

POPULATION STRUCTURE AND GROWTH OF THE HERMIT CRAB *DIOGENES PUGILATOR* (DECAPODA: ANOMURA: DIOGENIDAE) FROM THE NORTHEASTERN ATLANTIC

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ABSTRACT

A population of the hermit crab *Diogenes pugilator* from the northeastern Atlantic (Barbate, Straits of Gibraltar, Spain) was studied. The results show continuous recruitment throughout the year, within a size range from 0.4–1.02 mm in cephalothoracic shield length, as a consequence of the prevalence of ovigerous females throughout the year. The sex ratio was in favor of females. Results of size-frequency distributions from different locations show that there was no clear segregation of sizes by sexes or depths.

Five cohorts can coexist, although a decrease in the number of specimens was observed in the second year studied, perhaps induced by human influences in the area (the building of a new harbor and the restoration of the beach). The values of the Von Bertalanffy parameters (K and L_{∞}) showed slight differences between sexes and between years within sexes, as is shown in the ϕ' index analysis. The estimated maximum longevity of the individuals in the population studied was about 2 years, but normally the cohorts lived in the study area for approximately 1 year.

There are many studies on different biological aspects of species of hermit crabs, mostly related to relative growth and behavior, such as the use of gastropod shells where they live (Hazlett 1981, 1983, 1989, 1992; Bertness, 1980, 1981a, b, c; Blackstone, 1986a, b; Gherardi, 1991; Pessani *et al.*, 1990; Pessani and Premoli, 1993; and others).

However, studies on the population structure of hermit crabs are scarce, particularly for European species (Gherardi, 1991; Manjón-Cabeza and García Raso, 1994, 1995). Studies of *Diogenes pugilator* (Roux, 1829) are relatively few. However, there are studies on taxonomy (Forest, 1956; Ingle, 1993), larval development (Pike and Williamson, 1960), reproduction (Mouchet, 1931; Bloch, 1935), biometrics (Condreanu and Balcesco, 1968), and ecology (Guillén and Pérez Ruzafa, 1993).

This species is most abundant in shallow soft bottoms (Pèrès and Picard, 1964; Ledoyer, 1968) at depths between 0–126 m (Selvie, 1921; Forest, 1961, 1965). It occurs normally between 0.2–40 m (Zariquiey, 1968; Ingle, 1993).

The aim of this study is to analyze the structure of a population and absolute growth of *Diogenes pugilator* from southern Spain. The structure of the shallow soft-bottom decapod community where this population lives has recently been described by Manjón-Cabeza and García Raso (in press).

MATERIALS AND METHODS

The study area (Fig. 1) is located in Barbate Bay, province of Cádiz, in the vicinity of the Straits of Gibraltar, between 36°08'73"N, 05°55'19"W and 36°09'71"N, 05°53'59"W. The bottoms analyzed are at a depth of 15–24 m. Two transects, separated by 2.5 km, were selected for sampling, one in front of Barbate (B) and the other farther east, in front of Retin (R). Two samples were taken from each transect, at 15–18 m (B1, R1) and 24 m (B2, R2), respectively, in order to determine possible

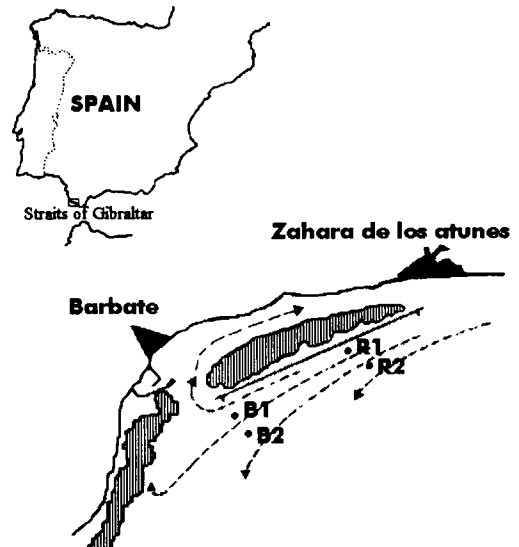


Fig. 1. Area of study and sampling points (R1, R2, B1, and B2). Arrows = tidal currents; lined areas = submerged rocky outcrops.

