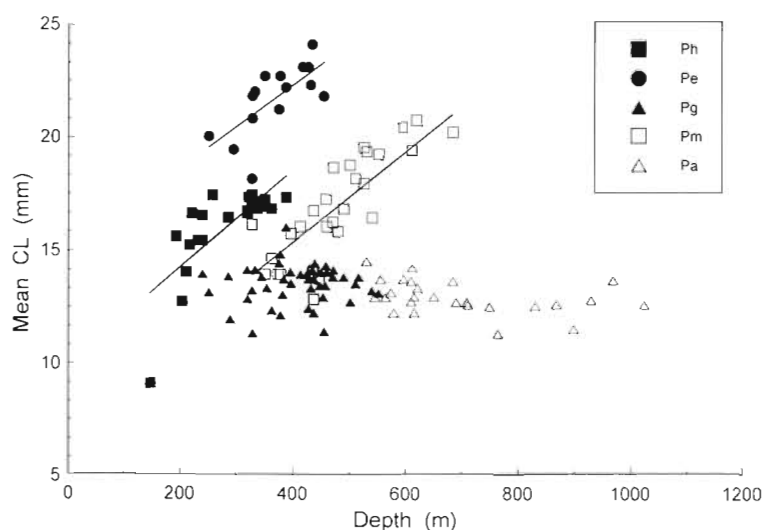

Fig. 7. Mean carapace length (CL) by depth. Regression lines were drawn for those species with a slope significantly ($p < 0.05$) different from 0. Regression equation parameters ($Y = a + bX$), coefficient of correlation (r) and significance level of the slope when different from 0 are: Ph ($a = 9.91$; $b = 0.0214$; $r = 0.76$; $p < 0.0000$); Pe ($a = 14.82$; $b = 0.0186$; $r = 0.69$; $p < 0.0043$); Pm ($a = 7.27$; $b = 0.0201$; $r = 0.77$; $p < 0.0000$). Species codes as in Table 1

authors have theorized that biological processes in high-latitude shallow water environments could be comparable to those found in the deep-sea environment (Thorson 1950, Lipps & Hickman 1982). Experiments carried out with a subeuphotic species of majid decapod, the subarctic *Chionoecetes opilio*, supports this conclusion. Field and laboratory experiments showed that larval release in this species was linked to phytodetrital deposition (Starr et al. 1994).

In the Mediterranean Sea measurements of material sinking from the photic zone to the deep sea are scant. Miquel et al. (1994) showed that the maximum annual peak of phytodetritus sedimentation in the Western Mediterranean (1000 m depth, off north Corsica) was in late June, which coincided with the maximum abundance of ovigerous females in the 5 pandalid shrimps studied here and with the seasonal peak of ovigerous females in the deepest species, *P. acanthonotus* (Fig. 1B). Evidence for seasonal deposition of primary production from the surface to great depths (below 4000 m) has been found in the Porcupine Sea Bight, where maximum deposition was also encountered between June and July (Lampitt 1985). Fusté (1982) found larvae of the genus *Plesionika* year-round at a station located at 60 m depth. The area of larval distribution reported by Fusté (1982) and the fact that larvae were found throughout the year suggest that these larvae most probably belonged to *P. heterocarpus*, since ovigerous females of this species occur year-round and it is the species with the shallowest distribution. Another fact to support this assumption is that a larger proportion of females and the smallest individuals are found in its shallowest depth range (< 200 m), in the neritic zone (Figs. 5 & 6, respectively). This neritic zone is more productive throughout the year than the adjacent oceanic zone, in relation to both phytoplankton biomass and zooplankton biomass (Estrada et al. 1985, Estrada & Salat 1989). This is one of the main factors which would allow the shallowest species, *P. heterocarpus*, to have an extended breeding season in contrast to the deepest species, *P. acanthonotus*, which is distributed in a less productive zone. This latter species would concentrate breeding in the months of maximum particulate sinking, which corresponds to June (Miquel et al. 1994).

