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LIFE HISTORY OF *PLESIONIKA EDWARDSI* (CRUSTACEA, DECAPODA, PANDALIDAE) AROUND THE CANARY ISLANDS, EASTERN CENTRAL ATLANTIC

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The life history of *Plesionika edwardsi* (Brandt, 1851) around the Canary Islands in the Eastern Central Atlantic was investigated, based on a total of 11 434 shrimps ranging in length between 8 and 40 mm carapace length (*CL*). The species carries out seasonal migrations; they concentrate in deep water during winter, move shallower in summer and return to deep water again in autumn. Ovigerous females occur throughout the year, but a spawning peak was determined between April and September. The size at maturity for females was approximately 26 mm *CL*. Shrimp size generally increased with increasing water depth. The growth parameters for males were L_∞ = 25.75 mm *CL* and K = 0.55 year^{-1}, and L_∞ = 28.28 mm *CL* and K = 0.66·year^{-1} for females. The species displays the typical reproductive pattern of tropical pandalids and is dioecious.

Plesionika edwardsi (Brandt, 1851) is a marine species of wide distribution at low latitudes. It is known from the Western Pacific (Philippines, Indonesia), the Western Atlantic (from South Carolina and North Bahamas to the Gulf of Mexico), the Eastern Atlantic (from North-West Spain to Sierra Leone, including the archipelagos of Azores, Madeira, Canaries and Cape Verde and most of the Mediterranean), and the South-Western Indian Ocean around the Seychelles (Crosnier and Forest 1973, Holthuis 1980, 1987, Chace 1985, Intès and Bach 1989, González *et al.* 1990, Fransen 1991, Martins and Hargreaves 1991, Biscoito 1993). Those authors have recorded the species at bottom depths of 54–700 m on mostly muddy substrata, but also on sandy or rocky bottoms over the continental shelf and upper continental slope.

P. edwardsi has been included in the F. A. O. catalogue of species of interest to fisheries (Holthuis 1980). Zariquiey Álvarez (1968) reported it as being caught by trawlers off the Mediterranean coast of Spain. It is believed to be of some economic interest in Spain, Italy, Morocco, Algeria and Tunisia, where it is sold in fish markets with other shrimps (Holthuis 1980, 1987). Since 1984, *P. edwardsi* has been caught in abundance with multiple shrimp traps on the steep grounds between 75 and 500 m deep in the Western Mediterranean (the east coast of Spain, Balearic Islands, Corsica, Sardinia and Sicily). During the period 1984–1991, annual Spanish catches varied between 80 and 100 tons (González *et al.* 1992). Intès and Bach (1989) reported the species to be of economic interest in the Seychelles. Despite its abundance and widespread distribution, *P. edwardsi* has not been studied in much detail (e.g. King 1986, Intès and Bach 1989, Martins and Hargreaves 1991).

The results of more than 20 fishing surveys in the deep waters around the Canary Islands have suggested that *P. edwardsi* and *Heterocarpus ensifer* are occasionally abundant and of possible, but restricted, economic interest (e.g. Santaella and Bravo de Laguna 1975, González *et al.* 1988, Caldentey *et al.* 1992, González 1995). Off the Azores, a trial fishery using bottom traps at depths ranging between 18 and 864 m showed that the most common and abundant shrimp caught there was *Plesionika narval,* followed by *P. edwardsi* (Martins and Hargreaves 1991). In the archipelago of Madeira, exploration with bottom traps down to 1 000 m (net at depth) revealed that *P. narval* was the most abundant pandalid shrimp, but large catches of *P. edwardsi* were taken between 130 and 360 m (Biscoito 1993).

Around the Canary Islands, *P. narval* is the target species of a small artisanal fishery on the narrow shelves and steep slopes of the western and central islands. Fishing is carried out with bottom shrimp traps set mainly between 100 and 150 m water depth. *P. narval* represents numerically and by mass about 85% of the total shrimp catch, the remaining percentage consisting of *P. edwardsi*, *H. ensifer* and other sublittoral shrimps. Although fisheries statistics are not available, up to 10 tons of pandalid shrimps might be caught annually.