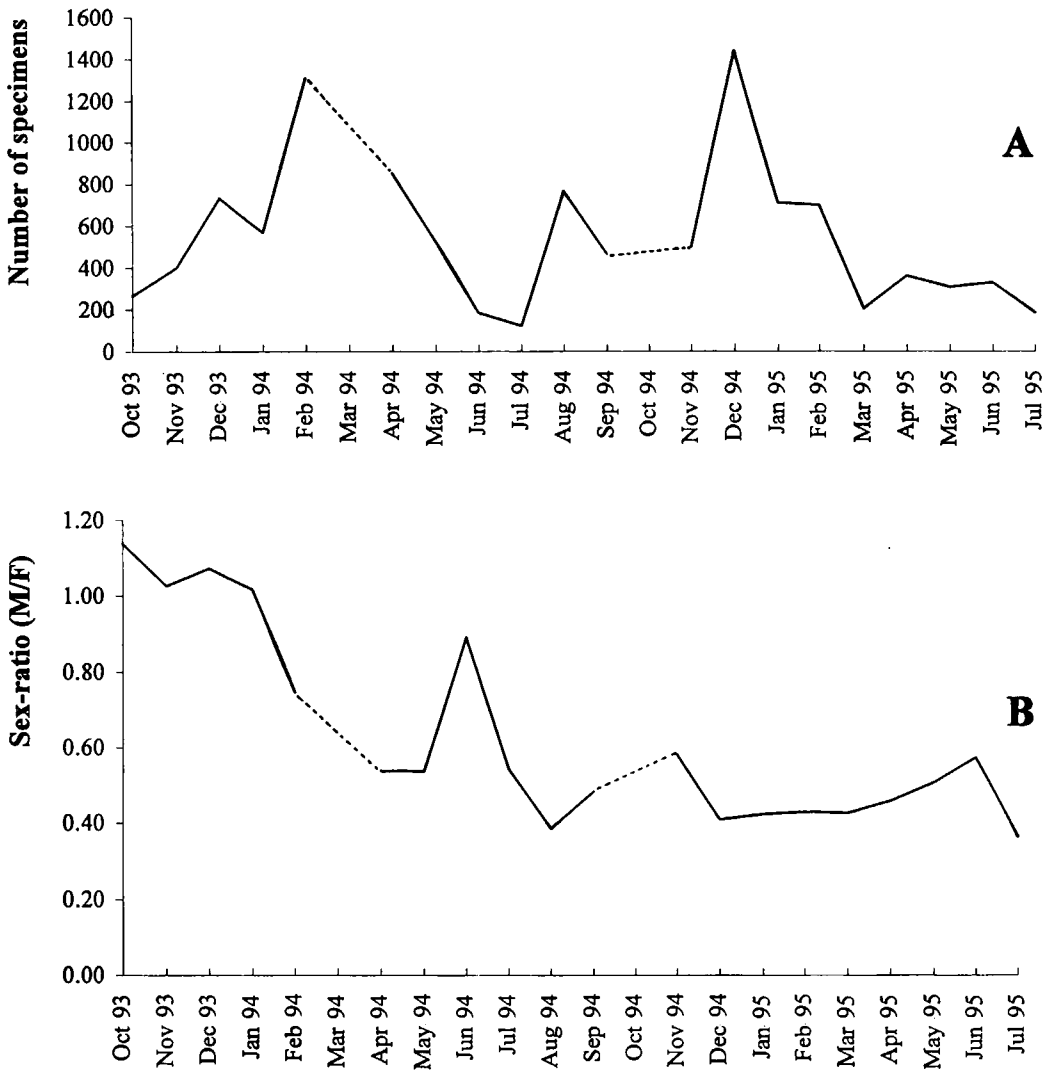


Fig. 2. Changes in a population of *Diogenes pugilator*. A, Monthly density throughout the two years; B, Changes in sex ratio (over a total of 10,535 individuals).

movements or migrations. The sediment is mostly detritic of mixed and coarse sand ($Q_{50} = 0.25\text{--}1.3$ mm), with some fine gravel and *Amphioxus* sand with abundant bioclastic remains. The sediment is fine-medium sand ($Q_{50} = 0.2$ mm) only in the B1 locality.

The main currents in this area are influenced by the proximity of Punta del Tajo and the Cape of Trafalgar. The frequent submerged rocky outcrops may play a role in the amplification and channeling of tidal currents. The surrounding shallow bottoms are sandy. For this reason, in the shallower sampling point B1, which is closer to the beach and the Barbate river mouth, the percentage of fine sand is higher (Manjón-Cabeza and García Raso, in press).

During two years (October 1993 to June 1995), monthly samples were taken using a small, heavy dredge, like those used for rock-dredging, with a rectangular frame of 42×22 cm and double net. The size of the inside mesh was 4.5 mm knot to knot. Despite this, we were able to get a good representation of small specimens, be-

cause of the characteristics of the sediment. For all sampling, the rock-dredging was carried out for 15 min, randomly in the selected locations, in the morning, and with good sea conditions.

In the laboratory, the sediment was washed through a sieve column with a mesh size between 1 cm and 1 mm. The fauna was separated and the hermit crabs were identified (Zariquiey, 1968; Ingle, 1993).