Low fecundity and large egg size is the general pattern found in deep-sea species (Thorson 1950, Mauchline 1972, Omori 1974, Gage & Tyler 1991). Our results, from species distributed between 150 and 1100 m, show a significant decrease of relative brood size with depth, although no relation was found between egg size and depth (Fig. 4).

In individuals of *Parapandalus narval* of the Eastern Mediterranean living between 5 and 140 m, Thessalou-Legaki (1992) reported a brood size of 8593 eggs

for a female of 20 mm CL, which is higher than the brood size found is this study for the shallowest species (*Plesionika heterocarpus*). King & Butler (1985) found increasing egg sizes, but not decreasing relative brood sizes, with depth in 8 species of deep-sea pandalid shrimps in the Pacific Ocean, distributed over similar depth ranges to the 5 species studied here. They also found a progressive increase in the maximum size of each species with depth, which was not observed in the Mediterranean pandalid species (Table 2). This different trend between deep-water Mediterranean and Pacific Ocean pandalid species could be related to the fact that the Mediterranean is isothermal below 200 m (~13°C), while a thermal gradient of 12°C between 200 m (17°C) and 600 m (5°C) exists in the Pacific Ocean. Vertical temperature variations such as those reported for the Pacific Ocean may reduce the probability of survival in larvae during their vertical migration (Mileikovsky 1971), which would be compensated for by an increase in egg size, as is found in pandalids of the Pacific Ocean. Under the isothermal conditions of the Mediterranean Sea, the pandalid species would not need to compensate possible larval mortality due to the thermal gradient with an increase in egg size.

Temperature is the main exogenous factor which can determine egg incubation duration in crustaceans (Wear 1974, Sastry 1983). In the Mediterranean this would imply that the number of spawnings per year would be lowest in the deepest species (Fig. 2). Both the lower number of spawnings and the lower relative brood size (Fig. 4) found in deeper species when compared to shallow ones would be responsible for the higher abundances observed in shallow species. The abundance of *Plesionika heterocarpus* is one order of magnitude greater than the abundance of *P. acanthonotus* (Abelló et al. 1988, Cartes & Sardà 1992, Cartes et al. 1994).

Four of the 5 species that we studied showed intraspecific size segregation by depth (Fig. 6) and interspecific size segregation among species was the rule (Fig. 7). This observation may be related to the diet composition of *Plesionika martia* and *P. acanthonotus*. They are similar with regard to resource type, but *P. acanthonotus* exploits smaller prey items (Cartes 1993). This author showed that for these 2 species there was a different size composition at depths where they co-occur Our results agree with this finding, and in their overlapping depth distribution range, 500 to 700 m, the size composition and mean CL of the 2 species was different. *P. edwardsi* and *P. martia* overlap extensively in their diet composition for individuals captured in submarine canyons (Cartes 1993). Our samples show that there is no size overlap between these 2 species over the depth range of 350 to 500 m. In an oligotrophic sea as the Mediterranean, where space

and food resources are limiting for species of similar morphology and trophic habits, segregation by depth could be an adaptation that allows co-existance.

Our observations show that for all 5 pandalid species the size and sex-ratio composition by depth showed parallel patterns. This distribution of sex-ratio and size by depth is considered to be associated with reproductive behaviour, in the sense that pandalid shrimps would have a preferential area for recruitment. The smallest individuals of *Plesionika heterocarpus* were associated with samples of high female percentage, and both were distributed in an area of higher productivity, the continental shelf, than the adjacent continental slope. As already pointed out, the smallest sizes and the samples with a higher proportion of females of *P. edwardsi*, *P. gigliolii* and *P. martia* occurred between 350 and 450 m. In the Western Mediterranean Sea, fronts have their point of contact with the sea bottom at around 350 to 450 m (Font et al. 1988). The interaction of the frontal system with the benthic environment could thus be related to the presence of small individuals of these 3 species at those depths.

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Mar Ecol Prog Ser 148: 49–58, 1997

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