This study provided information on the basic biology and biological parameters of *P. edwardsi* around the Canary Islands. The paper contributes to the

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Table I: Cruise and sampling information of shrimps taken between 1974 and 1994 around the Canary Islands

Cruise	Date	Island	Latitude (°N)	Longitude (°W)	Sample size	Size range (*CL*, mm)	Depth range (m)
AGAMENÓN 7406	June 1974	P	28°35´	17°57´	620	–	165–329
CANARIAS 85	June 1985	C	27°40´–28°06´	15°42´–15°52´	607	16–40	176–384
CANARIAS 85	June 1985	F	28°09´–28°45´	13°47´–14°02´	1	31	137
CANARIAS 85	June 1985	L	28°56´–29°16´	13°34´–13°51´	49	21–35	135–366
CANARIAS 85	June 1985	T	27°59´–28°25´	16°33´–16°38´	189	13–33	161–347
CANARIAS 85	June 1985	G	27°59´–28°15´	17°14´–17°21´	378	17–33	146–165
CANARIAS 85	June 1985	H	27°41´	18°02´	396	14–33	128–322
CANARIAS 85	June 1985	P	28°39´	17°58´	225	18–33	95–468
CANARIAS 85	July 1985	C	27°41´–27°43´	15°46´–15°47´	24	19–35	219–332
CANARIAS 85	July 1985	F	28°01´–28°47´	13°48´–14°27´	214	15–34	161–409
MOGÁN 8701	January 1987	C	27°46´–27°52´	14°50´–15°00´	354	–	135–405
MOGÁN 8701	February 1987	C	27°46´–27°52´	14°50´–15°00´	509	–	180–315
MOGÁN 8710	October 1987	C	27°43´–27°45´	15°47´–15°49´	3 751	8–34	125–270
MOGÁN 8802	February 1988	C	27°43´–27°45´	15°47´–15°49´	1 841	8–33	128–285
MOGÁN 8804	April 1988	C	27°43´–27°45´	15°47´–15°49´	449	12–36	121–286
MOGÁN 8804	May 1988	C	27°43´–27°45´	15°47´–15°49´	21	20–34	301
MOGÁN 8806	June 1988	C	27°43´–27°45´	15°47´–15°49´	85	16–33	247–265
TFMC ZM/90	January 1990	T	28°01´	16°44´–16°45´	15	17–28	262–357
TFMC ZM/90	February 1990	T	28°01´	16°44´–16°45´	2	17–21	98
TFMC ZM/90	July 1990	T	28°01´	16°44´–16°45´	14	9–24	128–201
TFMC ZM/90	August 1990	T	28°01´	16°44´–16°45´	12	10–26	121–158
TFMC ZM/90	September 1990	T	28°01´	16°44´–16°45´	25	8–23	140–160
GOMERA 9009	September 1990	G	27°58´–28°18´	17°12´–17°18´	361	8–31	54–266
TFMC ZM/90	October 1990	T	28°01´	16°44´–16°45´	73	9–26	113–200
TFMC ZM/90	November 1990	T	28°01´	16°44´–16°45´	138	9–25	112–144
CANARIAS 9206	May 1992	T	28°06´–28°20´	16°46´–16°57´	164	14–29	337–350
CANARIAS 9206	June 1992	T	28°01´–28°19´	16°43´–16°57´	393	12–29	119–403
TALIARTE 9403	March 1994	C	27°59´–27°59´	15°18´–15°20´	514	11–29	250–386
BOCINEGRO 9412	December 1994	C	28°08´–28°21´		10	19–29	100
Total	1974–1994		27°40´–29°16´	13°34´–18°02´	11 434	8–40	54–468

P = La Palma, C = Gran Canaria, F = Fuerteventura, L = Lanzarote, T = Tenerife, G = La Gomera, H = El Hierro