The cephalothoracic shield length (SL: maximum length, from the rostrum to the posterior part of the shield) was measured by a VID V computer program that processed stereoscopic microscope images taken by video camera, with a measurement error of 0.001 mm. The shield is the structure most frequently used to define size in hermit crabs. It is used as a reference measurement (McLaughlin, 1974; Blackstone, 1986a, b; Lancaster, 1990; Ingle, 1993; etc.), in spite of its narrow relationships with shell sizes (Bertness, 1981a; Lancaster, 1990). In the statistical analysis, nonparametric tests for equal-

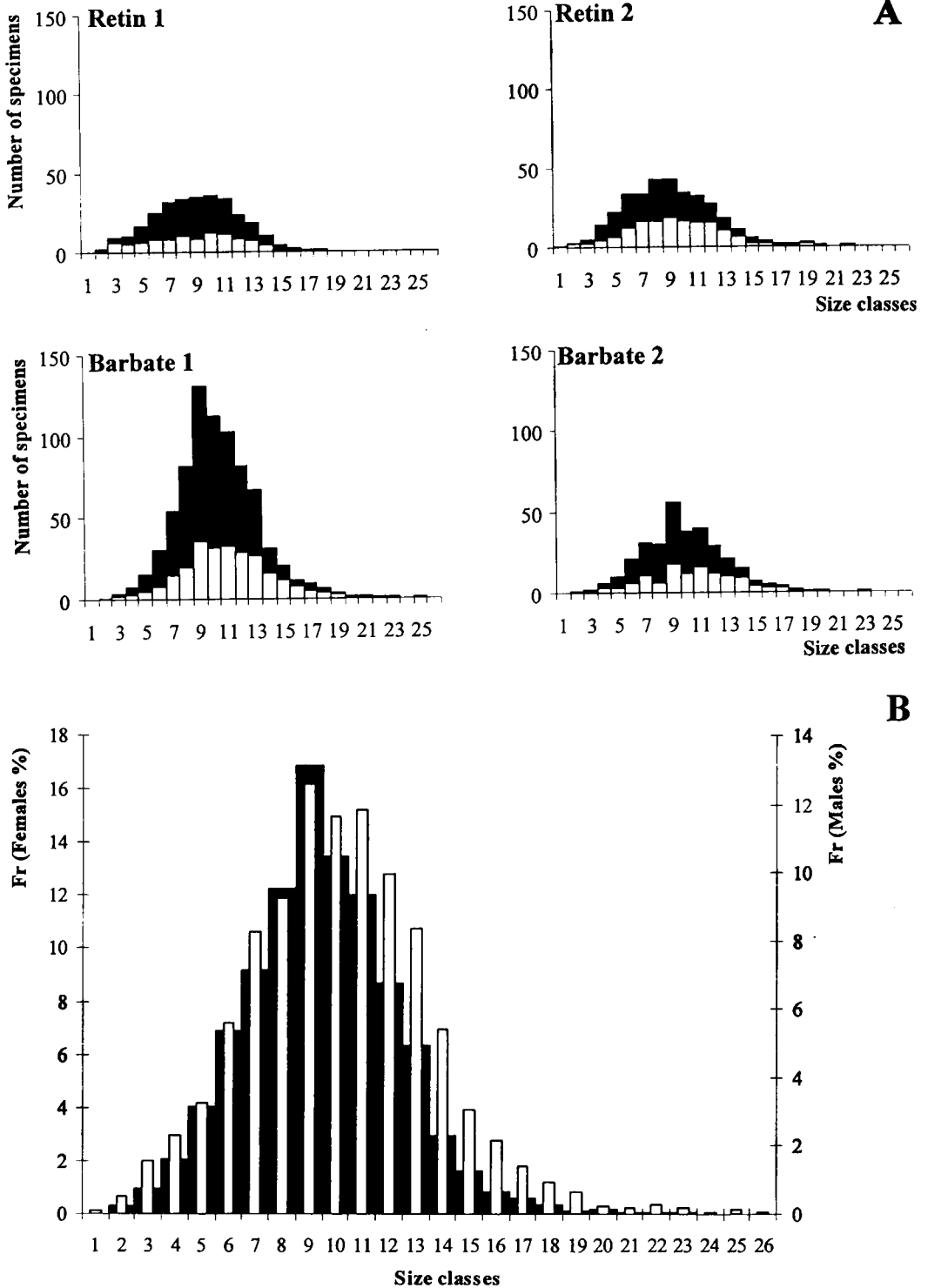


Fig. 3. Frequency histograms of size classes (cephalothoracic shield length in mm) of *Diogenes pugilator*. A, In different depths and localities (Retin and Barbate, 1 = 15–18 m, 2 = 24 m), all months combined. B, all localities and depths combined. Fr = frequency. White areas = males, black areas = females.

Table 1. Monthly mean size with the standard error (SD), the maximum (Max) and minimum (Min) of the cephalothoracic shield length for males and females of *Diogenes pugilator*. Sig. = Significance of the test of equality of the means between males and females (Mann-Whitney *U*-test, *significant difference $\alpha = 0.01$).

		Males		Females		Sig
		Mean \pm SD	Range (Min-Max)	Mean \pm SD	Range (Min-Max)	
1993	Oct.	2.49 \pm 0.72	1.16–4.51	2.52 \pm 0.58	0.83–3.78	
	Nov.	2.13 \pm 0.77	0.68–4.24	2.14 \pm 0.68	0.75–4.02	
	Dec.	2.68 \pm 0.92	0.80–5.33	2.69 \pm 0.83	0.94–5.13	
1994	Jan.	2.06 \pm 0.62	0.53–3.94	1.92 \pm 0.51	0.40–3.60	*
	Feb.	2.22 \pm 0.63	0.70–4.95	2.05 \pm 0.48	0.79–3.99	*
	Apr.	2.25 \pm 0.68	0.67–4.45	2.24 \pm 0.56	0.75–4.24	
	May	2.26 \pm 0.65	0.83–3.75	2.10 \pm 0.49	1.02–3.65	
	Jun.	2.01 \pm 0.53	1.00–3.20	1.91 \pm 0.50	1.09–3.24	
	Jul.	2.30 \pm 0.61	1.30–3.61	1.97 \pm 0.48	0.95–3.30	*
	Aug.	2.52 \pm 0.68	0.87–4.69	2.14 \pm 0.48	0.75–4.06	*
	Sep.	1.89 \pm 0.64	0.57–4.77	1.72 \pm 0.59	0.58–4.35	*
	Nov.	2.36 \pm 0.48	1.00–3.57	2.13 \pm 0.50	0.85–3.41	*
	Dec.	2.24 \pm 0.84	0.51–5.44	2.20 \pm 0.56	0.69–5.45	
1995	Jan.	2.38 \pm 0.39	0.72–3.14	2.19 \pm 0.38	0.68–2.99	*
	Feb.	2.45 \pm 0.31	1.56–3.01	2.35 \pm 0.38	1.03–3.01	*
	Mar.	2.81 \pm 0.48	1.46–3.74	2.34 \pm 0.50	0.60–3.74	*
	Apr.	2.56 \pm 0.47	0.98–3.46	2.48 \pm 0.52	0.72–3.61	
	May	2.38 \pm 0.58	0.92–3.82	2.27 \pm 0.50	0.93–3.42	
	Jun.	2.51 \pm 0.68	0.58–4.43	2.12 \pm 0.50	0.78–3.80	*
	Jul.	2.54 \pm 0.48	1.63–3.69	2.38 \pm 0.61	0.98–3.95	
	Total	2.34 \pm 0.71	0.51–5.44	2.19 \pm 0.57	0.40–5.45	*

ity of the means were made (Mann-Whitney *U* test) after determining the pattern of the distributions (Siegel, 1956; Sokal and Rohlf, 1969). In order to analyze the frequency histograms, these measurements were grouped in size classes (26), calculated according to the highest and lowest sizes (5.45–0.4 mm SL) (Christensen, 1983) with a size range of 0.2 mm. Modal progression analysis for males and females, using the method of Bhattacharya (1967), was applied in the determination of cohorts.

To determine the Von Bertalanffy parameters (Von Bertalanffy, 1934, 1938), the Bhattacharya and Ford-Walford methods were used (Walford, 1946; Bhattacharya, 1967) by the computer program FISAT, proposed by Gayanilo *et al.* (1989) and Gayanilo *et al.* (1994). For each year and sex, a cohort (presenting all or the maximum number of size classes) was selected. In order to determine the differences in these parameters and in the model of absolute growth obtained, the ϕ' index (Munro and Pauly, 1983), modified by Sparre (1987), was applied.

RESULTS

During the two years, a total of 11,748 specimens (6,885 females and 4,863 males) were captured. Changes in monthly density throughout the years is represented in Fig. 2A, where the number of specimens increases in winter (December–February) and decreases in April/ May–July, showing a clear seasonal variation. This trend is more acute in shallower locations (B1 and R1).

The sex ratio is clearly in favor of females in the period studied (Fig. 2B) and at all depths (Fig. 3A). Furthermore, ovigerous females are found throughout the year (monthly proportion of ovigerous females during the two years: OF/F% = 54.9, 15.7, 18.6, 51.8, 70.2, 68.1, 76.5, 40.2, 61.4, 84.9, 58.6, 58.7, 48.7, 71.9, 63.9, 62.2, 75.4, 62.1, 82.8, 59.9 (in a total of 6,685 females).

The study of the monthly means and the maximum and minimum cephalothoracic shield lengths are shown in Table 1. The results of the test of equality of the means showed differences between the sexes; in general, females are smaller than males, but monthly differences exist (Table 1).

The results of the analysis of size-frequency histograms of males and females (Figs. 3, 5) show that at all depths the dominant size classes are the same (class 9 = 2.0–2.2 mm SL) and have a similar population structure (Fig. 3A). However, at the B1 locality *Diogenes pugilator* is much more abundant than at the others (Fig. 3A).

Results of the application of modal progression analysis allow the determination of five cohorts in the annual cycle with different mean sizes for males and females (Fig. 4).