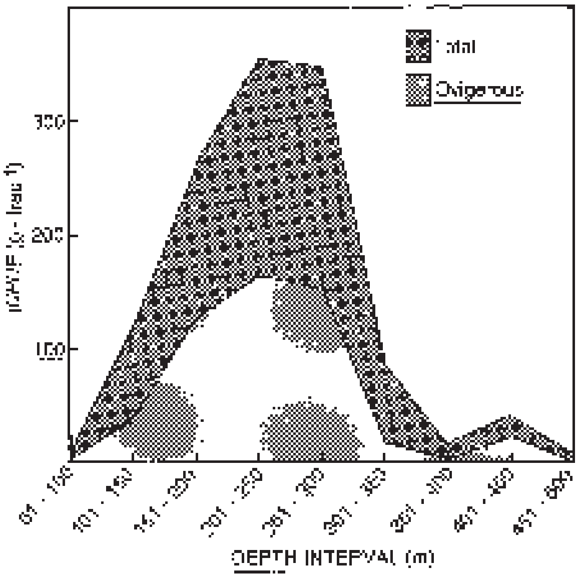

Fig. 1: Depth distribution of *P. edwardsi* off the Canary Islands, expressed in terms of *cpue*: total catches and catches of ovigerous females presented separately

knowledge of the life history of this pandalid species, and may be of future importance should it become necessary to assess and manage the stock.

MATERIAL AND METHODS

About 12 research surveys were made to the Canary Islands in the Eastern Central Atlantic be-

Table II: Effort and mass of total and ovigerous shrimps caught per 50 m depth interval

Depth interval (m)	Effort (number of traps)	Mass caught (g)	
		Total catch	Ovigerous shrimps
51–100	20	152	49
101–150	101	11 790	3 803
151–200	54	14 235	6 868
201–250	58	20 502	9 500
251–300	60	20 736	9 164
301–350	17	1 450	268
351–400	12	174	35
401–450	5	202	108
451–500	1	7	0
Total	328	69 248	29 795

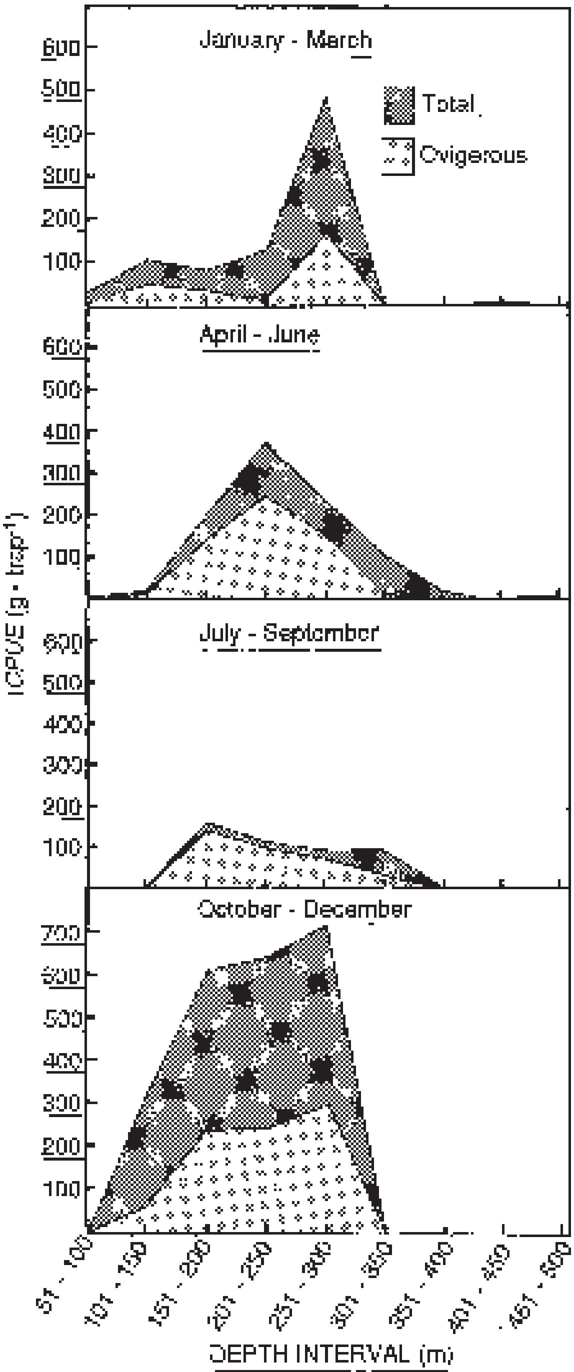

Fig. 2: Seasonal depth distribution of *P. edwardsi* off the Canary Islands. Data expressed in terms of *cpue*: total catches and catches of ovigerous females presented separately