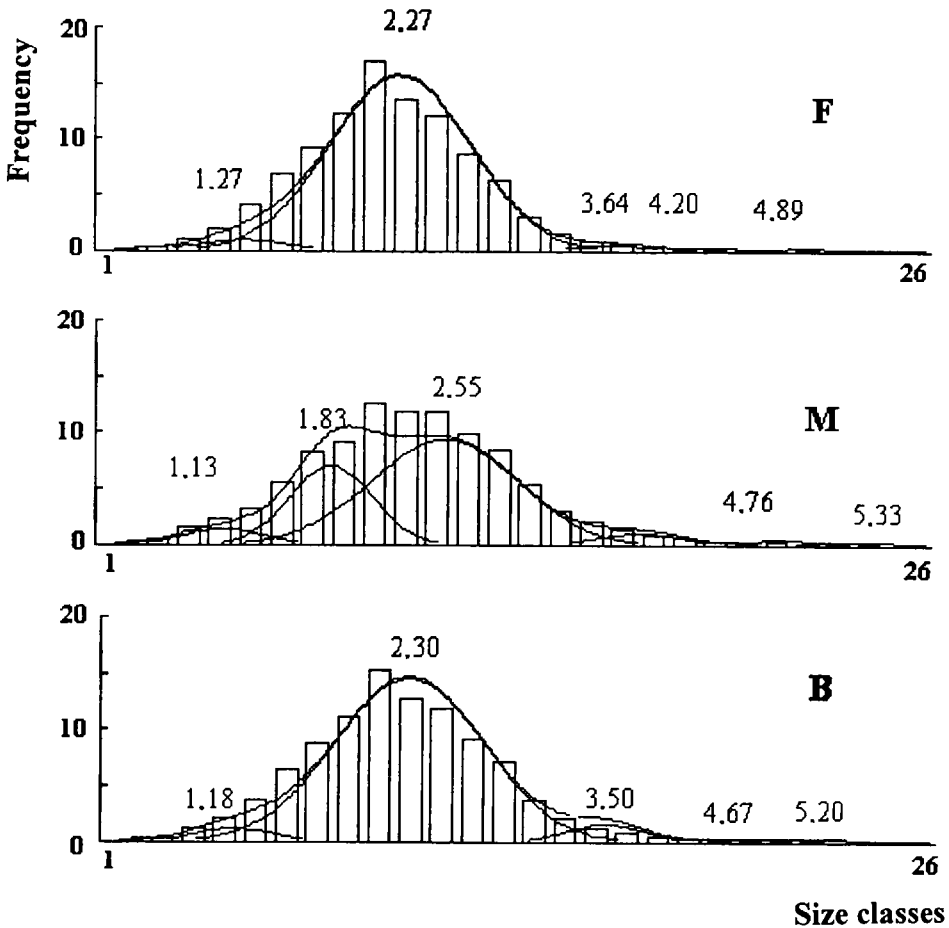


Fig. 4. Frequency histograms of size classes (cephalothoracic shield length in mm) of *Diogenes pugilator* showing the five cohorts that coexist. F = females, M = males, B = both sexes.

More cohorts coexist in December (Fig. 5A, B), in which the oldest cohort (with very few specimens) reaches a mean size of 5.20-mm SL.

Recruitment was continuous, although there was a greater abundance of small specimens (first size class) about every two months (mainly in the first year) (Fig. 5). In the second year, there was a decrease in the number of specimens and an absence of size classes larger than 19 (Fig. 5).