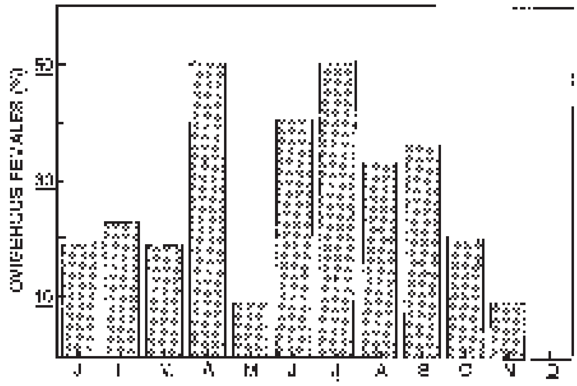

Fig. 3: Monthly frequencies of ovigerous females in the population of *P. edwardsi* off the Canary Islands

tween 27°41′–29°16′N and 13°34′–18°02′W during the period 1974–1994 (Table I). During these cruises, bottom traps were set on the insular shelf and slope regions at depths ranging from 54 to 468 m depth (e.g. Santaella *et al*. 1975, Santana *et al*. 1987, González *et al*. 1988, Lozano *et al*. 1990a, b, 1992, Hernández *et al*. 1991, López Abellán *et al*. 1994,

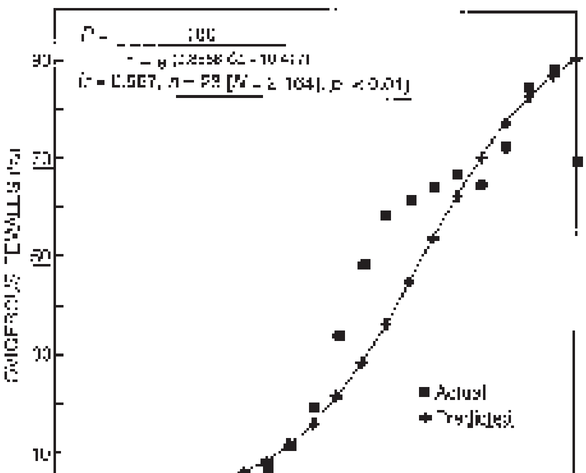

Fig. 4: Relationship between frequency of ovigerous females and carapace length of *P. edwardsi* off the Canary Islands

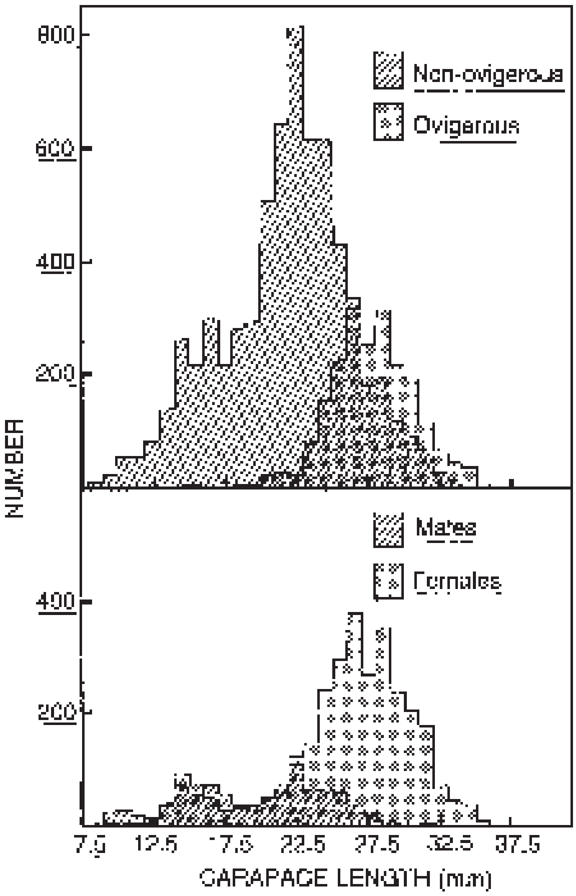

Fig. 5: Size frequency distributions of (a) non-ovigerous and ovigerous and (b) male and female *P. edwardsi* off the Canary Islands

González 1995). A total of 11 434 *P. edwardsi* was studied from these cruises, from which 75.6% were measured (size range 8–40 mm carapace length, Table I).