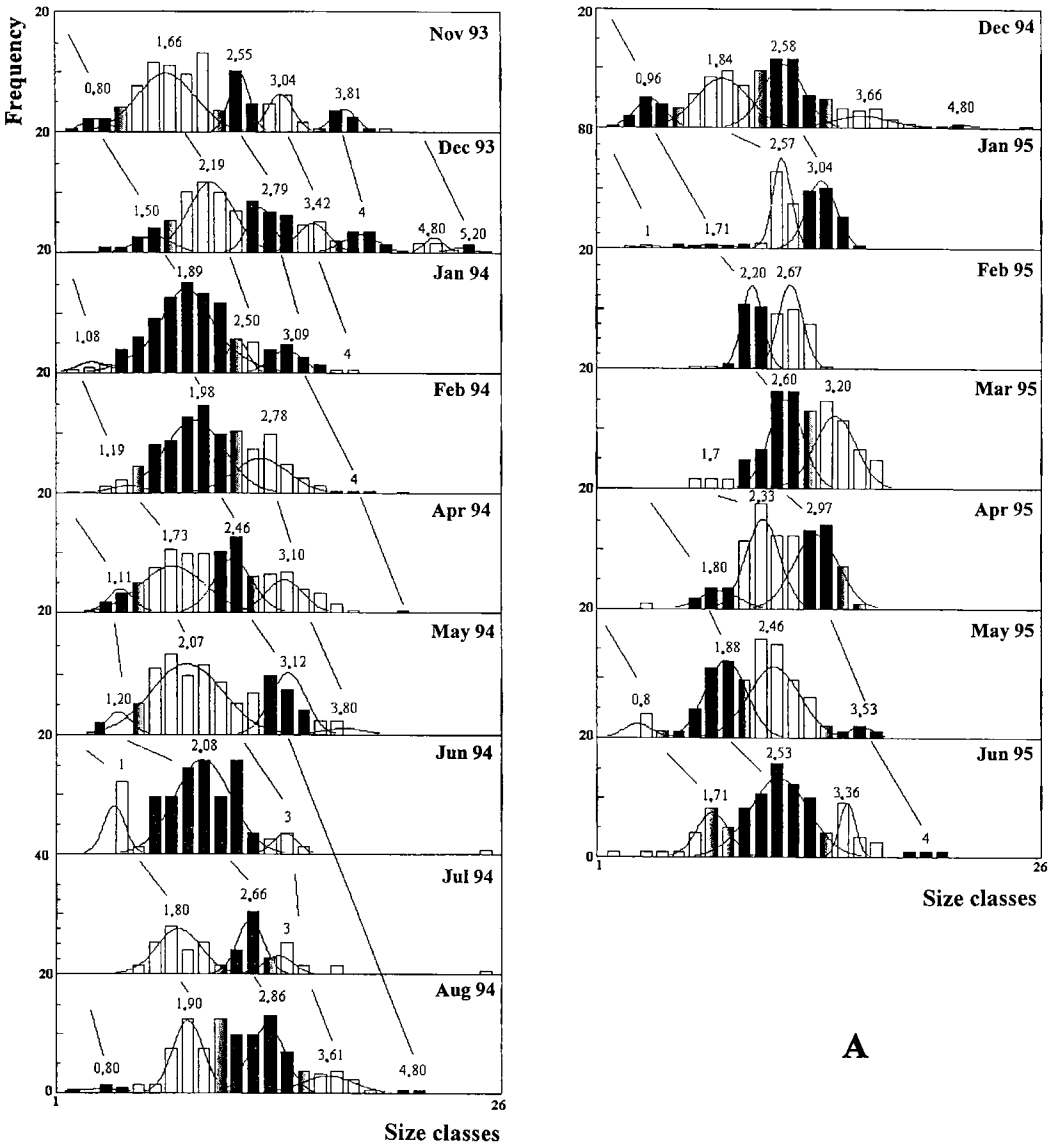
The parameters of Von Bertalanffy (L_{∞} , K) for two cohorts (one from each year) were determined for males and females (Table 2, Figs. 5A, B, 6). They show slight variation between sexes in the first cycle, as stated in the results of the ϕ' index analysis. According to the growth curve, the theoretical estimated maximum longevity of the individuals in the

population is about two years, but in the study area they normally live about one year.

DISCUSSION

In the study area, the population of *Diogenes pugilator* has a broad representation of different sizes, the medium sizes being dominant, although there are populations with larger sizes better represented in the southern Spanish Mediterranean littoral (unpublished data; García Raso, 1982). However, the maximum size found (5.45-mm SL) in this study is even larger than those quoted by Zariquey (1968) and Ingle (1993), who reported a cephalothoracic shield length of approximately 4.40 mm.

Furthermore, the mean size of females in this population is smaller than that of males.