P. edwardsi was not targeted during the research surveys, which formed part of a larger study on the entire pandalid shrimp assemblage. Therefore, fishing effort across the bathymetric range from 50 to 500 m was more or less equally distributed over each 100 m depth interval. Differences in the actual number of traps set per 50 m depth interval reflect variable weather conditions (Table II).

Most of the specimens caught were separated with respect to their ovigerous or non-ovigerous condition and counted. The carapace length (*CL*) of a subsample from each group was measured (± 0.1 mm) dorsally from the posterior edge of the eye socket to the posterior edge of the carapace using a vernier caliper. The total wet mass (*W*) of each shrimp was measured (± 0.1g), mostly from fresh material. The sex of non-ovigerous individual samples (females, males and sexually unidentified specimens) was determined after 1985, according to the presence/absence of the appendix masculina on the endopod of the second

Table III: Seasonality in mean size of shrimps per 50 m depth interval

Sex/Group	Value per depth interval (m)						
	Season	101–150	151–200	201–250	251–300	301–350	351–400
Males	January–March						
	Mean size (*CL*, mm)			14.1	19.6		21.6
	SD			1.8	4.6		3.8
	n			102	46		126
	April–June						
	Mean size (*CL*, mm)			21.4	19.7	22.1	
	SD			3.5	4.1	4.1	
	n			168	139	139	
	July–September						
	Mean size (*CL*, mm)		13.7				
	SD		5.2				
	n		124				
Females	January–March						
	Mean size (*CL*, mm)			14.5	24.9		25.6
	SD			2.6	4.0		3.4
	n			186	650		102
	April–June						
	Mean size (*CL*, mm)	23.6	25.4	26.6	27.1	25.2	
	SD	6.3	3.6	3.8	4.6	3.1	
	n	104	145	321	382	62	
	July–September						
	Mean size (*CL*, mm)		24.8				
	SD		4.0				
	n		163				
	October–December						
	Mean size (*CL*, mm)	25.8	26.9	27.4			
	SD	2.3	2.5	2.0			
	n	125	254	393			
Non-ovigerous shrimps	January–March						
	Mean size (*CL*, mm)			14.1	21.3		21.6
	SD			1.8	5.0		4.1
	n			281	1 428		151
	April–June						
	Mean size (*CL*, mm)	18.6	21.9	22.2	23.1	23.2	
	SD	3.9	3.5	3.5	4.9	3.3	
	n	69	127	346	433	181	
	July–September						
	Mean size (*CL*, mm)		16.1	18.3			
	SD		6.5	7.5			
	n		194	75			
	October–December						
	Mean size (*CL*, mm)	20.6	21.7	22.2	22.8		
	SD	3.3	3.1	3.6	5.0		
	n	1 106	672	1 317	72		

Table III *(continued)*

Sex/Group	Value per depth interval (m)						
	Season	101–150	151–200	201–250	251–300	301–350	351–400
Ovigerous females	January–March						
	Mean size (*CL*, mm)				26.4		26.5
	SD				2.3		1.6
	n				370		86
	April–June						
	Mean size (*CL*, mm)		26.4	28.1	29.2		
	SD		2.9	3.2	3.2		
	n		123	219	256		
	July–September						
	Mean size (*CL*, mm)		24.7				
	SD		3.7				
	n		144				
	October–December						
	Mean size (*CL*, mm)	25.8	26.9	27.4			
	SD	2.2	2.5	2.0			
	n	125	252	392			

pleopod (King and Moffitt 1984).

Shrimp abundance was estimated indirectly using catch-per-unit-effort (*cpue*) data (i.e. mass of shrimp per trap). The seasonal distribution of shrimp size and depth was investigated at 50 m depth intervals. The mass of shrimp per trap was calculated separately for ovigerous females and total shrimp. Sexes were treated separately, and samples consisting of <40 individuals were not analysed.

The spawning season was determined from the monthly frequency of ovigerous females. A sexual maturity curve was derived using a logistic function (Pope *et al*. 1983). The mean length (*CL*) at maturity in females was calculated as the length at which 25% of the population was ovigerous (King and Butler 1985).

Length frequency data were analysed to estimate growth of each sex, according to the method of Pauly (1983). Length frequencies of samples from September 1990 (for males) and June 1992 (for females) were repeated over five and six years respectively to simulate the time sequence of the samples according to the principles of Pauly's method. The Hasselblad's maximum likelihood method was used to separate the normal distribution of mixtured samples. The growth performance of both sexes (Munro's phi prime) was compared, according to Sparre *et al*. (1989).

Normality of the length data was determined using the Kolmogorov-Smirnov test (Sokal and Rohlf 1981) prior to comparing the mean size of different groups of shrimps. The same test was used to compare length frequency distributions. The Mann-Whitney *U* test was applied as a non-parametric test to compare independent samples (Sokal and Rohlf 1981). Sex ratios were analysed by size-class. The relationship between *CL* and *W* was calculated for each sex (or group) over the entire study period using the equation

$$W = aCL^{b} \quad .$$

Table IV: Statistical data on the size of the shrimps examined

Parameter	Males	Females	Non-ovigerous shrimps	Ovigerous females
Number of observations	906	3 014	6 574	2 164
Mean size (*CL*, mm)	19.1	25.3	21.2	27.1
SD	5.0	4.8	4.6	3.1
Range (mm)	8.0–34.0	8.0–39.9	8.0–35.0	12.6–39.9

RESULTS

P. edwardsi has been caught at depths from 54 m (cruise "Gomera 9009") to 468 m (cruise "Canarias 85") in the waters around the Canary Islands. Maximum estimates of abundance range between 264 and 353 g·trap^{-1} for total shrimps and between

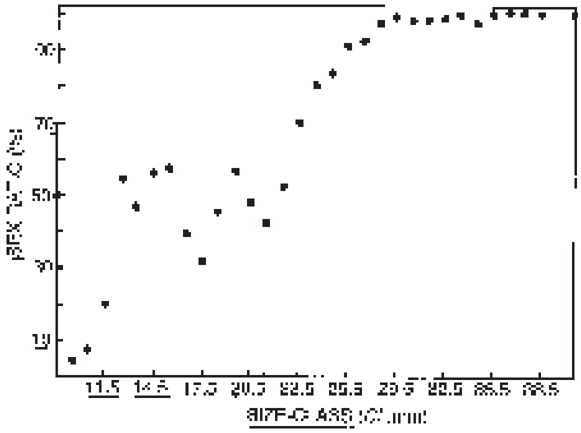

Fig. 6: Relationship between sex ratio frequency (females x 100/(males + females) and size of *P. edwardsi* off the Canary Islands

127 and 164 g·trap^{-1} for ovigerous females. These catches were taken from depths ranging from 151 to 300 m (Fig. 1).

The P. edwardsi population was concentrated between 250 and 300 m deep (total shrimps = 491 g.trap^{-1}, ovigerous females = 168 g.trap^{-1}) during the period January–March. The population was more homogeneously distributed from April to June, when it occurred over a wider depth range of 150–300 m (total shrimps = 198–241 g·trap^{-1}, ovigerous females = 144–155 g·trap^{-1}, Fig. 2). During the months July-September, *P. edwardsi* was concentrated at 150–250 m (total shrimps = 163–121 g·trap^{-1}, ovigerous females = 146–73 g·trap^{-1}). Although the population occupied a wide depth range (100–300 m) from October to December, it was most abundant at 250–300 m (total shrimps = 721 g·trap^{-1}, ovigerous females = 300 g·trap^{-1}, Fig. 2).