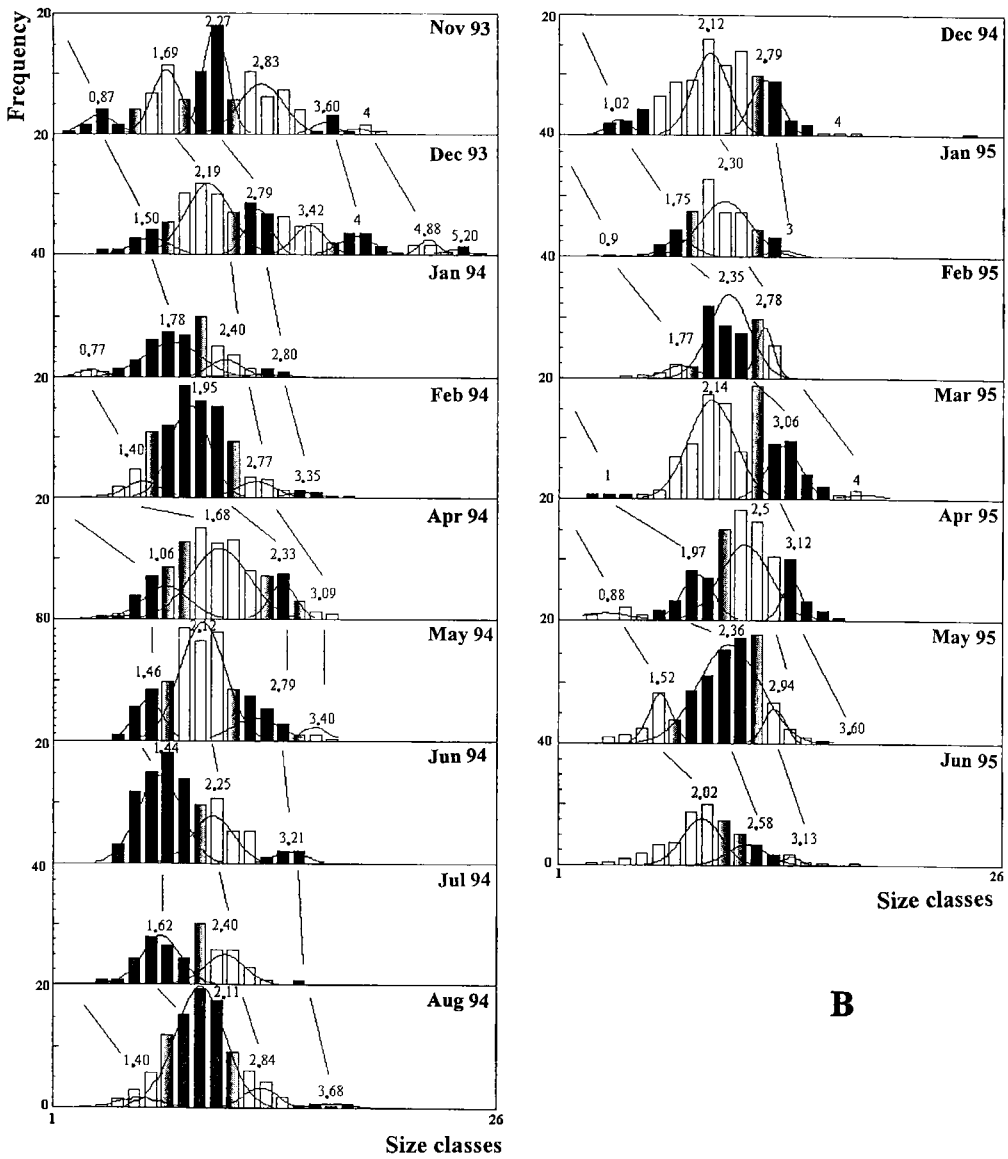
A

Fig. 5. Frequency histograms of size classes (cephalothoracic shield length in mm) of *Diogenes pugilator* showing the cohorts. A = Males, B = Females. The cohorts are indicated with diagonal lines and bars of different shading.

This dimorphism has been recorded in other species of the same genus, such as *Diogenes nitidimanus* Terao (see Asakura, 1992). This may be related to a slight growth reduction in females as a result of reproductive cost (Hartnoll, 1982, 1985). The sex ratio in the population was significantly female-biased, which is also in accordance with the results found by Asakura (1992) in *D. nitidimanus*.

Recruitment is constant throughout the year as a consequence of the abundant and continuous presence of ovigerous females. This

contrasts with the data from other Atlantic areas, such as Roscoff, where these are found from May–September (Bourdon, 1965), and with the reproductive patterns observed in other hermit crab species from southern Spain, such as *Cestopagurus timidus* (Roux, 1930) (see Manjón-Cabeza and García Raso, 1994) and *Calcinus tubularis* (Linnaeus, 1767) (see Amouroux, 1974; Manjón-Cabeza and García Raso, 1995), which have a well-defined reproductive maximum and seasonal recruitment.



B

Fig. 5. Continued.

The greatest abundance of *Diogenes pugilator* in the B1 locality is very probably due to the kind of sediment, richer in fine sands, which is preferred by this species and also because this is the shallower locality (Pères and Picard, 1964; Ledoyer, 1968, García Raso, 1987).

The winter increase of individuals is apparently not related to reproductive migrations, nor with maximum recruitment of first size classes, at least in our area of study. In fact, there is not a strong increase in the number of ovigerous females in previous months, which might increase the number of individuals.

However, another species of *Diogenes* (*D. nitidimanus*) undergoes migrations (Asakura, 1987b). In addition, *Diogenes pugilator* shows aggregations (Bourdon, 1965), with a maximum density of individuals in shallow bottoms, between 1–18 m in southern Spain, Mediterranean Sea (García Raso, 1982, 1987). This abundance may be due to migration related to environmental factors, perhaps as a consequence of the winter rains and the greatest river flow, which affect more intensely shallower localities (B1, R1) in which a more remarkable seasonality appears.