Females carried eggs throughout most of the year, with the percentage of ovigerous females in the population varying between 9.2 and 50.4% in May and July respectively (Fig. 3). The sexual maturity curve for female *P. edwardsi* (Fig. 4) shows that maturity (25% of the population) was reached at 26 mm *CL*.

The distribution of the mean shrimp sizes over each depth interval during each season is presented in Table III. In general, the size of females (both non-ovigerous individuals and ovigerous females) tended to increase with increasing depth. However, this trend was not apparent during the second quarter of the year for shrimps caught between 301 and 350 m deep. There was no clear trend in males because of insufficient data.

The length statistics of the shrimps examined by sex and reproductive group are summarized in Table IV. Material collected from around the Canary Islands ranged in length from 8 to 40 mm *CL*, and shrimps between 20 and 29 mm *CL* represented 66% of the total sample (Fig. 5). Males ranged from 8 to 34 mm *CL* and females between 8 and 40 mm *CL*. Non-ovigerous shrimps ranged from 8 to 35 mm *CL* and ovigerous females between 13 and 40 mm *CL* (Fig. 5).

There were significant differences in the length frequency distributions of *P. edwardsi* by sex and group (Table V). Females were significantly larger than males (25.3 mm and 19.1 mm *CL* respectively), whereas ovigerous females were significantly larger than non-ovigerous individuals (27.1 mm and 21.2 mm *CL* respectively).

Females dominated the bigger length-classes (20.0–40.9 mm), whereas sexes were equally represented in the 12–29 mm length range (Fig. 6). It was not possible to determine sex ratios in the smaller length-classes (8.0–11.9 mm).

Analyses of the length frequency data showed the presence of four modes in males and five in females (Table VI). Subsequent analysis of modal progression provided different values of L_∞ (25.75 and 28.28 mm) and K (0.55 and 0.69 year^{-1}) for males and females respectively. Based on the phi prime index, females (Φ' = 2.74) seem to have faster growth rates than males (Φ' = 2.56).

Table VII lists the relationships between carapace length and wet mass for each sex and group. Mass

Table V: Statistical comparison of length distributions and mean sizes of shrimps examined

Non-parametric test	Number of observations		Z	p	Number of observations		Z	p
	Males	Females			Non-ovigerous shrimps	Ovigerous females		
Kolmogorov-Smirnov	906	3 014	14.77	***	6 574	2 164	24.64	***
Mann-Whitney U	906	3 014	–30.46	***	6 574	2 164	–51.23	***

z = Density function of normal probability
*** $p < 0.001$

Table VI: Normal length distributions of male and female *P. edwardsi* derived by the maximum likelihood method

Number of observations	Mode (*CL*, mm)	*SD*	*SI*	χ^2	*df*
		Males			
66.00	9.792	1.132			
34.00	16.699	0.659	7.715		
37.95	20.329	1.350	3.614		
					3
		Females			
10.19	18.250	1.638	–		
31.43	21.318	1.325	2.071		
56.41	23.512	0.865	2.005		
45.87	25.697	0.709	2.777		
9.10	28.083	0.594	3.664	11.449	10

SI = Separation index

Table VII: Regression statistics ($y = ax^b$) for the relationships between carapace length (*CL*, mm) and wet body mass (g) by sex and reproductive group of *P. edwardsi*

Sex/Group	*a* (×10^{-4})	*b*	r^2	*n*
Males	34.964	2.439	0.874	906
Females	12.143	2.778	0.931	3 014
Non-ovigerous shrimps	12.193	2.757	0.941	6 574
Ovigerous females	59.448	2.298	0.843	2 164

For all regressions $p < 0.01$

increased with negative allometry, the coefficient b varying between 2.298 and 2.778. All relationships were significant ($p < 0.01$) and the high r^2 values indicated a good fit to the data.

DISCUSSION

Off the Canary Islands, *P. edwardsi* has been collected from 54 m to at least 468 m, mainly from 150 to 300 m. The species is commonly caught between 250 and 380 m off the Mediterranean coasts (Holthuis 1987) and at 300–500 m off the coast of North Africa (Crosnier and Forest 1973). Although the present results suggest that *P. edwardsi* inhabits shallower waters around the Canary Islands, it has been recorded from equally shallow water around the Azores (Martins and Hargreaves 1991). The other common pandalid shrimps, *P. narval*, is most frequently caught between 20 and 200 m off the Canary Islands, mainly from 50 to 175 m (González *et al.* 1997). The present results suggest that *P. narval* may be replaced by *P. edwardsi* with increasing depth.

P. edwardsi tends to concentrate in deep water in winter, moves shallower during spring, reaches its shallowest depths in summer and returns to deep water again in autumn. A similar distribution pattern, based on seasonal vertical movements, has also been reported for *P. narval* off the Canary Islands (González *et al.* 1997) and in the Eastern Mediterranean (Thessalou-Legaki *et al.* 1989).

Ovigerous females of *P. edwardsi* were present throughout most of the year, with peak spawning activity from April to September. Ovigerous females of this species were observed between January and March off the Azores (Martins and Hargreaves 1991), from January to August off the Iberian Peninsula (Zariquiey Álvarez 1968) and throughout the year in the Mediterranean (Holthuis 1987). Wide spawning seasons have also been reported for some congeneric species: *P. narval* off the Canary Islands (González *et al.* 1997), *P. heterocarpus* off the Mediterranean coasts (Holthuis 1987) and *P. martia* in the Mediterranean and the Eastern Central Atlantic (Zariquiey Álvarez 1968, Lagardère 1981, Holthuis 1987).

Given the seasonal nature of both distribution and spawning patterns in *P. edwardsi*, it is likely that the vertical movements of the population could be related to reproduction. Most shrimps, particularly ovigerous females, inhabit shallower waters during the second half (July to September) of the main spawning period. A similar pattern has been observed for *P. narval* off the Canary Islands (González *et al.* 1997).

These migratory and reproductive patterns become more difficult to interpret when analysing the bathymetric distribution in relation to shrimp length. Off the Canary Islands, the size of female *P. edwardsi* appears to increase with greater depth. A similar trend has been reported for other pandalids, e.g. *P. narval*, *Pandalus borealis, Pandalus montagui, Heterocarpus laevigatus, Heterocarpus sibogae* and *H. ensifer*, where larger individuals occupy deeper waters (Thessalou-Legaki 1989, González *et al.* 1997). In the present study, *P. edwardsi* showed no size gradient with depth in relating to spawning season. Non-return migrations towards deeper waters are believed to be the reason for such size differences in the inshore/offshore distribution of pandalids (Thessalou-Legaki *et al.* 1989).

The observation that female *P. edwardsi* are larger than males and that ovigerous females are larger than non-ovigerous individuals has been reported for shrimps off the Seychelles (Intès and Bach 1989) and the Azores (Martins and Hargreaves 1991). The predominance of females in the large size-classes suggests that *P. edwardsi* might be a protandrous hermaphrodite, as has been reported for many tropical and temperate deep-water pandalids, e.g. *Pandalus danae, Pandalus jordani, P. borealis, H. ensifer, H. laevigatus and H. sibogae* (King and Moffitt 1984, Thessalou-Legaki *et al.* 1989). However, the results are not conclusive. That females are larger than males and sex ratios favouring females in larger size-classes have traditionally been used as evidence for sex reversal. However, similar variations in size and sex ratios can occur in dioecious species where there are sex differences in relation to growth, mortality, migration and habitat preference. Differences in size and sex ratios appear to have been incorrectly used to support the hypothesis of sex reversal in other crustaceans (King and Moffitt 1984).

Growth parameters calculated in this study, particularly for females, are similar to those reported for *P. edwardsi* off the Fiji Islands (King 1986) and the Seychelles (Intès and Bach 1989). The present data show marked differences in growth patterns between the sexes where females have higher growth rates than males, which accounts for the observed patterns of sizes and sex ratios. González *et al.* (1997) found similar sex differences in relation to size, sex ratio and growth patterns in *P. narval* off the Canary Islands.

The data presented here regarding seasonal migrations, sex ratios and growth suggest that *P. edwardsi* is dioecious. Therefore, the species conforms to the reproductive pattern of tropical pandalids and demonstrates the complex nature of their life history.

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