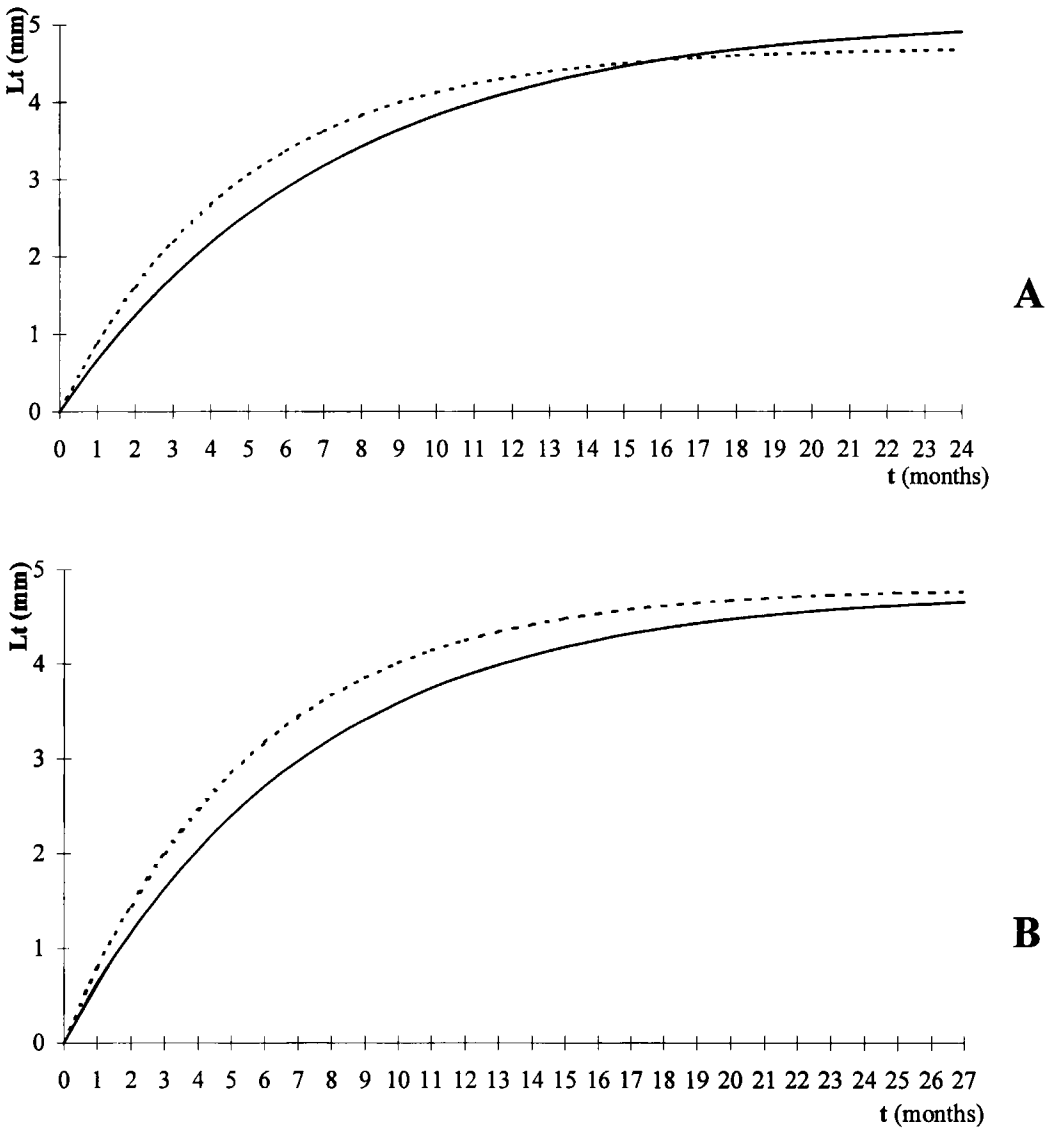


Fig. 6. Absolute growth curve of *Diogenes pugilator*. A, Males. B, Females. Continuous line = first cycle; discontinuous line = second cycle. Male equations: first cycle $L_t = 5.08(1 - e^{-0.14t})$, second cycle $L_t = 4.7(1 - e^{-0.21t})$. Female equations: first cycle $L_t = 4.76(1 - e^{-0.14t})$, second cycle $L_t = 4.7(1 - e^{-0.27t})$. L_t = cephalothoracic shield length.

We found differences in the growth patterns between sexes only in the second year and within sexes between years. However, these are very slight and, as is shown in Table 2, the ϕ' values are very close (around 1.2 in the first year and 1.5 in the second for both sexes). Differences in growth between cohorts and years are normal in decapods (García and Le Reste, 1986) and in other groups, such as fishes (Baro, 1996), as the result of many extrinsic and intrinsic factors. In our

Table 2. Growth in *Diogenes pugilator*. L_∞ and K = the growth parameters from the Von Bertalanffy equation. ϕ' = index of Munro and Pauly (1983).

	L_∞	K	$\phi' = L_n K + 2L_n L_\infty$
Males first period	5.08	0.14	1.28
Males second period	4.70	0.21	1.53
Females first period	4.76	0.14	1.15
Females second period	4.70	0.27	1.52

case, these differences may be related to interannual variability (more so in an area with strong hydrodynamic and fluctuating conditions) and to the decrease in the number of individuals (larger sizes) in the second year. The disappearance of these individuals may be due, at least in part, to human alteration of the environment. The construction of the new sports harbor inside the port of Barbate and the restoration of the beach produced temporal perturbations (in sediment composition) in the bottoms during the second year. However, the strong hydrodynamic conditions existing in the area tend to "wash" the bottoms quickly. These human acts cause alterations in the gastropod shells available and, perhaps, in food resources. This, in turn, may limit absolute growth, because both changes, particularly in the shells, are important factors in growth rate (Bertness, 1980, 1981a, 1982; Blackstone, 1986a).

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